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NOTES ON THE BEHAVIOR AND ECOLOGY OF THE  
RED-COTINGAS (COTINGIDAE: *PHOENICIRCUS*)

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**ABSTRACT.**—The two species of red-cotingas, *Phoenicircus*, are little-known birds with a patchy distribution in the rain forests of northern and central South America. We observed the foraging, displays, and vocalizations of the Guianan Red-Cotinga (*P. carnifex*) in Suriname and of the Black-necked Red-Cotinga (*P. nigricollis*) in northeastern Peru. Males of both species formed small, low-density leks. Almost all display occurred in the first hour after dawn, after which the birds dispersed and were rarely observed. Direct interactions between displaying males were infrequent, and male–male spacing at the lek appeared to be mediated through calling. Display consisted of repeated calling and horizontal flights between perches 5–15 m up in the understory. Display flights are often accompanied by mechanical whistling sounds. Although we observed female visits to the lek, no copulations or obvious pre-copulatory behaviors were seen. In courtship and vocalizations, as in morphology, red-cotingas exhibit characters of both manakins and cotingas. Received 19 Feb. 1991, accepted 28 May 1991.

The red-cotingas, genus *Phoenicircus*, are two closely related species inhabiting the lowland rain forests of northern and central South America. In both species, the male has a brilliant scarlet crown, breast, rump, and tail. The sides of the head, throat, back, and wings are black in male Black-necked Red-Cotingas (*P. nigricollis*) (see Frontispiece) and dark brown in male Guianan Red-Cotingas (*P. carnifex*). The females of both species are duller, with olive brown wings and backs and pale rosy un-

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COLOR PLATE

Male Black-necked Red Cotinga (*Phoenicircus nigricollis*) on a display perch in the rain forest of eastern Peru. Painting by Paul Donahue.



derparts. The Black-necked Red-Cotinga occupies upper Amazonia in Colombia, Ecuador, Peru, and Brazil, while the Guianan Red-Cotinga inhabits eastern Venezuela, the Guianas and lower Amazonian Brazil. Given the close similarity of the two forms, there is some question whether they are distinct species. The chief evidence for their being distinct is an area of possible sympatry along the southern tributaries of the Amazon, particularly the Rio Tapajós (Snow 1982).

The systematic position of *Phoenicircus* is uncertain. The outer and middle toes are united, as in manakins (Pipridae). Snow (1973) further suggested that the color of the plumage might indicate affinities with the manakins. Among the cotingas, *Laniisoma* also exhibits united toes as well as another character of *Phoenicircus*, modified seventh primary feathers. However, in *Phoenicircus* the seventh primaries are shortened and strongly recurved, while in *Laniisoma* they are slightly elongated and attenuated at the tip. Sclater (1888, cited in Snow 1973) linked *Phoenicircus* with the cocks-of-the-rock, *Rupicola*, apparently based on body color, the anterior crest (slight in *Phoenicircus*, extremely exaggerated in *Rupicola*), and the modified primaries (seventh in *Phoenicircus*, tenth in *Rupicola*, and differently shaped in the two genera). Snow (1973, 1982) concluded that in the absence of strong evidence to the contrary, it was best to retain *Phoenicircus* as an isolated genus within the Cotingidae.

The ecology and behavior of both species of red-cotingas are virtually unknown (Snow 1982). In this paper, we summarize observations on the diet, display, and vocalizations of both *P. nigricollis* and *P. carnifex* made during the course of other studies in Peru and Suriname.

#### STUDY AREA AND METHODS

Trail observed a small population of *P. carnifex* from December 19, 1985 to March 17, 1986 at the Brownsberg Nature Reserve, Brokopondo Province, Suriname. This 6000-ha reserve (4°53'N, 55°13'W) is located 130 km south of Paramaribo on the western shore of the Brokopondo Reservoir. The study area was at the northern end of the reserve's Mazaroni Plateau (elev. 500 m).

*P. carnifex* is rare and local in Suriname. Aside from Brownsberg and vicinity, it has been reported only from the Kayser Mountains in southern Suriname (Haverschmidt 1968). Trail never recorded the species in 24 months of fieldwork in the lowland rain forests of the Raleigh Falls-Voltzberg Nature Reserve (elev. 20 m), approximately 125 km WSW of Brownsberg.

