Differences in connections could be attributed to the differing general visceral functions of the nucleus. This source of confusion is absent in catfish, in which the general visceral nucleus is anatomically distinct and separated from the gustatory lobes.

The gustatory system of vertebrates, including perhaps mammals and humans, can thus be viewed as consisting of two (or more) subsystems that mediate different behaviors. Although differential parallel processing of inputs in other sensory modalities is well known (*11*), this is, to our knowledge, the first anatomical evidence for parallel subsystems of the gustatory sense.

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8. In mammals, the nucleus ambiguus is a migrated cell group; that is, during embryogenesis the neuroblasts leave the proliferative zone at the ventricular surface and move radially outward into the developing medullary tegmentum. In frogs and some fishes, the nucleus ambiguus does not travel far from the ventricular surface, and so the cell bodies come to lie dorsomedial to the position of the same cell group in mammals.
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10. The vagal lobe is also interconnected with the commissural nucleus of Cajal, which is the general visceral sensory nucleus of the caudal medulla. In catfish, the general visceral sensory nucleus is entirely separate from the more rostrally placed gustatory nuclei. This contrasts sharply with the situation in the nucleus solitarius, the homologous structure in mammals and birds.
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12. Supported by NIH grants RO-1 NS-15258 and KO-4 NS-00772. These results were presented in part at the 1984 meeting of the Association for Chemoreception Sciences.

14 September 1984; accepted 24 September 1984

Courtship Disruption Modifies Mate Choice in a Lek-Breeding Bird

Abstract. *The aggregation of displaying males in lek-breeding birds is often associated with disruption of courtship and mating but effects of this disruption on mate choice have not been shown. In a 4-year study of* Rupicola rupicola *in Suriname, interference among territorial adult males disrupted 31 percent of all female courtship visits and terminated 32 percent of all matings at a lek where there were an average of 55 territorial males. Disruption in this rain forest species caused females to modify their courtship and mating patterns, and males that used intense and persistent disruption received a disproportionate share of this redirected mate choice.*

Mate choice is a fundamental aspect of sexual selection and has emerged as a focus of evolutionary theory (*1*). Of particular interest is the degree to which members of the limiting sex (usually females) are able to control with whom they mate. The lek-mating system is generally considered to be particularly favorable for the operation of mate choice because females of lek species receive no resources from males, initiate mating by solicitation, and are not subject to forced copulation (*2*).

The one direct means of thwarting female choice that is available to the males of lek species is courtship disruption. This can be defined as any interference in courtship or mating that decreases the number of complete copulations performed by a male or that increases the time and energy required to perform them (*3*). Interruption of mating by competing males has been reported for all well-studied lek species, at levels ranging from 2 to 68 percent (*4*). However, because no direct benefits resulting from this behavior have been shown, the adaptive significance of courtship disruption is controversial (*2, 3*).

I present evidence that courtship disruption in a lek-breeding bird, the Guianan cock of the rock (Cotingidae: *Rupicola rupicola*), can provide direct benefits to disrupters by modifying female choice. These data were collected during a 4-year study of a color-banded population of *Rupicola* at the Raleigh Falls–Voltzberg Nature Reserve in Suriname, South America. The study lek, located in dense rain forest, had an average of 55 territorial males during the 1980 through 1983 breeding seasons (range, 51 to 61 males). Each *Rupicola* display territory is defended by a single male and consists of a cleared ground court (approximately 1 m in diameter) and the surrounding perches, to a height of 1 to 2 m above the court. The nearest-neighbor distance between court edges on this lek averaged 1.4 ± 1.26 m (mean ± standard deviation; $n = 96$), providing many opportunities for males to observe and disrupt each other's courtship.

Females come to the lek for courtship and mating, typically visiting the territories of a number of males over several days before copulating one or two times. Such a period is called a mating bout. Females initially observe the males from perches in the subcanopy and then enter individual display territories for courtship interactions (*5*). I limit the term "courtship disruption" to harassment of females actually visiting a male's territory.

During the study period 385 copulations and 3169 courtship visits by females to male territories were observed. As in other lek species, male *Rupicola* mating success is highly skewed, with the most successful male performing an average of 30 percent of all matings per year (range, 23 to 39 percent), and 67 percent of territorial males failing to mate at all each year (*5*). On average, adult males disrupted 31 percent of courtship visits (range, 28 to 36 percent) and 32 percent of matings (range, 21 to 41 percent) annually. Approximately half the territorial males, representing the full

Table 1. Courtship and mating of female *Rupicola* in relation to disruption during the first copulation of the mating bout. Disruption significantly increased the amount of courtship, number of males sampled, and degree of polygamy (all comparisons at $P < 0.05$ level, arcsin test for degree of polygamy; one-way analysis of variance for other measures). Means and standard deviations are shown.

