UNIVERSITY OF SOUTH BOHEMIA FACULTY OF SCIENCE



PERSONALITY, SOCIAL HIERARCHY AND HORMONES IN PRIMATES.

Martina Konečná PhD. thesis

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Annotation:

This thesis deals with two main issues: personality (stable individual differences in behavior) and behavioral endocrinology (or socioendocrinology) in nonhuman primates. The first part of the thesis comprises of two primate personality studies of two species: Hanuman langurs and Barbary macaques. Two basic methods of animal personality research (behavioral coding and trait rating) were compared. Stability of personality assessments has been demonstrated. Social rank of individuals was used to validate the questionnaire ratings as well as to illustrate the independence and stability of personality assessment. The second part of the thesis is based on two studies investigating hormone levels in female Barbary macaques. The relationship between cortisol, testosterone, dominance hierarchy and behavior was investigated. And the possible effect of maternal hormone levels around the time of conception on the sex of an infant was evaluated.

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List of original papers and author contribution:

Paper 1:

Konečná, M., Lhota, S., Weiss, A., Urbánek, T., Adamová, T. & Pluháček, J. (2008): Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: Subjective ratings and recorded behavior. Journal of Comparative Psychology, Vol. 122, 4, 379–389. [IF 2.08]

Martina Konečná collected part of the behavioral data, prepared personality questionnaire, completed questionnaire ratings, analyzed behavioral and questionnaire data and together with A. Weiss wrote the paper.

Paper 2:

Konečná, M., Weiss, A., Lhota, S. Wallner, B. Personality in Barbary Macaques (*Macaca sylvanus*): Social rank and temporal stability.

submitted to Journal of Comparative Psychology

Martina Konečná collected half of the behavioral data, prepared personality questionnaire, completed questionnaire ratings, analyzed behavioral and questionnaire data and wrote the paper under the supervision of A. Weiss.

Paper 3:

Konečná, M., Roubová, V., Wallner, B. Testosterone, not cortisol, related to dominance hierarchy in female Barbary macaques (*Macaca sylvanus*).

manuscript to be submitted to Hormones and Behavior

Martina Konečná collected half of the behavioral data and hormone samples, run laboratory analysis for cortisol and testosterone metabolites, compiled and analyzed the behavioral and hormone data and wrote the paper.

Paper 4:

Grant, V., Konečná, M., Sonnweber, R. S., Irwin., J., Wallner, B. Primate mothers' pre-conception testosterone levels relate to both dominance and sex of offspring. manuscript to be submitted to Proceedings of the Royal Society B

Martina Konečná collected half of the behavioral and hormonal data for the subset of Gibraltar females, run the laboratory analysis of testosterone metabolites, compiled the data, provided relevant information for the methods section and contributed to other parts of the manuscript.

Co-authors agreement:

Martina Konečná, the author of this PhD thesis, is the first and corresponding author of three papers (manuscripts). She collected the major part of all behavioral and hormone data and performed all the laboratory analyses. She evaluated the data and computed a significant part of the statistical tests. She wrote the three papers with the help of coauthors. For the fourth manuscript, she participated in behavioral and hormone data collection for the subset of Gibraltar females, ran the laboratory analysis of testosterone metabolites, compiled the data, provided relevant information for the methods section and contributed to other parts of the manuscript.

The first and corresponding author of the fourth manuscript hereby consents to the publication of the manuscript in the PhD. thesis of Martina Konečná and supports it by her signature:

1712 August, 2010

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PART III Konečná, M., Weiss, A., Lhota, S. Wallner, B.: Personal Macaques (<i>Macaca sylvanus</i>): Social rank and temporal stabil submitted to Journal of Comparative Psychology	•
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Introduction

Introduction:

1. Personality in nonhuman primates

Individual differences in behavior or personality (also termed as behavioral syndromes, temperaments or copying styles) have received wide attention in animal behavior research, as evidenced by rapidly growing literature in the last few decades (for reviews see Bell, 2007; Gosling, 2001; Sih et al., 2004a; Sih et al., 2004b; Smith & Blumstein, 2008; Wolf et al., 2007). Personality can be defined as underlying behavioral tendencies that differ across individuals, that are stable within individuals over time and that affect the behavior consistently across different contexts (Gosling, 2001). Personality traits have been documented in wide range of taxa, from invertebrates to primates (for reviews see Gosling, 2001; Gosling and John, 1999; Sih et al., 2004a).