Donahue observed *P. nigricollis* on 10 days between November 29, 1988 and January 11, 1989 at the ExplorNapo camp of Explorama Tours, Dpto. Loreto, Peru (3°15'N, 72°55'W). This camp (elev. 140 m) is located approximately 72 km NE of Iquitos, along Sucusari Creek, a left bank tributary of the Rio Napo. Donahue has not encountered the bird elsewhere in the course of repeated visits to the species' range in NE Peru and E Ecuador.

It is worth noting that neither of us has seen or heard red-cotingas more than 1 km from the display areas at either of our study sites. Localized distributions and small population sizes appear to be typical of both species of red-cotingas across their entire range (Snyder 1966, Hilty and Brown 1986).

Observations of displaying birds were made using 8× or 10× binoculars and a 15× spotting scope. Vocalizations were recorded on cassette tape, using Sony and Marantz recorders and Sennheiser directional microphones. Analysis of vocalizations was carried out using a Kay DSP-5500 Sonagraph.

## RESULTS

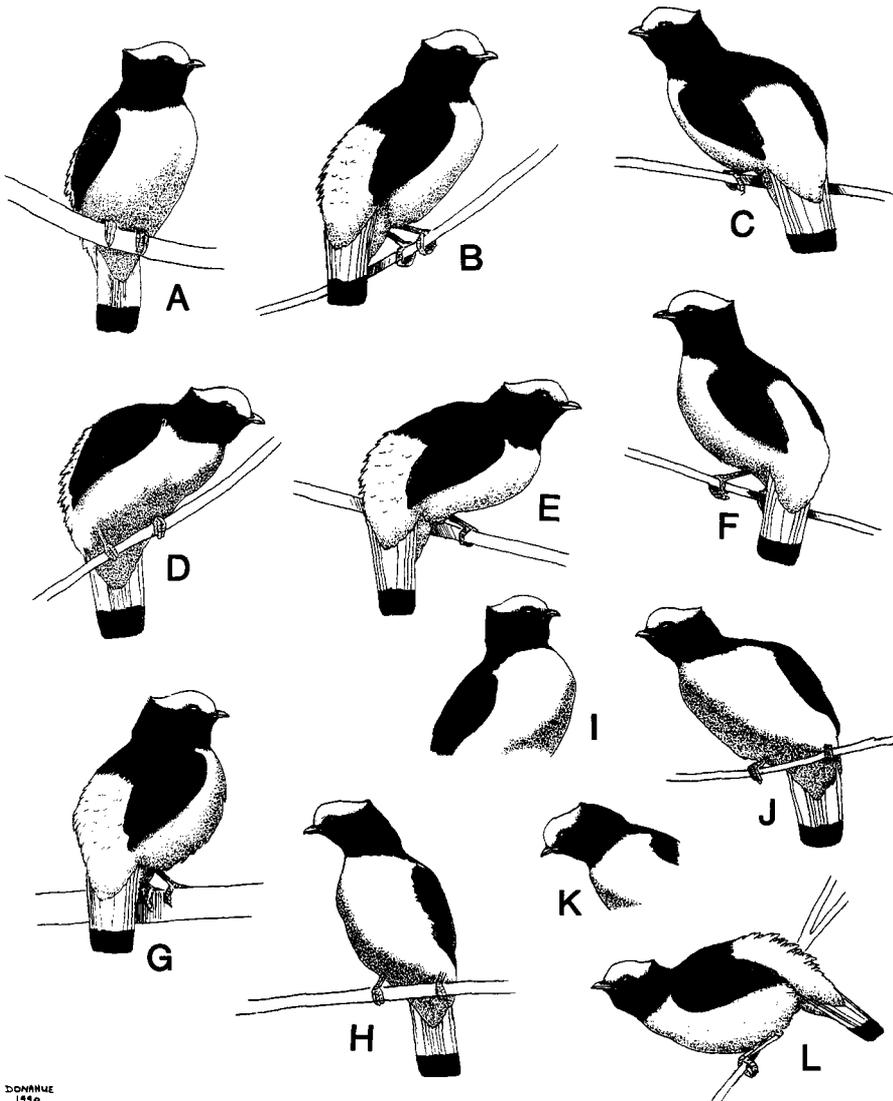
*Measurements.*—One adult male *P. carnifex* was mist netted two times, on January 24 and February 15, 1986. The wing length was 94 mm; culmen 10.5 mm; gape width 18.5 mm; weight 77 g (Jan. 24) and 78 g (Feb. 15). All feathers appeared new, and there was no molt on either date. Some of the soft part colors differed from those given in Snow (1982). The strikingly large eyes were dark brown; the bill was horn color; the gape was pale yellow; and the legs were pinkish-flesh in color. The soft part colors of *P. nigricollis* are similar, but the bill is yellow ochre.

