PREDATION AND ANTIPREDATOR BEHAVIOR AT GUIANAN COCK-OF-THE-ROCK LEKS

PEPPER W. TRAIL[1]

Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853 USA

ABSTRACT.—I documented predator attacks and antipredator behavior at four display sites of Guianan Cock-of-the-Rock (*Rupicola rupicola*) in Suriname from 1980 to 1985. Most observations were made at a large lek that averaged 55 territorial males, with supplemental data on display groups of 1, 2, and 6 males. Males at the main lek were attacked by 6 species of raptors, 1 mammal species, and 1 snake species. A total of 56 attacks and 2 kills by raptors were observed (0.22 attacks/day). Two kills of displaying males by the snake *Boa constrictor* were also observed.

Male Cock-of-the-Rock were very wary. I observed 832 spooks (complete or partial flushes) at the Main Lek, more than 90% of which were apparently false alarms. Males at the smaller display sites were much less likely to spook. The raptor attack rate was inversely correlated with group size, supporting the hypothesis that social antipredator behavior reduces risk for displaying males. There was no evidence that peripheral or young males were especially vulnerable to predators.

Snake predation represents a previously unrecognized cost of lek display for tropical birds. The Cock-of-the-Rock failed to exhibit any effective antipredator behavior against snakes and may rely for protection on the infrequency with which snakes locate leks. *Received 14 July 1986, accepted 11 March 1987.*

THE selective importance of predation at leks has been long debated. Because most vertebrate leks are conspicuous traditional aggregations, they presumably attract both resident and transient predators. The combined attention of the lek males, however, may make it difficult for a predator to approach undetected. Most authors have concluded that males displaying on leks are safer from predators than are males at solitary display sites, at least in open habitats (Lack 1968, Hjorth 1970, Oring 1982). The enhanced safety of social display has been proposed as a factor that favors the evolution of leks and the preference of females for clustered males in a number of prairie grouse species (Koivisto 1965; Lack 1968; Hjorth 1970; Wittenberger 1978, 1979).

Few data are available on predation at leks. Long-term studies of Greater Prairie-Chickens (*Tympanuchus cupido*; Berger et al. 1963), Sharp-tailed Grouse (*Tympanuchus phasianellus*; Oring 1982), White-bearded Manakins (*Manacus manacus*; Lill 1974), and Golden-headed Manakins (*Pipra erythrocephala*; Lill 1976) revealed extremely low rates of attempted predation, while higher rates were found for populations of Sage Grouse (*Centrocercus urophasianus*; Wiley 1973, Hartzler 1974) and Eurasian Black-Grouse (*Tetrao tetrix*; Koivisto 1965).

I observed predation and antipredator behavior during a 6-yr (1980–1985) field study of the lek-breeding Guianan Cock-of-the-Rock (*Rupicola rupicola*). This large (200–230 g) cotinga inhabits tropical rain forest in the Guianan region of northern South America. The brilliant orange plumage and active display of adult males make Cock-of-the-Rock leks conspicuous to humans, and presumably to predators as well. I studied a color-banded population of *Rupicola* at the Raleigh Falls–Voltzberg Nature Reserve of Suriname (Trail 1985a–c, Trail and Koutnik 1986). In this wilderness area Cock-of-the-Rock are exposed to a large natural assemblage of predators, including raptors, felids, and snakes.

I describe and analyze Cock-of-the-Rock antipredator behavior, and then use data on predation at different-size display sites to examine hypotheses concerning the role of predation in lek evolution. Specifically, I tested if lek behavior made males more or less vulnerable to

[1] Present address: Department of Ornithology and Mammalogy, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118 USA.

predation, and if a male's position on the lek correlated with his exposure to predation.

Study Area and Methods

The Raleigh Falls–Voltzberg Nature Reserve (4°40′N, 56°10′W) is a 560-km² area of lowland tropical rain forest surrounded by the much larger undisturbed forests of the Coppename River drainage (Fig. 1). The study area was centered around the Voltzberg, a 240-m-high granite dome located 5 km southeast of the river. Large boulders on the forested slopes of the Voltzberg provide the sheltered sites female Cock-of-the-Rock require for their mud nests. A large population of Cock-of-the-Rock is found in this area in association with the abundant nest sites, and I located 3 leks and 1 solitary male display site.

Male Cock-of-the-Rock maintain lek territories year-round, but active courtship and mating occur only from late December to April. The majority of matings are performed in January and February. I made daily observations from approximately 0645 to 1630 during December 1980 to April 1981, January–February 1982, January–March 1983, January–February 1984, and January 1985.

My primary research site was the Main Lek, which comprised an average of 55 territorial males per year from 1981 to 1984 (range 52–61). Display territories of males at this lek were small and densely clustered. Each territory consisted of a cleared display court, usually 0.8–1.2 m in diameter, and the adjacent perches to a height of 1.5–2.0 m over the court. The mean nearest-neighbor distance between courts was 1.4 ± 1.26 m (n = 96 courts).

I observed activity from a blind located approximately 6 m from the nearest courts. With the exception of a small number of the most peripheral territories (≤5/yr), all courts could be monitored simultaneously. Whenever the Cock-of-the-Rock gave alarm calls or spooked from the lek I recorded the time, the approximate proportion of males involved, and the apparent cause. If a predator was seen, I recorded its behavior until it left the area.