Emphasizing the importance of individual differences in animal behavior and considering these differences as adaptive strategies changed the science of animal behavior at least in two important ways. First, traditional behavioral ecology assumed intra-specific differences in behavior to be a non-adaptive variation of presumably adaptive averages (Dall et al., 2004) and treated behavior as being potentially infinitely plastic (Sih, 2004b). However, personality theory implies that behavior has only limited plasticity. Second, correlations among traits can act as evolutionary constraints, and thus the personality approach emphasizes the need to study behaviors together rather then as isolated units in particular context. The limited plasticity and across-context carryovers can explain behaviors that appear strikingly non-adaptive in an isolated context (Sih et al., 2004). For example, individuals with a high activity personality type are limited in how much they can reduce their activity in response to growing predatory pressure; individuals who are highly aggressive to same-sex conspecifics are not able to reduce their aggression enough when interacting with potential mates.

Animal personality theory has already been fully established and implemented into evolutionary theory. Issues such as heritability of personality traits (for review see van Oers et al., 2005), physiological and neuroendocrine correlates of personality traits (Carere et al., 2003; Koolhaas et al. 1999; Veenema et al., 2003), evolution and stability of different personality types (Wolf et al., 2007), and consequences for individual fitness (Smith and Blumstein, 2008) have been already investigated. Although the interest in personality studies is growing, some of the basic questions about personality traits per se remain unanswered (Bell, 2007).

1.1.2. Methods in animal personality research

To address further questions, standard methodological criteria have to be established. Despite its popularity in recent behavioral research, methodology for personality studies remains nonstandardized (Gosling 2001, Bell, 2007). Standard methods would allow for interspecies comparisons without the danger of methodological bias. Although some progress has been made in the last years, the basic question: "How to measure personality?" still represents one of the main methodological problems for researchers.

Currently, two basic methodological approaches are used in this type of research: i) behavioral coding, derived from classical ethological observation in test situations or everyday life and ii) trait rating, derived form human psychology and based on questionnaire rating of knowledgeable observers. Both of these two approaches have their pros and cons (Gosling 2001) and are widely used by primatologists to study personality in nonhuman primates. The trait rating method has been employed in studies aimed to investigate personality structure as a whole by revealing a personality model for a given species. This method has traditionally been used in nonhuman primates because of its easy applicability and the possibility of direct comparison with human personality research. Moreover, primatologists are often anthropologists by education and are thus familiar with methods of psychological research. The validity of animal personality ratings by

observers was supported by high interrater agreement, meaningful inter-species differences, predicting the behavior in different situations (Capitanio, 1999) and its relationship to other characteristics of individuals (Gosling & Vazire, 2002).

Behavior coding has been used to study particular personality domains, e.g. aggression (e.g. Petit, 1999) or sociability (e.g. Shepherd & French, 1999). To address personality structure using the behavioral coding method, observation of a wide range of behaviors in numerous situations is required. In most recent studies, behavioral coding is instead used to record a limited set or even a single behavior, which is subsequently labeled as a personality trait. However, the recorded behaviors differ among studies and it is only assumed that they belong to the same personality trait. For example, as Bell (2007) pointed out, predator inspection behavior (Dugatkin, 1992), behavior in an open field (Gosling, 2001) or feeding under risk (Bell, 2005) were all termed as "bold." However, the question is if each of these behaviors are equivalent and correlated with other behaviors in the same way. This approach deserved some critique, as personality is a complex concept and should include measurement of at least several behaviors under different conditions to actually fit within the realm of personality theory.

In general, there is a tendency to organize personality traits into some logical structure. Human personality researchers have investigated how personality traits are organized and presumed that a hierarchical organization of these traits exists. In humans, personality traits have been included in several personality dimensions that comprise a personality model. For example, the Five Factor personality model describes individual differences on the basis of five dimensions labeled as Extraversion, Neuroticism, Agreeableness, Conscientiousness, and Openness to Experience (McCrae & Costa, 1999). This organization allows for easier description of the interindividual variability within a population. Personality dimensions thus represent an economical way to summarize how one individual differs from another and how any given individual will behave across a range of situations and over long periods of time (John & Gosling, 2000). Moreover such organization enables investigation of personality development throughout an individual lifetime and also allows for interspecies comparisons. Comparative personality research may also describe which personality traits and dimensions play an important role in a given species and highlight evolutionary changes within personality structure (Gosling and Vazire, 2002).

