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Juvenil black uakari monkey
(*Cacajao hosomi*)

Cover photo: Juvenil black uakari monkey (C*acajao hosomi*) eating a ripe fruit of the palm Mauritia flexuosa in Pico da Neblina National Park, Brazil.
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SOCIOECOLOGY OF BLACK UAKARI MONKEYS, *CACAJAO HOSOMI*, IN PICO DA NEBLINA NATIONAL PARK, BRAZIL: THE ROLE OF THE PECULIAR SPATIAL-TEMPORAL DISTRIBUTION OF RESOURCES IN THE NEBLINA FORESTS

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Key words: Uakaris, Neotropical Primates, Pithecine, Pico da Neblina, Grouping patterns, Resource Distribution

Abstract

Data from a year study of one group of approximately 70 individuals black uakaris, *Cacajao hosomi* in Pico da Neblina National Park, Brazil, revealed that animals carried out daily activities as a non-cohesive unit; fission-fusion was never witnessed. We hypothesize that large groups of black uakari monkeys in Neblina result from the peculiar spatial-temporal distribution of resources in their ever-wet caatinga/terra firme/chavascal forest mosaic in Neblina. *C. hosomi* may form large groups in Neblina because: 1) preferred foods in occur in patches (trees) which are large, dense and clumped, 2) there is a long period of food availability as fruits are slow to mature and are consumed at all stages of maturity, and 3) there is an interannual variation in the availability of productive patches at the landscape level forcing the animals to range far and wide in order to keep tract of productive patches.

Introduction

Black uakaris remain among the least known of all New World primates. They are diurnal, medium sized monkeys with males slightly larger and more robust than females (2.4-4.5 kg, Boubli et al., in press). Recently, three species have been proposed (Boubli et al., in press), Neblina black uakari, *C. hosomi*, from the left bank of Rio Negro in Brazil and Venezuela, golden backed black uakaris, *C. melanocephalus* from the right bank of the Rio Negro and Colombia, and Ayres uakari, *C. ayresi*, from the Aracá River, a left ban tributary of Rio Negro (Boubli et al., in press). *Cacajao hosomi*, (henceforth black uakari) is found between the upper Orinoco and upper Negro Rivers. This area, located on the equator, corresponds to the western limit of the 'Tepui' mountains, the natural divide between Brazil and Venezuela. Part of this area lies within Pico da Neblina National Park in Brazil and Parque Serrania de la Neblina in Venezuela, forming a large transboundary protection area (Boubli et al., 2005). Pico da Neblina National Park is one of the most isolated parts of Amazonia, and is inhabited only by the Yanomami people. This Park is located on the left bank of the Rio Negro, in the extreme north-western part of Brazilian Amazonia, on the border of Brazil and Venezuela.

In Pico da Neblina these monkeys have been observed in very large groups of around 100 individuals, corresponding to the largest reported groups for pithecine primates (Boubli, 1997, 1999). To date, the reasons for the formation of such large groups remain obscure. Here, we examine aspects of the ecology of black uakaris in Neblina that are peculiar in relation to the ecology of other pithecines studied elsewhere and that might help explain the formation of unusually large groups in this species. In particular, we look at the spatial-temporal distribution patterns of preferred foods for several closely related taxa: the white uakaris, *Cacajao calvus,* and bearded sakis, *Chiropotes albinasus*, *C. satanas*, *C. chiropotes*, and *C. sagulatus*. These species are morphologically very similar (Ayres, 1989; Hershkovitz, 1987), and yet are found in different habitat types: Neblina black uakaris are found in a catinga/ chavascal/ terra firme forest mosaic, white uakaris are found in holocenic flooded forests or várzeas and *Chiropotes* spp. are predominantly found in upland terra firme forests.

Whereas predation risk has been hypothesized to set the lower limit of group size in primates, the upper limit is usually thought to be given by increased levels of intragroup feeding competition experienced by individuals in larger groups associated with the spatial-temporal distributional patterns of preferred foods (Alexander, 1974; Terborgh and Janson, 1986). Thus, we examine how the peculiar pattern of spatial-temporal distribution of preferred food species in Pico da Neblina might be setting a high upper limit for black uakaris in this region.

Black uakaris, *C. hosomi in Pico da Neblina National Park, Brazil*

One group of black uakaris was followed by Boubli (1997) in Pico da Neblina National Park, Brazil (Fig. 1), as part of a study of the autoecology of this elusive primate. The study group had approximately 70 individuals that carried out daily activities as a non-cohesive unit. Fission-fusion was never witnessed. The forest at the study site consisted of a mosaic of caatinga forests (forest on white sandy soil *sensu* Klinge et al., 1979), terra firme forest (sensu Pires and Prance, 1985) and chavascal (swamp forest).

Fig. 1: Pico da Neblina National Park and Estação Ecológica do Mamirauá.

In total, black uakaris included seeds of ripe or unripe fruits in 77.8 % of all feeding records (Boubli, 1997). Seeds of unripe fruits alone accounted for 63.8 % of the feeding records. Overall, black uakaris tended to eat fruit species that were protected by medium and hard husks, that were animal dispersed (synzootically or endozootically) and green in coloration. In terms of size, most fruit species eaten by uakaris fell within the 1 to 9 cm range. The majority of fruit species eaten by black uakaris had only one seed. Most seeds eaten by the monkeys measured from 2 to 3 cm in length (Boubli, 1999).

In Pico da Neblina, 30 % of the diet of black uakaris was composed of 3 fruit species: *Micrandra spruceana* (Euphorbiaceae) ranking first, *Eperua leucantha* (Caesalpinoidea) ranking second and *Hevea cf. brasiliensis* (Euphorbiaceae) ranking third. These tree species were spatially clumped as tested by Total Local Quadrant Variation method (TTLQV-, Ludwig and Reynolds, 1988; Boubli, 1997).

Micrandra spruceana, was available in the forest for at least 8 to 9 months as unripe and ripe fruits (Boubli and Couto-Santos, 2007)). *Hevea cf. brasiliensis* was available for 6 months (Boubli and Couto-Santos, 2007). Whereas *E. leucantha* was available from December through April, *E. purpurea* was available from April through August, thus these combined food sources were available to black uakaris for 9 months of the year. During the times of lowest overall food availability in the phenological samples (non-peak time), August through October, *Sloanea durissima* was fruiting. This tree species is one of the largest in the forest (DBH 107 ± 23.4 cm, n=3) and produces a very large fruit crop (no data is available for the relative density and spatial distribution of this tree species at the study site, Boubli, 1997). Also at this time the palm *Mauritia flexuosa* and several liana species were producing fruits that were readily taken by black uakaris (Boubli, 1997). In addition, several tree species in Neblina had individuals producing fruits on more than one occasion during the year long study (e.g., *Eperua leucantha*, *Gustavia pulchra*, *Ecclinusa bullata*) (Boubli and Couto-Santos, 2007); this asynchrony contributed to the relatively even temporal distribution of fruit favoring low level of intra-group feeding competition experienced by black uakaris year around.

An examination of the size of most individual trees used by black uakaris as food sources in Neblina showed that the monkeys were choosing trees that had an average DBH that was significantly larger than the average size for trees sampled in the 2 ha botanical sample (Boubli, 1997). Though data are limited for day ranges, on ten days that black uakaris were followed from dawn to dusk in Pico da Neblina (including wet and dry seasons), average day range was 2,300 ± 1,197 m (range 1220 to 4,400 m).

White uakaris, *Cacajao calvus*

Cacajao calvus as studied by Ayres (1986) at Estação Ecológica de Mamirauá (Fig. 1) lives in Amazonian flooded forests in groups of 30 to 50 individuals. Approximately 65 % of this primate's diet was composed of seeds of immature fruits -a diet with high energy content. Three fruit species (*Eschweilera turbinata*, *Cheiloclinium cognatum* and *Xylopia frutescens*) accounted for 35 % of the diet of *C. calvus* (Ayres, 1989). The flooded forest habitat, locally known as várzea, is characterized by a high degree of synchrony in fruit production which is associated with the flooding regime of várzeas. During the high water periods, many tree species (55 species) are fruiting simultaneously while in the dry season few species bear fruits (18 species)[Várzea has about 109-135 tree species per hectare.].Changes in day range and group size in *C. calvus* were correlated with the flooding regime. During the high water season, *C. calvus* groups traveled as a unit and up to 6 km in one day. In the low water season, groups split into small foraging parties (12 to 15 individuals) that stayed apart (1-2 km) for several days. Day ranges at this time of the year were around 1 to 2 km. The amount of traveling was greatly increased during high water season. During low water periods, when animals were in small subgroups, the amount of travel was reduced. Throughout the year, *C. calvus* used fruit trees that were on average greater than 30 cm diameter at breast height (DBH); higher than the modal distribution of diameter classes within the botanical plots at the study site (mode = 10 cm DBH).

Bearded sakis

Bearded sakis (*C. albinasus*, *C. satanas*) are restricted to terra firme forests. Data from Ayres (1981, 1989), van Roosmalen et al. (1988), Frazão (1992), Peetz (2001) and Veiga (2006) show that group sizes and diet of *Chiropotes* have some parallels with that of *Cacajao. Chiropotes* group sizes have been reported to vary from 8 to 56 individuals. Seeds make up 30 to 75 % of *Chiropotes* annual diet with marked seasonal variation in some sites where the consumption of seeds can go up to 95 % in some months (Frazão, 1992). In Surinam, the 3 top ranking species in the diet of *C. satanas* accounted for 27 % of all feeding records (*Ecclinusa guianensis*, *Eschweilera corrugata* and *Tetragastris altissima*) (Van Roosmalen et al., 1988). In Rio Aripuanã, three top ranking species in the diet of *C. albinasus* contributed 28.12 % of the feeding records (*Astrocaryum vulgare*, *Caryocar villosum*, *Goupia glabra*) (Ayres, 1989). In the Minimum Critical Size Ecosystem reserves of the Smithsonian Institution (MCSE) in Manaus, Brazil, *Chrysophyllum sanguinolentum* made up 12.1 % of the diet of *C. satanas*, and the three top ranking species corresponded to 20 % of the diet (*Chrysophyllum sanguinolentum*, *Inga cf. paraensis*, *Pouteria anomala*) (Frazão, 1992). Like *Cacajao*, *Chiropotes* day ranges are usually large for their body size varying from 1 to 4 + km (Peetz, 2001; Veiga, 2006; Ayres, 1981; Frazão, 1992).

Grouping patterns

Theory predicts that group size is affected by patterns of spatial and temporal distributional of food resources in a primate's home range (Terborgh and Janson, 1986). In a general way, for *Cacajao* and *Chiropotes*, food is potentially more evenly distributed temporally than is the case for most other frugivores, as these monkeys eat fruits at all stages of maturity (Ayres, 1981, 1986; Boubli, 1999). In addition, fruits eaten by *Cacajao* and *Chiropotes* have a high caloric content. That counteracts the additional costs to traveling resulting from large groups. Consequently, large day ranges potentially result in greater numbers of food patches encountered by the animals each day, i.e. more food available and potentially lower intragroup feeding competition.

Although *Cacajao calvus* and *Chiropotes* spp. live in groups of similar sizes, they differ in their grouping patterns. In contrast to *C. calvus*, most studies of *Chiropotes* spp. describe large groups year round that travel from food patch to food patch as a unit. The group is usually non-cohesive but individuals are never more than 300 meters apart (Ayres, 1981; van Roosmalen et al., 1988, Frazão, 1992; Norconk et al., 1994; Pereira, 2002; Vieira, 2005). Recently, exception to this pattern has been observed in groups of *C. albinasus* and *C. satanas* (Veiga et al,. 2006).

Ayres (1989) believes that the difference in grouping patterns between *C. calvus* and *Chiropotes* spp. can be explained by the different pattern of tree species distribution in várzea versus terra firme forests. In várzea, tree species show a fairly even distribution due to the manner in which seeds are dispersed: through the water (Ayres, 1986; Goulding, 1980). Thus, during the low water season in várzea, preferred fruiting trees are rare and widely distributed, forcing the large groups of *C. calvus* to split into small foraging groups, so as to reduce intra-group feeding competition. In the high water period, fruit is superabundant, allowing individuals to travel in large foraging groups.

In the terra firme of *Chiropotes*, most tree species tend to occur at very low densities (with the exception of one or two common species) and are spatially clumped (Gentry, 1988, 1990). Thus, in terra firme forests, potential *Chiropotes* spp. food patches are scarcer yet larger than in the várzea, due to clumping of tree species. As suggested by Norconk et al. (1994), remaining in large groups and traveling from clump to clump as a unit and fissioning locally, within a clump of fruiting trees, are probably good strategies for exploiting large (clumped) and widely dispersed food patches. In addition, in terra firme forest, fruit (particularly immature fruit) availability is presumably more even throughout the year when compared to várzea habitats since, in terra firme, trees are not subject to seasonal flooding such as is the case of várzeas (Ayres, 1986). Terra firme forests do show peaks and low points in overall fruit abundance; however, such oscillation is apparently far less pronounced than is the case in várzea forest (Ayres, 1986). Thus, *Chiropotes* is possibly experiencing lower variability in levels of intragroup feeding competition year round than *Cacajao calvus* in várzea habitats.

Large groups of black uakaris in Pico da Neblina National Park, and the caatinga forest, a hypothesis

We hypothesize that the formation of very large permanent groups of black uacaris in Pico da Neblina National Park may be a result of the peculiar pattern of food abundance and spatial/temporal distribution in this region. Black uakaris in Neblina were found in a caatinga/chavascal/terra firme forest mosaic that differs in several important respects from várzea, where *Cacajao calvus* lives, and terra firme where the *Chiropotes* spp. are found. The forest in Pico da Neblina was characterized by the dominance of trees that produced dry, large seeded barochorous fruits preferred by black uakaris. Caatinga forest in particular held the highest proportion, where 86 % of the trees produced dry large seeded fruits (Boubli 1999). The forest (and again the caatinga forests in particular) was also characterized by a high degree of tree species dominance. In a two hectare botanical sample, Boubli (2002) found that 3 tree species, namely *Eperua leucantha* (Caesalpinoidea), *Hevea cf. brasiliensis* (Euphorbiaceae), and *Micrandra sprucei* (Euphorbiaceae) accounted for 33 % of all marked trees. These same tree species accounted for 66 % of all sampled trees in the caatinga forest (Boubli, 2002). Whereas *E. leucantha* and *H.cf. brasi-*

liensis ranked second and third in black uakari diet, *M. sprucei* did not produce fruits during the year long study in Neblina and thus were not consumed by black uakaris at the study site. Seeds of this species however, were readily eaten by black uakaris in other parts of Pico da Neblina and the local Yanomami people consider it as one of the main foods of this primate.

