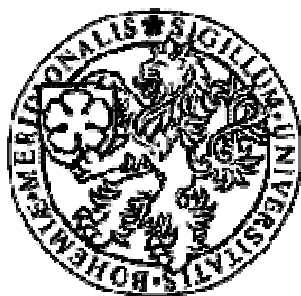
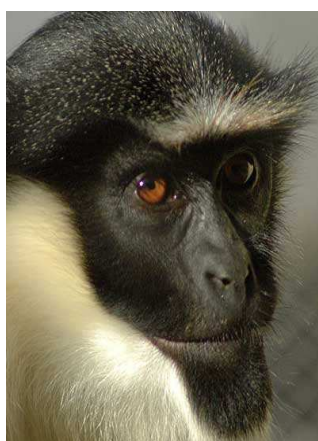


PŘÍRODOVĚDECKÁ FAKULTA
JIHOČESKÉ UNIVERZITY V ČESKÝCH BUDĚJOVICÍCH
KATEDRA ZOOLOGIE



**COMPARISON OF PLAY BEHAVIOUR OF FOUR GUENON
SPECIES: DIANA MONKEY (*Cercopithecus diana*), DE BRAZZA
MONKEY (*Cercopithecus neglectus*), PATAS MONKEY
(*Erythrocebus patas*) AND VERVET (*Chlorocebus pygerythus*)
WITH REGARD TO SELF-HANDICAPPING**



DIPLOMOVÁ PRÁCE

Hereby I declare that I elaborated this MSc. thesis myself with use of the referred-to literature.

I declare that in conformity with the law § 47b Act nr.111/1998 Collection of Law as amended, agree with publication of unshortened version of my MSc. thesis electronically by the Faculty of Natural Sciences on a publicly accessible part of the STAG database run by the University of South Bohemia in České Budějovice on its website.

In České Budějovice, January 4, 2008.

Autor: Bc. Veronika Charvátová
Vedoucí práce: Mgr. Stanislav Lhota, PhD.

České Budějovice 2008

Charvátová V. (2008): Comparison of play behaviour of four guenon species: Diana monkey (*Cercopithecus diana*), de Brazza monkey (*Cercopithecus neglectus*), Patas monkey (*Erythrocebus patas*) and Vervet (*Chlorocebus pygerythus*) with regard to self-handicapping; diploma thesis [in English] - 61 pp. Faculty of Natural Sciences, University of South Bohemia, České Budějovice, Czech Republic.

Annotation:

In order to compare play behavior of the four guenon species - diana monkey (*Cercopithecus diana*), de Brazza monkey (*Cercopithecus neglectus*), patas monkey (*Erythrocebus patas*) and vervet (*Chlorocebus pygerythus*) – with special focus on occurrence of specific self-handicapping features, these species were studied at captive settings: at Zoo Ostrava, Zoo Plzeň, Zoo Ústí nad Labem, Zoo Ohrada, Zoo Leipzig, Zoo Frankfurt, and Zoo Basel. The aim of this study was to complete a complete ethogram of play behaviour of the four studied species and to test a hypothesis explaining play behaviour with its self-handicapping elements as “training for the unexpected” (Špinka et al. 2001). The outcomes of this study are qualitative (play behaviour repertoire) as well as quantitative (statistical data) analyses. Our findings generally support the tested hypothesis although further research is needed.

Acknowledgements:

I would like to thank to many people. At the first place to my tutor Stanislav Lhota for a great deal of advice and support. I also thank to my colleagues which were very helpful in many aspects of my work – Richard Štochl, Marek Špínka, Milada Petrů, Alena Kozlová, Petr Veselý and Simona Poláková. For the help with statistical analyses I thank to Aleš Kuběna. Special thanks belong to all the friendly and helpful staff in the zoos – for their hospitality, provided information and support. Last but not least, I would like to thank my mother, who has been supporting me throughout all my life.