The first goal of our personality study in Hanuman langurs (Semnopithecus entellus) (part II) was to compare the two methods of personality assessment and their application in a field study. Personality structures revealed by trait rating and behavioral coding methods were compared. Such a direct comparison of these two methods is almost absent in previous studies. Ours was the first personality study in the species of Colobinae subfamily and also the first to use a personality questionnaire based on the human Five Factor personality model in monkeys. In the second personality study (part III) we aimed to investigate personality structure in Barbary macaques (Macaca sylvanus) and evaluate its stability across time. We were also interested if and how changes in dominance rank effect the personality ratings of the individuals. Both studies represent an important contribution to comparative personality research.

2. Behavioral endocrinology

Field endocrinology is undergoing a period of rapid growth due to the development of noninvasive techniques for monitoring physiological functions. Researchers can examine hormone-behavior relationships and address questions and hypotheses through the study of animals in their natural habitats and social settings (Hodges & Heistermann, 2003; Touma & Palme, 2005; Whitten et al., 1998).

It is worth to note that hormones do not make the behaviors to happen in a deterministic

manner. Rather, hormones are one of several factors that interplay in the decision-making system of an individual. They may change the thresholds for other factors that enter into the decision, but are normally not the sole triggering agent. They rather "permit behavior" to occur than "cause behavior" (Adkins-Regan 2005). In the connection with social behavior, hormones allow a great deal of flexibility, allowing, for example, primate females to mate outside of fertile periods or differentiate behavioral reaction according to a particular social partner and current situation (Anestis, 2010).

2.1. Stress hormones and dominance

Social hierarchy (dominance or rank) represents an important concept in all social living primates. Position in dominance hierarchy and its relationship to other characteristics of individuals has been investigated in a wide range of species. The acquisition and maintenance of high dominance status is often species-specific and can be dependent on physical strength, age, reproductive state of female, or can be inherited. Higher ranking individuals usually enjoy priority of access to important resources, e.g. food or mates. In some nonhuman primates, the relationship between dominance and higher reproductive success has been documented (Rodriguez-Llanes et al., 2009; Silk et al., 1981; Wolfe, 1984).

It may therefore seem that being low ranking is completely disadvantageous due to limited access to resources and higher possibility of being a target of aggression from dominants. The majority of previous studies on physiological stress have been conducted in a laboratory or with captive animals, more often with males. Unfortunately, the methods commonly used in a laboratory to generate stress, e.g. footshock, restraint, forced swim, or cold, bears little resemblance to the natural conditions under which social stress appears. This approach may elicit behavioral and physiological responses different from those resulting from social and physiological stressors, such as social defeat or social hierarchy formation (Tamashiro et al., 2005). In captivity, social and environmental conditions usually differ from that found in natural habitats, which may restrain the possibilities of alternative coping strategies with stress, especially in subordinates (Creel et al., 1996).

These studies most often led to the conclusion that a higher levels of stress hormones in subordinates indicates that low social status is a stressful position for group-living individuals. However, recent studies of free-ranging populations in a wider range of species are beginning to show a different pattern of results (Abbott et al. 2003; Cavigelli et al. 2003; Creel, 2001; Ray & Sapolsky 1992; Virgin & Sapolsky 1997). It has been suggested that there is no uniform relationship between stress physiology and position in dominance hierarchy. In general, several important characteristics have been identified, including dominance acquisition and maintenance, as well as the number of stressors and availability of coping mechanisms (Abott et al., 2003). Moreover, species- and even sex-specific characteristics play an important role. The finding that elevation of stress hormones can be a consequence of subordination or a cost of dominance complicates the conventional view of social stress, with broad consequences for the evolution of dominance and sociality (Creel, 2001).

We investigated the role of stress hormones in female Barbary macaques (*Macaca sylvanus*) (part IV). Barbary macaques represent a species with a rather tolerant social organization, less strict dominance hierarchy and low rates of aggression. As previous studies were mainly focused on macaque species that have despotic dominance style with high rates of aggression and steep dominance hierarchy, the comparison could bring interesting insights about the importance of species-specific dominance style for a particular individual living in a given society.

