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Genital Displays by Adult Male and Female Mantled Howling Monkeys, *Alouatta palliata* (Atelidae): Evidence for Condition-Dependent Compound Displays

Clara B. Jones

Introduction

Behavioral displays are thought to have arisen for the inter-individual assessment of information to resolve conflicts of interest and to avoid the risks of serious injury that may result from costly fights (Krebs and Davies, 1993). Displays

are considered to represent stereotyped or ritualized intention movements, ambivalent responses, or redirected acts (Tinbergen, 1952). The stereotyped and ritualized behaviors of mantled howling monkeys (*Alouatta palliata*) have been noted by several authors (Carpenter, 1934; Crockett and Eisenberg, 1987; Jones, 1980, 2000), although most reports are anecdotal. This brief report provides empirical data on stereotyped genital displays of adult male and female mantled howlers, concluding that they represent elements of compound, condition-dependent displays.

Methods

Study site and animals

The study (Jones, 1980, 1985, 2000 and references) was conducted in 1976 and 1977 at Hacienda La Pacifica, Cañas, Guanacaste, Costa Rica (10°18'N, 85°07'W). Marked animals (Scott *et al.*, 1976) in two *A. palliata* groups were studied in two habitats (Frankie *et al.*, 1974) of seasonal tropical dry forest (riparian habitat, Group 5: three adult males, 15 adult females, 401 h observation; deciduous habitat, Group 12: two adult males, eight adult females, 114 h observation).

In Group 5, Y male was highest-ranking, G male, second-ranking, and R male, lowest-ranking. The sub-adult, LT male, entered the hierarchy in 1977. In Group 12, S male was dominant, and Z male subordinate. In previous reports (e.g., Jones, 1980), Z male was labeled "R_{12}", but to avoid confusion with R male of Group 5, this Group 12 male has been re-labeled "Z." Procedures for determining dominance hierarchies may be found in Jones (1980). Group 12 was followed by radio-tracking (AVM SM-1 sending at 296 Mhz with a model LA 12 receiver [AVM Instrument Company, U.S.A.]).

Results are based upon randomized focal and *ad libitum* observations (Altmann, 1974). Modal social organization of mantled howlers is multimale-multifemale, yielding a polygynandrous mating system (Carpenter, 1934; Glander, 1980; Jones, 1980, 1985, 2000; Jones and Cortés-Ortiz, 1998; Crockett and Eisenberg, 1987). Mantled howler males are characterized by a predominantly white scrotum against dark pelage (Jones, 1999), and the females' labia are a variegated mix of black and white pigmentation (Jones, 1997). Cycling females exhibit genital swelling and color change (Glander, 1980; Jones, 1985), presumably corresponding to cycle stage.

Definitions

In this short report, "display" means one event. Genital display by males (GDM) signifies an adult male exposing his scrota to another individual, usually with the tail extended vertically. Genital display by females (GDF) indicates an adult female exposing her genital region to another individual, usually with her tail in a vertical position. These postures were considered to be "stereotyped" or "ritualized" because, when expressed, the animal's behavior appeared to "freeze" (Lorenz, 1951 quoted in Eibl-Eibesfeldt, 1970) and to occur with "typical intensity" (Morris, 1957). The initiation and termination of a GDM or a GDF event was determined by the beginning and ending, respectively, of the frozen posture. The recipient (the "receiver") of the display's signal was presumed to be the nearest neighbor of the displaying individual (the "sender"). "Copulation" means dorso-ventral mounting with intromission, with or without ejaculation. "Displacement" means that one animal (sender or receiver) moved at least 1 m away from the other (sender or receiver). Two males were judged to be in coalition against a third if the two were observed to cooperatively displace the third (Jones, 1980, 2000).

Data analysis

The non-parametric Chi square (χ^2) "goodness of fit" test is employed with alpha set at 5%. All tests are two-tailed.