The number one species in the diet of black uakaris in Pico da Neblina, *Micrandra spruceana* (Euphorbiaceae) was the 4th most abundant tree in terra firme forest and second in total basal area (Boubli, 2002). This species was exclusive to terra firme and was among the largest trees in the forest making an important contribution to the structure of this habitat. It occurred in large groves or clumps and produced dry fruits containing three large seeds each.

These results suggest that black uakari food patches in Pico da Neblina were clumped and large, resulting in low intra-group feeding competition experienced by these primates (sensu Terborgh and Janson, 1986). In addition, most fruits consumed by black uakaris were available as unripe fruits for long periods of time. Consequently black uacaris in Pico da Neblina were potentially experiencing low levels of intra group feeding competition year round, explaining why fission-fusion was never observed (Boubli, 1999). Thus, the spatial-temporal distribution of black uakari preferred foods in Pico da Neblina appeared to be favoring the formation of the unusually large groups observed/reported.

The above scenario however, implies that black uakaris should attain high population densities in Pico da Neblina as well as large group sizes. The same idea does not accommodate the fact that these monkeys traveled relatively far each day and occurred in low densities(but still more abundant than other sympatric species, Boubli, 1997). Although no systematic population census was ever conducted in Pico da Neblina, during several primate surveys (1993-94), my encounter rates with groups of black uakaris were relatively few suggesting low population density.

This situation can be explained however, if at the level of the landscape, fruit production/availability on different parts of the forest exhibited an interannual variation, i.e., if different patches of same species resources fruited at different times and not in synchrony. In Pico da Neblina, large food patches of some tree species appeared to follow this pattern. As discussed above, the tree species *Micrandra sprucei*, failed to produce a fruit crop even though, in other areas, this species was observed fruiting. As a consequence, a large potential food patch at the study site could not be used by the monkeys whereas other patches of this resource could be potentially available a few kilometers away. We suggest then that black uakaris in Pico da Neblina were adopting a strategy of traveling far each day in large permanent groups to more efficiently exploit unpredictable resources that occur in large patches.

Another important variable that could be contributing to this strategy is the renewal rate of resources at food patches. If resources have a slow renewal rate than it makes sense for the monkeys to cover a large area and only return to a feeding patch after allowing enough time for it to recuperate (e.g., Kirkpatrick, 1996). A similar situation was observed in *Rhinopithecus bieti* from Southern China. Unlike other primates of its genus, *R. bieti* was reported to live in very large cohesive groups of up to 175 individuals and to use a very large home range of 25 km^2 (2,500 ha) (Kirkpatrick, 1996). Kirkpatrick (1996) believes that, because *R. bieti* main food source, lichens, are very abundant, evenly distributed and available all year around, these monkeys are experiencing low levels of intra-group food competition, which would explain the large groups observed. Moreover, the slow renewal rate of such resource might be contributing for the large home range size used by this primate species in Southern China.

In conclusion, we believe that *C. hosomi* form large groups in Neblina because: 1) preferred foods occur in patches (trees) which are large, dense and clumped, 2) there is a long period of availability as fruits are slow to mature and are consumed at all stages of maturity, and 3) there is an interannual variation in the availability of productive food patches at the landscape level forcing the animals to range far and wide in order to keep tract of these resources.

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PRELIMINARY REPORT: ANTIPREDATOR BEHAVIORS OF MANDRILLS

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Key words: alarm calls, Cercopithecidae, *Mandrillus sphinx*, mobbing calls, predation, primate vocal communication

Abstract

Predation has likely been a major selective force shaping the evolution of primates. As a result of this current and past force, primates display a variety of antipredator behaviors. Because natural encounters with predators are infrequently observed, we do not have knowledge about the antipredator behaviors of many primate species. The aim of this study was to investigate how one such primate, mandrills (*Mandrillus sphinx*), responds to its predators. We presented visual models of leopards and crowned hawk-eagles to semi-free ranging mandrills and recorded their behavioral and vocal responses. The results indicated that mandrills tended to respond appropriately to different predator stimuli by running into trees for leopard presentations and seeking cover for eagle presentations; the mandrills emitted alarm calls at higher rates and for longer amounts of time in the leopard presentations compared to the eagle presentations.

Introduction

Predation has likely exerted a strong selective pressure on the evolution of primates. This pressure may have affected their group size and composition, ecological niche, reproductive and social behavior, body size, and cognitive abilities (van Schaik, 1983; Cheney and Wrangham, 1986; Cords, 1990; Hill and Dunbar, 1998; Stanford, 1998; Uster and Zuberbühler, 2001; Zuberbühler and Jenny, 2002; Isbell 2005). Because of this predation pressure, primates currently exhibit a variety of antipredator behaviors (Stanford, 2002).

The antipredator behaviors of primates include vocal and behavioral defenses. Primates often emit alarm calls that can convey specific information about the level of danger associated with the predator and the type of predator (Seyfarth et al., 1980; Pereira and Macedonia, 1991; Zuberbühler, 2000; Manser, 2001; Manser et al., 2001; Zuberbühler, 2001; Fichtel and Kappeler, 2002; Kirchhof and Hammerschmidt, 2006). Depending on the level of danger and the type of predator, they can flee, mob, or increase their vigilance to avoid being attacked (Cheney and Wrangham, 1986). Because natural encounters with predators are infrequently observed (Isbell, 2005), we still do not know how many primate species respond to their predators.

One of these species whose antipredator behaviors are not well known is the mandrill (*Mandrillus sphinx*). Mandrills are cercopithecine monkeys that live in multimale, multifemale groups (Abernethy et al., 2002). They are mainly terrestrial and are likely predated on by leopards (*Panthera pardus*), crowned hawk-eagles (*Stephanoaetus coronatus*), Gabon vipers (*Bitis gabonica*), and rock pythons (*Python sebae*)(Jouventin 1975; Lahm, 1985; Harrison, 1988). Because mandrills are extremely difficult to study in the wild, few detailed reports of their behaviors exist (e.g., Kudo, 1987; Rogers et al., 1996; Setchell et al., 2006). During one reported encounter with a leopard in the wild, mandrills climbed up trees or fled on the ground and also emitted vocalizations (Harrison, 1988). We are unaware of any reports that describe how mandrills respond to their other predators.

The purpose of this study was to examine the behavioral and vocal responses of semi-free ranging mandrills to model predators. Because of the difficulty of observing mandrills in the field, we studied a semi-free ranging population. We presented model predators of leopards and crowned hawk-eagles to assess whether the mandrills reacted differently to these different classes of predators. Because these different classes of predators employ different techniques for capturing primates (Mitani et al., 2001; Zuberbühler and Jenny 2002), we expected the mandrills to display different responses to each predator class.

Materials and Methods

We studied the responses of a semi-free ranging group of mandrills (*Mandrillus sphinx*) to predator presentations between July and September 2004. Presentations were conducted between 8:00 and 17:00 h. The mandrills were housed at the Centre de Primatologie, Centre International de Recherches Médicales (CIRMF) in Gabon, Africa and enclosed within a 1.5 hec area of rainforest that was surrounded by about 5-10 m of mowed grass. The group consisted of 25 individuals: two adult males, ten adult females, five juvenile males, three juvenile females, two infant males, and three infant females. All individuals were identifiable by their ear tags and/or tattoo markings.They were provisioned daily and habituated to the presence of the observers.

The mandrills in this study group had limited experiences with natural predators. With the exception of four individuals, all of the mandrills were born at CIRMF. The captive-born mandrills were descendents of the original 15 wild-born mandrills that established the captive colony over twenty years ago (Feistner et al., 1992). Because large eagles and raptors (e.g., crowned hawk-eagles) inhabit the study area, it is likely that the mandrills are familiar with these predators but no direct observations of predation have been observed (J. Yorzinski, pers. obs; J. Wickings, pers. com.). Leopards do not inhabit the area so the mandrills had no experience with them. The other four individuals were likely captured in the wild and brought into captivity as infants (B. Salle, pers. com.); they therefore had minimal exposure to predators in the wild.

Predator presentations

The mandrills were exposed to leopard and crowned hawk-eagle models. The leopard models were constructed by attaching a 2D paper printout to a cardboard base of the same shape. The paper printouts were copies of high quality photographs of leopards that were enlarged to approximate the actual size of the animal. Round rhinestone crystals were glued to the eyes of the models. These types of 2D models elicit natural antipredator behaviors (Coss et al., 2005; Stankowich and Coss, 2007). Most of the crowned hawk-eagle models were also constructed similarly. However, one of the eagle models had a plastic head and a cotton-filled fabric body with eagle markings and feathers (made by Carl Gage, Bio Models, Co.). A different model was used in each presentation.

The models were presented outside of the enclosure. The leopard models were placed face-up on the ground and were revealed by pulling forwards on a stick that was attached to the backside of the model. Most of the eagle models were presented by raising the models vertically on a levy system made of clear fishing line attached to tree branches. However, one of the eagle models glided across a clear fishing line that was connected to two posts. The person revealing these models was fully concealed within the dense understory surrounding the enclosure. The models were visible for about 30-45 sec.

For each presentation, at least one observer watched the reaction of the monkeys and another person revealed the predator model. All presentations were recorded with a Canon ZR-60 and/or Canon ZR-40 digital video camcorder (Canon USA, Inc., Lake Success, NY, USA). Before the predator model was revealed, the observer(s) recorded the position and identities of all visible monkeys; after the predator model was revealed, they recorded the behavioral responses of these visible monkeys. The response of each monkey was categorized as (1) running up a tree, (2) running into cover, or (3) remaining stationary and flinching. Because it was not usually possible to observe the behavioral responses of all visible monkeys during the actual presentation, the behavioral responses of many of the monkeys were scored from the video recordings. Audio recordings were made with a Tascam DA-P1 DAT recorder (Teac America, Montebello, California, USA) and Audio-Technica (Akron, Ohio, USA) AT4071a directional microphone.

Measurements and statistical analysis

The behavioral responses of the mandrills were compared between predator classes using Fisher’s exact tests with a Bonferroni correction. Selected comparisons were made by pooling the responses of individuals to a given predator class into two categories (e.g., individuals running into trees versus all other behavioral categories). Only the responses of adult females and juveniles that were initially located on the mowed grass (open area without vegetation) were analyzed. Some individuals were exposed to the same predator class on multiple occasions; because these individuals always responded in the same way to a given predator, they were only counted once per predator type. The responses of individuals that were initially located in the trees or bushes were excluded because of low sample sizes. The responses of the dominant adult male were considered separately because they were different from those of the other age-sex classes; the other adult male of the group was never visible during the predator presentations so we have no information about his antipredator behaviors.

The alarm calling behavior of the mandrills was compared between treatments. Because we were rarely able to identify the individual that was vocalizing, the acoustic analyses are based on the pooled vocalizations from all individuals. Even though the alarm calls of mandrills are sometimes emitted in a series of two syllables (Kudo, 1987), each syllable of an alarm call was considered a separate alarm call. Based on the audio recordings, we calculated the total number of alarm calls given within the first 10 sec of a predator presentation (call rate). We also calculated the total amount of time that mandrills emitted alarm calls (the difference between the last and first alarm call emitted; amount of time alarm calling). Mixed models (PROC MIXED) were used to analyze the call rate and amount of time alarm calling. All analyses were performed with SAS (SAS Institute 2003). Means and SE are provided in graphs to illustrate effect sizes.

Results

Four leopard and four eagle presentations were successfully conducted. More mandrills tended to run into the trees in the leopard compared to the eagle trials (Fisher's exact test: p=0.0310). More mandrills tended to run into the bushes in the eagle compared to the leopard trials (p=0.0849) (Table 1). The responses of the dominant adult male to the predator presentations differed (his responses were only visible for three leopard presentations and three eagle presentations). In two of the leopard presentations, he remained on the ground and paced back and forth while looking in the direction of the predator; in one of the presentations, he ran away after hearing the alarm calls but never turned to look at the leopard model. In the eagle presentations, he always remained stationary and sometimes also flinched.

Table 1: Behavioral responses of adult female and juvenile mandrills after seeing different predator types. All of these mandrills were initially located on the mowed grass (open area without vegetation) when the predator was presented.

Predator	**Run into trees**	**Run into cover**	**Stationary and flinch**
Leopard	6	0	0
Eagle	3	4	1

Mandrills emitted many alarm calls in response to the different predator classes. The call rate was higher in response to the leopard trials compared to the eagle trials ($F_{1,6}$=23.07, p=0.003; Fig. 1). Mandrills continued giving alarm calls for longer in response to the leopard trials compared to the eagle trials ($F_{1,6}$=38.61, p=0.0008; Fig. 2).

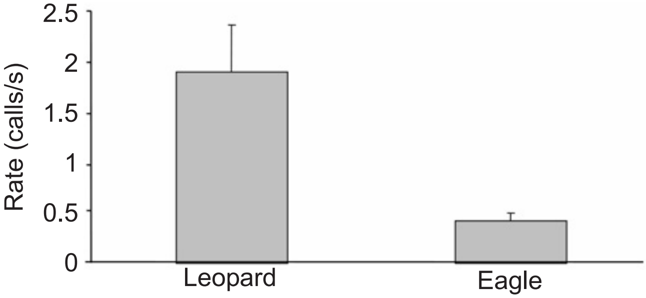

Fig. 1: Statistically significant difference in the rate of alarm calls between predator classes.

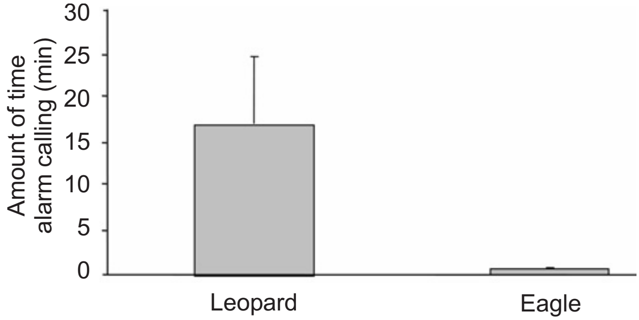

Fig.2: Statistically significant difference in the amount of time emitting alarm calls between predator classes.

Discussion and Conclusions

The results indicated that mandrills tended to run into trees for leopard presentations and to run into cover for eagle presentations. The mandrills emitted alarm calls at a higher rate and for longer amounts of time in the leopard presentations compared to the eagle presentations.

Leopards and eagles use different hunting techniques to capture primates (Mitani et al., 2001; Zuberbühler and Jenny, 2002). Many primates can evade leopard attacks by running into trees and eagle attacks by running into cover (Seyfarth et al., 1980). The behavioral responses of the mandrills were consistent with the hunting strategies of the predators presented.

The different predator classes likely represent different levels of danger to mandrills. Leopards likely represent a high level of danger to all age-sex classes because they are known to prey on juvenile and adult mandrills (Jouventin, 1975; Harrison, 1988). Crowned hawk-eagles may only prey upon juvenile and subadult mandrills (Jouventin, 1975; Lahm, 1985; Harrison, 1988) and therefore may not be dangerous to all group members. These different levels of danger could explain why the mandrills called at a higher rate and for longer amounts of time in the leopard presentations (higher overall danger) compared to the eagle presentations (lower overall danger).