CONTENTS:

1. Introduction	7
2. Review of literature	8
2.1. Play itself.....	8
2.2. Functions of play.....	9
2.3. Self-handicapping in play.....	12
2.4. External factors influencing quantity of play	14
3. Aims of the study	15
4. Methods.....	16
4.1. Studied species	16
4.1.1. Biology of the studied species.....	16
4.1.2. Observed animals	18
4.2. Video recording.....	19
4.3. Data processing.....	20
4.3.1. Ethogram of play behaviour.....	20
4.3.2. Selection of self-handicapping elements.....	20
4.3.3. Data recording.....	22
4.3.4. Statistical analyses.....	22
5. Results	24
5.1. Play behaviour ethogram.....	24
5.2. Videorecorded play behaviour.....	33
5.3. Comparisons of occurrence of the selected self-handicapping elements.....	34
5.3.1. Kendall's coefficient of concordance	34
5.3.2. Percentages of self-handicapping elements performed on terrestrial and arboreal substrates.....	40
6. Discussion.....	41

6.1. Play behaviour repertoire.....	41
6.2. Comparison of occurrence of self-handicapping elements.....	43
6.3. Percentages of self-handicapping elements performed on terrestrial and arboreal substrates.....	46
6.4. Further analyses.....	47
7. Conclusions.....	48
8. References.....	49
9. Appendices	54

1. INTRODUCTION

Among all kinds of behaviour, play is one of the most elusive ones. We can often easily tell when certain individuals (animals including humans) are playing but when it comes to explaining what play actually is and what function does it have, we are not very confident (Bekoff 2001).

Play certainly has its importance in ontogeny and as an infant develops, its play behaviour develops as well (Chalmers 1980, Loizos 1967, Špinka *et al.* 2001). By playing, we learn many things but what all do animals learn in play remains clouded. In this study, we focused on one of the recent hypotheses explaining play as a training for unexpected situations (Špinka *et al.* 2001). This hypothesis is based on the fact, that mammalian immatures actively self-handicap and the authors suggest that by doing so, the animals prepare for unexpected situations in life. Therefore, the main aim of this study was to test this hypothesis by comparison of play of four guenon species living in different environments.

2. REVIEW OF LITERATURE

2.1. PLAY ITSELF

Play behaviour is characteristic for young, developing animals rather than for adults (Martin & Caro 1985) although in many mammalian species play is present in adulthood as well (Bekoff 2001, Burghardt 1999, Fagen 1981, Loizos 1967, Pellis and Iwaniuk 1999, 2000). But what exactly play is? Although we can often recognize play when we see it, we cannot precisely define play as it includes a wide variety of behaviours and differs more or less from species to species (Bekoff 2001). We can distinguish play from other kinds of behaviour with similar behavioural components by perceiving its *Gestalt* (Vick & Conley 1976). Nevertheless, many authors agree on certain common features of play behaviour (Bekoff 1984, Bekoff & Byers 1998, Fagen 1981, Hinde 1970, Loizos 1967): combination of motor patterns from several serious functional contexts; exaggeration and repetition of motor acts; and reordering of behavioural sequences. This list has been extended by some other characteristics such as: sequences of motor acts may be fragmented or incomplete (Loizos 1967); animals may self-handicap and reverse their roles (Bekoff & Allen 1998, Fagen 1981); special “play signals“ are often used before or during a play sequence (Loizos 1967, Bekoff 1976); play may have sudden onset as well as termination, and playing animals don't vocalize very much (Vick & Conley 1976). Barber (1991) mentions other three characteristic features of play: vigor, emergency behaviour (which corresponds with the „sudden onset and termination“ from the previous reference), and three-dimensional movement. Power (2000) shows the link between immature play behaviour and adult serious behaviour: Among mammals, locomotor play generally contains elements of antipredator behaviour, object play contains elements of predatory behaviour and food handling, and social play contains elements of affiliative, agonistic, and sexual behaviour.

Last but not least, play is inseparately connected with emotions of fun, well-being or joy (Bekoff & Allen 1998, Špinka *et al.* 2001) and with non-stressful conditions (Burghardt 1998, 1999).

There are three generally recognized types of play (e.g. Bekoff & Byers 1981):

1. locomotor play - includes all kinds of locomotion and static postures which are not directed at anything and anyone else
2. object play – play directed at an object, body-part, or prey
3. social play – play directed at conspecifics

2.2. FUNCTIONS OF PLAY

Although play is an activity which seems purposeless (Bekoff & Byers 1981, Martin & Caro 1985), to be maintained in course of evolution, it needs to have a distinct function (Martin & Caro 1985, Power 2000). The function of play may be different in different species (Barber 1991), and within a species, it can vary according to age, sex, context, and environment (Bekoff 2001, Breuggeman 1978, Dolhinow 1999, Fagen 1981, Martin & Caro 1985, Paquette 1994, Poirier *et al.* 1978). Many authors (e.g. Dolhinow 1999, Fagen 1981, Loizos 1967, Martin & Caro 1985, Poirier *et al.* 1978, Thompson 1998) acknowledge the possible multiple function of play, which means that play serves as physical training, practice of social skills including social bonding and anticipating behaviour of others, and play is also means of learning specific skills and abilities needed in life . There are numerous theories on the main function of play but among all, the following are the most widely discussed:

- **MOTOR/PHYSICAL TRAINING** - play may be a mechanism for providing physical training and training for adult activities (Byers 1984, Fagen 1981, Groos 1898 in Burghardt 1998, Smith 1982). This specific training is possibly linked with muscle-fibres differentiation and cerebellar synaptogenesis (Byers & Walker 1995, Byers 1998). Development of motor skills related to play might have immediate benefits to young animals such as providing important physical exercise that develops endurance, control of body movements, and/or perceptual-motor integration (Nunes *et al.* 2004). According to Biben (1998), squirrel monkeys (*Saimiri sciureus*), namely males, play mostly to win, to gain dominance over play partner. Biben claims that this is clear evidence that play serves as a training for adult fighting. In juvenile Belding's ground squirrels (*Spermophilus beldingi*), motor skills improved throughout the period in which juveniles engaged in play, especially in social play (Nunes *et al.* 2004). On the other hand, Sharpe (2005b) examined whether young meerkats (*Suricata suricatta*) that play-fought more or that won play-fights more frequently would have

greater success later in serious fights but her findings did not support this hypothesis.

- **SOCIAL SKILLS HYPOTHESIS** - play may be a safe mechanism for testing personal, and partner's abilities, for learning social skills, and for learning about qualities of others (Pellis and Iwaniuk 1999, 2000, Poirier *et al.* 1978, Thompson 1996,1998). During social play, while individuals are having fun in a relatively safe environment, they learn basic rules that are acceptable to others (how hard they can bite, how roughly they can interact) and how to resolve conflicts (Bekoff 2001). Testing social roles, and improving communication skills that contribute to current survival in the juvenile stage and social-bonding might be the key role of play in ontogeny (Burghardt 2005, Dugatkin & Bekoff 2003, Palagi, Cordoni, & Borgognini Tarli 2004, Palagi, Paoli & Borgognini Tarli 2006, Špinka *et al.* 2001). Palagi, Cordoni and Borgognini Tarli (2004) studied play behaviour in captive chimpanzees (*Pan troglodytes*), and found that play was most frequent in pre-feeding time, from what they concluded that the “practising of social skills“ function of play might be most effectively pronounced during periods of high social tension (pre-feeding time) when animals need to reduce the tension. This reduction of social tension may be effectively achieved only when animals learn and perfect their social skills. Studies of rhesus monkeys (*Macaca mulatta*) (Symons 1974) and olive baboons (*Papio anubis*) (Chalmers 1980) revealed that aggressive gestures and vocalizations were not present in play and that gestures and vocalizations given during play occurred only rarely in other contexts. Therefore these authors suggest that play cannot provide adequate practising of specific adult social skills.
- **ESTABLISHING SOCIAL RELATIONSHIPS** - play might help to establish social relationships among individuals likely to interact with each other in future (Baldwin & Baldwin 1974, Bekoff 1974, Fagen 1981, Holmes 1994, Maestriperi & Ross 2004, Palagi 2006). Paquette (1994) conducted a longitudinal study in captive chimpanzees (*Pan troglodytes*), and suggested that “social play during their adolescent period functioned in establishing and maintaining the dominance ranks within dyads“. During her field studies Sharpe (2005a) found that strengthening of long-term bonds between potential dispersal partners is probably not the function of social play in meerkats (*Suricata suricatta*). Meerkats did not favour play with the most appropriate

potential partners (did not prefer their own sex although they disperse with animals of the same sex only) nor did they strive to play with younger animals (that they could dominate in a future group) or avoid playing with older animals (that they could not dominate), and preferred playmates were not favoured as prospecting partners.