To estimate mean daily group size at the Main Lek I conducted full-day censuses at least once a week through each season. On these days I counted all visible males at half-hour intervals from 0700 to 1700 (21 censuses/day). I calculated 42 weekly means for group size spanning the period January–April 1981–1984. These were compared with the frequency of spooks and predation (see Results).

Female visitation at the Main Lek occupied an average of 28% of the time from 0700 to 1700 daily. During female visits males displayed on their courts (described by Trail 1985c). During the remainder of the day territorial males typically perched near their courts, from just above the ground to 3 m. Nonterritorial males usually remained in the subcanopy 8–12 m above the lek. The dispersion of males in the vicinity of the Main Lek thus included a dense cluster of males low over the display courts, with a scattering of other males in the subcanopy and at varying distances around the lek periphery.

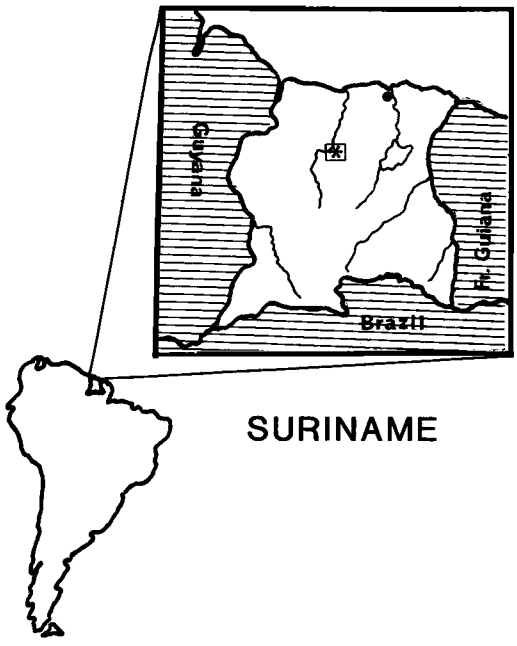

Fig. 1. Suriname, South America. The Raleigh Falls–Voltzberg Nature Reserve is indicated by the asterisk. The dot indicates the capital, Paramaribo.

The interior of tropical rain forest is characterized by structurally complex and stratified layers of vegetation and by low light levels. To assess visibility at the height of the perched males at the Main Lek, I used a square of pink plastic flagging with an area of 25 cm². Flagging was mounted on poles at the height of 2 m and was moved progressively away from a sample court in each of the four main compass bearings. An observer standing on the court noted the distance at which the flagging was hidden completely by foliage. For 15 courts, representing every area of the lek, the mean visibility was 15.7 ± 1.21 m (n = 60 measurements, range 4–30 m). I also measured the height from the ground to the lowest foliage above each of 30 courts, again representing all areas on the Main Lek. The mean height was 3.3 ± 1.75 m (n = 30, range 1.0–8.0 m). These measurements suggest that visibility was sufficiently restricted at the Main Lek to make detection of predators difficult. During periods of display, the calls of the males could be heard for several hundred meters through the forest, and predators (except snakes) presumably first detected the Main Lek by sound.

In addition to intensive studies at the Main Lek, I

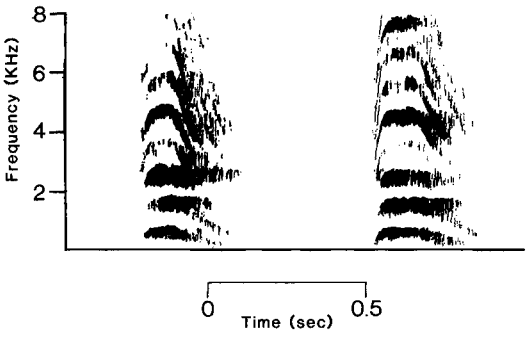

Fig. 2. Two alarm calls (the "hey" vocalization) of Guianan Cock-of-the-Rock, recorded at the Main Lek in 1981.

observed 3 other display sites: the Creek Lek, the Nest Slope Lek, and the Solitary Male site. The Creek Lek consisted of 6 territorial males and was located in dense liana forest near a small stream approximately 2 km southeast of the Voltzberg dome. The almost impenetrable vegetation of this lek was a marked contrast to the more open Main Lek. All-day observations were made 1–2 times per week at the Creek Lek during January–March 1983.

The Nest Slope Lek consisted of only 2 territorial males (briefly joined by a third in 1981) and was located on the boulder-covered slope of the Voltzberg. This was the center of Cock-of-the-Rock nesting activity, and 6 nests were located within 50 m of this display site. The Nest Slope Lek was approximately 300 m from the Main Lek, and the chorusing of Main Lek males was heard there easily. The vegetation on the rocky nest slope was more open than at the Main Lek, with widely spaced trees and almost no lianas or understory palms or shrubs. The forest in this area resembled the Cock-of-the-Rock lek in the Kanuku Mountains, Guyana, described by Gilliard (1962) and Snow (1971). The Nest Slope Lek was observed at least once a week in the 1981 and 1982 breeding seasons.