The behavior of the dominant adult male of our group in response to the predator models was striking compared to the responses of the other mandrills. Rather than fleeing in response to seeing the leopard models, he remained in front of the leopards and paced back and forth; he also did not flee in response to the eagle models. Because male primates often serve an important role in defending against predators (Crook and Gartlan, 1966; van Schaik and van Noordwijk, 1989; Hill and Lee, 1998), it would be interesting to determine whether this behavior of a male mandrill is widespread within the species. This would be an especially interesting finding since it has been suggested that adult male mandrills contribute little to group protection because of their seasonal presence in mandrill hordes (Abernethy et al., 2002).

Although the mandrills had limited experience with natural predators, they still responded to all of the models. In particular, they responded to the models of leopards even though most of the mandrills had never seen this predator before. Their responses to the leopard models may represent a generalized response to novel, terrestrial animals rather than leopards per se (Yorzinski and Ziegler, 2007). Because the mandrills continued alarm calling long after the leopard models were revealed, it is unlikely that their behaviors were simply startle responses. It would be informative to compare the responses of these mandrills to those in the wild. More research exploring the antipredator behaviors of mandrills could help us further understand their group dynamics.

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URINARY GLUCOCORTICOID LEVELS IN RELATION TO SOCIO-BEHAVIORAL AND REPRODUCTIVE PARAMETERS IN CAPTIVE-HOUSED MALE CHIMPANZEES

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Key words: chimpanzee, glucocorticoids, testosterone, dominance rank, social behavior

Abstract

The secretion of glucocorticoids in primates is known to be influenced by a variety of endogenous and exogenous factors. Among great apes, however, little information exists on the effect of social variables on glucocorticoid output. Here, we investigated the effect of dominance rank, received aggression and affiliative behaviour on urinary glucocorticoid excretion in eight male chimpanzees housed in two captive groups. Furthermore, we examined the relationship between glucocorticoid and androgen output in these males. Our data show that basal glucocorticoid excretion was unrelated to male dominance rank and frequency of received aggression. In some individuals an increased amount of affiliative behavior was related to a subsequent decrease in glucocorticoid output and one individual showed an increase of affiliative behavior when having increased glucocorticoid level. We also found that basal androgen levels were unrelated to basal levels of glucocorticoids. The data suggest that under stable conditions glucocorticoid levels in captive chimpanzees are not markedly affected by socio-behavioral variables. Moreover, the results indicate that rank-related reproductive success reported in captive chimpanzee males is not a result of rank-related differences in adrenal function, but rather modulated by behavioral mechanisms.

Introduction

In primates, as in many other mammals, high physical or psychological loads are associated with increased glucocorticoid output. While short-term elevations of glucocorticoids are part of a mechanism to maintain homeostasis, a chronic increase in glucocorticoid secretion due to a prolonged exposure to stressors can lead to exhaustion of energetic resources and, as a result, can impede physiological functions or result in pathology (Sapolsky, 2002).

The secretion of glucocorticoids is known to be influenced by a variety of endogenous and exogenous factors. For example, glucocorticoid output is higher at the beginning of daily activity than before sleep (Weitzman et al., 1971; Coe and Levine, 1995; Muller and Lipson, 2003), is elevated during situations of increased body demands (von der Ohe and Servheen 2002) and can also be affected by social parameters. Regarding the latter, received aggression can increase glucocorticoid secretion (Wallner et al., 1999), while social positive interactions with conspecifics are capable of reducing glucocorticoid output (DeVries et al., 2003; Abbott et al., 2003). The impact of social factors (e.g., dominance status, mating patterns) upon glucocorticoid production, however, varies considerably between primate species (Mendoza and Mason, 1986; Abbott et al., 2003). Identifying the factors influencing glucocorticoid output is thus important for better understanding stress physiology in a particular species.

Among the great apes, little information exists on this topic. Previous studies focused mainly on validation of measurement techniques (Bahr et al., 2000), effect of day time on glucocorticoid excretion (Czekala et al., 1994; Stoinski et al., 2002; Muller and Lipson, 2003) or age-related developmental effects (Robbins and Czekala, 1997; Stoinski et al., 2002; Maggioncalda et al., 2002). Data on the relationship between social factors and glucocorticoid secretion are more limited since only rough social parameters such as dominance rank (Robbins and Czekala, 1997; Muller and Wrangham, 2004) or group composition change (Jurke et al., 2000) were investigated. Whether high glucocorticoid levels affect reproductive (i.e. testicular) function in male great apes, as reported for males of other primate taxa (Sapolsky, 1985; Hayashi and Moberg, 1987), has not been studied.

In the present study on captive male chimpanzees, we investigate the relationship between glucocorticoid levels and specific social parameters (rank, aggression received, performance of affiliative behavior) on the one hand and between glucocorticoid and androgen levels on the other hand. In a recent study on wild chimpanzees (Muller and Wrangham, 2004) it has been reported that dominant males tended to have higher glucocorticoid levels than subordinate males, probably as a result of increased energy expenditure due to higher rates of aggression. The impact of received aggression and behaviors of social support (e.g. affiliative behavior), which have recently been identified as two major predictors of basal cortisol levels in primates (Abbott et al., 2003), on the variation in glucocorticoid excretion was not addressed. To what extent glucocorticoid output is related to endocrine testicular function in-individual chimpanzee males has also not been examined. Compared to the wild, in captivity spatial constraints may influence both socio-behavioral factors as well as physiology and might be more important than energetic expenditure in shaping glucocorticoid secretion across individuals. Acquiring knowledge about factors associated with glucocorticoid secretion in captive chimpanzees might therefore not only be of scientific interest, but also help to improve the welfare and reproductive management of this species in captivity. The aims of our study therefore were to investigate under conditions of captivity: 1) if and how glucocorticoid levels are related to socio-behavioral parameters (dominance rank, rates of received aggression and affiliation) and 2) whether a relationship between glucocorticoid and androgen levels exists.

Material and Methods

Animals and housing conditions

The subjects of the study were two groups of chimpanzees, housed in the Amersfoort and the Arnhem zoos, the Netherlands. The Amersfoort group consisted of 4 adult males (10-36 years, Table 1), 11 adult females (9-37 years) and 7 infants/juveniles of both sexes (< 6 years). The Arnhem group consisted of 4 adult males (12-26 years, Table 1), 2 adolescent males (7-8 years), 17 adult females (9-45 years), 4 adolescent females (7-8 years) and 7 infants/juveniles (< 6 years).

Table 1: Demographic data of study males and number of urine samples analyzed

Zoo	**Name**	**Age (years, months)***	**Dominance rank****	**Rearing**	**# of urine samples analyzed**
Amersfoort	Mike	~ 36Y	$1\text{-}2_M$	unknown	28
	Drum	21Y, 3M	$1\text{-}2_D$	parent	22
	Cees	22Y, 4M	3	parent	35
	Utta	10Y, 4M	4	parent	22
Arnhem	Jelle	15Y, 2M	1	parent	-
	Jing	20Y, 9M	2	parent	69
	Fons	26Y, 4M	$3\text{-}4_F$	parent	61
	Giambo	12Y, 11M	$3\text{-}4_G$	parent	56
	Zouly	8Y, 6M	5	parent	49

* at the onset of the study
** males with identical numerical indices were similar in ranks

Chimpanzees in the Amersfoort zoo could use a 150 m^2 indoor cage and a 500 m^2 outdoor enclosure; in the Arnhem zoo the animals were held in either a 250 m^2 indoor or 700 m^2 outdoor enclosure. During the day and hence behavioral observations, the animals were maintained together in one enclosure (Amersfoort: outdoor; Arnhem: indoor (mostly) and outdoor (when temperatures exceeded 8° C). At night, Amersfoort animals stayed together, whilst in Arnhem the subject males were housed alone and remaining animals stayed together or were separated in smaller matrilineal groups. In both zoos animals were fed three times per day with fruits and vegetables (in the Amersfoort zoo also gruel) and with mineral pellets once a day, while water was available *ad libitum*.

In the Arnhem group, one of the males (Jelle) was treated once per month with trilafone, an antipsychotic drug, to prevent him from being overaggressive. As a result, Jelle´s level of aggression was "normalized" (i.e. was comparable to that of the α-male(s) of the Amersfoort group; Klinkova et al., 2004) and received aggression by Arnhem males were in the same range as those recorded for the Amersfoort males (Table 2). Since, furthermore, glucocorticoid (this study) and testosterone levels (Klinkova et al., 2004) of the Arnhem males were comparable to those recorded for the males in Amersfoort, it is unlikely that the treatment of Jelle affected group dynamics and the behavior and hormone levels of Jelle´s group members in an unnatural way. However, since the treatment caused some side effects (trembling and impaired locomotion) during 2-6 days post-treatment, as a rule, all males were separated from the group and no data were collected during this period.

Behavioral observations

Behavioral observations were conducted in the Amersfoort zoo from June to September 2001 (total 295 observation hours) and in the Arnhem zoo from December to April 2002 (total 432 observation hours). All study males >8 years were observed simultaneously as focal subjects (Table 1) for usually 4-7 hours per day.

Agonistic events (aggressive and submissive behaviors) were registered by all occurrences technique and affiliative behavior by scan sampling with 20 min intervals (Altman, 1974). Aggressive elements included threat, charging display, chase, grasp, push, throw an object, kick, hit, jump, stamp, drag, lift, tug hair, bite. Registered elements of submissive behavior were scream, grin, crouch, rapid oh-oh vocalizations and fleeing. Affiliative behavior was defined as involvement in grooming or playing interactions with one or more other animals. Detailed definitions of the behavioral elements are described by van Lawick-Goodall (1968) and van Hooff (1973). For each social interaction, we noted the identity of the performer and the receiver. Behavioral data were recorded using "The Observer" program of Noldus Information Technology (Base Package for Windows and Support Package for the Psion Workabout – version 3.0).

Behavioral analysis

Agonistic interactions and assessment of dominance ranks

We defined the onset of an agonistic interaction as the first occurrence of agonistic behavior directed to a particular animal. Agonistic interactions were considered to be independent if they were evenly distributed in time. According to this, elements of agonistic behaviors performed within a time interval of 240 sec. were considered belonging to the same agonistic interaction (Klinkova et al., 2004).

Dominance ranks among males were assessed as described in detail by Klinkova et al. (2004) and were usually based on direction of rapid "oh-oh" vocalizations, a submissive behavior that is uni-directionally performed by subordinate individuals to the more dominant ones and is usually accompanied by submissive crouching (Noe et al., 1980).

Rates of received aggression and proportion of affiliative behavior

The overall (over the entire study period) and daily rates of received aggression were calculated as the number of agonistic interactions in which a particular male was a subject of aggression of any other individual divided by the number of observation hours. Daily rates of received aggression were calculated only for those days in which the total observation time of a particular male exceeded 4 hours.

The overall (over the entire study period) and daily proportions of affiliative behavior were calculated as the number of scans in which a particular male was involved in affiliative interactions divided by the total number of scans. Daily proportion of affiliative behavior were calculated only for those days in which 16 or more scans were made.

Urine collection and hormone analysis

For determination of glucocorticoid excretion, we collected morning urine samples because we were mainly interested whether dominance rank and the patterns of behaviors studied have an impact on basal glucocorticoid output (as an index of chronic stress) which is more reflected by morning urinary glucocorticoid levels while afternoon levels are more influenced by waking activity patterns (Muller and Wrangham, 2004). Samples were collected around 8:00 a.m. from all focal males (except of Jelle, whose hormonal levels might have been affected by the treatment, see above) either from individual night cages (Arnhem) or after early morning separation (Amersfoort). All samples were frozen at -20° C within an hour after collection and stored at this temperature until hormone analysis.

Since native cortisol is quantitatively of only minor importance in the urine of primates, including the chimpanzee (Bahr et al., 2000), samples were analyzed for immunoreactive 5β-androstane-3α,11β-diol-17-one (3α,11β-dihydroxy-CM), a group-specific measurement of 3α,11β-dihydroxylated cortisol metabolites (Ganswindt et al., 2003), which has been shown to reliably detect increased glucocorticoid output in various primate species (Heistermann et al., 2004, 2006, Fichtel et al., 2007). In order to proof the biological validity of the assay in reflecting adrenocortical activity in the chimpanzee, 25 IU of a long-acting slow-release ACTH preparation (Synacthen Depot, Novartis, Switzerland) were injected intramuscularly into one non-study male chimpanzee from Leipzig zoo and urine samples were collected for glucocorticoid measurement. Post-treatment, a 5-fold increase above baseline was obtained in urinary 3α,11β-dihydroxy-CM levels, indicating that the measurement is reliable for monitoring adrenal activity in the chimpanzee. HPLC analysis of urine samples from one of the study males also showed that >90 % of the immunoreactivity measured was associated with a single peak co-eluting at the position of authentic 5β-androstane-3a,11β-diol-17-one (data not shown), indicating that the glucocorticoid measurement was also specific.

The same urine samples were in parallel measured for concentrations of immunoreactive testosterone (T) using a specific testosterone assay (Klinkova et al., 2004).

Urine samples were hydrolyzed and extracted with diethylether according to the method described by Klinkova et al. (2004). Urinary extracts were diluted in assay buffer and 50µl measured for concentrations of 3α,11β-dihydroxy-CM and T by microtitreplate enzymeimmunoassay (EIA) procedures as described in detail by Heistermann et al. (2004) and Klinkova et al. (2004), respectively. Sensitivity of the glucocorticoid assay at 90 % binding was 1 pg. Inter-assay coefficients of variation were 9.7 % (n=33) for high and 16.7 % (n=31) for low concentrated quality controls. Respective figures for intra-assay coefficients of variation were 6.3 % (n=16, high) and 8.7 % (n=16, low). Sensitivity and coefficients of variation of the testosterone assay are described in Klinkova et al. (2004).

In order to compensate for variations in the volume and concentration of the voided urine, creatinine (Cr) concentrations were measured in each urine sample as described by Bahr et al. (2000) and all hormone values are expressed as mass/mg Cr.

Statistical analysis

Statistical analyses were carried out using the software package Statistica 5.1 (1984-1998, StatSoft Inc., Tulsa, OK, USA). All analyses were performed using two-tailed non-parametric tests with the overall α-level of significance set at 0.05. Jelle, the treated α-male of the Arnhem group (see above), was excluded from all analyses.

Inter-male differences in glucocorticoid values were tested by Kruskal-Wallis ANOVA with post-hoc pairwise multiple comparisons using the Mann-Whitney U test in which α-level was adjusted according to the Holm-procedure (Holm, 1979).