First mating	Mating bouts	Courtship visits	Males visited	Polygamous females (%)
Disrupted	17	15.3 ± 10.74	4.2 ± 3.32	47
Complete	55	6.7 ± 5.82	2.8 ± 1.58	18

range of territory locations and mating success on the lek, performed courtship disruption each year (mean 48 percent, range 43 to 56 percent (*6*). None of the differences between years is statistically significant, indicating that courtship disruption is a normal aspect of adult male *Rupicola* behavior (*7*).

I observed 161 cases of disruption in which both the specific female and male involved were identified. Using this sample, I was able to examine the effects of courtship disruption on: (i) subsequent female courtship and mating, (ii) the mating success of the victimized male, and (iii) the mating success of the disrupting male.

Interruption of the first copulation of a mating bout has a clear effect on female behavior in *Rupicola*. Interrupted females subsequently performed significantly more courtship visits and visited more males than did others, and they were more likely to mate with more than one male (Table 1). This tendency of females to redirect their mate choice away from males with whom they were interrupted constitutes a direct reduction in male mating success due to disruption.

Because of the skew in *Rupicola* male mating success, it is not meaningful to calculate an average probability of mating between disrupter males and the females that they disrupt. Instead, I focused on the actual sample of potential mates considered by each female. Each female *Rupicola* visits only a few males at the lek (mean, 3.1 ± 2.2; n = 72 mating bouts by banded females) and chooses her mate from this group. Among 230 observed combinations of banded males and females, 29 were between a female and a male that had disrupted her, and 201 involved pairs where there had been no prior disruption. Disrupting males obtained more matings (62 percent, 18 of 29) than nondisrupters (41 percent, 83 of 201; a few females mated with a male in each category). This statistically significant difference [$P < 0.05$, $\chi^2(1) = 4.44$] suggests that disrupters can gain reproductive benefits as a result of disruption. Since reproductively successful males do not perform more disruption overall (*6*), this result is not due to a restriction of disruptive behavior to the most attractive males.

Does disruption redirect mate choice to particular disruptive males, or does it merely reopen the choice process of females? Evidence that specific redirection can occur comes from an analysis of the various types of disruptive behavior. Adult *Rupicola* males perform several different disruptive behaviors, which can be classified as confrontational or nonconfrontational (Fig. 1). Confrontational disruption involved direct physical conflict between the two males and takes three forms: male-male fighting, direct interruption of copulation (*8*), and attempted mounting of a female on another male's territory. Nonconfrontational disruption, in contrast, does not involve physical conflict between the males and thus may be less costly for the disrupter. It takes two forms: supplanting of the female and threat display directed at the courting pair (calls and wing-beating). Supplanting of a visiting female from her perch in another male's territory was by far the most common form of disruption observed, and the two types of nonconfrontational disruption together accounted for 64 percent of all disruption.

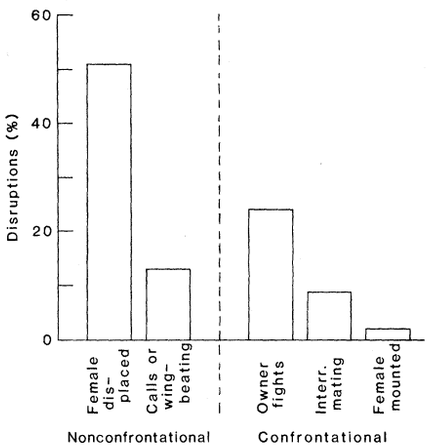

Fig. 1. Types and frequencies of courtship disruption performed by adult male *Rupicola*. Observations are of disruption by identified adult males (n = 991).