The Solitary Male display site was also located on the rocky eastern slope of the Voltzberg, approximately 200 m from the Nest Slope Lek. The display court of this male was located in the bottom of a small basin (ca. 30 × 15 m) completely closed in by 10–20-m-high boulders. Five nests were located on the adjacent boulders. The Solitary Male site was observed at least once a week in 1981 and 1982.

RESULTS

Antipredator behavior.—Male Cock-of-the-Rock were extremely wary at leks. Antipredator behavior took two forms: spooks and alarm calling. Spooks were headlong flights off the lek by subgroups of neighboring males or by the entire group. Alarm calling consisted of directing the ringing "hey" call (Fig. 2) toward a particular stimulus, and was performed by Cock-of-the-Rock of all age and sex classes. Males occasionally gave alarm calls without spooking when large mammals visited the lek. This response was given to humans, to felids (jaguar, *Felis onca*; puma, *F. concolor*; ocelot, *F. pardalis*), and, rarely, to other mammals (e.g. brocket deer, *Mazama* spp.; and tamandua, *Tamandua tetradactyla*).

At the Main Lek spooks were the most common response to startling stimuli. Given the risk of surprise attack in the rain forest, the most appropriate reaction to threat appeared to be headlong flight, often preceded by a few abrupt "hey" calls. Following a false alarm males typically returned to their territorial perches at once (in less than 30 s) and resumed their previous activities.

I recorded 832 spooks on the 254 observation days of the 1981–1985 breeding seasons (3.28 spooks/day), spanning the months December–April. The rate of spooks varied through the breeding season. The mean number of spooks per day was significantly less in December (2.1 ± 1.9, $n = 23$ days), March (1.6 ± 2.1, $n = 19$ days), and April (0.8 ± 0.8, $n = 10$ days) than in January (4.0 ± 2.8, $n = 107$ days) and February (3.3 ± 2.5, $n = 95$ days), the height of the breeding season (Duncan's multiple-range test, 247 df, $P < 0.05$). Frequencies of spooks were not significantly different in January and February. This seasonal pattern in number of spooks paralleled a decline in group size following the peak of female visitation in January and February (Trail 1984).

I eliminated seasonal effects by considering observation days only during January and February 1981–1984 in the analyses of the frequency and causes of spooks (Table 1). Only one of the differences between years was statistically significant. Spooks caused by fights and chases were significantly more frequent in 1983 and 1984 than in the two previous years (Duncan's multiple-range test, 6 df, $P < 0.05$). This was associated with intense competition following the disappearance of the most successful male in 1983 (Trail and Koutnik 1986).

More than half of the spooks at the Main Lek had an unknown cause: Cock-of-the-Rock simply flew explosively away from their perches without previous alarm calls and without an

TABLE 1. Causes of spooks observed at the Main Lek, January and February 1981–1984. Mean number of spooks per day were 3.4 (1981), 3.7 (1982), 4.5 (1983), and 3.0 (1984).

Cause	1981	1982	1983	1984	Total (%)
Observed attacks	6	21	18	5	50 (6.7)
Possible attacks	7	11	7	3	28 (3.8)
Cock-of-the-Rock alarm calls	22	33	30	13	98 (13.2)
Harmless animals	20	17	42	21	100 (13.4)
Cock-of-the-Rock fights and chases	1	2	8	10	21 (2.8)
Falling vegetation	8	5	6	0	19 (2.6)
Unknown	117	88	143	81	429 (57.6)
Total	181	177	254	133	754 (100.0)
n[a]	54	48	56	44	202

[a] Number of observation days.

evident stimulus. The magnitude of these spooks varied from just a few males to as many as half the birds on the lek. All "cause unknown" spooks appeared to be false alarms, and the birds returned immediately and resumed their previous activities. Complete, lekwide spooks were rare and never occurred without an obvious cause, in most cases an actual predator attack.

Documented attacks on Cock-of-the-Rock accounted for only 50 spooks, less than 7% of the total. In an additional 28 spooks I saw no predator, but the behavior of the males indicated they had detected one in the area. In these cases a minimum of one-third of the males left their territories; they remained off the lek for minutes, not seconds, and the spook was followed by sustained alarm calling. I classified these instances of severe and sustained alarms as "possible attacks."

Cock-of-the-Rock "hey" calls triggered 98 spooks (13.2%). In 89 of these cases the cause of the calls was unknown and the spooks appeared to be false alarms. In 5 instances the cause was the presence of a mammalian predator (2 jaguar, 1 puma, 2 ocelot) at the lek. The pattern of alarm calling given to a felid was distinctive. The alarm began beyond the lek and usually continued for many minutes, gradually shifted location, and finally faded in the distance as a few males followed the cat off the lek. In 4 instances I heard this pattern of alarm calling without seeing the cause. In these cases a felid presumably passed near the lek out of my view.