We tested for an overall correlation between median glucocorticoid value and overall rates of received aggression using all males. We also examined whether daily changes in received aggression rates caused changes in glucocorticoid values in individual males. For this, we tested for correlation between the difference in received aggression rates on days 1 and 2 of any consecutive 3-day window and the change in glucocorticoid values (expressed in ratio) on days 2 and 3 of the same window. This analysis was performed only for males from the Arnhem group, since such a procedure required daily urine samples. Similarly, we tested for correlations between proportion of affiliative behavior and glucocorticoid levels on an overall (using data from all males) and daily basis (within individual males, only Arnhem group). In addition, we tested on a daily basis within each male whether glucocorticoid level affected the amount of affiliative behavior by correlating morning glucocorticoid values with the proportion of affiliative behavior performed by the individual on the same day. The Spearman rank correlation test was used for all approaches.

In order to test whether glucocorticoid levels were synchronized between males during the course of the study, we tested for correlations between smoothed glucocorticoid values of male group members. Pair-wise Spearman rank correlation tests were used for this purpose with α-levels adjusted according to Holm-procedure (Holm, 1979).

In order to test for an interrelationship between glucocorticoid and androgen levels, we tested overall for the 8 study subjects a correlation between median urinary glucocorticoid and androgen values. In addition, within each male of the Arnhem group, we also tested for a correlation between daily fluctuations of glucocorticoids and androgens.

Results

Relationship between glucocorticoid levels and dominance rank

In both groups of chimpanzees, glucocorticoid concentrations differed significantly between males (Amersfoort: H_3=49.43, N=107, P<0.0001; Arnhem: H_3=11.36, N=235, P=0.01). Post-hoc analysis indicated that differences in glucocorticoid levels were significant between almost all males in the Amersfoort group and between two males in the Arnhem group (Fig. 1a, b). These differences were, however, not obviously rank-related. Among the ten dyads where male dominance ranks differed from each other, in three the more dominant males had a higher glucocorticoid level, in other three the opposite effect was found and in the remaining four cases there were no significant differences in glucocorticoid levels.

Relationship between received aggression and glucocorticoid levels

As shown in Table 2, in both study groups median rates of received aggression differed considerably between males and were in both groups negatively associated with rank (r = 0.96, p<0.0001 for both groups combined, n=8). Overall, for the 8 study subjects, there was, however, no significant relationship between median rate of aggression received and median urinary glucocorticoid level (R=0.33, n=8, NS). There was also no significant relationship between the two variables on a day-to-day basis within individual males (R=-0.12-0.21, N=33-55, NS, only tested for Arnhem males, see above).

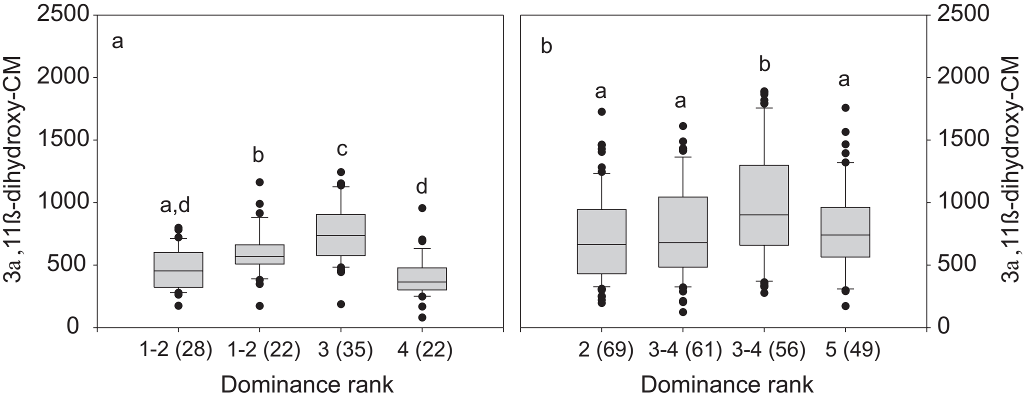

Fig. 1: Inter-male differences in urinary 3α,11ß-dihydroxy-CM levels in relation to dominance rank for Amersfoort (a) and Arnhem (b) males. Number of urine samples from each male is indicated in brackets. Different superscript letters indicate significant differences in male glucocorticoid levels as determined by multiple pairwise comparisons using Mann-Whitney U test.

Relationship between glucocorticoids and affiliative behavior

Proportions of scans (median values for the complete study) in which affiliative behavior was performed did not vary markedly between males (Table 2). Overall, for the 8 males, no significant relationship between median glucocorticoid levels and proportion of affiliative behavior performed was obtained (R=0.43, n=8, p=0.29). Within males (only tested for Arnhem group), on a day-to-day basis, however, increasing amount of affiliative behavior was significantly related to the following decrease in glucocortioid output in the next morning sample in 2 of the 4 males (R=-0.41, N=33, P=0.02 and R=-0.34, N=39, P=0.03); whilst in the other 2 individuals, this relationship was non-significant (R= -0.09 – -0.16, N=36 - 50, NS). In addition, in one male (from the Amersfoort group), high morning glucocorticoid levels were significantly positively related to high frequencies of affiliative behavior shown on the same day (R = 0.51, N=19, P=0.03; for other males R = -0.24 – 0.27, N=13-62, NS).

Correlation between glucocorticoid levels of different males

In the Arnhem animals, glucocorticoid output of all males was highly correlated (R = 0.88 - 0.99, P<0.000001, N=52-68) and showed a continuous increase during the course of the study (Fig. 2a). In contrast, there were no correlations in glucocorticoid concentrations between individual males in the Amersfoort group (R = -0.20 – 0.45, N=10-16, NS) and levels did not systematically change during the course of the study (Fig. 2b).

Table 2: Median rates of received aggression and proportion of affiliative behavior in individual males.

Zoo	**Male**	**Median**	
		Rate of received aggression (N/hour)	**Proportion of affiliative behavior (%)**
Amersfoort	Mike	0.04	8
	Drum	0.04	10
	Cees	0.11	13
	Utta	0.39	17
Arnhem	Jing	0.06	26
	Fons	0.10	16
	Giambo	0.13	20
	Zouly	0.55	21

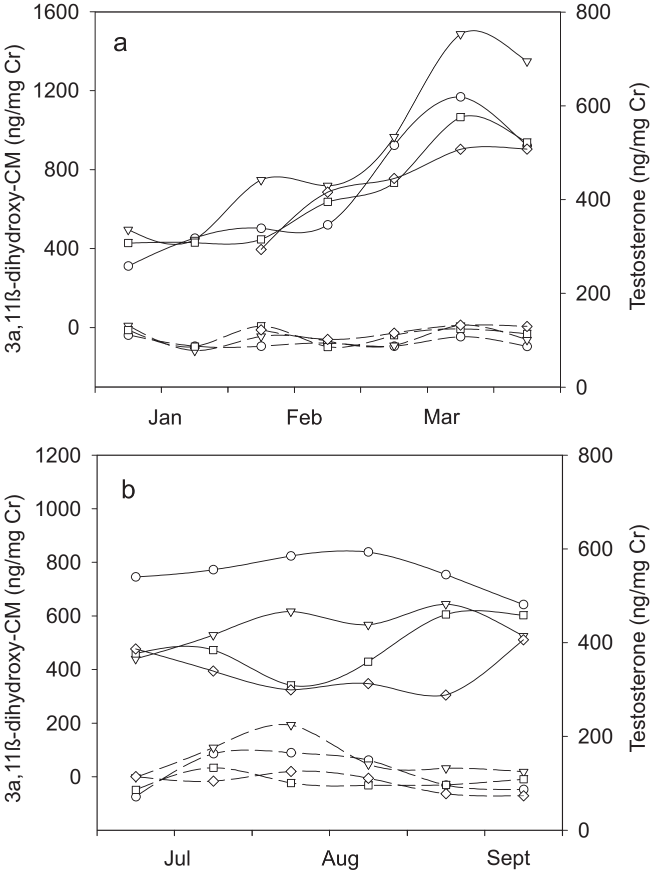

Fig. 2: Smoothed curves of urinary 3α,11β-dihydroxy-CM (solid line) and testosterone (dashed line) changes during the course of the study in the 4 males of a) the Arnhem and b) the Amersfoort group. Each symbol represents the median hormone level of an individual calculated over various half month periods throughout the whole study period.

Relationship between glucocorticoid and androgen levels

Median glucocorticoid and androgen levels were not significantly related to each other for the 8 males studied (Fig. 3). Moreover, the increase in glucocorticoid level in the Arnhem group during the course of the study was not accompanied by similar changes in urinary testosterone concentrations (Fig. 2a). However, within individuals, daily fluctuations in glucocorticoid and androgen levels were significantly correlated in Arnhem males (R = 0.32-0.60, P= 0-0.004, N= 55-78).

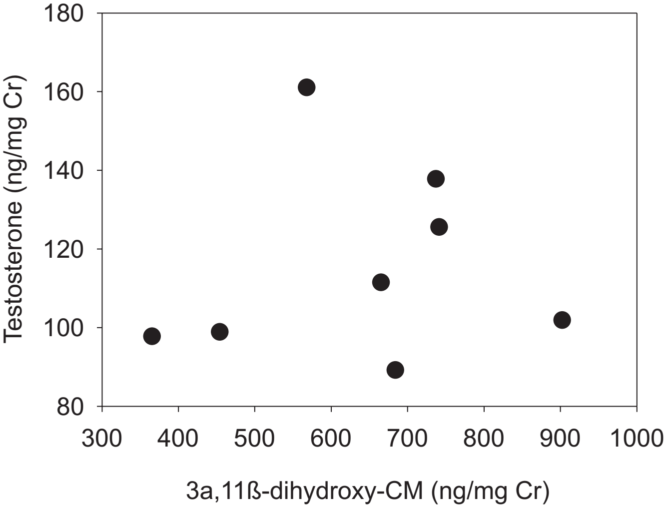

Fig. 3. Relationship between individual urinary 3α,11β-dihydroxy-CM and testosterone levels in the 8 study males (R=0.38, N=8, P=0.35).

Discussion

Glucocortioid levels differed significantly between individual males in both groups of chimpanzees, but these inter-male differences were not obviously related to dominance rank. This finding is in line with that of a recent study on wild male chimpanzees in which also no rank-related differences in urinary glucocorticoid values were obtained when morning samples were measured (Muller and Wrangham, 2004). Interestingly, in the same study a positive correlation was found between male rank and glucocorticoid values when afternoon samples were analyzed. The authors concluded that glucocorticoid levels in afternoon samples are influenced by short-term changes in adrenal function as a result of daily activity pattern associated with increased energy expenditure in dominant males, while levels measured in morning samples more likely reflect basal glucocorticoid production. Whether a similar relationship between rank and afternoon glucocorticoid levels may have existed in our study groups is unclear since we were mainly interested in the effects of social parameters on basal glucocorticoid output and therefore collected morning urine. In captivity, however, it is unlikely that animals of different ranks differ much in energetic expenditure and it is therefore questionable whether dominant males in captivity would also show elevated glucocorticoid levels during daytime activity as found for the free-ranging animals. Our results on captive chimpanzees together with those of Muller and Wrangham (2004) on free-ranging individuals, however, clearly suggest that dominance rank per se does not significantly affect basal adrenal activity in males of either dominance status and thus is not associated with chronically elevated glucocorticoid levels in either dominant or subordinate individuals.

Irrespective of whether a relationship between glucocorticoid level and dominance rank exists, the spatial constraints under captivity conditions and high rates of received aggression, especially over prolonged periods of time, might nevertheless lead to chronic psychosocial stress reflected in increased basal glucocorticoid output in primates (Wallner et al., 1999; Abbott et al., 2003). In our study males, we found no such relationship, although in both groups rates of received aggression differed considerably across individuals, with low-ranking males receiving the highest level of aggression. There are two likely, not mutually exclusive, explanations for this finding. First, the rates of aggression received by individual males were in general relatively low (maximum one act every two hours) and therefore may have not been sufficient to induce marked changes in glucocorticoid secretion. On the other hand, we found a negative relationship between amount of affiliative behavior and subsequent glucocorticoid levels in some of our study males. This suggests that individuals might have mitigated the potentially negative effect of received aggression by engaging in higher rates of affiliative behavior as part of a coping strategy to avoid increased level of stress associated with increased glucocorticoid output (e.g. Koolhaas et al., 1999). If this is the case, our data would be in agreement with findings of other studies demonstrating that opportunities for social support are capable of reducing stress response in primates (Sapolsky et al., 1997; Abbot et al., 2003). If low-ranking males which were the main receivers of aggression use increased levels of affiliation to mitigate the effect of aggressive acts received from dominants, then this would also explain the lack of a relationship between glucocorticoid excretion and rank in our study. Due to the limited number of males per group, it is, however, difficult to make firm conclusions and more studies preferably on groups with a larger number of males would be needed to confirm our preliminary contentions.

Interestingly, there was a continuous increase in glucocorticoid values over the course of the study in Arnhem, which was apparent in all males. The reason for this change in adrenal function is not clear, but since social relationships did not obviously change during the study period and all males were affected in the same way, it is unlikely that the factor(s) mediating the rise in glucocorticoid output were of a social nature but rather indicate the possibility of an environmental influence. Since it is known from studies in other vertebrate species (Romero and Remage-Healey, 2000), including primates (Strier et al., 1999; Weingrill et al., 2004) that glucocorticoid production can be affected by seasonal changes in metabolic profiles and, thus, can have a circannual pattern, it is possible that photoperiod-induced changes in metabolic rates may account for the rise in glucocorticoid excretion seen in the Arnhem males.

The increases in glucocorticoid values from the beginning to the end of the study in Arnhem males was not accompanied by changes in androgen levels. Furthermore, no relationship between median glucocorticoid and androgen levels was apparent when tested over all males. In a previous study on the same males we found that individuals which were subject to high levels of aggression showed decreased testosterone secretion (Klinkova et al., 2004). Our present findings now clearly suggest that this testosterone suppression was not mediated by elevated basal levels of glucocorticoids and that therefore mechanisms other than enhanced adrenal activity are responsible for this effect in low-ranking captive-housed male chimpanzees which are the target of high levels of aggression. A lack of correlation between overall glucocorticoid and androgen levels was also reported in other primate species, such as rhesus macaques (Bercovitch and Clarke, 1995), long-tailed macaques (van Schaik et al., 1991) and muriquis (Strier et al., 1999), all of which were studied in their natural environment. In contrast, in laboratory rats, glucocorticoids were reported to decrease the production of testicular androgens (Stalker et al., 1989) and in male rhesus macaques, chronic glucocorticoid treatment resulted in testosterone suppression (Hayashi and Moberg 1987). It seems, therefore, that the duration and dosage of glucocorticoid exposure are crucial for its potential suppressing effect on testicular endocrine function in primates. On the other hand, we found a synchronous change in daily glucocorticoid and testosterone fluctuations within individual males on a day-to-day basis. Although the physiological mechanisms underlying this relationship are not clear, simultaneous elevations in both testosterone and cortisol have been reported for a number of primate species (Martensz et al., 1987; Lynch et al., 2002; Stoinski et al., 2002). As a functional explanation for such a relationship Bercovitch and Ziegler (2002) suggested that metabolic adjustments related to male reproduction might promote elevations in both adrenal and gonadal steroids to meet the energetic demands of mate guarding and mate acquisition and thus cope with the challenges of male reproduction. Our data suggest that this might also apply to chimpanzees.