2.2. Testosterone in female nonhuman primates

The relationship between social hierarchy and testosterone in females represents one of the

currently unexplored and exciting research questions. In vertebrate males, Challenge hypothesis (Hirschenhauser and Oliveira, 2006; Wingfield et al., 1990) explains changes and differences in testosterone levels among individuals. Recent interest in the investigation of the role of a traditionally "male hormone" prompted suggestions about testosterone levels and its relationship to rank in females (Archer, 2006). The theory predicts that if dominance is related to higher reproductive success and to the success in female competition, then we may expect dominant females to have higher levels of testosterone than subordinate ones. The elevated testosterone levels should provide advantage in female competition via dominance and aggression related behaviors. However, at the same time, elevated levels of testosterone are costly, thus reproductive advantage is important for elevated levels to evolve (Anestis, 2010). Females may compete over food as well as mates and their investments, particularly in monogamous species. In humans, women with high testosterone also scored high on personality traits related to dominance and aggression (Grant and France, 2001) and thus match these predictions very well. Previous studies on male and female nonhuman primates again report mixed results. These inconsistencies suggest that a more detailed investigation of important species- or sex- specific characteristics is needed.

In our study (part IV) of female Barbary macaques (*Macaca sylvanus*), we have investigated the relationship between testosterone, dominance rank and aggression rates during two breeding seasons, aimed to evaluate the role of female competition in a species with a rather tolerant dominance style.

2.3. Maternal hormones and offspring sex

Barbary macaques are seasonal breeders with a distinct mating season; where females resume cycling and can usually conceive after the first or second cycle. We have collected behavioral as well as hormonal data during two consecutive mating seasons (part V). This setting of our study allows for testing the possible effect of maternal pre-conceptional levels on subsequent infant sex. Although the debate whether mammalian mothers have adaptive control of the sex of their offspring is still on going, theoretically such control should be beneficial. The first theoretical framework for the investigation and interpretation of the data showing atypical mammalian sex ratios was provided by the Trivers and Willard hypothesis (Trivers and Willard, 1973) suggesting that mammalian mothers in good condition would derive a fitness advantage if they conceived and raised male offspring.

This theory generated numerous studies with conflicting results. Some reported dominant mothers have more male infants; others reported dominant mothers have more female infants. This illustrates the importance of investigation of the physiological mechanism of possible female manipulation. In the maternal personality hypothesis, derived from the human data, Grant (1996, 2007) suggested that mammalian females play a role in pre-determining the sex of their offspring by means of fluctuations in maternal testosterone levels. In humans, women who score high on personality questionnaires designed to measure dominance are more likely to conceive sons than less dominant women. Moreover women scoring high on dominance related traits have higher testosterone levels (Grant and France, 2001). Several observations suggest that the level of testosterone in a mammalian female's follicular fluid affects the probability of male or female infant conception (Garcia-Herreros et al., 2008; Grant & Irwin, 2005; Grant et al., 2008). The effect of testosterone levels on subsequent infant sex have been reported in other species (Helle et al., 2008; Shargal et al., 2008).

Moreover, female testosterone levels are interconnected with stress hormone levels as they are both controlled by the adrenal cortex (Mazur, et al., 1997). Maternal personality theory thus represents the possibility to explain some of the apparent failures to confirm the Trivers and Willard theory by taking into account the fact that female testosterone levels rise in response to environmental stressors.

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Part II

Konečná, M., Lhota, S., Weiss, A., Urbánek, T., Adamová, T., Pluháček, J. (2008): Personality in free-ranging Hanuman langur (Semnopithecus entellus) males: Subjective ratings and recorded behavior. Journal of Comparative Psychology, Vol. 122, 4, 379–389.

Personality in free-ranging Hanuman langur (Semnopithecus entellus) males: Subjective ratings and recorded behavior.