*Characteristics of *Phoenicircus leks*.*—The only published description of red cotinga courtship indicates that males of *P. nigricollis* display in groups of up to 12 individuals and that these groups may move widely (Olalla 1943, cited in Snow 1982). Displaying male Black-necked Red-Cotingas observed in Brazil were described as very tame (Olalla 1943, cited in Snow 1982), but we found both species to be difficult to approach closely.

Fig. 1 illustrates typical postures of male *P. nigricollis*. Drawings A, B, and G show birds in relaxed perching postures; drawings C, F, H, and I illustrate different states of alertness. Display postures are shown in drawings D, E, J, K, and L; these are described in more detail below. Note that the tail is often twisted slightly to the side both during perching (Fig. 1F) and calling (Fig. 1D, E). This emphasizes the conspicuous rump.

The display area of *P. nigricollis* at ExplorNapo was in terre firme forest, along a low, wide ridge. All displays and calling took place within an area measuring approximately 300 × 150 m, with the most intense activity centered in an area about 75 × 150 meters. Although the wide spacing and frequent flights of the males made accurate counts difficult, a total of 6–10 males probably displayed regularly in this area. Display and foraging took place in the understory from 8–15 m above the ground.

At Brownsberg, all observed *P. carnifex* displays occurred in an area measuring approximately 100 m × 50 m. The forest in this area was characterized by scattered tall emergent trees reaching a height of 40 m, a canopy at approximately 30 m, a well-developed understory level of small trees at about 10–15 m, and little growth beneath this understory. The red-cotingas occupied the understory level, typically displaying and foraging at a height of 8–12 m. A lek of eight male Capuchinbirds (*Perissocephalus tricolor*, Cotingidae) occupied the lower canopy in this same site, at a height of 15–25 m.



DONAHUE  
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FIG. 1. Postures of male *Phoenicircus nigricollis*, based on field sketches. A, B, G. Relaxed perching. C, F, H, I. Various alert postures, ranging from low (C) to high (H) intensity. D, E, L. Bowing postures of calling males. J, K. Male between calls, showing head-bobbing.

On most days, two male red-cotingas displayed in the area. One male was captured and color banded on January 24 and was resighted repeatedly through the remainder of the observation period. The other male was unbanded but could be individually recognized by a horizontal band of lighter feathers on his upper breast. A third male was observed calling infrequently in this area (less than one day per week).

During our one to three month observation periods, males displayed daily within adjacent, largely exclusive ranges, and did not appear to display elsewhere. The display ranges were very small in relation to the similar surrounding habitat, and contained no concentration of resources used by visiting females. Although there were some fruiting trees in the display areas, the same tree species appeared widespread in the surrounding forest. These characteristics of the display sites and the display behavior of male red-cotingas fulfill the criteria for lek behavior (Bradbury 1981).

*Male-male interactions at the lek.*—In *P. carnifex*, the two regular males maintained adjacent, slightly overlapping regions of display activity, typically remaining at least 20 m apart. At this distance, they were frequently out of visual contact but in continual auditory contact. The display area of the banded male was elliptical, measuring approximately 60 m × 20 m; that of the unbanded male was more nearly circular, measuring about 30 m in diameter. The display areas of the male *P. nigricollis* appeared to be in this same size range, or slightly larger.