Concerning male reproductive success in chimpanzees, we have previously shown that in the Arnhem group this is clearly related to male dominance rank (Klinkova et al., 2005), but not associated with rank-dependant differences in androgen levels (Klinkova et al., 2004). Our present data indicate that reproductive success in these captive chimpanzees is also unrelated to glucocorticoid output. Based on these findings we suggest that the rank-dependent reproductive success in captive male chimpanzees is thus mainly achieved by rank-related differences in agonistic and reproductive behavioral patterns (see Klinkova et al., 2005), rather than by differences in adrenal and testicular endocrine function.

In conclusion, the present study provides preliminary insight into some social and possibly environmental factors influencing glucocorticoid excretion in captive male chimpanzees and the relationship between glucocorticoids and androgens. The information generated will hopefully help to better understand the factors influencing adrenal function in male chimpanzees, and, by doing so, may also provide a basis for improved assessment of animal well-being and captive management of the species.

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RECENT OBSERVATION ON RESIDENT MALE CHANGE FOLLOWED BY INFANTICIDE IN HANUMAN LANGURS (*SEMNOPITHECUS ENTELLUS*) AROUND JODHPUR

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Key words: *Semnopithecus entellus*, resident male, take over, infanticide, Potentiality show.

Abstract

Two cases of infant attacks were observed after take over in a free-living unimale bisexual troop (B-19) of Hanuman langur (*Semnopithecus entellus*) around Jodhpur, Rajasthan (India). This one- male bisexual troop (comprising 11 members total) was attacked in second week of May 2005 by an all-male band of three adult males and the resident male was driven form the troop. The most potent male of three males took over on May 18, 2005.The youngest infant, about three weeks was fatally wounded by an attack from the new resident male on May 20, 2005. The black coat infant, who was severely injured, died next day. A white coat infant, about six months old was also injured but who survived. The new resident was noted aggressive many of the time after these attacks and observed running behind female carrying white coat infant for about two months. And now in July 2005, he looked normal. It is proposed that such infanticidal attacks take place incidentally because of aggression arised and or explained by a show displayed by the new male to rival males and the troops members let them realize his potentiality (terror strategy). It seems that the earlier given reprodvetive strategy and resource competition hypotheses are do not strong enough.

Introduction

The Hanuman langur (*Semnopithecus entellus*) is the best-studied and most adaptable South Asian colobine. They live in wide range of habitats, from most deciduous forest to scrub and open rocky areas, like Jodhpur and in villages, and towns and on cultivated land (Roonwal and Mohnot, 1977; Wolfheim, 1983). Two basic types of social groups are bisexual troops and all-male bands. Troops are matrilineal groups of adult females and offspring with either one adult male (unimale bisexual troop) or more than one adult male (multi-male troops). Around Jodhpur 99 % of the bisexual troops are unimale bisexual troops (Mohnot et al., 1987; Rajpurohit, 1987).

A variety of social changes are met in this species. Resident male change or replacement is one such important social change, periodically seen in the unimale bisexual troops. The present paper describes the process of adult male replacement followed by and infanticide in a bisexual troop of langurs at Jodhpur.

Infanticide has been observed in many mammals including several primate species (see Hrdy, 1979; Hansfater and Hrdy, 1984). Male replacement and infant killings in Hanuman langurs have been reported at several study sites in India: Dharwar (Sugiyama, 1965), Jodhpur (Mohnot, 1971; Makwana, 1979; Sommer and Mohnot, 1985; Agoramoorthy and Mohnot, 1988; Rajpurohit and Chhangani, 2003; Rajpurohit et al., 2003), Mount Abu (Hrdy, 1974), Kanha (Newton, 1986), in Nepal (Borries, 1997) and Tirunelveli (Ross, 1993). It is notable that all the sites where infanticide has been reported, the bisexual troop structure was either predominantly one-male or after the take-over (resident male change) seemed to be functionally one-male. It has been difficult to explain the form and function of infanticide in term of modern evolutionary theory. Hrdy's hypothesis that infanticide has evolved primarily to procure reproductive advantage to males has received much attention. A new resident male could speed up the mother's sexual receptivity by eliminating young infants unlikely to be his own, so that she could then bear his offspring (Hrdy, 1974). However, questions regarding wounding and disappearances of older infant and juveniles at the time of take over and after resident male change remain unclear (Vogel and Loch, 1984; Agoramoorthy and Mohnot, 1988). The second important hypothesis suggests that an infanticide male might kill infants in order to increase the resources available for himself and his relatives (Rudran, 1979). This paper proposes a 'terror strategy' hypothesis just to explain the exhibition of the male potentiality to rival males as well as to troop members.

Material and Methods

Hanuman langurs were studied in and around the city of Jodhpur, which lies at the eastern fringe of the Great Indian Desert in Rajasthan, India. The habitat was described by Mohnot (1971, 1974). The climate of Jodhpur and its vicinity is arid and characterised by uncertain and variable rains (annual mean rainfall ca 390 mm) and extremes of temperature (hot summers with maximum temperatures up to 50° C and cold winters with minimum temperatures of 0° C). The langur population around Jodhpur is geographically isolated. The troops are distributed over a 30 km diagonal ridge running from the village of Chonkha in the west to Daijar in the northwest, passing through Jodhpur Fort (fig. 1). This genetically isolated pocket population of about 1800 langurs organised in 48 groups (34 bisexual troops and 14 all-male bands). The total area used by these animals comprises about 150 km^2. There are no other langur troops within a radius of 100 km. Water is available throughout the year for all the troops through artificial lakes, tanks, and ponds. Langur troops dwell close to human habitation and people regularly feed the monkeys.

Study group Kailana – I (*Bisexual troop B-19*)

The troop B-19 a focal group for study lives near Kailana lake guest house (8 km north west to Jodhpur city). In May, 2005 first week the troop size was 11, including the former resident male, 7 adult + 1 young adult female, 1 male white coat and 1 new born (black-coat) infants. On May 18, 2005 new resident took over. The youngest infant (i.e. black coat) was attacked by new resident on 20th may. The severely injured infant died next day, and troop size remained 10 animals.

Animals are easy to observe, as they are not shy and available on ground for maximum time of the day. The present study based on scan and all-occurrence samplings (Altman, 1974) during last 6-7 months. The group composition of this focal troop (Kailana – I) during study period is given in table 1.

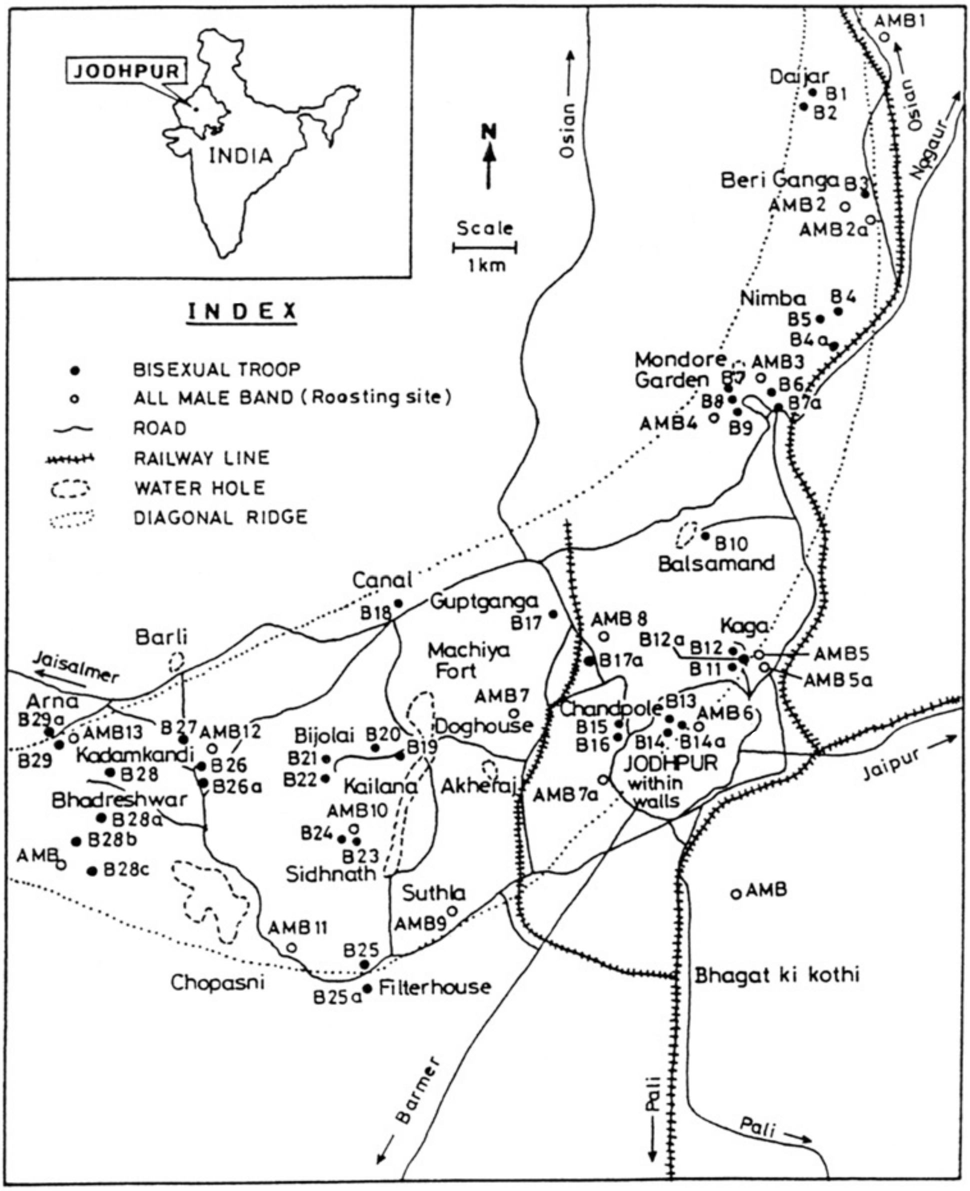

Fig. 1: Location of Hanuman langur troops and bands around Jodhpur and study cite.

Table 1: Group composition of focal bisexual troop Kailana – I (B-19) during January-December, 2005.

S.NO.	Month	Composition													Remark
		adult		subadult		juvenile		WCI		CCI		BCI		Total	
		M	F	M	F	M	F	M	F	M	F	M	F		
1	Jan	1	7	0	1	0	0	1	1	0	1	0	0	12	
2	Feb	1	7	0	1	0	0	1	1	0	0	0	0	11	One CC Infant disappear
3	March	1	7	0	1	0	0	1	0	0	0	0	0	10	One WC infant also missing
4	April	1	8	0	0	0	0	1	0	0	0	0	0	10	
5	May	1	8	0	0	0	0	1	0	0	0	1	0	11	New birth (F-7)
6	June	1	8	0	0	0	0	1	0	0	0	0	0	10	New born attacked & killedby new resident
7	July	1	8	0	0	0	0	1	0	0	0	0	0	10	
8	Aug	1	8	0	0	0	0	1	0	0	0	0	0	10	
9	Sept	1	8	0	0	0	0	1	0	0	0	0	1	11	New birth (F-1)
10	Oct	1	8	0	0	0	0	1	0	0	0	0	1	11	
11	Nov	1	8	0	0	0	0	1	0	0	0	0	1	11	
12	Dec	1	8	0	0	0	0	1	0	0	1	0	1	12	New birth (F-4)

Abbreviations: M=male; F=female; WCI=white coat infants; CCI= changing coat infants; BCI=black coat infants

Observation and Results

In the first week of the focal troop B-19 (Kailana – I) comprised of 11 langurs in May and 12 in December 2005 (see table 1) with former resident male who was continuously there as resident for about last three years (i.e. male changed in March-April, 2002). The troop found normal and there were two infants one male white coat infant of about six months old and another new born (black coat) infant only of 8-10 days old.

Take over process

On May 16, 2005,at 8.30 the B-19 troop seen normal and located near new temple. At 8.50, the resident male climbed up top of tree and whooped twice, then came down and jumped, from park wall to tree branched. At 8.55, he ran towards south where three adult male were seen. He approached for a while and stoped. The resident now (at 9.00 am) observed sitting about 50 meters before those intruders. And he continuously teeth grinded, air bitten and looked aggressive towards them. Teeth grinding heard from opposite side also (i.e. from all-male band males). This situation continued for about 10-12 minutes.

At 9.12, the resident suddenly approached them and tried to attack one of them, but rechased by all those three males. And resident once come back to the troop, which was at the same place (about 500 meters from the event). Now the invaders (three males) followed the resident and teased him.

At 9.25, the resident once again resisted these intruders and tried to chase them away, who have already near the B-19 troop. And there was fighting, the resident male was bitten severely at right arm which was bleeding. However, one of the intruder male also injured at left leg. Now at 9.35, those three males have mingled with bisexual troop B-19 and the resident seen sitting on wall about 10 meters apart, looking to the bleeding arm.

There was no more fights or protest from the resident male who was seen sitting still at the same place for last 40-45 minutes. And the troop was under the possession of those three invading males. Two adult females (not with infants) were seen presenting to one of those outside males but no mating were observed. After 10.30 am, animals were resting and the resident had moved same distance from the troop and seen sitting on a tree. The wound seemed serious and the resident male became weak, who was not in position to chase the invaders away from his territory now.

At 5.00 pm, the B-19 troop was seen with those three males and the resident male was not found nearly. We have reached for the resident male in area, but he was not found.

It was observed that both mothers one carrying white coat and another black coat infant were keeping distance from those three males and not allowing allomothing.

On May 17, 2005 at 7.30 am, the focal troop found with those three males, the former resident was not located nearby. Today the most potent male from those three males started chasing to remaining two. He was seen followed them and not allowed to sit near females of the troop. But those two of his colleagues were not ready to leave the site and sitting here and there.

At 8.40 am, the new male having right hand one (last) finger missing (the most potent one) succeeded to chase the two males little bit and now they were seen sitting about 10-12 meters apart from the troop.

At evening 5.30 pm, the troop B-19 was seen exclusively under the possession of new males. And those two of his gang males were not observed nearby, which might have drew with and left the site.

On May 18, 2005, the focal troop B-19 was now seen under the possession of that new male and this way he took-over this troop and became new resident.