- **SELF-ASSESSMENT** – Thompson (1998) suggested that main function of play may be that it provides young with immediate feedback on their physical abilities. When a young animal succeeds several times in performing certain task, it may attempt to succeed in a more challenging task. This development of play describe e.g. Byers (1987) and Gomendio (1988) in ungulates. According to the presumptions of Thompson (1998), play should have immediate benefits and these benefits should be mostly at the cognitive level.
- **TRAINING FOR THE UNEXPECTED** (Špinka *et al.* 2001) – according to this hypothesis, the main function of play is to rehearse situations in which an animal loses full control over its movements, position or sensory perception and to rehearse how to get from these situations as quickly as possible; coping with unexpected situations includes physical training, learning how to regain control over self body and also learning how to cope emotionally wit these situations. Špinka *et al.* (2001) suggest that animals should actively seek and create unexpected situations in play through self-handicapping. Therefore the functions of play may be: to increase versatility of movements and to enhance ability of animals to cope with unexpected situations. According to the “training for the unexpected“ hypothesis, play should be beneficial immediately by “increasing locomotor versatility within the current phase of ontogeny“, and by improving ability to cope emotionally with unexpected situations – these may be immediate as well as long-lasting benefits.
Before this hypothesis was proposed, Biben (1998), made several conclusions about play, which would also support this hypothesis. These are: play promotes behavioural flexibility; play may promote learning about the intentions of others; play-fighting may reduce the stress of close bodily contact; play provides experience in both dominant and subordinate roles; play-fighting increases tolerance to pain thus making an animal more persistent and “brave“.

- **SURPLUS ENERGY HYPOTHESIS** – Barber (1991) modified the hypothesis put forth by Friedrich Schiller and later Herbert Spencer – he claims that young mammals living on low-quality vegetation may often consume excess of energy in order to ensure adequate protein intake, therefore they are not limited in energy and have to let off the excess energy in play. By doing so, their sympathetic nervous system is activated, their metabolic rate increases and thermogenesis in brown adipose tissue is stimulated which may produce defence against cold and obesity and enhance resistance to pathogens.

Martin's findings (1984) on domestic cats (*Felis catus f. domestica*) do not strongly support this hypothesis very much: The amount of energy expended on play by kittens was 4-9% of the total daily energy expenditure and the time spent daily by playing was on average 4% of the total time. Neither do findings of Nunes *et al.* (2004) who studied Belding's ground squirrels (*Spermophilus beldingi*) support this hypothesis. Their observations revealed that juveniles who engaged in play (both social and non-social) less ate more frequently. On the other hand, juveniles who played more had greater body fat than the others - this supports the idea that “energetic variables such as body fat limit the expression of play behaviour“.

2.3. SELF-HANDICAPPING IN PLAY

Self-handicapping occurs when the stronger, bigger or more skilled of two mismatched play partners adjusts its play intensity to match that of the other individual (Aldis 1975, Symons 1978, Watson & Croft 1996) or when an individual performs a behavioural pattern by which it may compromise itself (Špinka *et al.* 2001). Self-handicapping elements may or may not resemble serious motor pattern as they can mimic movements that occur without an animal's active contribution (Špinka *et al.* 2001). Self-handicapping may also be of a great importance in maintaining fair-play as animals must rely that their play partner will not harm them when they disadvantage themselves. Animals who don't behave fairly in this aspect are often avoided as play partners (Bekoff 2001).

There are numerous examples of self-handicapping. Watson and Croft (1996) found that red-necked wallabies (*Macropus rufogriseus banksianus*) adjusted their play to the age of their partner. When a partner was younger, the older animal adopted a “defensive, flat-footed posture“, and pawing rather than sparring occurred. In addition, the older player was more tolerant of its partner's tactics and took the initiative in prolonging interactions. Bekoff

(1974, 1977) described characteristic features of social play in canids where self-handicapping elements such as „play bow“ occur very often. Pereira & Preisser (1998) observed two modes of self-handicapping in hamadryas baboons (*Papio hamadryas*) - disproportionately gentle play behaviour and confinement of the roughest play behaviour to occur predominantly in proximity to his young partner's stronger allies.

Shimada (2006) studied “social object play“ in Japanese macaques (*Macaca fuscata*). This kind of play requires certain amount of self-handicapping (such as not using full power or moving more slowly) to be maintained otherwise only the strongest would possess the object. He found that the object holder is likely to be chased by others and as a role of object holder is changing, different animals are being chased. This finding is in concordance with other findings which suggest that self-handicapping serves as a means of maintaining play or training for different situations.