Overt aggression between male red-cotingas was observed only once. This occurred at the *P. carnifex* lek outside the usual display area of either resident male, but nearer the unbanded male's range. The birds were perched in adjacent saplings, only 4 m apart. For 10 min, the males made occasional short flights (with wing-whistling, described below) but gave no calls and engaged in no direct interactions. Then the banded male flew to within 2 m of the other bird, who promptly supplanted him with a strike or near-strike. Shortly thereafter, the banded male flew out of sight in the direction of his normal display range. He gave an advertising call from his new location (at least 20 m away), which the unbanded male immediately answered. When Trail then gave an imitation of this call, the unbanded male responded by flying assertively around the area, looking for the source. On other occasions, these males were observed feeding together without aggression at fruiting trees near the lek.

*Descriptions of courtship displays and vocalizations.*—The display of both *P. carnifex* and *P. nigricollis* occurred almost exclusively during the first one to two hours after first light, with only occasional calling later in the day. During 13 observation days on *P. carnifex* from December 24,

1985–February 4, 1986, the mean time of the first call was 05:48 h (range 05:39–05:55). The mean time of the first call for *P. nigricollis* was almost identical: 05:42 h (range 05:36–05:46, N = 4 mornings). This was approximately 15 min after first light in the forest interior. Display activity appeared to be more intense on sunny mornings than when there was overcast. On most days, calling continued actively until 06:30–07:00 h, after which the males were rarely seen.

In both species, this dawn period was usually the only bout of display, although on some days there was sporadic calling at other times, particularly in the late afternoon. If one male began calling after dawn, the other male usually returned to his display area and joined in. This pattern is presumably the basis for the statement that the group of displaying males in *P. nigricollis* is “called up” by one individual (Olalla 1943, cited in Snow 1982). The brief daily display of *Phoenicircus* contrasts with the more extensive display of most other lekking cotingas and manakins and may help to explain the paucity of observations on red-cotingas.

All the displays that we observed were associated with the production of vocalizations and mechanical noises. The most common vocalization of *P. carnifex* was the advertising call (Fig. 2A) which can be rendered as “pee-chew-eet.” This call was always the first vocalization given at dawn. The preferred calling perches were small horizontal branches or lianas, free from foliage, 8–10 m up. Each male called from at least a dozen perches within his range and did not have obvious favorites.

During bouts of “pee-chew-eet” calling, the males typically maintained an upright posture with their tails straight down and their scarlet rump feathers fluffed out and very conspicuous. They also erected their short crown feathers, which then partially covered the base of the bill. As they produced the call, the males pulled their heads back in a pumping motion. The interval between “pee-chew-eets” during calling bouts averaged 16 sec (range 4–44 seconds, N = 59).

The advertising call of *P. nigricollis* is a loud note which can be rendered as “whea”; this was often preceded by a soft “wur” note (Fig. 3A). “Whea” calls were always the first vocalization to be heard at dawn. They were sometimes given in series, with either increases or decreases in volume from the first to last call. During intense calling, the “whea” sometimes became distinctly two-syllabled: “whee-ah,” with the accent on the first syllable.

During calling, the males bowed forward on their perches, with conspicuously ruffled rump feathers (Fig. 1D, E, L). Between calls, the male remained in a slightly bowed posture and commonly performed a rapid forward head bobbing or bowing (Fig. 1J, K). This was similar to the head-pumping of *P. carnifex* but did not accompany the production of the call itself. Each male appeared to have 3–5 favorite calling sites within