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Abstract

The authors obtained behavioral observations and personality ratings for 27 free-ranging Hanuman langur males. Subjects were rated using a questionnaire based on the human Five-Factor Model (FFM). Behavioral observations were taken over 5 months using an ethogram that included 50 behaviors. Principal Component Analysis (PCA) of ratings revealed Agreeableness_R, Confidence_R, and Extraversion_R components. Each personality dimension was associated with a unique set of observed behaviors. PCA of 36 behavioral indices revealed Dominance_B, Involvement_B, and Activity_B components. Bivariate correlations showed that Agreeableness_R was negatively correlated with Dominance_B; Confidence_R was positively correlated with Dominance_B and Involvement_B but negatively correlated with Activity_B; and Extraversion_R was positively correlated with Activity_B. Dominance rank was positively correlated with Confidence_R and Dominance_B but negatively correlated with Agreeableness_R and Activity_B. These results highlight the comparability of behavioral coding and personality ratings and suggest that some aspects of personality structure were present in the common ancestor of Old World monkeys.

Abstrakt

V této studii byla získána data o chování a hodnocení osobnosti pro 27 volně žijících samců hulmanů posvátných. Jedinci byli hodnoceni prostřednictvím dotazníku založeném na pětifaktorovém modelu používaném v lidské psychologii. Záznam chování byl pořízován po dobu pěti měsíců na základě etogramu, který obsahoval 50 prvků chování. Výsledkem analýzy hlavních komponent (PCA) dotazníkového hodnocení jsou tři dimenze osobnosti označené jako Přívětivost_d, Sebejistota_d a Extraverze_d. Každá z těchto dimenzí byla spojená s pro ni unikátní sadou zaznamenaných prvků chování. PCA třicetišesti behaviorálních indexů odhalila komponenty Dominantnost_{ch}, Zapojení_{ch} a Aktivita_{ch}. Dimenze Přívětivost_d byla negativně korelovaná s Dominantností_{ch}, a Eapojením_{ch} ale negativně s Aktivitou_{ch}; a Extraverze_d byla pozitivně korelovaná s Aktivitou_{ch}. Pozice v sociální hierarchii pozitivně korelovala se Sebejistotou_d a Dominantností_{ch} a negativně s Přívětivostí_d a Aktivitou_{ch}. Tyto výsledky ukazují porovnatelnost obou metod, subjektivního hodnocení vlastností a záznamu prvků chování. A také naznačují, že některé aspekty struktury osobnosti byly přítomné už u předka všech dnešních strarosvětských primátů.

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Part III

Konečná, M., Weiss, A., Lhota, S. Wallner, B.: Personality in Barbary macaques (Macaca sylvanus): Social rank and temporal stability. submitted to Journal of Comparative Psychology Personality in Barbary Macagues (Macaca sylvanus): Social rank and temporal stability.

Martina Konečná^{1*}, Alexander Weiss², Stanislav Lhota^{1,4}, Bernard Wallner³

Abstract

We used a questionnaire based on the human Five-Factor Model to assess the personalities of 26 semi-free-ranging Barbary macaques at two time points. We compared the compositions of these dimensions to those of rhesus macaques and Hanuman langurs. Finally, we modeled the relationships between personality ratings and a behaviorally measure of rank. Principal-components analysis revealed four personality dimensions that we labeled Friendliness, Activity/Excitability, Confidence, and Opportunistic. The interrater reliability of ratings and temporal stability of personality dimensions over one year were excellent. Comparing the make-up of these dimension to rhesus macaques and Hanuman langurs we found that Confidence, Friendliness, and Activity/Excitability had analogs in all three species, though there was no analogue of the Opportunistic dimension in these species. The Opportunistic dimension combined traits related to rank acquisition and low agreeableness. Finally, we showed that Confidence and rank were interrelated and that the stability of Confidence over time could not be explained by rank but that the stability over time of rank could be explained by personality stability. These findings demonstrate the role of species differences in ecology and social organization in shaping personality dimensions and the impact of personality on the social lives of Barbary macaques.