Results

In Group 5, 42 GDMs were displayed by Y male, 47 by G male, 26 by R male, and four by LT male ($\chi^2 = 37.8$, df = 3, $p \leq 0.001$). Thus, males of this group were not likely to display equally, and Y and G males were most likely to exhibit GDMs. GDMs occasionally escalated; six times to displacements and four times to chases, but never to fights. GDMs occurred in association with sexual behavior ("lingual gestures" [Carpenter, 1934; Jones, 1985], sexual solicitations [Jones, 1985], herding, copulation [Jones, 1985]: n = 18), vocalizations (see Jones, 1980, 2000: n = 26), "branch-break" displays (Glander, 1975; Jones, 2000: n = 12), urination (Glander, 1975, 1980; Jones, 2002, 2003: n = 4), and branch marking (Glander, 1975: perineal or chin marking: n = 3). Thus, GDMs may be components of "compound displays" (Bradbury and Vehrencamp, 1998) including visual, auditory, and olfactory signals. Females who were the recipients of GDMs or who were associated with displaying males were noted to be cycling on 14 occasions.

Y male displayed 13 times to G, eight times to R, four times to LT, 10 times to G and R males in coalition against Y, and six times to females ($\chi^2 = 5.96$, df = 4, $p > 0.05$). Thus, Y male displayed equally to his recipients. The recipient of one GDM by Y male was undetermined. G male exhibited GDMs 17 times to Y male, 15 times to R, three times to LT, three times to Y and R in coalition against G, once to R and LT in coalition against G, once to an adult male of another group (Group 10), once to a transient, subadult male, and six times to females ($\chi^2 = 50.14$, df = 7, $p \leq 0.001$). G male, then, was most likely to display to Y and R males. R male displayed eight times to Y, 11 times to G, twice to LT, and five times to females ($\chi^2 = 6.94$, df = 3, $p > 0.05$). Thus, R male was equally likely to display to his recipients.

In Group 12, GDMs by S male occurred 37 times, by Z male, 18 ($\chi^2 = 6.56$, df = 1, $p \leq 0.02$). Thus, the dominant male, S, was more likely than the subordinate, Z, to display. S male exhibited GDMs 19 times to Z and 16 times to females ($\chi^2 = 0.26$, df = 1, $p > 0.05$). The dominant male in

Group 12, then, is equally likely to display to his recipients. Z male exhibited GDMs eight times to S and nine times to females ($\chi^2 = 0.06$, df = 1, $p>0.05$). Thus, Z male, also, was equally likely to display to his recipients. The recipient of one GDM by Z was undetermined.

Females of Group 5 exhibited 42 GDFs, nine times to Y male, 15 times to G male, eight times to R male, once to LT male, three times to G and R males in coalition against Y, twice to Y and R males in coalition against G, and four times to other females ($\chi^2= 24.68$, df = 6, $p\leq0.001$). Thus, females were most likely to display to G male. GDFs occurred in association with female-female displacements (n = 11), vocalizations (n = 1), chasing (Jones, 2000: n = 2), fighting by females (Jones, 2000: n = 1), genital inspection by males (n = 4), urination (Jones, 2002, 2003: n = 3), copulation (n = 1), grooming (Jones, 1979: n= 1), and huddling (Glander, 1975; Jones, 1980: n= 1). As for males, then, GDFs may be components of "compound displays." Females (either sender or receiver) were noted to be cycling on three occasions.

Females of Group 12 exhibited GDF's nine times, twice to S male, three times to Z male, and four times to other females ($\chi^2 = 0.66$, df = 2, $p>0.05$). Females of Group 12, then, are equally likely to display to their recipients. In this group, GDF's by one female to another occurred in association with copulation (Jones, 1985: n = 2) or fighting (n = 1), and these displays were exhibited on four occasions when either the displaying female, the receiver, or both were cycling. Vocalizations were noted to accompany GDFs on one occasion in Group 12.