Cooperative tactics in social play include self-handicapping (when participants make themselves more vulnerable to attacks by their opponents) and role reversal (when individuals that are more dominant in the non-play context appear in subordinate roles during play (Altmann 1962, Fagen 1981, Špinka *et al.* 2001). Role-reversal occurs when a dominant animal performs an action during play that would not normally occur during real aggression“ (Bekoff 2001) - for example, a bigger, stronger animal or momentarily superior animal would not deliberately roll-over on his back during fighting, but would do so while playing. Sometimes, both role-reversal and self-handicapping might occur together in play (a dominant individual might roll over and inhibit the intensity of a bite). As Biben (1998) points out: “One function of role reversal is to keep play bouts going, but intentionally losing is not what happens in a real fight.“ She made an important point when she wrote that it would be beneficial for any young male monkey to find himself engaged in a mismatch because only then he learns that the best way out of it is not to panic but to “assume the subordinate role and make the most out of a bad situation.“

To establish or to maintain a playful mood many animals evolved signals (Bekoff 2001, Bekoff & Allen 1998, Loizos 1967, Pellis & Pellis 1996). Play signals are often derived from self-handicapping actions and they often involve elements similar to those used by weak, tired, subordinate or injured animals (Špinka *et al.* 2001). Study of domestic dogs (*Canis lupus f. domestica*) by Bauer & Smuts (2007) showed a link between occurrence of self-handicapping and play signals. Both kinds of behaviour might function to reassure older/dominant dogs that play manoeuvres by their partners pose no serious threat. Another

possibility is that dogs use self-handicapping to communicate that they want to play and this function is most commonly attributed to play signalling. According to observations of Bauer & Smuts (2007) older/dominant dogs are far more likely to perform self-handicapping behaviours towards disadvantaged partners when the latter are young puppies. This was also observed in chimpanzees (*Pan troglodytes*) by Mendoza-Granados & Sommer (1995).

Petrů (2005) studied self-handicapping in Hanuman langurs (*Semnopithecus entellus*), and its relation to possible ritualised play signals. She found that the function of selected self-handicapping elements – head rotation, play tumble, and suspensions - in play of Hanuman langurs was probably making play more unpredictable and variable rather than functioning as ritualised play-signals.

2.4. EXTERNAL FACTORS INFLUENCING QUANTITY OF PLAY

Animals play only when they are free from environmental as well as social and physiological stress (Biben 1998, Fagen 1981, Loizos, 1967, Martin & Caro 1985, Špinka *et al.* 2001). “Playtime generally is safe time — transgressions and mistakes are forgiven and apologies are accepted by others especially when one player is a youngster who is not yet a competitor for social status, food, or mates“ (Bekoff 2001).

Environmental conditions are very important factor influencing occurrence of play. Rhesus monkeys (*Macaca mulatta*) living under semi-natural conditions on a Puerto Rican island played less during hot weather than at other times (Levy 1979). Kenyan vervets (*Chlorocebus pygerythrus*) living in wild played only rarely during dry season but after the start of wet season, when vegetation began to grow, the amount of play increased substantially (Lee 1981). Baldwin & Baldwin (1973) found out that squirrel monkeys (*Saimiri oerstedii*) living in Panamanian forests play little when food is in short supply because they spend more time searching for food. Sommer & Mendoza-Granados (1995) studied two male groups of Hanuman langur monkeys (*Semnopithecus entellus*) – one living in rich habitat with abundant resources and the other one living in a relatively poor habitat. They found out that monkeys living in the rich habitat played 6-7 times more frequently than the other group and that their play lasted significantly longer. When the monsoon rains caused increase in availability of plant food in the poor habitat, the play activity of the monkeys living there increased rapidly.

We can therefore assume that juvenile mammals play in a relatively safe environment, when weather conditions are good and when they have enough food.

3. AIMS OF THE STUDY

- 1) To complete ethogram of play behaviour of the four guenon species.

- 2) To compare repertoires of play behaviour and especially of self-handicapping elements in the four guenon species living in different environments.

- 3) To compare occurrence of selected self-handicapping elements among the four guenon species and assess whether prevailing (preferred) types of self-handicapping in each species support the hypothesis that the main function of play could be training for the unexpected

4. METHODS

4.1. SPECIES STUDIED

4.1.1. Biology of the studied species

Diana monkeys (*Cercopithecus diana*) inhabit western Africa - from Sierra Leone to Ghana (Booth 1958). They inhabit forests with large trees and they spend most of the day in canopy (Byrne *et al.* 1983) but during the day they move between lower and higher forest strata. In their locomotion prevail faster modes of moving such as leaps (McGraw 1998). Diana monkeys are threatened by commercial hunting as reported by several studies (e.g. Refisch & Koné 2005).