One hundred spooks (13.4%) were associated with the calls of nonpredatory animals, including 5 bird species (*Monasa atra, Cacicus cela, Daptrius americanus, Ortalis motmot, Querula purpurata*) and 3 mammal species (*Saguinus midas, Dasyprocta* sp., *Sciurus* sp.). These calls were loud and abrupt, and apparently startled the Cock-of-the-Rock into spooking. The movements of monkeys (*Cebus apella, Saimiri sciureus, Saguinus midas*) through the lek triggered spooks in 11 cases, and 6 more were caused by the sound of small mammals running on the ground. The flight sounds of unidentified birds caused 19 spooks, including 3 in response to large birds (probably Black Vultures, *Coragyps atratus*), display diving above the canopy. The flight of Red-billed Toucan (*Ramphastos tucanus*), Gray-fronted Dove (*Leptotila rufaxilla*), Black-faced Hawk (*Leucopternis melanops*), and Barred Forest-Falcon (*Micrastur ruficollis*) through the lek triggered 1 spook each. None of these species attack adult Cock-of-the-Rock. A small number of spooks were triggered either by Cock-of-the-Rock fights (21 cases, 2.8% of the total) or by the sounds of branches breaking or trees falling (19 cases, 2.6%).

This analysis emphasizes the wariness of Cock-of-the-Rock at the Main Lek. At most 12% of the spooks were responses to potentially dangerous situations. This is the sum of actual attacks, possible attacks, and the 9 cases in which felids passed near the lek. All remaining spooks were false alarms, as indicated by the males' immediate resumption of normal behavior.

Predation at the lek.—Cock-of-the-Rock at the Voltzberg are exposed to three classes of predators: birds, mammals, and snakes. The study area supports a diverse community of 23 species of diurnal raptors and 3 species of owls. Although owls attack Temperate Zone lek grouse (Berger et al. 1963, Rusch et al. 1972), they probably are not important predators on lek birds in the tropics, where dawn and dusk are brief. Crested (*Lophostrix cristata*) and Spectacled (*Pulsatrix perspicillata*) owls occurred at the Voltz-

TABLE 2. Raptor attacks observed at the Main Lek during 254 observation days, January–April 1981–1985. Lined Forest-Falcon, Barred Forest-Falcon, Black-faced Hawk, and Black Hawk-Eagle were also seen at the Main Lek, but did not attack the Cock-of-the-Rock.

Species	No. days with attacks	Total no. attacks	No. kills
Ornate Hawk-Eagle (*Spizaetus ornatus*)	8	8	2
Collared Forest-Falcon (*Micrastur semitorquatus*)	7	28	0
Bicolored Hawk (*Accipiter bicolor*)	3	3	0
White Hawk (*Leucopternis albicollis*)	1	1	0
Great Black-Hawk (*Buteogallus urubitinga*)	1	1	0
Crested Eagle (*Morphnus guianensis*)	1	1	0
Unidentified	14	14	0
Total	35	56	2

berg, but neither were seen at Cock-of-the-Rock display sites.

Six species of raptors were seen to attack Cock-of-the-Rock during this study (Table 2). The unidentified raptors (Table 2) were probably Collared Forest-Falcons (*Micrastur semitorquatus*), Slaty-backed Forest-Falcons (*M. mirandollei*), or Bicolored Hawks (*Accipiter bicolor*), similar-size species that can be difficult to distinguish. Four additional potential predators, the Harpy Eagle (*Harpia harpyja*), Black-and-white Hawk-Eagle (*Spizastur melanoleucus*), Black Hawk-Eagle (*Spizaetus tyrannus*), and Slaty-backed Forest-Falcon, occur in the area but were not seen to attack Cock-of-the-Rock.

I observed 56 attacks by raptors at the Main Lek. I defined an attack as an instance in which a hawk flew rapidly onto the lek and triggered a sustained spook. This definition excludes flights through the lek by small, nonthreatening raptors (e.g. Lined Forest-Falcon, *Micrastur gilvicollis*). Strikes at Cock-of-the-Rock were observed in 75% of attacks. In the remainder no strike was seen, either because of limited visibility or because of evasive behavior by all of the males. Two of the 56 attacks resulted in kills, for a success rate of 3.6%.

There were an additional 35 possible raptor attacks during the 254 observation days. In these cases no raptor was seen, but all or almost all males spooked from the lek and stayed away for several minutes to give persistent alarm calls. Such behavior never accompanied known false alarms (e.g. in response to nonthreatening animals or falling limbs). The total rate of raptor attacks was thus 0.22 confirmed and 0.36 possible attacks per day at the Main Lek.

Compared with other lek birds, Cock-of-the-Rock are subject to a high rate of attempted predation. Lill witnessed no attacks on either White-bearded Manakins in 835 h (Lill 1974) or Golden-headed Manakins in 2,000 h of observation (Lill 1976). His study site on Trinidad, however, lacked the bird-eating *Micrastur* and *Accipiter* hawks. Wiley (1973) observed 8 Golden Eagle (*Aquila chrysaetos*) attacks on Sage Grouse during 86 mornings of observation (0.09/day). Berger et al. (1963) witnessed only 3 raptor kills in 4,745 mornings of observation at Greater Prairie-Chicken leks, but did not specify the number of actual attacks. Koivisto (1965) observed 17 visits by Northern Goshawks (*Accipiter gentilis*) to Eurasian Black-Grouse leks in Finland during approximately 195 mornings of observation (0.09/day). Oring (1982) reported only 1 raptor kill seen on approximately 600 mornings of observation at Greater Prairie-Chicken and Sharp-tailed Grouse leks. Ammann (1959), Moran (1966), Blus (1967), and Moyles (1979) provided additional descriptions of raptor predation at leks, but without information on attack rates.