Infanticide in troop B-19

The new resident male was seen normal on 18th of May and both the infants were safe with their mothers. Then we couldn't visit the troop for 2-3 days. On May 22, 2005, at 7.00 the troop B-19 found on roadside near new temple on Kailana lake turn. Today, we found only 10 individuals and the youngest infant (black coat) was not seen with its mother. We looked around but the black coat infant was neither found dead nor alive. Then we cheeked the white coat infant and found an injury on right buttock. That injury looked not too old may be of day or two. Mother was observed not allowing infant to go apart from her lap. The new resident seen very aggressive, two females observed to the resident male. But the male shown no interest. The ousted resident or other two males were not seen around even after searching here and there.

On May 28, 2005, at 7.00 am, the new resident observed with troop B-19 which was found on the trees at same Kailana turn. There were total 10 animals (8 females, a white coat infant and the resident male) in this focal troop now. We saw a dead (dry) infant hanged on a branch of *Prosopis juliflora*. And also found female 7 sitting close to that dead and nearly dried black coat. This female might be mother of that victim black coat, most probably killed by the new resident some time on may 20th.

Now the new resident was nearly accepted by the female of this focal troop. But still the white coat mother was seen keeping distance with him. There is no new birth in during last two months (i.e. May 28 to July 28, 2005), and the troop observed normal. The resident was observed bit aggressive on few occasions but seen attacking the only infant available in the troop again.

Discussion

The sexual selection hypothesis suggests that infanticide results in increased reproductive output for the incoming male. Hence infanticide behaviour is selected for (Hrdy, 1974, 1977). Leland et al. (1984) suggest that infanticide behaviour is more likely to occur in one-male groups than in multimale groups. In multimale groups, paternity may be confused, leading to the possibility that more than one male may defend an infant from attack and the chances of an infanticide male siring the mother's next infant are lower than in an one-male groups. Hence the costs of infanticide are increased, whereas the benefits are decreased in multimale groups. Although, the present infanticide attacks occurred in a one-male situation.

Curtin and Dolhinow (1978) suggested that infanticide is linked to an unnaturally high primate population density brought about by human disturbance. However, other studies have seen infanticide in undisturbed populations of langurs (Newton, 1986) and other primate species (Struhsaker and Leland, 1987). This study offers little support for the social pathology theory. Although the Jodhpur langur population is found near human habitation, the density of langurs in the area (approx. 14.5/km^2, this study and Rajpurohit et.al., 2003) is not high.

Cudran (1979) suggest that an infanticide male might kill infants in order to increase the resources avaible for himself and his relatives. However, this hypothesis does not explain why the male attacked the youngest infant (the animal consuming the least resources) but not older infants and juveniles who consume more (Hrdy, 1977; Sommer and Mohnot, 1985; Agoramoorthy and Mohnot, 1988).

Another hypothesis explains infanticide as arising from high levels of aggression being reflected during take-over (Mohnot, 1971). This idea is not contradicted by the recent infanticide attacks in Jodhpur langurs. In this study, the new resident male of troop B16 attacked two youngest infants (changing coats) only in very aggressiveness and extreme tension. However, he did attack in one instance only, after that he was observed normal. It is proposed here that the function of infanticide can be explained by the exhibition of the male potentiality or terror strategy to rival males near by and the troop members just to let them understand his supremacy. It might be simply coincident that more male infant are victimized, as they are bit more in number in infant sex ratio. The sexual selection, resource competition or social pathology hypotheses are not that suitable in this study site. However, there is a little support for the idea that infanticide is associated with a period of high aggression during male replacement (Mohnot, 1971).

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ETHOLOGY, NEUROETHOLOGY, AND EVOLVABILITY IN VERTEBRATES: A BRIEF REVIEW AND PROSPECTUS

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Key words: behavioral accommodation, evolvability, genetic accommodation, neuroethology, neuromuscular conflict, transposable behavioral elements

Abstract

The implications of recent developments in cellular and developmental biology are discussed for vertebrate ethology, describing behavior as neuromuscular elements with the potential to generate non-lethal phenotypic novelty induced by environmental stimuli (*evolvability*). I present a modified schema of a recent model for the origin of adaptive phenotypic novelties. *Behavioral accommodation* is hypothesized to lead to *genetic accommodation* if recurrence of environmental effects upon biochemical pathways of novel genetically correlated neuromuscular elements enhances survival and reproduction. I review, discuss, and interpret findings which have been implicated in neural plasticity and subsequent reorganization of the phenotype (e.g., "trial-and-error" learning), emphasizing, in particular, the importance of *hypervariable exploratory systems*. It is suggested that hypervariable neuromuscular elements and subsequent phenotypic plasticity may be induced by long-term potentiation (LTP), potentially deconstraining conserved action patterns and exposing novel patterns of response to selection. The idea that the phenotype is a heterogeneous landscape of neuromuscular elements varying in function from selfish, including parasitic, to mutualistic is proposed, and I suggest that conflict may be ubiquitous, enhancing the potential for deconstraint. A simple theoretical treatment is applied to my proposal that semi-autonomous, antagonistic *transposable behavioral elements* (TBE) may parasitize one another within and between individuals, inducing hypervariability. I suggest topics for future research, in particular, the role of environmental stressors as inducers of hypervariability and evolutionary adaptability.

Introduction

Among the unresolved topics in organismal biology are the origin, evolution, and consequences of behavioral diversity. Before the 1990s, most studies in ethology, the biology of behavior, investigated animal action or motor patterns and development without analyzing molecular, cellular, or genetic levels of analysis (e.g., Rowell et al., 1964; West, 1967; Van Hoof, 1969; Eibl-Eibesfeldt, 1970; Fentress, 1983; Jones, 1984; but see, for example, Weiss, 1941a,b; Morris, 1956; Ewer, 1960). Cellular switches controlled by gene products, however, regulate all behavioral and developmental responses (e.g., Nüsslein-Volhard, 2006; Manoli et al., 2006; Hull, 2006; Guido, 2006; Frank, 2006; Whitfield et al., 2006), creating a link between the behavioral phenotype and the genome. Because of the association between behaviors, cells, and their products, recent advances in cellular and developmental biology require assessment for what they imply about the proximate and ultimate causation of behavior (e.g., Metzner and Juranek, 1997).

Classical ethology has historically emphasized species-typical, discrete, stereotyped, and ritualized signals and displays responsive to predictable environmental stimuli (e.g., Tinbergen, 1952) rather than non-stereotyped, graded, intraindividual, interindividual, or other variable behaviors favored in heterogeneous regimes (e.g., abiotic and biotic regimes varying in time and space: Suvanto et al., 1999; Jones, 2005a). The study of behavioral and developmental plasticity (polymorphisms and polyphenisms: Jones, 2005b), however, is likely to gain a central focus in ethology as a result of renewed interest in the ways that behavioral responses, modified by environmental stimuli, can induce genetic and, by consequence, phenotypic variability. The purpose of this commentary is to provide an overview of *ethology*, *neuroethology*, *and evolvability*, "the capacity to generate nonlethal phenotypic variation" ("evolutionary adaptability": Kirschner and Gerhart, 1998, p. 8420; also see Guido, 2006; Sniegowsky and Murphy, 2006) by way of cellular, genomic, and developmental effects.

Although Kirschner and Gerhard (1998) held that addressing evolvability at the morphological level is more challenging than at the cellular level, herein we address how variability of phenotypic expression in vertebrates might be induced beyond those thresholds of response resulting from existing heritable variation within and between individuals of a population. I suggest that conceptualizing behavior at the neuromuscular and, by extension, morphological levels of analysis will advance theoretical and empirical treatments of phenotypically-induced evolvability. Introducing several new terms, I discuss the benefits of my approach for demonstrating how endogenous perturbations (e.g., molecular and cellular plasticity) might facilitate adaptation through the exposure of novel neuromuscular elements to the environment.

Consistent with most other treatments of phenotypic plasticity, I do not highlight differences between *behavioral plasticity* and *developmental plasticity*, assuming, instead, that behavior is a product of developmental processes (Pigliucci, 2001; Piersma and Drent, 2003; Kingsolver and Pfennig, 2007) differentially influenced by and with differential responsiveness to the environment. Although phenotypic plasticity might be induced by neutral effects (mutation, recombination, drift) or other mechanisms (see Jones, 2005a, Table 1.1, p 6), in this paper we exclusively discuss its induction by environmental stimuli. Future studies, however, should investigate the utility of Sih's (2004) schema which conceptualizes a continuum from highly plastic and reversible behavior to relatively unresponsive developmental effects.

A General Model of Phenotypic Change

In order to appreciate the significance of evolutionary adaptability, it is important to highlight ethology's historical concern for conserved action or motor patterns. The capacity for evolvability implies a breakdown of the conserved or constrained functions (after Kirschner and Gerhart, 1998). The present paper addresses the *deconstraint* (emancipation or release of mechanism or function) of conserved action or motor patterns by environmental perturbations, potentially exposing novel combinations of neuromuscular response to the environment (after Kirschner and Gerhart, 1998). In the present treatment of the evolutionary adaptability of behavior, two constructs are fundamental (see West-Eberhard, 2003, 2005; also see Groves, 1989): *behavioral* (phenotypic) *accommodation* and *genetic accommodation*. Behavioral accommodation refers to the organism's capacity to respond proximately to environmental change (behavioral plasticity). Genetic accommodation, on the other hand, is a longer term, adaptive process. Although processes functionally equivalent to those currently discussed as evolvability have been proposed since the 1800's (e.g., the "Baldwin effect": see reviews in Downes, 2003; West-Eberhard, 2005), our current understanding of cellular and developmental biology and genetics permits a clearer understanding of the (non-Lamarckian) ways in which novel phenotypes might arise as a result of environmental induction. Of particular import to ethologists will be the consequences of stochastic biochemical and neural events, epistasis (multiple-gene effects), pleiotropy (multiple effects of a protein), epigenomics (e.g., maternal effects), "trial and error" learning and other examples of phenotypic modification (e.g., "superstitious behavior"). By way of these and related processes (e.g., endocrinological) basic to the organism's capacity for reorganization (remodeling), the (prenatal or postnatal) phenotype may be modified adaptively by experience. Related to the latter effects, West-Eberhard (2003; also see Groves, 1989) discusses how the capacity for remodeling may increase the speed of evolution, not only facilitating the expression of novel phenotypic characters but also the fixation of these traits.

West-Eberhard (2005, p. 612; also see West-Eberhard, 2003; Groves, 1989) proposed a "general model for the origin of adaptive phenotypic novelties" permitting a straightforward assessment of changes in the behavioral phenotype and their implications for evolvability. Table 1 is a modified version of West-Eberhard's (2005) schema, displaying necessary and sufficient conditions for "the evolutionary origin of all kinds of adaptive traits-morphological, physiological and behavioral" (p. 612). These concepts are presented in relation to a recent example of developmental plasticity reported by Jones (2006a). A noteworthy feature of Table 1 is the concept that "initial spread" (#4) will depend upon repeatability or recurrence of environmental events in relation to neuromuscular activity, in particular, the morphological, endocrinological, physiological, and cellular, including molecular and genetic, rearrangements dependent upon the formation of novel presynaptic contacts (Ferreira and Paganoni, 2002). Finally, #2 [Behavioral (Phenotypic) Accomodation] and #5 (Genetic Accomodation) show the potential for behavioral (phenotypic) and genotypic conflict before and after exposure to selection since response competition may arise in neuromuscular pathways within and between individuals at all levels of analysis (e.g., genetic: Rice, 2000; Burt and Trivers, 2006; neuronal: Hull, 1934; Proekt et al., 2004; genetic and phenotypic: Hager and Johnstone, 2006; Moore et al., 2006; Roncadin et al., 2007; and, phenotypic: Bharati and Goodson, 2006; Deco and Rolls, 2006). This topic will be discussed in greater detail below. Support for genetic accomodation will require documentation such as changes in "the role of different synaptic proteins in the cellular events leading to the formation of synapses among neurons in the central nervous system" (Ferreira and Paganoni, 2002, p. 1).

Table 1: West-Eberhard's (2005) "general model for the origin of adaptive phenotypic novelties" slightly modified to include five, rather than four, "concepts" and to highlight the behavioral component of the phenotype. Examples based upon a putative case of developmental plasticity in mantled howler monkeys (*Alouatta palliata palliata*: Jones, 2006a).

	West-Eberhard's "Concept"	**Example**
1	Novel environmental stimulus induces response in one or more individuals	Anthropogenic effects create novel habitat which mantled howlers inhabit
2	Phenotypic accommodation: response(s) by individual(s) induces novel phenotype	Diet change and/or increased seasonal effects (environmental stochasticity) in new habitat (?: see Stern and Emlen, 1999)
3	Behavioral accommodation has potential to induce stochastic and/or perturbing effects (e.g., in biochemical pathways)	Fluctuating and recurrent environmental variables (e.g., variations in temperature, humidity, or rates of interaction with competitors) induce variability in gene expression (?: Mousseau and Fox, 1998; Martin, 2005; Volfson et al., 2006)
4	The frequency of common or "ubiquitous" environmental effects may increase rapidly within a single generation	Adult female mantled howlers in irrigation habitat had a smaller chest circumference than females in riparian or deciduous habitat ($p < .05$: Jones, 2006a)
5	Genetic accommodation (change in gene frequencies induced by selection): assuming genetic variation in phenotypically accommodated trait(s), the initial spread of the novel phenotype enhances responsiveness of some individuals in population to stimulus(i) which is, then, subject to selection.	Smaller chest circumference among mantled howler females in irrigation habitat may be a result of natural selection (?: Jones, 2006a)

Evolvability Potential: Phenotypic Accomodation as the Precursor of Genetic Accomodation

Following Kirschner and Gerhart's (1998) discussion of evolvability in cellular and developmental biology, neuromuscular elements may be assessed in relation to *compartmentation*, *redundancy*, *robustness*, *weak linkage*, and *exploratory systems*. As West-Eberhard (1998) pointed out, compartmentation implies hierarchical organization of modules controlled by switches (Ptashne, 2004; Choi et al., 2005; Manoli et al., 2006), a topic of inquiry in the animal (including human) behavior literature whereby neural, especially brain, modules are conceptualized as inducers of motor patterns (see Schall, 2004). Ethologists have typically studied motor patterns or action patterns as *behavioral units* (e.g., Van Hoof, 1969; Mc Cleery, 1978; Fentress, 1983) analyzable sequentially with a variety of statistical procedures (e.g., "transition probabilities": Jones, 1983; Calabi and Rosengaus, 1988). The concept of *behavioral units* implies *compartmentation* of cellular functions which may be re-framed as independent or differentially emancipated *neuromuscular elements*. In this paper, I suggest that neuromuscular elements may be evaluated objectively for their likelihoods of expression, their combinatorial (transposable) capacity (*weak linkage*), and their repeatability (*redundancy*, recurrence) if they are conceptualized as products of cells (neurons) or cellular networks. For example, Figure 1 displays musculature involved in many facial expressions, and the outputs of muscles alone or in concert with other muscles in the body provide examples of the neuromuscular elements comprising the focus of this paper.