De Brazza monkeys (*Cercopithecus neglectus*) live in eastern and central Africa, in parts of Gabon, Cameroon, the Central African Republic, Zaire, Ethiopia, northern Angola, in the basin of the Congo River, the southern part of Ethiopia, the valley of White Nile, and parts of Uganda and Kenya (Decker 1995, Napier & Napier 1967). Mostly, they inhabit riverine and swamp forests but they have been also observed in mountain forests (Rosen 1974 in Oswald & Lockard 1980). De Brazza monkeys have been described as arboreal quadrupeds (Napier & Napier 1967), which reportedly also spend much of their time on the ground (Oswald & Lockard 1980). Their daily range is the shortest among all guenons – about 500m (Butynski 2002, Wahome *et al.* 1993). Populations of de Brazza monkeys are endangered because of forest fragmentation and devastation and because of hunting for their meat (in Kenya: Brennan 1985).

Vervet monkeys (*Chlorocebus pygerythrus*) belong to a widely distributed genus living in eastern and southern Africa – from Senegal to Ethiopia and south to the South Africa (Nowak 1991, Rowe 1996). Their natural environment is savannah and riverine woodlands (Chism and Rowell 1988). The taxonomy of vervet monkeys has been widely discussed. While some authors treat them as a single species (Rowe 1996), Groves (2001) recognizes six species: *Chlorocebus aethiops*, *C. djamdjamensis*, *C. pygerythrus*, *C. tantalus*, *C. sabaenus*, *C. cynosuroides*.

Patatas monkeys (*Erythrocebus patas*) inhabit open country from Senegal to Ethiopia and south to Tanzania (Chism & Rowell 1988, Oshawa 2003). They prefer grass and

woodland savannahs and avoid areas where trees are denser (Chism & Rowell 1988; Nakagawa 2000). With maximal speed about 55 km/h they are considered to be the fastest of all primates (Nowak 1991).

Most of these four species form troops of one adult male, several adult females and their offspring (Butynski 2002, Byrne *et al.* 1983) but vervets typically live in troops with several adult males and many females (Rowe 1996). De Brazza monkeys were reported to be living in monogamous family groups (Gautier-Hion & Gautier 1978) but other observations suggest that they are living in polygynous family groups (Rowell 1988, Wahome *et al.* 1993). Females are philopatric and establish a dominance hierarchy within a troop (Nowak 1991).

Body weight is between 4-9 kg with males being significantly bigger and heavier than females (Nowak 1991). Gestation period is 160 – 180 days and normally a single young is born (Nowak 1991). Food of these guenons comprises mainly of fruits, seeds and leaves, and also of arthropods, gum, roots, worms, lizards, etc. (Butynski 2002, Nowak 1991). They are diurnal, active mainly in the early morning and late in the afternoon or evening (Nowak 1991). Their potential predators are lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), caracals (*Caracal caracal*), servals (*Leptailurus serval*), three jackal species (*Canis* sp.), wild domestic dogs, eagles (*Polemaetus bellicosus*) and eagle-owls (*Bubo lacteus*) (Chism & Rowell 1988).

4.1.2. Observed animals

Seven immature individuals of each species were observed. The young of all four species were observed and filmed in captive settings – at zoos. For details of zoos and group compositions see Appendix I. A summary of observed individuals is presented in Table 4.1.

Table 4.1: Observed individuals, periods and places (zoos) of videorecording and lengths of obtained videorecordings

species	zoo	period	observed subjects	video recording length
<i>Cercopithecus diana</i>	Leipzig	October 14- 23, 2005	2♀	710 min
	Ostrava	March 8 – 20, 2003	2♀	700 min
		November 11 – 22, 2004	2♀, 1♂	680 min
<i>Cercopithecus neglectus</i>	Ústí n.L.	October, November 2002 (continuously)	2♀, 1♂	320 min
	Plzeň	March, April 2002 (continuously)	3♂	1200 min
		September 1 – 15, 2005	1♂	510 min
<i>Chlorocebus pygerythrus</i>	Basel	September 16 – 28, 2007	1♀, 6♂	670 min
<i>Erythrocebus patas</i>	Ohrada	August 2007, continuously	2♀, 2♂	450 min
	Frankfurt	September 13- 25, 2002	1♀, 2♂	700 min

4.2. VIDEO RECORDING

Before the beginning of video recording at each zoo, I consulted the situation of animals and their daily regime with the zookeepers and I spent some time (approximately a day) observing the group to be able to recognize individuals and to get an insight into daily activities of the group.

