Articles

MIMICRY IN PRIMATES: IMPLICATIONS FOR HETEROGENEOUS CONDITIONS

Unrelated organisms may sometimes look alike. Mimicry (convergence due to exploitation or mutual advantage) is a Darwinian mechanism which may explain such similarities. In 1974, Cody concluded that, for mammals, virtually nothing is known of character convergence to facilitate aggressive spacing or of social mimicry to facilitate gregariousness (see also Pough, 1988; Vencl, 1977), although both forms of mimicry are well documented for birds (see Wickler, 1968; Moynihan, 1968, 1981; Cody, 1969, 1974). These studies concluded that different organisms in the same populations, guilds or communities may exhibit similar structures as conventional mechanisms to promote mutual recognition in predator-prey, competitive, mutualistic or social interactions. Convergent features may help to explain certain patterns of exclusion, coexistence, social parasitism, hyperparasitism, co-operation or "interpersonal attraction" within and between species (see Moynihan, 1968), and this note reviews for the primates traits that may represent convergence to facilitate recognition.

Table 1 summarizes preliminary evidence for the Order Primates. In brief, 20 species or genera exhibit characters that are likely candidates for the above interpretations. Eight of the 21 species or genera are Neotropical, 13 (62%) are Paleotropical. Each example involves some apparent type of mimicry among potential competitors for food, mates or space: five apparent examples of intraspecific modeling to a pregnant morphology (prominent abdomens) by one or both sexes: six of intraspecific mimicry of genitalia (four of six cases exhibit female mimicry of male sexual structures; Fig. 1); one of interspecific mimicry of genitalia; nine of interspecific vocal mimicry; two of interspecific mimicry of facial signals; two of generic morphological mimicry; two of paedomorphosis and neoteny which may involve convergence to juvenile forms; and three of mimicry of an estrus model ("pseudoestrus").

Convergence may entail a one-way (e.g., *Cercocebus* to *Macaca* and *Papio*) or a two-way (e.g., prominent abdomens in both sexes of *Ateles*) change whereby mutant organism B may become more similar to the phenotype of organism A (one-way) or both may model each other more or less mutually (two-way). In order to demonstrate one-way or two-way dominance, despotism or competition in a two-organism

dyad, it would be necessary to test the effects of clinal variation and to show deleterious effects for one or both interactants in the absence of the modeled trait. Subsequent measures of the effects of interactions in the presence of the modeled trait would be expected to demonstrate less deleterious consequences, no deleterious consequences or facilitation by one or both interactants. It is unlikely that rigorous tests meeting these criteria can be conducted in the field. However, the examples of modeled structures displayed in Table 1 may provide rich tests of hypotheses concerning the evolution or proximate advantage of obligatory relationships in general and competitive and social mechanisms in particular (see Jones, 1985a; West Eberhard, 1979; Briand and Cohen, 1984), especially where investigators employ the tools of game theoretical analysis, removal experiments, or comparative approaches (see Axelrod and Hamilton, 1981; Jones, 1982).

For example, imagine a hypothetical set of interactions between two organisms, A and B (a "payoff matrix", see Axelrod and Hamilton, 1981) and the relative costs and benefits (genetic or other) in each of four conditions: (1) A mimics B; (2) B mimics A (both one-way mimicry); (3) A and B mimic each other or a third model (two-way mimicry); and (4) neither A nor B mimic the other. Assuming that A and B use some limiting resource in common, the competitively inferior organism will experience the lowest relative payoff across conditions. These four conditions may correspond, respectively, to social parasitism (W. C. Dilger, pers. comm; see also West-Eberhard, 1979) or hyperparasitism; to mutualism or co-operation (see Moynihan, 1968, 1976); and to "active competition" (see Emlen, 1973, Chapter 12) where B or A may competitively exclude the other in certain environmental regimes. Features that are mimicked or modeled are assumed to be morphological, physiological (including chemical), behavioral, or developmental.

The frequency of mimicry may be much higher than Table 1 indicates since the subject has rarely been investigated systematically. Pseudoestrus provides a good example. Hrdy (1981) is of the opinion that pseudoestrus facilitates the female's ability to "manipulate" potential mates, and adult female howler monkeys (*Alouatta palliata* Gray) provide a rich example of such manipulation among Neotropical primates (Jones, 1985b). A recent report by Zucker *et al.* (1994) suggests that genital swelling may not be a reliable measure of estrus stage in mantled howlers. Males employ visual and olfactory cues to assess female condition and may in part base decisions to copulate upon these cues (Jones, 1985b). Although the

methods for evaluating genital swelling employed by Zucker *et al.* may require refinement, this study suggests that females may deceive males about their true estrus condition by mimicking an unreliable estrus stage. Studies of the confidence of estrus signals need to be undertaken in other primates.