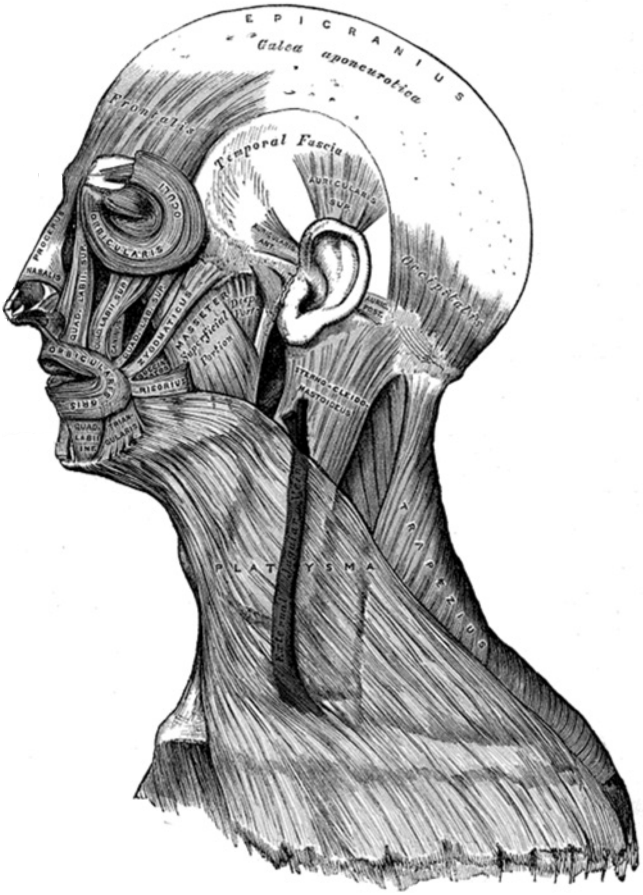

Fig. 1: Muscles associated with some human facial expressions (after Niedenthal, 2007) representing neuromuscular elements as described in the present paper. These motor elements may be expressed alone or in concert with other neuromuscular elements in the face or elsewhere in an actor's or a recipient's body. Hypervariability of response may occur where neuromuscular elements are expressed with greater frequency, rate, duration, or intensity than is required to effect successful communication between sender and receiver(s), potentially deconstraining conserved action patterns. See text for additional discussion.

Neuromuscular Elements as Exploratory Systems

Like transposable elements (TE) at the genetic level of analysis, evolution appears to have designed neuromuscular elements as "tinkering" mechanisms (Jordan, 2006), sometimes generating diversity and complexity. I expand Kirschner and

Gerhart's (1998) discussion of *exploratory systems* by evaluating the "tinkering" functions of neuromuscular actions as exploratory systems with *hyperflexible*, *hypervariable*, or unstable properties (see Khersonsky et al., 2006), overproducing elements leading to phenotypic variability, *deconstraint* of conserved activities (Kirschner and Gerhart, 1998), and facilitation of evolvability by increasing exposure of the phenotype to the environment. This construct of evolutionary adaptability is similar to energy models of motivation proposed by early ethologists (Lorenz, 1937, cited in Hinde, 1960; Tinbergen, 1951) and psychologists (Mc Dougall, 1913; Freud, 1940). These schemas advanced the idea that behavior is "spontaneous", resulting from an overproduction (hypervariability) of energy, the "drive" for neuromuscular elements (see Hinde, 1960). Another idea related to the concept of hypervariability as well as to energy models is Leigh Van Valen's (1973) Red Queen Hypothesis whereby organisms are obligated to maintain their fitness by coevolutionary "arms races" with their competitors, and coevolving systems may be particularly prone to favor enhanced, novel responses. The particular focus of the present paper is the potential for and initiation of the capacity to maintain the ability to respond to environmental perturbations.

Similar to all definitions of variability, hypervariability may imply excessive frequency, rate, duration, intensity, and/or quality of behavioral display, and overproduction, exaggeration, or extravagance of neuromuscular actions may be investigated as potentially adaptive responses to environmental heterogeneity, exposing novel neuromuscular elements and patterns of these to the environment. Thus, behavioral accommodation may enhance the capacity of hypervariable neuromuscular elements to respond to environmental heterogeneity. In some conditions, then, individuals or phenogroups with a broader range of genetically correlated responses (phenotypic variation) may be favored by selection. The likelihood of expression of these potential responses may be determined by differential *robustness* (canalization) or design (e.g., genetic, morphological: Wagner, 2005). Similar to the overproduction of eggs by many bird taxa (Saether, 1988) or to the display of exaggerated traits in sexual contexts (Andersson, 1994; Alexander et al., 1997; Jones and Van Cantfort, 2007), overproduction of neuromuscular elements may minimize fitness costs by maximizing robustness to environmental perturbations (e.g., perturbations in resource availability; see Kirschner and Gerhart, 1998). Safran et al. (2005), studying barn swallows (*Hirundo rustica*), demonstrated increased mating success in males whose plumage color was experimentally enhanced.

Examples of hyperflexibility may be found in the ubiquitous multimodal (multichannel, multisensory) responses of vertebrates. These may take the form of audiovisual, olfactory-visual, tactile-auditory signals, and the like. Rowe (1999) and others have proposed that multimodal signals increase the reliability of information sent to receivers and/or increase the ease of signal reception. Other sources suggest that multimodal signals enhance adaptive psychological processes (Rowe, 2002; Guo and Guo, 2005) and, importantly, generate novelty effects (Rowe and Guilford, 1999). The latter possibility combined with MØller and Pomiankowski's (1993) conclusion that complex signals may function as "multiple messages" or "redundant signals" support the view that neuromuscular elements may be components of exploratory, hyperflexible systems enhancing the potential for evolvability.

One robust example of such a system may be found in the "spur marking" behavior of male ring-tailed lemurs (*Lemur catta*). Following the reports of Jolly (1966) and Gould and Overrdorff (2002), these animals mark their home ranges with visual and olfactory signals using glands in their forearms. Additionally, however, these males spread their secretions by cutting into a sapling's bark with a "spur" covering the gland. These behaviors include *redundancy* and are apparently designed for emphasis, consistent with the notion that they are hyperflexible and hypervariable responses. The presence of a specialized spur indicates that these exaggerated marking behaviors have been favored by selection. Thus, hypervariable (exploratory) responses may be adaptive rather than an indication of neutral effects or error. Additional examples of hypervariable, exaggerated responses can be found in the literature on ethology and evolution such as emotions (Darwin, 1965), "handicaps" (Zahavi and Zahavi, 1997; Maynard Smith and Harper, 2003), wasteful, impulsive, and risky behaviors (e.g., impulsive homicide: Anderson and Bushman, 2002), ritualized signals and displays (Tinbergen, 1952; Jones, 2007), displacement activities (e.g., Sevenster, 1961), and many sexually selected indicators, classically, ornaments (Andersson, 1994; see Miller, 2001) and genitalia of either sex (Eberhard, 1985; Jones, 1997). Concerning the latter example, sexually selected responses in males appear to be ubiquitously hypervariable in relation to potential mates, often imposing costs upon females without apparent restraint (Rice, 2000; Smuts and Smuts, 1993; but see Jones, 1996). These topics are amenable to empirical investigation.

Neuronal Plasticity and the Potential For Behavioral Accommodation

Following Khersonsky et al.'s (2006, p. 498) discussion of hypervariability at the enzyme level, studies of *behavioral* and *genetic accommodation* will need to evaluate (1) what mechanisms generate these effects (e.g., Li et al., 2006), (2) how "latent activities" (i.e., the potential for *behavioral* and *genetic accommodation*) arise (e.g., Budd, 2006), and (3) how *behavioral* and *genetic accommodation* can arise "without severely compromising the original activity" (e.g., Brakefield, 2006; Lee et al., 2006; also see Kirschner and Gerhart, 1998). As Kirschner and Gerhart (1998) suggest, long-term potentiation [LTP: the long-term enhancement in communication between neurons resulting from simultaneous stimulation (Cooke and Bliss, 2006; Hebb, 1949)] is one mechanism generating plasticity that is thought to be highly conserved across vertebrates, possibly responsible for *behavioral accommodation* with adaptive potential (evolvability: see, for example, Ribeiro et al., 2002). LTP may be viewed as a special case of plasticity where long-lasting cellular changes can be produced affecting genetic and, presumably, phenotypic expression (Cooke and Bliss, 2006). LTP has been established as a strong molecular and cellular mechanism underlying learning and memory (Whitlock ετ al., 2006) and has been demonstrated in a number of systems (see review in LØmo, 2003).

The second criterion identified by Khersonsky et al. (2006) as a necessary condition for an understanding of *evolvability* is a description of how the "latent activities" (*evolvability* potential) arise. In vertebrates, "latent activities" are likely to arise from four primary sources. Following Kirschner and Gerhart (1998), I dicuss one of these, learning, in relation to LTP (see Wada et al., 2004). A property of some learning mechanisms is "trial-and-error" output which has been interpreted as excitatory activity responsible for "variability of response" (Hull, 1934; see Thorndike, 1911).

As discussed by these authors, *exploration* and *hypervariability* characterize trial-and-error activities and, according to the psychological literature, are latent properties of neuromuscular elements (see review in Mazur, 2006). Another latent activity, is *noise* or *stochasticity* inherent to all forms of computational activity which might be expected to produce a baseline degree of error or inaccuracy in response. Noisy responses are expected to be favored by selection if a genetically correlated synaptic or neural network "error" proved adaptive (i.e., beneficial to survival or reproductive success). To my knowledge, this line of evidence for the evolution of *evolvability* has not been explored empirically in vertebrates (but see Martin, 2005).

A third source of "latent" activity with the potential to facilitate *evolvability* might be represented by selective appropriation of molecules from one function or set of functions to others (see Kirschner and Gerhart, 1998). Candidate molecules that may have generated the potential for evolvability *via* LTP are PKC (Huang et al., 2007); MAP kinase (Satoh et al., 2007); and, PKA (Aragona and Wang, 2007), suggesting that the investigation of "latent activities" may yield important insights for research on phenotypic plasticity.

Finally, epigenomics (gene-environment interactions: e.g., Katz, 2006), pleiotropy (e.g., Abdolmaleky et al., 2005), and epistasis (e.g., Sambandan et al., 2006; De Luca et al., 2006) are also likely to be important "latent" mechanisms implicated in the potential for *behavioral* and *genetic accommodation.* All of these mechanisms may facilitate the expression of novel responses, increasing the exposure of neuromuscular elements to the environment.

Antagonistic Properties of Neuromuscular Elements: Potential Costs

In humans and other social taxa, social and non-social contexts are likely to have favored the evolution of novel neuromuscular elements and neuromuscular networks (circuits), and both the inputs and the outputs of these different contexts may conflict. Sometimes the combinations and recombinations of neuromuscular elements may be adaptive and, like phenotypic plasticity in general, evolutionary rates of neuromuscular actions may be subject to selection (but see Sniegowski and Murphy, 2006). Phenotypic plasticity, however, is expected to be associated with costs (Jones, 2005c), and, although the study of *ethology*, *neuroethology*, *and evolvability* is in its early phases, it is possible to explore in a preliminary way how behavioral and genetic accommodation might be constrained in heterogeneous regimes. Exploratory behavioral systems, for instance, may appear to violate the "phenotypic paradigm" of neo-Darwinism (Bowen and Jordan, 2002; Burt and Trivers, 2006; also see Kirschner and Gerhart, 1998) such that extravagant and excessive (hypervariable) behavioral repertoires seem costly to the bearer’s inclusive fitness. Such responses, however, may promote lifetime reproductive success rather than constrain it. For example, females may prefer males with hypervariable (extravagant: see Andersson, 1994; Alexander et al., 1997) repertoires as signs of higher quality in heterogeneous regimes. This type of female selectivity might be especially beneficial in heterogeneous regimes where potential mates are likely to be unpredictable to one another and where the potential for male monopolization of females will be compromised (see Jones, 1995b). Hypervariable trait repertoires may indicate that males bear superior genes and/or are capable of providing direct benefits such as food or breeding sites (Andersson, 1994; Zahavi and Zahavi, 1997; also see Maynard Smith and Harper, 2003). The logic of deconstraint of conserved activities is advanced by Kirschner and Gerhart (1998).

Nonetheless, conflict (e.g., genetic conflict: Rice, 2000; Burt and Trivers, 2006) may constrain or may be harmful to inclusive fitness. Thus, it is important to understand the ways in which conflict is resolved within and between individuals. Hypervariable behaviors of the same phenotype (intraindividual) may appear to be incompatible where, for instance, the biochemical pathways of genetically correlated neuromuscular elements conflict and/or compete with the biochemical pathways of an accommodated response. For example, in cichlid fish (*Astatotilapia burtoni*), "social opportunity" (i.e., the opportunity for subordinate males to become dominant breeders) triggers a molecular cascade resulting in increased fitness and access to resources (Burmeister et al., 2005). One might think of the range of possible responses–subordinate to dominant, in this case–as a continuum of neuromuscular elements corresponding to differential efficiency of biochemical pathways, including cellular and developmental function. It is reasonable to assume that certain positions along the continuum are associated with greater, possibly, optimal, efficiency of biochemical function.

Neuromuscular actions may conflict (Hull, 1934; see Biro et al., 2006; Crowley, 2003; Van Veen and Carter, 2006), such as, in a situation where a male may "decide" to exhibit either affiliative (e.g., *Papio* "friendship": Smuts, 1985) or aggressive (e.g., *Papio* infanticide: Palombit, 2003) behavior towards a female and her offspring. Endogenously, exogenously, or epigenetically induced switches (Ptashne, 2004; Chow, 2005; Hull, 2006) may select one response over another by a process similar to "behavioral contrast" (Gutman, 1977). In these conditions (e.g., males' sexual advances to receptive females), the successful behavior or combination of behaviors is that providing the greatest level of stimulation (hypervariability) to reward systems (see Sanfey et al., 2003). Behavioral contrast may minimize the likelihood of deleterious conflicts among responses that are likely to be nonlethal by increasing competition among neural and, possibly, neuromuscular elements, ensuring that novel combinations and recombinations of neuromuscular elements may be reinforced and exposed to the environment.

In another case, neuromuscular actions may conflict where some characters, traits, or responses depend upon others. For example, neuromuscular actions may "hitchhike" on one another (*phenotypic hitchhiking*) where some behaviors temporarily compensate for others, possibly to pass through a *phenotypic bottleneck* (a situation with few or no options to reproduce; see Kirschner and Gerhart, 1998, p. 8426; see Groves, 1989). Phenotypic hitchhiking may represent a condition in which severe constraints upon an individual's prospects for survival or reproduction favor the use of responses, possibly ones detrimental to fitness, over the short-term that increase phenotypic and/or genotypic benefits over the long term. It is in this sense that neuromuscular elements employed for phenotypic hitchhiking are *exploratory* and *hyperflexible* responses. These actions are employed to "test the waters" in a "last ditch" effort to survive or reproduce and, in this sense, are "best of a bad job" tactics (see Jones and Agoramoorthy, 2003).