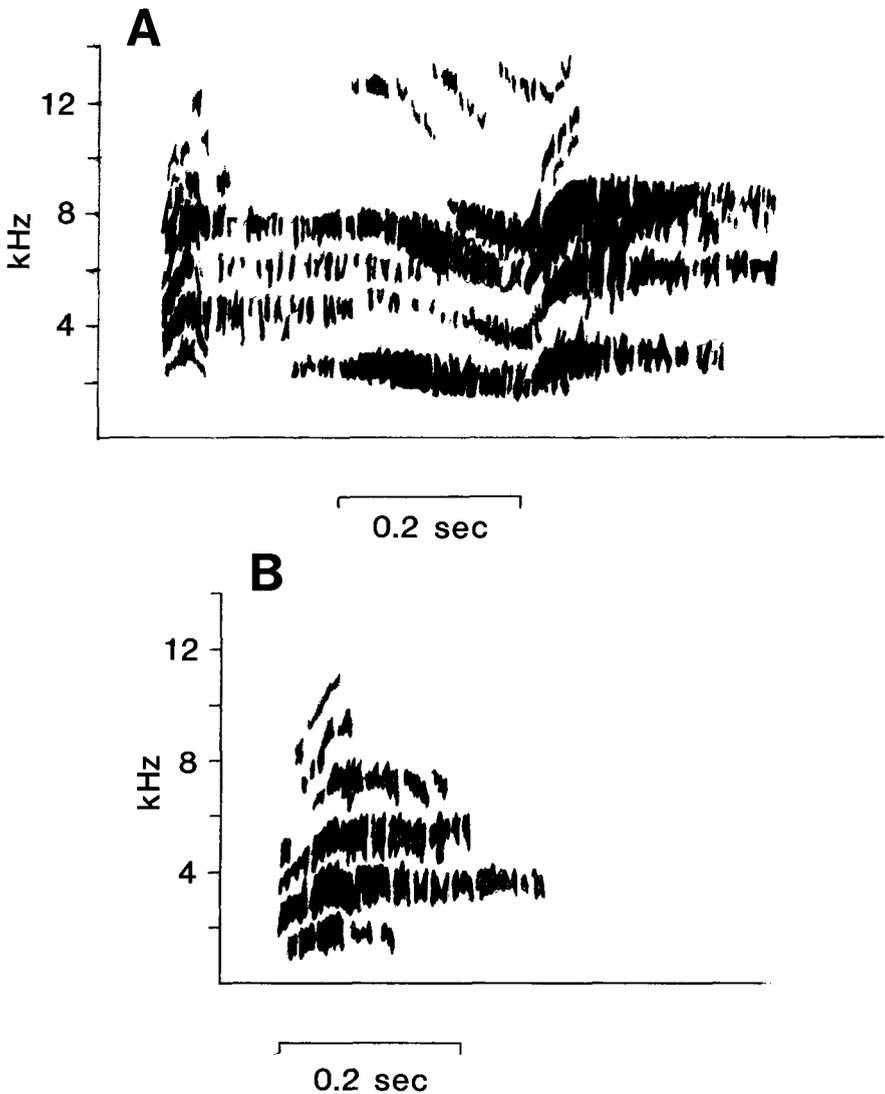


FIG. 2. Vocalizations of *P. carnifex*. A. The “pee-chew-eet” advertising call. B. The “wheep” call, which is given in contexts of arousal and alarm. See text for further information.

his display area. Horizontal sections of hanging lianas were the overwhelmingly preferred calling perches.

The most obvious display in both species of red-cotingas was the horizontal flight display. Males flew rapidly between calling perches 6–20 m apart, swooping up to land on the new perch. During all display flights,