Discussion

Similar to patterns of marking (Eisenberg, 1981), genital displays by adult mantled howlers are most likely to be derived from "simple movements of elimination." While it is possible that genital displays function as "contact-promoting behavior" (Eisenberg, 1981), less likely, as appeasement, I have observed these displays by mantled howlers in Panama (*A. p. aequatorialis*) and Mexico (*A. p. mexicana*), as well as Costa Rica (*A. p. palliata*), and, in all cases, genital displays appear to be used to control other individuals (see Jones, 1980, pp.394-395) and, possibly, to communicate threat. Supporting the latter view is the finding that GDMs and GDFs sometimes escalate to agonistic behavior(s), although wounds have never been observed on the scrota of male mantled howlers (N. J. Scott, Jr., pers. comm.; C. B. Jones, pers. obs.) or on the perineal area of females (C. B. Jones, pers. obs.).

In Groups 5 and 12, high-ranking males were most likely to exhibit GDMs. If genital displays are costly to males in time, energy, exposure to predation, and/or risks from fights, they may represent reliable ("honest") displays of quality which only high-ranking males can afford (see Andersson, 1994). Males of both groups displayed to their recipients with equal frequency with the exception of Group 5's second-ranked male, G, who was most likely to display to Y and R males. This pattern may reflect the complexity of interactions which results when the number of males in a group increases as well as G's reliance upon a display unlikely to escalate in his competitive relations with other males. G's employment of genital displays, then, may reflect a safe strategy in highly competitive conditions.

Supporting the interpretation that G's displays to other males reflected male-male competition is the finding that females of Group 5 were most likely to exhibit GDFs to G male, although females of Group 12 were equally likely to display to S and Z. The "skew" in copulations in Group 12, however, was much higher than in Group 5 (Jones, 1985), possibly demonstrating, again, the complexity of interactions with an increase in male numbers. The present results support the view that GDMs and GDFs reflect interindividual competition since they occurred in association with sexual behavior as well as displacements, chases, and related agonistic responses. GDMs and GDFs appear to be conditional signals dependent upon phenotype or environment ("best of a bad situation rules": Brockmann, 2001), which are likely to be displayed for purposes of assessment when individual quality varies over time (e.g., because of nutritional state, fatigue, cycling stage, health: see Payne and Pagel, 1996). Future research is required to further document stereotyped and ritualized responses (including vocalizations) and their functions in howlers, and to assess the relative significance of elements of "compound displays" in *A. palliata*, other members of this genus, and, particularly, adults of other polygynandrous primates (see, for example, Smuts and Watanabe, 1990).

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SQUIRREL MONKEY (*SAIMIRI SCIUREUS*) REHABILITATION IN FRENCH GUIANA: A CASE STUDY

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Introduction

Rehabilitation can be an effective conservation tool (Kleiman, 1989). Although controversial (Soave, 1982; Harcourt, 1987), some experiences are undoubtedly positive (Rijksen, 1974; McGrew, 1983; Dillon Morin, 1994; Nogueira *et al.*, 1994; Ades, 1998; Harding, 1998). One of the difficulties of rehabilitation attempts is the lack of available referenced case studies, whatever their success. Since the late seventies, the Pasteur Institute of French Guiana has used the squirrel monkey (*Saimiri sciureus*) as an experimental model for the study of human malaria. In addition to the captive colony, the Institute managed an island where 150 wild monkeys originating from French Guiana and Suriname were introduced in 1981 (de Thoisy and Contamin, 1998). To date, the resident population totals approximately 100 animals (de Thoisy *et al.*, 2002). The initial aim of this study, requested by the manager of the colony of the Pasteur Institute, was to conduct a rehabilitation experiment with a group of common squirrel monkeys in order to assess the reliability of this management option for unwanted individuals, either post-experimental or old breeders.

Basic recommended rules, as indicated for any primate transfers (Konstant and Mittermeier, 1982), concern (i) *the release area*: suitability of the habitat, availability of feeding resources for both the resident population and the introduced animals, (ii) *the candidate animals' potential for successful rehabilitation*: ability to support the inherent stress, ability to feed according to needs, and (iii) *the release protocol*: methodology, accounting for ecological features such as seasonality and phenological patterns (for instance, fruiting patterns in the area). Since optimal conditions were indicated for this case study, this attempt also aimed to contribute to the knowledge of the ability of primates to be rehabilitated.