All raptors that attacked Cock-of-the-Rock made rapid rushes onto the lek, apparently from not far beyond the periphery. The larger species (*Morphnus, Spizaetus, Buteogallus, Leucopternis*) made fast, shallow dives onto the lek, while the smaller *Micrastur* and *Accipiter* flew in with rapid wingbeats. In most cases the males spooked off the lek with loud alarm calls before I saw the raptor. After making their strikes the raptors typically perched on or near the lek (4–10 m up) for only a few minutes, while males concealed in the subcanopy foliage gave continuous alarm calls.

The males quickly returned following attacks by *Micrastur* and *Accipiter,* and even resumed display while these hawks were perched on the lek itself. On one occasion an adult Collared Forest-Falcon remained on the lek for more than 2 h, during which time it made 15 unsuccessful strikes. These small raptors probably were capable of subduing a Cock-of-the-Rock only by

surprise and were not treated as a serious threat while in view. Similar responses by lek grouse to relatively nonthreatening raptors were reported by Berger et al. (1963) and Hartzler (1974).

In contrast, Cock-of-the-Rock reacted with panic to Ornate Hawk-Eagles. This species made both of the observed raptor kills at the Main Lek. Ornate Hawk-Eagles are reported to feed on both mammals and birds (Brown and Amadon 1968) but probably specialize on large birds (Lyon and Kuhnigk 1985). In both successful attacks the hawk-eagles dived and struck males on or near the ground. Both kills were instantaneous. In one case the hawk-eagle pinned its prey between the buttresses of a tree, possibly stunning itself in the process, as it remained motionless with outflung wings for at least 30 s after the strike. It remained perched at the base of the tree for 2 min before flying off easily. This hawk-eagle plucked its Cock-of-the-Rock on a fallen tree trunk approximately 30 m beyond the periphery of the lek. In the other case the hawk-eagle apparently carried its prey away from the lek before feeding on it. After all Ornate Hawk-Eagle attacks, the male Cock-of-the-Rock remained very wary for hours and repeatedly spooked without apparent cause.

There was probably a third kill by raptors at the lek. On 18 February 1983 there was a lek-wide spook followed by more than 90 min of alarm calling. This coincided with the disappearance of the bird that had been the top male (in terms of number of copulations) for the previous 3 yr and was third ranked in 1983. He had been seen earlier that morning, and had never previously been absent from the lek for a full day. His disappearance, coinciding with the massive spook, suggests strongly that he was killed by a predator, probably a raptor.

The impact of mammalian predators at leks is poorly understood. Mammals may account for more kills of displaying grouse at leks than do the more frequently observed raptors (Hartzler 1974, Maxson et al. 1979).

The potential mammalian predators observed at Voltzberg were jaguar, puma, ocelot, and tayra (*Eira barbara*). Margay (*Felis wiedii*), little spotted cat (*F. tigrinus*), and jagarundi (*F. yagouaroundi*) probably occur in the area but were not seen. Jaguars were seen at the Main Lek 5 times, puma once, and ocelot twice. Tayras were never seen at the Main Lek, although one was seen at the Nest Slope Lek.

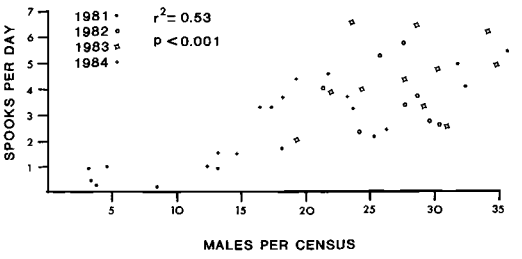

Fig. 3. Correlation between male group size and frequency of spooks at the Main Lek. For each of the 42 weeks of observation at the Main Lek from January through April 1981–1984, the mean number of spooks per day and the mean group size were calculated. Group size was determined by counts of all visible males taken every half hour from 0700 to 1700 on 1–3 census days/week.

I observed only one possible attack by a mammal. Shortly after dawn, when it was still very dim in the forest, an ocelot ran to the edge of the lek, sprang onto a tree trunk, and looked toward the displaying males. The Cock-of-the-Rock spooked well before the ocelot could have attacked, and no pounce occurred. The other felids passed through the lek without exhibiting hunting behavior, but caused the birds to fly into the forest subcanopy and give alarm calls. Gilliard (1962) also reported an ocelot at a Cock-of-the-Rock lek, but did not observe an attack. Ocelots exhibit behavioral specializations for bird hunting (Ewer 1973) and are probably the mammal that poses the greatest threat to displaying birds. Jaguars and pumas prey primarily on medium-size to large mammals, and occasionally on large ground birds such as curassows (Ewer 1973, Koford, 1983, pers. obs.). The tayra, a large mustelid, is omnivorous (Janzen 1983), but probably cannot capture fast-flying birds.