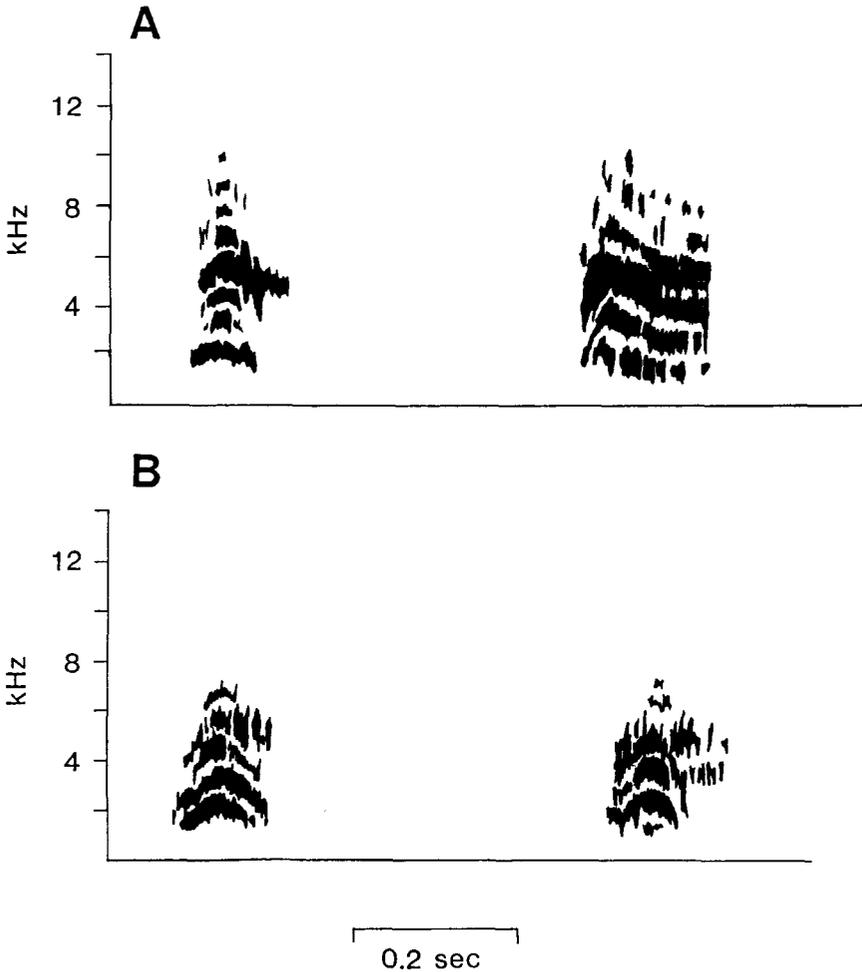


FIG. 3. Vocalizations of *P. nigricollis*. A. The advertising call: a quiet "wur" followed by a loud "whea." The "whea" was frequently given without the introductory note. B. Two examples of the "yip" arousal or alarm call. See text for further information.

the males in both species produced a characteristic mechanical sound, presumably with their modified seventh primary feathers (illustrated in Snow 1982). This was a two-part ringing sound, recalling a rapid pair of cricket calls (Fig. 4).

Male *P. carnifex* frequently produced a high-pitched whistle vocalization (Fig. 4) as the male swooped onto a perch at the end of a flight display.

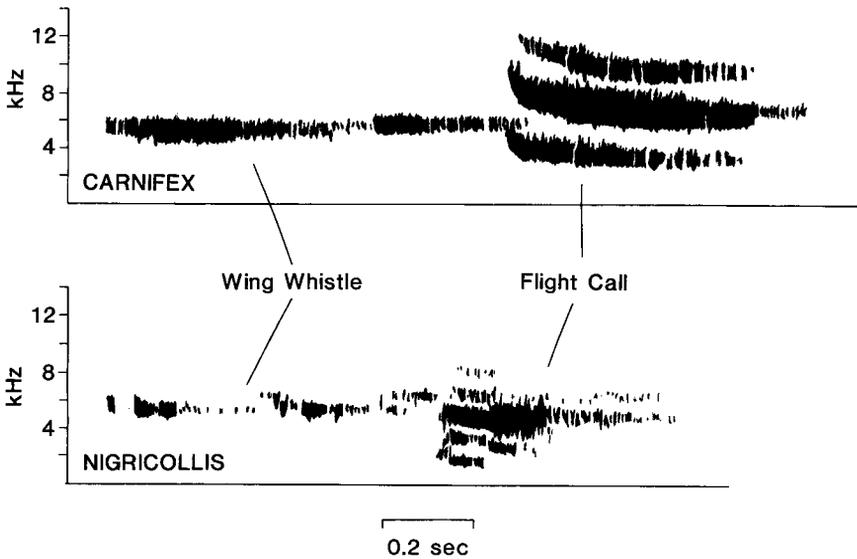


FIG. 4. Flight sounds of *Phoenicircus*: mechanical wing whistles followed by flight calls. A. *P. carnifex*: wing whistle followed by flight whistle. B. *P. nigricollis*: wing whistle followed by abbreviated version of the “whea” call given in flight.

This whistle was never given independent of flight display, but the flight display was sometimes performed without the whistle call. When the flight whistle vocalization was given, it followed the mechanical wing whistle, never preceded it.

Male *P. nigricollis* apparently did not call in flight as frequently as did *P. carnifex*. However, they did sometimes produce an abbreviated version of the “whea” call at the end of a display flight, following the mechanical wing whistle (Fig. 4). This was much lower-pitched than the *P. carnifex* flight whistle, and sounded more like a squawk than a descending whistle.