Most primates are obligately social, and systems of mimicry assume potential or ongoing interactions among coexisting individuals or populations within or between species. These systems of cues, signals, and signs represent mechanisms of social regulation and symmetry which facilitate interpersonal organi-

Table 1. Mimicry in primates and its possible origins. A = adult(s), AF = adult females, AM = adult males; RC = resource competition (including food, mates and/or space); MP = mimicry of pregnancy; MM = mimicry of males; MY mimicry of young.

Genus or Species	Trait	Origins	Source
Alouatta	Prominent abdomens (AF)	RC; MP	Jones, 1985b
	Genital hypertrophy (AF)	RC; MM	Pers.obs., Coelho, pers. comm.
	Neotenous vocalizations (AM)	RC; MY	Jones, 1980
	Morphological convergence[a] (A)	RC	Pers.obs.
	Pseudoestrus (AF)	RC	Jones, 1985b
Aotus	Vocalizations adapted to nocturnal life	RC (bats?)	Napier & Napier, 1967; pers.obs.
Ateles	Prominent abdomens (A)	RC[b]: MP	Napier & Napier, 1967; pers. obs.
Brachyteles	Prominent abdomens (A)	RC[b]; MP	Napier & Napier, 1967
Callicebus	"Howler-like" and/or bird-like vocalizations	RC	Napier & Napier, 1967; Vencl, 1977; pers.obs.
Callimico	Tamarin-like vocalizations	RC	Napier & Napier, 1967
Cebus	Genital hypertrophy (AF)	RC[b] (*Alouatta*?; *Ateles*?); MM	Napier & Napier, 1967; pers. obs.
	Scrotum sessile (AM)	RC[b]; MF	Napier & Napier, 1967; pers.obs.
	Vocal mimicry (A)	RC[b]; (birds?; *Alouatta*?)	Napier & Napier, 1967; pers.obs.
Cercocebus	*Macaca* & *Papio*-like facial signals (A)	RC	Napier & Napier, 1967
	Papio-like vocalizations	RC	Napier & Napier, 1967
Cercopithecus	Bird-like vocalizations (A)	RC	Napier & Napier, 1967
Cynopithecus	*Macaca*-like facial signals (A)	RC	Napier & Napier, 1967
Hapalemur	*Lemur*-like vocalizations (A)	RC	Napier & Napier, 1967
Homo	Prominent abdomens (A)	RC	Bjerre, 1958
Macaca	Pseudoestrus (AF)	RC	Hrdy, 1981
Microcebus	"High-pitched", possibly "supersonic" vocalizations	RC (bats?)	Napier & Napier, 1967
Pan paniscus	Paedomorphosis & neoteny (A)	RC; SM	Shea, 1983
Papio	Pseudoestrus (AF)	RC	Hrdy, 1981
Papio papio	Perianal area of male mimics estrus	RC	Napier & Napier, 1967
Papio leucophaeus	Estrus female resembles *Cercocebus* in estrus	RC	Napier & Napier, 1967
Perodicticus	Genital hypertrophy (AF)	RC; MM	Napier & Napier, 1967
Presbytis	Prominent abdomen (A)	RC; MP	Napier & Napier, 1967
Saguinus	Ultrasonic vocalizations (A)	RC (bats?)	Napier & Napier, 1967
Simias concolor	Morphological convergence to *Macaca nemestrina*	RC	Napier & Napier, 1967

[a] Striking morphological similarity apparent for *Alouatta* physiognomy (single adult at rest), *Cathartes* physiognomy (single vulture at rest), *Nasutitermes* nests and *Sciurus* nests.

[b] Possibly an adaptation to mixed-species feeding aggregations (see Klein and Klein, 1973; also pers. obs.; pers.comm. from D. Boucher, C. Freese, and A. Coelho).

zation. These systems of mimicry may enhance species integrity in disturbed habitats where patchy conditions prevail, and the organization of communication is expected to impose a conservative homeostatic force under heterogeneous conditions caused by habitat degradation and other factors. Such features may contribute to the optimization of survival and reproductive success in distressed regimes. Other examples of "stereotyped" or "ritualized" characteristics may be interpreted as traits functioning homeostatically to promote individual recognition within or between species (see, for example, Smuts and Watanabe, 1990; Wickler, 1968).