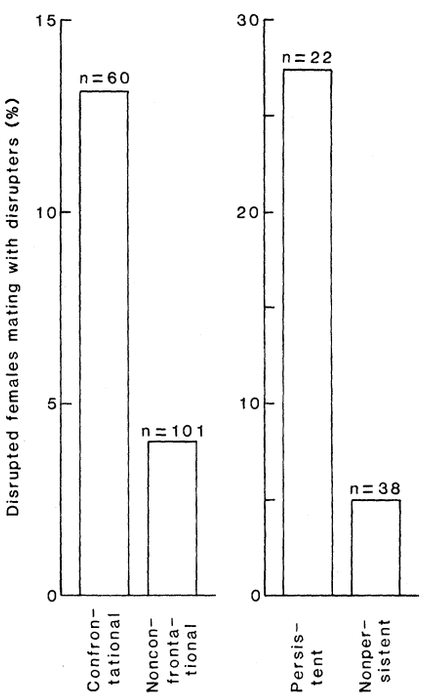

Fig. 2. The effect of disruption intensity and persistence on female mate choice in *Rupicola*. (A) Males using confrontational disruption were significantly more likely to mate than were nonconfrontational disrupters [$P < 0.05$, $\chi^2(1) = 4.79$]. Because these data are not limited to the subset of disrupting males actually visited by the disrupted females, the probability of actually mating is relatively low. (B) Males using persistent disruption were significantly more likely to mate than were nonpersistent males [$P < 0.05$, $\chi^2(1) = 5.84$].

Males that performed the more intense confrontational disruption were significantly more likely to mate with the females that they disrupted than were nonconfrontational males (Fig. 2). Among confrontational males, the greatest benefits were to those that carried out a persistent form of disruption (that is, directed at least four disruptions toward a specific visiting female within 1 week) (*9*). Because these males directed their disruptive behavior toward specific females, they appeared able to focus the choice of the disrupted females on themselves more effectively.

If disruption confers reproductive benefits, why isn't it even more widespread in the *Rupicola* mating system? Highly disruptive males may suffer because of the decreased time and energy that they spend defending and displaying on their own courts. For example, in 1983, the mating success of one male fell from 12 percent (8 of 67 matings) to 3 percent (2 of 60 matings) after he became extremely disruptive. Moreover, the intense confrontational disruption that appears to confer the greatest benefits may also incur the greatest energetic cost and risk of retaliation. Disrupting males were subjected to immediate retaliation in 70 percent of interrupted copulations (n = 124), being either chased or grappled with by the disrupted males. These costs appear to limit the overall incidence of courtship disruption in the *Rupicola* lek-mating system, with the result that female mate choice is largely free of direct male control.

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6. Mating males were divided into three classes: high success (performed >10 percent of all matings in a given year; $n = 6$), moderate (>5 and ≤10 percent of the matings; $n = 13$), and low (≤5 percent of the matings; $n = 15$). There were no statistically significant differences between the mean amount of disruption performed by males in these three classes. Neither disruption nor mate choice is directly affected by dominance in *Rupicola*. See P. W. Trail (*Natl. Geogr. Res.*, in press) on territoriality and dominance in this species.
7. Male *Rupicola* gain adult plumage as 3-year olds. Although younger males and females sometimes disrupt courtship, they never interrupt matings and are not included in this discussion.
8. Copulation in *Rupicola* typically lasts 10 to 15 seconds and is terminated by the female. I classified any copulation terminated by an intruding male as interrupted, regardless of its duration.
9. The mean number of courtship visits per female during this study was 8.7 ± 8.1 ($n = 72$ mating bouts by banded females). A persistent disrupter thus interrupted approximately half of the female's visits.
10. This research was made possible through the cooperation of STINASU, the Foundation for Nature Preservation in Suriname. I thank D. Clark, G. Farley, K. Fristrup, L. Kellogg, B. McCaffery, D. Smith, and G. Tabor for help in the field. This report was greatly improved by comments from J. Bradbury, S. T. Emlen, D. Koutnik, A. S. Rand, and N. G. Smith. Financial support was provided by the National Geographic Society, NSF grant BNS 79-11231, the National Academy of Sciences Henry Fund, the Harris Foundation, the Chapman Fund, and Sigma Xi. This report was prepared while P.W.T. was a postdoctoral fellow at the Smithsonian Tropical Research Institute.
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Continued Expression of Neonatal Myosin Heavy Chain in Adult Dystrophic Skeletal Muscle

Abstract. *The expression of myosin heavy chain isoforms was examined in normal and dystrophic chicken muscle with a monoclonal antibody specific for neonatal myosin. Adult dystrophic muscle continued to contain neonatal myosin long after it disappeared from adult normal muscle. A new technique involving western blotting and peptide mapping demonstrated that the immunoreactive myosin in adult dystrophic muscle was identical to that found in neonatal normal muscle. Immunocytochemistry revealed that all fibers in the dystrophic muscle failed to repress neonatal myosin heavy chain. These studies suggest that muscular dystrophy inhibits the myosin gene switching that normally occurs during muscle maturation.*

Myosin heavy chain (MHC) has been shown to undergo an isoform transition from embryo to neonate to adult in a variety of muscle systems (*1*). Since these MHC isoforms appear to be products of separate genes, a precise program of gene switching must be maintained during normal muscle development. Avian muscular dystrophy, like Duchenne's muscular dystrophy, is a single-gene disorder of myogenic origin (*2*). Muscles in dystrophic individuals often have many characteristics of immature muscle (*3*), suggesting that the disease is a failure of normal developmental regulation. To explore this possibility, I prepared a monoclonal antibody that reacts with the neonatal MHC but not the embryonic or adult MHC of the chicken pectoralis major (PM). I found that virtually all fibers in the PM of 6-month and 1-year-old dystrophic chickens reacted with this antibody, while no fibers in the PM of normal birds of these ages reacted. Furthermore, by using an "immunofingerprinting" technique, I was able to demonstrate that the immunoreactive myosin in the adult dystrophic PM was identical to that in the neonatal normal PM.