The third *Phoenicircus* vocalization was a short, loud monosyllable, which sounded like “wheep!” (in *P. carnifex*) or “yip!” (in *P. nigricollis*). The versions of this call produced by the two species were similar, although the *P. carnifex* version was higher-pitched (Figs. 2B and 3B). Unlike the advertising and flight calls, the “wheep” call was given by both male and female red-cotingas. It appeared to signal a high degree of arousal or alarm, as it was given both in response to human disturbance and during female visits to the display area. In such situations, long series of “wheep” calls were sometimes given without any other vocalizations. This call was reminiscent of the “hey” alarm call of another cotinga, the Guianan Cock-of-the-Rock, *Rupicola rupicola* (see Trail 1987, Fig. 2).

The final sound produced by *P. carnifex* was the wing buzz. This two-

part mechanical sound was short and loud, very different from the high-pitched wing whistle. Trail heard the wing buzz very rarely and saw it being produced only once. On this occasion, three male red-cotingas were in close proximity at a fruiting tree on the edge of the display area. One male made a short ( $\leq 2$  m) flight upward at a  $45^\circ$  angle, during which this two-part buzz was produced. No further details were seen, and the significance of this sound remains unknown. Male *P. nigricollis* were never heard to produce a loud wing buzz. Given the rarity of this sound in *P. carnifex*, however, it may still be recorded in *P. nigricollis*.

*Male-female interactions.*—Drably colored *P. carnifex* were observed at the Brownsberg lek on five occasions. These were probably all females. The plumage of young male red-cotingas resembles that of females but is brighter (Snow 1982); no such intermediate plumages were seen. During these visits, the males concentrated their activity in the vicinity of the female, and the rates of “pee-chew-eets” and especially flight displays and flight whistles increased. In the absence of females, the ratio of “pee-chew-eets” to flight whistles was about 5:1, but during female visits this ratio dropped to approximately 2:1. This supports the interpretation of “pee-chew-eets” as advertising calls, with display flights and flight whistles representing more directed courtship behavior.

Despite their increased rates of calling and flight displays, male red-cotingas did not attempt to intercept or perch adjacent to females visiting the display area. We recorded no novel displays or calls associated with female visits, and observed no direct courtship interactions or matings. Female red-cotingas either simply passed through, or stopped for a few minutes to feed on fruits in the display area. They frequently gave “wheep” calls, but we were unable to determine whether these were given to attract males, in response to the males’ displays, or in response to our presence.

Female visits to the *P. nigricollis* lek at ExplorNapo Camp were not observed. Periodically during observations, the rate of “whea” calling would increase dramatically. This presumably signalled the approach of a female, but the large distances between males and the wariness of the birds precluded confirmation.

*Behavior away from display sites.*—During the course of studies at Brownsberg, Trail and assistants spent much time walking through the forests of the northern Mazaroni Plateau, an area of approximately 4 km<sup>2</sup>. We rarely heard red-cotingas away from the display area (always giving “wheep” calls) and sighted them only once. On this occasion we located two female-plumaged red-cotingas giving a series of “wheep” calls, at least 0.5 km from the display area. These birds remained 4–5 m apart, but they moved together, apparently foraging for fruit 6–10 m up in the thick understory foliage. An unbanded male was also present, actively flying around the area with wing-whistles, but without giving “pee-chew-

eet" or "flight whistle" calls. This male never directly interacted with the females but remained in their vicinity. He had a pale ring of feathers on his breast and may have been the same individual as the similarly marked unbanded male at the display area.

*P. nigricollis* were observed away from the lek only twice, despite extensive walking by Donahue over the surrounding 4–5 km<sup>2</sup> of forest. Both these observations were brief glimpses and occurred within approximately one-half kilometer of the lek.

*Observations on feeding.*—Red-cotingas appear to be completely frugivorous, with recorded food items from the families Palmae (*Euterpe*), Moraceae (*Ficus*), and Passifloraceae (Snow 1982). At Brownsberg, *P. carnifex* was observed feeding on the fruits of Myrtaceae (*Eugenia*), Guttiferae (*Clusia*), Melastomataceae (*Miconia*), and Lauraceae (genus unidentified). At ExplorNapo camp, *P. nigricollis* was observed feeding on the fruits of Meliaceae (*Trichilia*).