Is mimicry inherently more common in the Paleotropics than in the Neotropics, or are the present trends a result of sampling error? Some observations are suggestive. First Paleotropical species are more terrestrial than Neotropical, possibly favoring the expression of visual features. Most of the examples in Table 1 are signs of visual communication, possibly biasing the results in favor of Old World taxa. Second, for arboreal species, studies are needed of the differential architecture of forests inhabited by primates since such studies may reveal the selective pressures associated with mimicry in primates in Paleotropical and Neotropical forests (see Richards, 1973). Third, it may be productive to study interspecific mimicry in modalities other than the visual, in particular the potential for vocal mimicry with birds. Species with which primates compete for food and space are likely candidates for mimicry. Finally, most studies of "coalitions and alliances" in primates have been conducted on Paleotropical species. Nonetheless, it seems clear that mimicry in both Old and New World primates can be viewed in the context of symmetrical communication and can be related to the growing literature on reciprocal relationships in primates (e.g., de Waal and Luttrell, 1988).

Research on convergent features in primates has the potential to unify this literature with that of other taxa (e.g., Mason and Crews, 1985; Pietsch and Grobecker, 1978; Bawa, 1980; references for birds cited above). In particular, the morphometric quality of traits exhibited in Table 1 allows a high degree of quantitative precision in measurement and empirical evaluation permitting analysis relative to variations in size, sex, and vital parameters (e.g., age, fecundity, and survivorship) as well as aggressive and non-aggressive behaviors, structures, signals, and displays. Where populations are polymorphic for convergent traits, as Bushmen and Australian aboriginals may be for prominent abdomens (see Bjerre, 1958; E. Hagmann, pers. comm.), studies may be undertaken

to reveal the heritability of convergent features as well as their biogeographical distribution and possible relationship to population differentiation (W. C. Dilger, pers. comm.; Cody, 1974). Future investigations of mimicry in primates and other mammals may produce more than "anecdotal" results (Cody, 1974, p.260).

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GEOGRAPHIC DISTRIBUTION OF NIGHT MONKEYS, *AOTUS*, IN NORTHERN BRAZIL: NEW DATA AND A CORRECTION

The geographic distribution of *Aotus trivirgatus* Humboldt, 1812 was recently extended eastwards as far as the state of Amapá on the basis of four specimens collected at Carmo do Macacoari, Itaubal, eastern Amapá, and on the island of Caviana in the Marajó archipelago, Pará (Fernandes, 1993). In 1994, fieldwork at these two sites resulted in the collection of a further two specimens of *Aotus* from the former (Museu Paraense Emílio Goeldi MPEG 24035 and Instituto de Pesquisas do Estado do Amapá IEPA 041) and three from the latter (MPEG 24130, 24131 and 24132).

All ten specimens now collected at these two sites were analyzed using the diagnostic characteristics used by Hershkovitz (1983). According to Hershkovitz, *Aotus trivirgatus* and *Aotus infulatus* Olfers 1818 belong to the gray-necked and red-necked groups, respectively. His phenetic key to the *Aotus* species and subspecies (1983, p.213), showed that *A. trivirgatus* and *A. infulatus* may be distinguished by just two characteristics: the coloration of the side of the neck, and the presence (or absence) of a whitish band at the lateral corner of the eye. The remaining characters cannot be considered diagnostic. The entire side of the neck behind and below the ear is grayish agouti or brownish agouti in *A. trivirgatus*, as are the flank or the outer side of the arm, and whitish bands are found at the lateral corners of the eyes. In *A. infulatus*, the neck is partially or entirely orange or buff, and two small whitish patches are found above the eyes.

All ten specimens exhibit the diagnostic characters of *A. infulatus*. The animals from Carmo do Macacoari were indistinguishable from those of Caviana Island, and the Goeldi Museum specimens of *A. infulatus* from Marajó Island and the Rio Tocantins. All these thus represent a single species, *A. infulatus*, the geographic distribution of which is extended to the left (north) bank of the lower Amazon, in Amapá (Fig. 1). Consequently, the known eastern limit of the geographic distribution of *A. trivirgatus* is still the Rio Trombetas, as described by Hershkovitz (1983). Contrary to Fernandes (1993), then, the occurrence of night monkeys in the remainder of Amapá, west of the Rio Trombetas in Pará remains to be confirmed, especially as the genus was not reported from previous primate surveys in Amapá (Carvalho, 1962), Suriname (Mittermeier and van Roosmalen, 1981), and French Guiana (Roussilhon, 1988).

The presence of *A. infulatus* north of the Amazon is consistent with the occurrence of other closely related taxa on both sides of the lower reaches of the river: *Cebus apella apella, Cebus nigrivittatus/kaapori, Chiropotes satanas* ssp., *Saguinus midas* ssp. and