I found no published records of snake predation on lek-breeding birds, and snakes are not likely to be important predators on any Temperate Zone lek species. In the Neotropics, however, there are numerous species of bird-eating snakes, including the bird snake (*Pseustes poecilonotus*), the tree boas (*Corallus caninus* and *C. enydris*), the boa constrictor (*Boa constrictor*), the tiger rat snake (*Spilotes pullatus*), and the fer-de-lance (*Bothrops atrox*). These species occur in the rain forests of Suriname, and I saw the latter three species at the Voltzberg. I saw a boa constrictor kill two male Cock-of-the-Rock at the

Main Lek, and a third male was almost certainly killed by the same snake. These observations are described in detail below.

On 12 December 1980 I spotted a male Cock-of-the-Rock lying on the forest floor, wrapped in the cryptically patterned coils of a boa constrictor. The snake was approximately 1.75 m long and had already swallowed the bird's head. The bird's band combination confirmed that the dead male was the owner of the adjacent court, 0.5 m away. He apparently was struck while displaying on or perched near his court. The boa finished swallowing the Cock-of-the-Rock in approximately 15 min, then climbed out of sight into a small tree 3 m from the edge of the dead male's court. No mobbing or alarm calls were directed at the snake, and a few males remained perched within 3–4 m of the boa as it ate its victim.

On 11 January 1981 I found the dead male's numbered metal band and one of his color bands embedded in a mass of digested bone beneath the tree into which the boa had disappeared. Under the same tree I found another metal band, belonging to a male that had not been seen in the current field season. This male may have been an earlier victim of the boa. The band could not have been removed from a living bird, and it is unlikely that raptors or mammalian predators would consume their prey on the lek itself, given their observed intolerance of Cock-of-the-Rock alarm calls.

The boa killed another male the following day, 12 January, at 1317. There is no doubt that the same snake was involved, as it was the same size and coloration and attacked males on the same site only 4 weeks apart. The strike must have occurred only seconds before I noticed it, as the bird was still struggling feebly. The time from strike to death was less than 1 min. The surrounding males did not react to the snake's activity, and neither they nor the victim gave alarm calls. The victim was the new owner of the court where both kills occurred. To read his bands I had to prod the coils of the boa, and this disturbance caused the snake to drop its prey. It apparently then left the area, as there was no further evidence of its presence.

The effect of display group size.—For a group-displaying frog subject to intense predation pressure, Ryan et al. (1981) showed that predation risk was inversely correlated with increased chorus size for individual calling males and that overall predation rate was not correlated with group size. To assess the effect of display group size in Cock-of-the-Rock, I examined the frequency of spooks and predation at the Main Lek as group size declined seasonally and compared the Main Lek with the three smaller display sites.

There was a highly significant positive correlation between number of spooks per day and display group size at the Main Lek (Fig. 3). In contrast, the number of actual attacks appeared to be related inversely to group size. Attacks were observed 3 times more often when the lek was small that when it was large (Fig. 4), although these differences were not statistically significant ($\chi^2 = 4.18$, 3 df, $P > 0.10$). Thus, the increased incidence of spooks for large group sizes cannot be explained by a greater number of predator attacks. Instead, it presumably resulted from the transmission of individual false alarms through the group. The flushing of one male, even in the absence of apparent threat, frequently precipitated a major spook. For large group sizes there were many potential alarm instigators, resulting in frequent spooks, most of which appeared to be false alarms. For smaller groups the males were exposed to fleeing conspecifics less often and appeared less wary. The ratio of total spooks to actual attacks increased dramatically with group size at the Main Lek. For very small groups (<10 males, $n = 9$) it was 2:1, for small groups (10–19.9 males, $n = 18$) it was 7:1, for medium-size groups (20–20.9 males, $n = 36$) it was 13:1, and for large groups (≥30 males, $n = 15$) it was 50:1. The increased incidence of false alarms represents a cost of social display that could impose an upper limit on group size.

I also examined the effect of display group size by comparing the incidence of spooks and predation at the Main Lek and the three smaller display sites (Table 3). During January and February 1981–1983, we observed the Creek Lek (6 males) for 11 days, the Nest Slope Lek (2 males) for 12 days, and the Solitary Male display site (1 male) for 6 days. On these days simultaneous observations were made at the Main Lek, allowing matched comparisons between sites.

More spooks occurred at the Main Lek than the other sites, both in absolute numbers and in number of days with spooks. The only spook observed at a small site accompanied an Ornate Hawk-Eagle attack. This confirms the positive

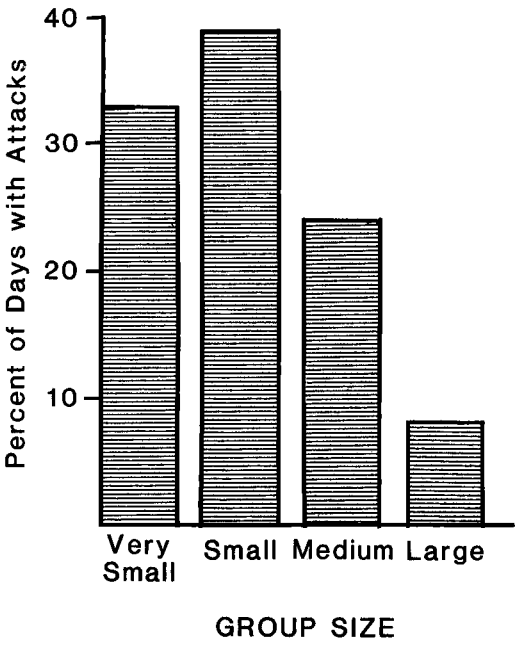

Fig. 4. Frequency of attacks at the Main Lek in relation to male group size. For each census day the daily mean group size was determined and assigned to the appropriate size class: very small (<10 males, n = 9 days), small (10–19.9 males, n = 18 days), medium (20–29.9 males, n = 38 days), or large (≥30 males, n = 13 days). The frequency of days with attacks was then calculated for each group size class.