Abstrakt

K hodnocení osobnosti u 26ti volně žijících makaků magotů jsme použili dotazník založený na lidském pětifaktorovém modelu a to ve dvou časových obdobích. Porovnali jsme složení nalezených osobnostních dimenzí s dimezemi u makaků rhesus a hulmanů posvátných. Nakonec jsme namodelovali vztah mezi hodnocením osobnosti a postavením v sociální hierarchii určené na základě pozorovaného chování. Výsledkem analýzy hlavních komponent byly 4 dimenye osobnosti oynačené jako Přátelskost, Aktivita/Vzrušivost, Sebejistota a Přizpůsobivost. Spolehlivost hodnocení vlastností a jejich stabilita v čase byly vynikající. Porovnáním výsledné struktury osobnosti s modely osobnosti u makaků rhesus a hulmanů posvátných jsme zjistili, že Sebejistotu, Přátelskost a Aktivitu/Vzrušivost nebo jim analogické dimenze můžeme najít u všech tří druhů. Pro přizpůsobivost jsme žádný analog u těchto druhů nenašli. Tato dimenze kombinuje vlastnosti, které se vztahují k dosažení vysokého postavení v hierarchii a k malé přívětivosti. V neposlední řadě jsme ukázali souvislost mezi Sebejistotou a postavením v sociální hierarchii. A také že stabilitu hodnocení vlastností souvisejících se Sebejistotou nelze vysvětlit sociálním postavením ale naopak stabilita sociálního postavení může být vysvětlena stabilitou hodnocení osobnostních vlastností. Naše výsledky dále ukazují důležitost vlivu mezidruhových rozdílů v ekologii a sociální organizaci na formování osobnostních dimenzí a také vliv osobnosti na sociální život makaků magotů.

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Part IV

Konečná, M., Roubová, V., Wallner, B.: Testosterone, not cortisol, related to dominance hierarchy in female Barbary macaques (Macaca sylvanus).

manuscript to be submitted to Hormones and Behavior

Testosterone, not cortisol, related to dominance hierarchy in female Barbary macaques (Macaca sylvanus).

Martina Konečná^{a*}, Veronika Roubová^a, Bernard Wallner^b

Abstract

Within the genus Macaca Barbary macaques represent a species with a rather tolerant dominance style, characterized by low levels of aggression and less steep dominance hierarchy. In this study we investigated the relationship between rank, aggression and hormone levels in female Barbary macagues. We collected behavioral and hormonal data on 17 free-ranging females in two consecutive mating seasons. We analyzed 605 samples for fecal cortisol (fC) and testosterone (fT) metabolites. Our results indicated that high ranking females have higher levels of fT then subordinate females. No relationship between fT and aggression was found across subjects. These results are consistent with previous studies, although the number of studies on fT-rank-aggression relationships is very low in female nonhuman primates. We found no relationship between fC and female dominance rank. The absence of fC-rank relationship suggests that subordinate females do not suffer from chronic stress and the results are in agreement with equal relative allostatic load of dominance and subordination in Barbary macaque females. Our results also indicated that females with higher rates of received aggression had lower fC levels. The possibility of change in stressor interpretation and the effect of provisioning are discussed to explain this counter-intuitive relationship.

Abstrakt

V rámci rodu *Macaca*, jsou makaci magoti řazení k druhům se spíše tolerantním stylem dominance, který je charakterizován nízkými frekvencemi agresivních interakcí a méně strmým gradientem sociální hierarchie. V těto studii jsem zkoumali vztah mezi postavením v sociální hierarchii, aggresivním chováním a haldinou hormonů u samic makaků magotů. Data o chování a hormonálních hladinách jsme získali od 17ti volně žijících samic v průběhu dvou sezón páření. Hladina metabolitů kortisolu a testosteronu byla stanovena u 605 vzroků trusu. Naše výsledky ukazují, že vysoce postavené samice mají vyšší hladinu testosteronu než samice níže postavené. Nebyl prokázán žádný vztah mezi hladinou testosteronu a agresivním chováním u samic. Tyto výsledky jsou v souladu s některými předchozími studiemi, ale podobných prací zabývajících se vztahem testosteronu, sociální hierarchie a agrese u samic primátů není mnoho. Postavení v sociální hierarchii nemělo žádný vztah k hladině kortizolu u jednotlivých samic. Tento výsledek ukazuje, že nízko postavené samice makaků magotů netrpí chronickým stresem. Toto zjištění je ve shodě s předpoklady shodné relativní alostatické zátěže stanovené pro dominantní a nízko postavené samice makaků magotů. Další výsledky naznačují že samice, které byli často cílem agresivních interakcí měli nižší hladinu kortisolu. Tento na první pohled kontraintuitivní výsledek je diskutován z hlediska možnosti změny interpretace stresoru a vlivu přikrmování.