Consequently, on an observation day, if possible we attempted to video record any playful activity that was seen during the whole day. The recording of a play activity started shortly before (e.g. when noticing “play intention movements”) or when the activity started or as soon as possible after its beginning and the recording was ended only after the activity ended (animals switched to another activity, juveniles went to their mother, etc.). When playing individual/s were being recorded, and some other individual began to play, we did not pay attention to the other play activity in order to have entire play sequences videorecorded. The aim of the videorecording was to record play behaviour of selected individuals, and therefore we did not film whole group but only playing individuals. Video recording was conducted during opening hours of the zoos – i.e. usually between 8:00 and 18:00. The recording time was limited by the durability of camera batteries, and we attempted to videorecord as many play activities as possible when animals were active and we recharged batteries mainly when animals were feeding or when they were resting.

Hand-held cameras Sony DCR-TRV 110E, 160E or 730E and Panasonic NV-GS27, with automatic focus were used. The animals were filmed from a distance of approximately 1,5 - 10 m, from visitors' viewing areas.

Videorecordings were recorded by the author, and in Frankfurt and Ústí nad Labem zoos by several colleagues.

4.3. DATA PROCESSING

4.3.1. Ethogram of play behaviour

The ethogram of the four guenon species was constructed on the basis of observation, and on a detailed analysis of videorecordings. The ethogram is based on ethograms of Kozlová (2002) and Štochl (2004) – these ethograms were revised and extended. The ethogram contains elements that were observed in any of the four guenon species and in each element the occurrence in each of the species was marked as well as its possible self-handicapping function.

The complete ethogram is presented in the chapter 5.1. - Table 5.1.

4.3.2 Selection of self-handicapping elements

For the purpose of this study 30 self-handicapping elements were chosen according to a previous study performed by Štochl (2004) – for definitions see the ethogram (chapter 5.1.) It was also marked in each element whether it is performed only in locomotor, social or both types of play (based on personal observations and previous study by Štochl 2007):

- 1. play tweak (rough touch); 2. play bend; 3. play tumble; 4. play gallop; 5. scamper;**
- 6. bipedal stance; 7. bipedal walk; 8. brachiation; 9. moving in quadrupedal suspension; 10. fore- and hindlimb suspension; 11. suspension by forelimbs; 12. suspension by hindlimbs; 13. swinging; 14. unstable sitting; 15. play jump; 16. hop;**
- 17. bridging; 18. overturn; 19. handstand; 20. flip; 21. somersault; 22. somersault in the air; 23. jump off by a somersault; 24. leap up “on a wall”; 25. leap “on twigs”;**

26. leap up “on a ledge”; 27. play jumping on; 28. jump on; 29. object carrying; 30. object transporting

When selecting the behavioural elements, self-handicapping was considered in a broadest possible sense, so that all the range of *possibly* self-handicapping patterns is included. Therefore, the list also includes elements, self-handicapping nature of which may be questionable. The selected elements may disadvantage monkeys in one or more of the following ways (Štochl 2002, 2004, Lhota – personal communication):

1. Restricting or deteriorating sensory perception

A monkey performs a movement or adopts a position, which alters its visual or kinetic perception. These elements usually include neck or back bend, body positioned upside down, quick turns or fast, acrobatic movements.

2. Physically demanding movements and postures

A monkey performs a movement or adopts a position which demands increased physical effort (e.g. bipedal stance, brachiation, somersault), disadvantages an animal in performing normal movement (e.g. play gallop, leap on twigs, object carrying) or forces an animal to quickly change the direction (e.g. bounce, leap up on a wall).

3. Balance disturbance

A monkey deliberately performs certain behaviour which may disturb its balance and increase the probability of an accident (e.g. bipedal walk, unstable sitting, handstand).

4. Restriction towards a partner

A monkey may adopt a disadvantageous position (e.g. play tumble); use more harsh behavioural patterns than in normal play therefore risking vigorous reaction from its play partner (e.g. play tweak, jump at); not use its full power in order to match its younger play partner; perform an acrobatic feature in social play; carry

an object during play chase, etc.