Moermond and Denslow (1985) have suggested that red-cotingas may rely on hovering and stalling flight maneuvers to gather fruits, based on the short, highly slotted wings and high wing loading of these species. In stalling, a bird uses a steep wing attack angle stop briefly in front of the fruit, which is then seized. Twenty-one fruit captures by *P. carnifex* were observed. Fruits were taken in flight in 12 cases, using the following methods: snatch (5 times), stall (4 times), and hover (3 times). In the remaining 9 foraging observations, red-cotingas picked fruit from a perched position. The picked fruit was a berry in a panicle in seven cases and a drupe in the other two cases.

All observations of feeding in *P. carnifex* took place at the lek and its immediate vicinity. Males typically made between one and three fruit captures, and then returned to display perches. Feeding was usually solitary, although the resident males sometimes fed together. Red-cotingas were never seen accompanying the mixed species flocks that fed on fruit in the forest canopy at Brownsberg. The observation, described above, of three red-cotingas travelling together away from the lek suggests that the birds sometimes forage socially, although feeding was not observed.

On the only occasion when feeding was observed in *P. nigricollis*, a male and a female were seen feeding on the fruits of a *Trichilia* tree located near the center of the lek. Feeding with them in the same tree were Black-spotted Barbet (*Capito niger*), Lawrence's Thrush (*Turdus lawrencii*), and White-tailed Trogon (*Trogon viridis*).

#### DISCUSSION

Our observations support the traditional classification of *P. carnifex* and *P. nigricollis* as separate species. Although the displays are similar, the vocalizations are distinct. If these species do come into contact south

of the Amazon, it is likely that the differences in their lek behavior would be sufficient to prevent interbreeding. Given the apparent affinities of *Phoenicircus* with both the cotingas and the manakins, it is of particular interest to compare the courtship displays of red-cotingas with those of other members of these two families. The evolution of displays in manakins has been extensively discussed (Snow 1963, Sick 1967, Prum and Johnson 1987), and Snow (1982) has reviewed the information available on courtship behavior in the cotingas (see also Trail 1985, Bierregaard et al. 1987).

In vocalizations and displays, as in morphology, *Phoenicircus* recalls both manakin and cotinga species. The posture of a male *P. carnifex* giving the "pee-chew-eet" call, with fluffed rump and erect crown, resembles that of the cocks-of-the-rock (*Rupicola*), a similarity noted by Robert Ridgley (cited in Hilty and Brown 1986). The advertising calls, and particularly the accompanying head-pumping motion in *P. carnifex*, recall another group of cotingas, the pihas (*Lipaugus*). The flight display resembles that of the *Pipra* manakins, particularly *P. erythrocephala* (Snow 1962a, Lill 1976), while the wing buzz is strikingly like sounds produced by the manakins of the genus *Manacus* (Snow 1962b, Lill 1974). The wing whistle accompanying the red-cotinga flight display is more unusual, but recalls the sounds made by male Guianan Cock-of-the-Rock in flight. In the cock-of-the-rock, however this sound (produced by elongated tips on the tenth primaries) is not part of a special flight display. Finally, the alarm call of *Phoenicircus* resembles that of *Rupicola*.

The blend of cotinga and manakin courtship behaviors exhibited by red-cotingas emphasizes the closeness of these families. Observations of precopulatory behavior and mating in *Phoenicircus* may provide further insight into the affinities of this fascinating genus. As in the manakins in which acrobatic flight displays are important elements of courtship (especially *Pipra* and *Chiroxiphia*), male *Phoenicircus* are significantly smaller than females (Snow 1982). This suggests that the as-yet-unreported precopulatory displays of male red-cotingas may involve more elaborate flight maneuvers than those we observed.

#### ACKNOWLEDGMENTS

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dedicated to David and Barbara Snow in admiration of their pioneering field studies of cotinga behavior and ecology.

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## COLOR PLATE

The frontispiece painting by Paul Donahue has been made possible by an endowment established by George Miksch Sutton.