Myosin from 20-day-old normal chicks was prepared and MHC was electrophoretically eluted from a sodium dodecyl sulfate–polyacrylamide gel (*4*). The MHC was mixed with Freund's complete adjuvant and injected intraperitoneally into BALB/c mice, and hybridomas were prepared from the spleens of immunized mice (*5*). One clone that arose from this fusion (subseqently referred to as 2E9A) produced an antibody that reacted with myosin from the PM of neonatal chicks but not with myosin from the PM of embryonic or adult chickens. Solid-phase enzyme-linked immunoassay (ELISA) demonstrated that 2E9A reacted with myosin from the PM of 20-day-old chickens but not with myosin from the PM of 12- to 13-day-old embryos or with myosin from the PM of 1-year-old chickens (Fig. 1A). Immunoreactive myosin first was detectable shortly before hatching, increased to a maximum by 3 weeks, and then decreased until becoming undetectable by

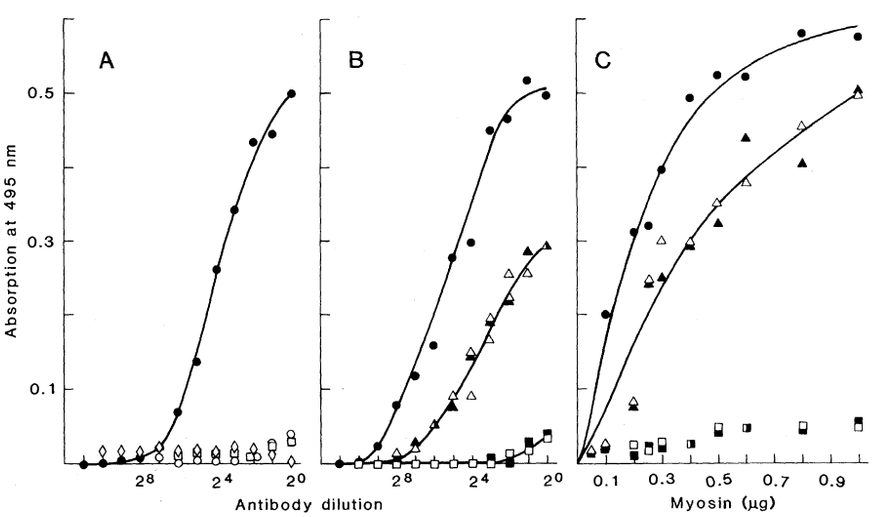

Fig. 1. Analysis by ELISA of myosins with 2E9A antibody. Myosins were plated on 96-well microtiter dishes at 0.5 μg per well (A and B) or as indicated (C). Wells were subsequently blocked with 2 percent horse serum and incubated with 50 μl of 2E9A antibody for 30 minutes at 37°C. Wells were washed three times with phosphate-buffered saline (PBS) and bound antibody was detected with the Vectastain screening kit (Vector Laboratories). Absorbance at 495 nm was measured in a microtiter plate reader. Data points are the averages of duplicates. (A) Myosin (0.5 μg) from the PM of 12-day normal embryos (○), 20-day normal chicks (●), 1-year normal adults (□), and control wells containing no myosin (◇) was reacted with 2E9A antibody diluted 1:4 in PBS. (B) Myosin (0.5 μg) from the PM of 20-day normal chicks (●), 6-month normal chickens (■), 1-year normal chickens (□), 6-month dystrophic chickens (▲), and 1-year dystrophic chickens (△) was reacted with 2E9A antibody diluted in PBS. (C) Myosin from the PM of 20-day normal chicks (●), 6-month normal chickens (■), 1-year normal chickens (□), 6-month dystrophic chickens (▲), and 1-year dystrophic chickens (△) at the indicated concentration was reacted with 2E9A antibody diluted 1:4 in PBS. The results demonstrate that 2E9A antibody reacts only with neonatal myosin during development of the PM in normal chickens but continues to react with myosin from the PM of adult dystrophic chickens.