relation between group size and spooks documented for the Main Lek. Because of fewer observation days at the smaller sites, I was unable to analyze precisely the risk per male at the different-size sites. The long-term persistence of small display sites and the occupancy of territories there by the same individuals for at least 3 breeding seasons indicates predation was not intense enough to preclude display groups of various sizes.

The effect of male attributes.—A final question concerning predation on leks is whether males differ in their vulnerability based on territory position, age, or both. Wiley (1973) suggested that peripheral male Sage Grouse should be taken by predators more often than central males, but he observed too little predation to test the hypothesis. Hartzler (1974) found 5 predator-killed male Sage Grouse during his study, of which 3 were adults with central territories, 1 was a peripheral male of unknown age, and 1 was unidentified. He concluded that central

TABLE 3. Incidence of spooks and attacks during simultaneous observation days at the Main Lek and smaller display sites. Main Lek = 55 territorial males, Creek Lek = 6, Nest Slope Lek = 2, and Solitary Male site = 1. Observations were made from 0700 to 1700 on each day. "Probable attacks" includes all cases in which an attacking predator was seen or inferred from Cock-of-the-Rock behavior.

	Main/ Creek	Main/ Nest Slope	Main/ Solitary
No. observation days	11	12	6
Days with spooks	11/0	12/1	6/0
Days with confirmed attacks	1/0	0/1	2/0
Days with probable attacks	3/0	4/1	4/0
Total spooks	56/0	37/1	29/0
Total confirmed attacks	1/0	0/1	2/0
Total probable attacks	5/0	4/1	5/0

males might be *more* vulnerable to predators than peripheral males.

Cock-of-the-Rock leks are irregular in shape because of the thick vegetation of the rain forest. The Main Lek was composed of three lobes of courts in a relatively open area, surrounded by thicker understory vegetation. Males with territories in the thicker vegetation were on the margins of the lek and rarely received female visits. During the course of the study 40 courts were occupied in this peripheral area, compared with 108 courts inside. There was no evidence of predation on the peripheral males, whereas 5 males on 4 of the more central courts were taken by predators (the ownership status of the remaining victim was unknown).

I determined the density of males in the area of each court by counting the territories falling inside a 5-m-diameter circle centered on that court. Two of the courts where predation occurred were in the area of greatest male density on the lek (0.9 courts/m^2). The other two courts were in areas with only slightly lower clustering (0.5 and 0.6 courts/m^2). These densities are very high compared with almost all other lek birds (see Trail and Koutnik 1986: table 1). These data reject the hypothesis that males in low-density or peripheral areas of leks are particularly vulnerable to predators.

Successful, older male Cock-of-the-Rock were equally likely to be killed by predators as young and unsuccessful males. Males attain full adult plumage at 3 yr of age, generally defend courts for the first time as 3- or 4-yr-olds, and mate for the first time at 4 or more years of age. I saw

no subadult 1- or 2-yr-old male attacked by predators. All 6 Cock-of-the-Rock for which there was direct or indirect evidence of predation were banded in adult plumage before the first breeding season of the study (1980). The ages at death of the four confirmed predation victims were: ≥3 yr (1 male), ≥5 yr (2 males), and ≥6 yr (1 male). The male whose band was found beneath the boa's tree was ≥4 yr old, and the male that disappeared immediately after the intense panic was ≥6 yr old.

Four of the males were killed after mating was under way for the year, and two of them mated before being killed (on average, only 33% of territorial males mated each year; Trail 1984). One victim was the most successful male on the Main Lek for the three breeding seasons before his death and occupied a court in the densest part of the lek. Overall, the yearly mortality rates of successful and unsuccessful court owners did not differ significantly. Based on returns of banded individuals, males that mated in a given season experienced an annual mortality rate of 0.24 ($n = 90$), vs. a rate of 0.20 for males that did not mate ($n = 171$, $G = 0.718$, not significant).

DISCUSSION

To understand the role of predation, detailed studies of both the behavior of predators (e.g. Schaller 1972, Spencer and Zielinski 1983) and the antipredator behavior of prey (e.g. Greene et al. 1978) are required. Such necessarily descriptive accounts are basic to the development and testing of models of selection, and as such are an indispensible part of modern evolutionary biology (Greene 1986).