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Part V

Grant, V., Konečná, M., Sonnweber, R. S., Irwin., J., Wallner, B.: Primate mothers' pre-conception testosterone levels relate to both dominance and sex of offspring

manuscript to be submitted to Proceedings of the Royal Society B

Primate mothers' pre-conception testosterone levels relate to both dominance and sex of offspring

Valerie J. Grant^{1*}, Martina Konečná², Ruth-Sophie Sonnweber³, R. J. Irwin⁴, Bernard Wallner⁵

Abstract

Evolutionary biologists argue that fitness benefits must accrue to animals that can influence the sex of their offspring according to environmental conditions. There is increasing evidence to support the maternal dominance hypothesis which suggests that such influence may originate pre-conceptually in the mammalian female. Testosterone, already known to be related to dominance behaviour, is present in follicular fluid and recent evidence suggests the ovum might emerge already adapted to receive an X- or a Y-chromosome-bearing spermatozoon. Higher maternal levels of both serum and faecal testosterone have been shown to be associated with an increased number of male offspring. Here we report data showing a strong relationship between low pre-conception faecal testosterone in female Barbary macaques (*Macaca sylvanus*) and the subsequent birth of more female offspring (a two-sample randomization test of mean difference between maternal testosterone samples for subsequently male and female offspring resulted in p < 0.001). Also consistent with the maternal dominance hypothesis, high testosterone levels were associated with both high dominance rank and the birth of male offspring.

Abstrakt

Schopnost ovlivňovat pohlaví vlastních potomků podle podmínek prostředí, by měla dle předpokladů evolučních biologů být pro daný druh výhodná. Hypotéza mateřské dominance (maternal dominance hypothesis) předpokládá, že tuto schopnost může savčí matka uplatnit v období před početím. Testosterone, který souvisí s dominantním chováním, je přítomný ve folikulární tekutině a dle výsledků současných studií se zdá, že vajíčko je předpřipravené přijmout spermii nesoucí buď X nebo Y chromozóm. Předchozí studie ukázaly souvislost mezi vyšší hladinou testosteronu v krvi či vzorcích trusu a zvýšeným počtem samčích potomků. V této studii přinášíme data, která ukazují vztah mezi nízkou hladinou testosteronu ze vzorků trusu v období před početím u samic makaků magotů (*Macaca sylvanus*) a vyšší pravděpodobností následného narození samičího potomka (signifikantní randomizační test průměrných rozdílů v hladinách testosteronu samic, kterým se následně narodil samčí a kterým samičí potomek, p<0.001). Vysoká hladina testosteronu souvisela také v souladu s teorií mateřské dominance jak s vysokým postavením v sociální hierarchii tak narozením samčích potomků.

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Summary:

This thesis brings new results and insights concerning personality and behavioral endocrinology of nonhuman primates. Our findings represent contribution towards understanding how personality traits and hormonal levels relate to social behavior of studied individuals.

Our major findings:

Two basic methods in animal personality research (behavioral coding and trait rating) have been compared in field study of free-ranging Hanuman langur males. We validated questionnaire ratings by observed behavior and demonstrated comparability of both approaches. Both methods were used to establish personality model of given species.

Personality study of Barbary macaques demonstrated temporal stability of questionnaire findings. The revealed personality model was compared with studies that used similar methodology. The results of this inter-species comparison suggest that some aspects of personality structure were present in common ancestor of Old World monkeys. Moreover we demonstrated that changes in dominance rank did not lead to changes in personality assessment. And thus we conclude that assessment of personality traits related to social dominance is to some degree independent of actual rank.

Cortisol and testosterone metabolites and their relationship to dominance rank and aggressive behavior were investigated in female Barbary macaques. The results revealed strong positive relationship between female rank and testosterone levels. On the other side, cortisol was not related to rank and thus it can be concluded that low ranking females do not suffer chronic social stress in this species.

We tested the effect of maternal testosterone levels at the time of conception on subsequent infant sex in female Barbary macaques. Our data showed significantly higher probability of male conception in dominant high testosterone females. These results provide strong support for the maternal personality theory and thus imply the important role of mammalian mothers in pre-determining the sex of their offspring by means of fluctuations in maternal testosterone levels. Our study represents the very first study testing this relationship in nonhuman primates.

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Konečná M., Weiss A., Lhota S. (2008): Relationship between questionnaire rating and recorded behavior in personality study of Hanuman langur males. Contribution to the symposium "How do we know that primate personality is real and useful?". Convenors: Alex Weiss & Martina Konecna. 22nd Congress of the International Primatological Society, Primate Eye, 96, pp.112-113

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