Neuromuscular Elements as Transposable Behavioral Elements (*TBE*)

At a point in time, an organism's behavior may be viewed as an organic, multidimensional space definable as active and inactive, semi-autonomous neuromuscular elements (active, inactive, and interacting neuromuscular elements= Behavioral Phenotype at T_0) so that the unifying level of analysis of this description of the organism's behavior= the cell and its products, including genes and biochemical pathways. Some of these neuromuscular elements may have the potential to function selfishly (i.e., in their own replicative interest) or in cooperation with other neuromuscular elements (Kidwell and Lisch, 2001) and may exhibit varying frequencies, rates, durations, intensities, and qualities of association with other elements (see Kidwell and Lisch, 2001). The environment determines the selective value of different neuromuscular elements, and an empirical and sequential analysis of individual and interindividual behavior based upon the concept of neuromuscular elements is, in principle, possible.

Goodson and Wang (2006), for example, recently demonstrated differential sensitivity of vasotocin-immunoreacitve neurons in asocial and gregarious species, supporting the idea that neuromuscular elements are measurable along the continuum that I suggest (from selfish or parasitic to cooperative). Additional research is required to determine the proportion of a phenotype exposed to a given stimulus or stimulus array represented by selfish and mutualistic neuromuscular elements and whether some neuromuscular combinations rarely or never occur. Kirschner and Gerhart (1998, pp. 8422-8423) discuss immunological reactions as exploratory mechanisms, and vertebrate systems (e.g., endocrine, neural) interacting with the immune system are likely, as well, to have the potential to promote deconstraint of conserved actions, facilitating evolvability.

Objective measurement of neuromuscular elements is possible because they will usually be defined as a subset of all observable, genetically correlated neural events (neuron= N), especially, muscle actions (M), of an organism. In light of recent developments in cellular and developmental biology (Wong et al., 2005), classical ethology's treatments of behavioral traits as integrated and coordinated units (Tinbergen, 1952) require modification. In this paper, I propose a more heterogeneous view of the behavioral phenotype derived from the literature on "selfish genetic elements" (e.g., Kidwell and Lisch, 2001; Hurst and Werren, 2001; Burt and Trivers, 2006). I advance the idea that neuromuscular actions are best viewed as *transposable behavioral elements* (TBE), semi-autonomous, replicable, thus, "movable" (e.g., *via* social learning) components of phenotypes with the potential to gain differential advantage and, thus, to *parasitize* one another when operating selfishly. It is important to understand the semi-autonomous nature of TBE since this property affords the potential for flexibility and deconstraint of conserved neuromuscular elements. All modes of conflict, then, including parasitic modes, are likely to favor evolutionary adaptability.

Extending the discussion of Burt and Trivers (2006; also see Kidwell and Lisch, 2001) for transposable elements (TE), selfish TBE may be viewed as phenotypic parasites with the capacity to display *self-parasitism* where one or more behavioral responses competes with others (e.g., Gaskin and White, 2006). Selfish TBE will also demonstrate the capacity for *non-self-parasitism* involving movement from one individual or group to another (e.g., *via* selection and recombination: Fischer and

Schmid-Hempel, 2005; Agrawal and Otto, 2006; social learning: Fragaszy and Perry, 2003; cultural "memes": Gavrilets and Vose, 2006; units of language: Santi and Grodzinsky, 2006; phenotypic manipulation: Jones, 2005a, c; or, phenotypic drift: Jones, 2006b). The fundamental similarity between TE and TBE, then, is their "replicative capacity".

It seems likely to us that, similar to TEs (Kidwell and Lisch, 1997; Bowen and Jordan, 2002), TBE have played a significant, if not major, role in eukaryotic complexity and variability as exploratory mechanisms, facilitating deconstraint of conserved activities and promoting reorganization of the phenotype. Following the speculations of Kidwell and Lisch (1997) for TE, TBE, then, may promote evolvability due to their "intrinsic parasitic nature". This property may take the form of their exploitative replicability, making them candidate exploratory mechanisms; potential coadaptations between parasitic TBE and their hosts such as other TBE and individual phenotypes, including non-TBE neuromuscular elements including the copulatory patterns discussed by Dewsbury (1972; see comment on mating by Kirschner and Gerhart, 1998, p. 8427); and, exploitation of parasitic TBE by their hosts (e.g., *self-parasitism*). Stereotyped and ritualized motor responses classically emphasized by ethologists (e.g., Tinbergen, 1952) may be examples of neuromuscular elements originally favored by *behavioral accommodation* that, through recurrent exposure to the environment leading to *developmental bias*, were refined through selection in a process of *genetic accommodation*.

For example, males of one species may *parasitize* males (and females) of a second species by inducing costs from hybridization, possibly leading to speciation or to an evolutionary chase. The possibility for *coevolution* of these characters may explain certain patterns of "female choice" and reproductive isolation (e.g., biased reproduction *via* "reinforcement": Servedio, 2004) as counteradaptations to costs imposed by (intrasexual and intersexual) sexual conflict (Rice, 2000). As suggested above, these costs represent hypervariable responses by males, and hypervariable interactions among individuals (e.g., neuromuscular elements resulting from intrasexual as well as intersexual selection) may be analyzed similarly. Figure 2 displays the directionality of interactions most likely to be implicated in interindividual conflict, including parasitic and other coevolved responses where one class or category of individual imposes (fitness) costs upon another class or category of individual to which the lat-

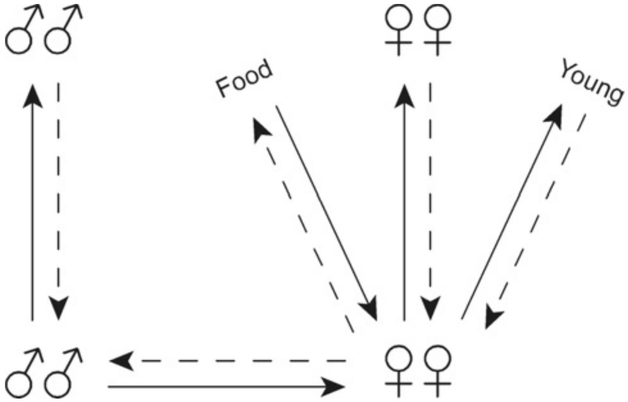

Fig. 2: Suggested direction of potential conflict(s) (differential optima) where one class or category of individuals (phenogroups: Jones, 2005a) imposes costs in inclusive fitness upon another class or category of individuals (closed arrows) to which the latter may adaptively respond (broken arrows).

ter may respond. Some of these responses are likely to be genetically correlated and, if adaptive, are expected to be favored by selection. All forms of conflict, then, may be viewed as driving forces with the potential to deconstrain conserved responses.

Parasite-host models, thus, should prove helpful for treatments of TBE where parasitic TBE are viewed as exploiters of other TBEs or non-TBE muscle patterns (hosts). In particular, TBE of "weedy", colonizing, or invading species such as ants, cockroaches, rabbits, rats, and macaque monkeys selfishly exploit their own and others' phenotypes for gains in fitness, changing the landscape of one's own and of others' phenotypes (possibly a special case of "niche construction": see Lewontin, 2000). Similar to weedy species, humans inhabit a broad range of environments and are capable of existing opportunistically in marginal habitats (Groves, 2001) and should be good models for ethological studies of adaptations to heterogeneous regimes and potential tradeoffs between *robustness* (canalization: Lerner, 1970; Flatt, 2005; Lenski et al., 2006) and *evolvability*.

A Model of Parasitic TBE

Applying the treatment of MAY and ANDERSON (1990) to the present discussion, these authors define the fitness of a parasite (exploiter) as reproductive rate (R_0), a density-dependent value. This equation can be generalized to TBE where R_0 is defined as *rate of replication* (reproduction). Where TBE interact, the effectiveness of the parasite (TBE alone or in combination with other neuromuscular actions) is related to a measure of cost (e.g., in time or energy) to the host (other neuromuscular actions), all other things being equal. The host might be the whole phenotype of one or more individuals, including the behavioral phenotype on which a TBE resides, or the host might be some proportion of another individual's phenotype. May and Anderson's (1990) equation can be labeled for TBE parasitism such that

$$R_0 = y\,(N) / (a+b+v)$$

where y is effectiveness of the parasite (actor), N is population density of the host (recipient–within or between behavioral phenotypes), a is rate of the recipient's cost from interacting with actor, b is rate of cost to recipient from all but a, and v is ability of the recipient to completely or partially escape the deleterious effects of the actor.

For example, in a classic paper, Bolles (1970) discussed *species specific defense reactions* (SSDR) as three different strategies: freezing, fleeing, and fighting. This researcher proposed that learning a novel avoidance behavior would be positively associated with its similarity to the SSDR. Bolles provided several examples of his inference, most of the cases relying upon studies of laboratory rats avoiding electric shock. If a rat's propensity to avoid danger by running (SSDR) is a TBE (parasite) and if a rat's cumulative muscular system *other than that associated with its SSDR* is the host, effectiveness of the parasite, y, can be expressed as the proportion of times a rat runs in the face of danger (e.g., electric shock) out of the total times the rat is exposed to danger and adopts another defensive response. The value, a, is the cost to the rat's phenotype imposed by TBE (e.g., injury or error rate), while b is the rate of all other costs save cost of a to the host (say, energetic maintenance costs). The expression, v, is the host's (non-TBE phenotype) ability to escape the deleterious effects of the SSDR (e.g., efficiency of behavioral switch mechanisms, flexibility of response threshold). In this manner, the equation by May and Anderson (1990) might be employed to evaluate SSDRs and, by extension, TBE, in the laboratory or field.

Related to this, May and Anderson's (1990) treatment may be applied to all cases of "internal conflict" as recently developed by Livnat and Pippenger (2006). In a theoretical paper, these authors show that "conflict can emerge within a collective even when natural selection acts on the level of the collective only" (p. 3198).The arguments in this paper support the view that *transposable elements* may arise at all levels of the individual's organization, not simply the genetic level, consistent with the present report's proposal that neuromuscular elements may function independently and selfishly and that they may *parasitize* other neuromuscular actions. Although these ideas require both theoretical and empirical investigation, I suggest that the concept of biological conflict is likely to be ubiquitous as a mechanism of deconstraint, applicable to all levels of biological organization.

Caveats

As ethologists have historically been aware, biological processes are conservative in the sense that the same components and mechanisms can be identified repeatedly across a broad range of taxa (Ptashne and Gann, 1998), and pleiotropy (multiple effects of genes) appears to be "largely reproducible and even predictable" (Weinreich et al., 2006, p. 111; see also Brakefield, 2006). These reports document constraints on phenotypic plasticity, providing a *caveat* that the behavioral phenotype is not infinitely modifiable. Bershtein et al. (2006) have recently concluded, however, that proteins are "far less robust [i.e., functionally diverse] than generally assumed" (p. 929-931), supporting West-Eberhard's (2003, 2005; also see Kirschner and Gerhart, 1998) conclusion that *genetic accommodation* is a major evolutionary dynamic. Theoretical and empirical research is required to evaluate the nature and degree of phenotypic variability, including hypervariability, for organisms responding to quantified stimuli across a range of environmental regimes. Such studies will inform us of the potential for evolvability within and between species.

Another concern is highlighted by Nowak's (2006) treatment of "fitness landscapes". Although we suggest in the present paper that the phenotype and, thus, the patterns of activities of neuromuscular elements should be viewed as a heterogeneous fitness landscape, Nowak emphasizes that such a treatment implies that genotypes map to phenotypes and phenotypes to fitness. To quote this author, "In general, however, to understand the relationship between genotype, phenotype, and fitness is an extremely complicated problem." (p. 31). There is much work to be done, and ethology has the potential to contribute in fundamental ways to this enterprise, for example, by measuring covariations of genetic, cellular, behavioral, and environmental factors across a broad range of conditions, by documenting norms of reaction (Lewontin, 1974; Schlichting and Pigliucci, 1998) between neuromuscular elements and environmental variables, and by mapping the fitness values (reproductive and/ or replicative rates) of phenotypes.

Conclusions and Prospects: Ethological Heterogeneity as a General Biological Construct

In this paper, I emphasize the potential for evolvability, the behavioral phenotype as a heterogeneous landscape, and the potential for conflict among neuromuscular elements. Using empirical evidence, I expanded West-Eberhard's (2005) "general model for the origin of adaptive phenotypic novelties", pointing out the challenges of measuring several of the concepts fundamental to this schema. Table 1 shows that potential conflicts of interest between phenotype and genotype may arise at several stages from the environmental induction of *behavioral accommodation* to the final stage of *genetic accommodation*, where this stage is attained after selection acts on favorable genetically correlated phenotypic novelties, *remodeling* biochemical and neural networks. West-Eberhard's (2005; also see Hemmer, 1990; Badyaev, 2005) writings also support the idea that *stress*, a ubiquitous condition for organisms in nature, must commonly be the environmental trigger or switch inducing *behavioral accommodation* since environmental stressors may often establish endogenous states suboptimal to some range of response thresholds for which organisms are adapted, inducing hypervariable activities (see Viltart and Vanbesien-Mailliot, 2007). This perspective suggests a new field of research documenting the multilevel causes and consequences of novel behaviors, mechanisms, and functions. As West-Eberhard (2003, p. vii) proposes, this new field of development involves "the ontogeny of all aspects of the phenotype, at all levels of organization, and in all organisms".

I have also proposed that conflict may arise where TBEs function selfishly within and between individuals, discussing several possible examples of selfish TBE, including their potential to behave parasitically. Although the particular multilevel processes whereby behavior induces novel responses are poorly understood, this area of research will, no doubt, increase in status proportionately with the mainstreaming of "evo-devo" biology (the evolution of development), a domain of investigation that remains somewhat marginalized. Both additive and non-additive components of genetic processes may enhance robust (canalized) responses to environmental perturbations (Wagner, 2005), but recent research shows that, while mutation-induced (epistatic) perturbations are linked with robustness, mechanisms have evolved to promote deconstraint of conserved activities in response to environmentally-induced perturbations. These mechanisms enhance *behavioral accommodation* and increase the likelihood that this route to evolutionary adaptability is very common, indeed.

In summary, I conclude, that the study of *ethology*, *neuroethology*, *and evolvability* provides a rich domain of investigation for researchers interested in the causes and consequences of behavioral novelty and variation. Future research has the potential to enhance our understanding of variation within and between phenogroups, including population differentiation (speciation). Although tradeoffs may exist between *evolvability* and *robustness*, hypervariable modifications of conserved neuromuscular elements through environmental induction have the potential to enhance and to consolidate recurrent neural memories, serving, I suggest, to increase their exposure to evolutionary forces.

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