It is generally accepted that males are safer displaying on leks than alone (Lack 1968, Oring 1982). Some consider this to have been an important force in the evolution of leks (Hjorth 1970; Wittenberger 1978, 1979). Others argue that predation is too infrequent or variable among lek species to be a general explanation for lekking (Lill 1974, Borgia 1979, Bradbury and Gibson 1983). The available data have two limitations. First, almost all studies have been conducted in extensively man-modified areas, where the predator community has been reduced in diversity and abundance. Second, there is a lack of data comparing predation on display groups of different sizes. These are needed to test whether lek display is indeed safer than solitary display for males of a given species.

Cock-of-the-Rock at the Voltzberg inhabit undisturbed rain forest and are exposed to a natural predator community. The predation rate on males at the Main Lek was comparable to the highest level previously reported for lek birds (Hartzler 1974), and the significance of this predation pressure was emphasized by the well-developed antipredator behavior of lek males. The regular occurrence of predation at all avian leks studied in relatively undisturbed habitats (Koivisto 1965, Lumsden 1968, Wiley 1973, Hartzler 1974, this study) suggests that the importance of predation as a source of mortality on leks has been underestimated. This does not mean, however, that lek-displaying males are more vulnerable to predators than are conspecifics that display solitarily. Males on large leks could gain antipredator benefits from three consequences of group display: better detection and mobbing of predators, lower predator success through the flock-confusion effect, and lowered individual risk through the selfish-herd effect.

The benefits of increased vigilance in groups have been documented for a wide variety of organisms (Bertram 1978) and appear to apply well to Cock-of-the-Rock. Displaying males at the Main Lek were alert, spooked readily, and were rarely attacked successfully. I found a significant positive correlation between group size and frequency of spooks, and a suggestive but nonsignificant inverse correlation between group size and frequency of attacks. If the observed decline in attack rate with increasing group size is genuine, it suggests that raptors regard the largest display groups as unprofitable targets. I was able to judge group size at a distance by the volume of calling at the Main Lek, and raptors may do so as well.

Snakes are the only predators for which Cock-of-the-Rock lack effective antipredator behavior. The Cock-of-the-Rock were particularly vulnerable to the boa constrictor because of their terrestrial display, tightly clustered courts, and extreme site tenacity. Once a snake encounters a lek it may be able to kill a significant proportion of displaying males. The stability of Cock-of-the-Rock leks in the face of this threat suggests either that the feeding patterns of snakes are inconsistent with the methodical removal of all members of a group or, more likely,

that snakes rarely find leks (because of the rarity of large snakes or leks, or both, or because of the snakes' limited searching radius). This potentially significant hazard of lek display in the tropics is thus apparently mitigated by the rarity and limited mobility of snakes, rather than by direct or indirect benefits of group defense.

The increased wariness of males in large display groups resulted in a greatly increased frequency of false alarms. The significance of this cost is difficult to assess but could involve three different currencies: energy, display time, and female preference. False-alarm spooks were usually brief and involved most of the males on the lek. Thus, the time consumed by false alarms was probably small and equally distributed among the males. The energetic cost of headlong flight off the lek several times a day could be more important, but the risk of ignoring an alarm was apparently greater. Finally, if false alarms are frequent enough to disrupt female courtship visits on a regular basis, they could impose an upper limit on lek size through female preferences. Females could bypass the largest leks to mate at smaller groups where false alarms interrupt courtship less frequently. More data on display groups of different sizes are needed to test this hypothesis.

A second possible antipredator function of leks is the confusion of the predator by multiple fleeing prey, as demonstrated in fish schools (Neill and Cullen 1974). The shrill alarm calls and explosive flight of dozens of males scattering from the Main Lek in a spook could have made target selection difficult for predators, contributing to the very low attack success rate. It may be relevant that the drab females often remained on the lek during a spook. These females apparently relied on escaping the attention of predators in the confusion created by the colorful fleeing males. I never saw a predator attack a female.

Finally, males that display in groups could benefit from the "selfish-herd" effect (Hamilton 1971, Wittenberger 1979, Ryan et al. 1981). Individuals can reduce their predation risk by increased clustering, in effect seeking cover within a group (Hamilton 1971). Care must be taken, however, when extending this argument from mobile groups of animals to the immobile arrangements of territories on leks. Wittenberger (1979) suggested that females may reduce their predation risk by favoring central males or territories on leks. I found no data to support this hypothesis in Cock-of-the-Rock or other lek species. Territory position did not correlate with predation risk in Cock-of-the-Rock. None of the males taken by predators owned peripheral courts, and two were resident in the most densely packed area of the lek.

Male Cock-of-the-Rock at leks perform active behaviors, including surveillance, mobbing, and evasion, that provide effective defense against avian and mammalian predators. They appear to lack such defenses against snakes, perhaps because these potentially significant predators rarely encounter leks. It has been stated that forest environments are unfavorable for the evolution of leks because predator detection is difficult in thick vegetation (Wiley 1974; Wittenberger 1978, 1979). This hypothesis was proposed to explain why most forest grouse display solitarily, while most grouse of open habitats lek. Forest-dwelling birds in many other families form leks, however, including manakins (Lill 1974, 1976; Foster 1981), hummingbirds (Snow 1974, Stiles and Wolf 1979), and cotingas (Snow 1982, this study). The effective antipredator behavior exhibited by Cock-of-the-Rock in rain forest suggests that correlations between mating systems and habitats are unlikely to be due to predation.

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