4.3.3. Data recording

In each of the observed young, number of each of the 30 elements was traced and hand-written into a table while watching the video. In this procedure it was possible to stop the video whenever needed and mark the occurrence of a certain element. The total number of performed elements was summarized as well as the number of elements performed at each of following 8 substrates (supports):

1. ground, storey
2. tree trunk, bars of a cage
3. branch, ceiling of a cage, rope tied by both ends
4. terminal branches, twigs, rope tied by one end
5. bare wall
6. wall with extremities
7. object
8. another individual

For each observed individual a length of videorecorded locomotor play and social play was measured using the computer program Observer 3.0. The data were collected with precision to a nearest second. Locomotor, social play and times when an observed animal was not playing or was off view were specified as „states“. Object play was not measured separately but as a part of either locomotor or social play – the same arrangement was used in previous study by Štochl (2007). Overall length of play behaviour was calculated as the length of social play together with the length of locomotor play.

4.3.3. Statistical analyses

To ensure interobserver reliability, together with my colleague Richard Štochl, we performed an interobserver agreement test. We used a 2-hour videorecording of 2 patas monkey (*Erythrocebus patas*) juveniles aged 6 and 18 months in which we recognized and marked numbers of the 30 self-handicapping elements performed over the time of the whole videorecording – each of us separately. Afterwards, our results – i.e. frequencies of the selected elements - were compared by a nonparametric Wilcoxon pair match test.

According to the test results, there was no significant difference among the two observers (the younger juvenile: $Z=1.185$, $p=0.236$; the older juvenile: $Z=0.338$, $p=0.735$). We have therefore considered it safe to pool data from both observers and in order to keep number of variables low, we did not consider the difference between observers in following analyses.

To compare concordance (the degree to which multiple measurements of the same thing are similar – in this case the degree to which the animals favour the same elements) of the frequencies of the selected 30 self-handicapping elements in play of the four guenon species, the Kendall's W or Kendall's coefficient of concordance was used. This is a non-parametric test, which compares any number of measurements. Kendall's W ranges from 0 (zero concordance – i.e. each animal prefers different elements) to 1 (absolute concordance – i.e. animals tend to prefer the same elements) and its results are ranks – i.e. which element is the most frequently used, which is the second, etc. Because we compare preferences of behavioural elements within an individual, it is not necessary to control for the different time of videorecorded play behaviour among individuals.

This test was used to assess:

- 1) whether immatures of each species favour or don't favour the same self-handicapping elements or whether each individual has its own favourite elements
- 2) how high is the concordance in favouring the selected elements among all monkeys, among monkeys belonging to one species, and among monkeys belonging to one species living in one zoo

To assess whether young of each species performed self-handicapping elements more on terrestrial (ground, storey) or on an arboreal (tree trunk, bars of a cage, branches, ropes, terminal branches/twigs, wall, wall with extremities) substrates, percentages of the elements performed at these two types of substrate were counted.

5. RESULTS

5.1. PLAY BEHAVIOUR ETHOGRAM

The final ethogram is presented in the Table 5.1. All patterns are divided into several categories, and social play into subcategories, which are characterized by definitions.

Forms of performed patterns may differ slightly in each species and even among individuals.

Table 5.1:

Ethogram of play behaviour of four guenon species (EP – *Erythrocebus patas*, CP – *Chlorocebus pygerythrus*, CN – *Cercopithecus neglectus*, CD – *Cercopithecus diana*). In each element is also marked its possible self-handicapping function.

Pattern	Definition	Self-handicapping	Occurrence in species			
			EP	CP	CN	CD
GENERAL PLAY ELEMENTS	Elements occurring in any of the categories of play (object, locomotory, social). These elements are specific only for play and are not performed by adults or in other than play contexts.					
play face	monkey's mouth is wide open for several seconds (much longer than during agonistic behaviour), teeth are only slightly exposed, eyes open or closed; no attempts to bite	no	+	+	+	+
play bend	a monkey bends its neck or whole body backwards	yes	+	+	+	+
play tumble	a monkey lays down and welters from side to side (once or repeatedly), exposing its belly	yes	+	+	+	+
eyes closing	an active monkey is closing its eyes (not only blinking), often for several seconds; it does not include eyes closing when mouthing or biting play partner	yes	-	-	+	-
play intention movements	a monkey performs a detectable mark of a play movement but it is not fully performed	no	+	+	+	+
OBJECT PLAY	Object play is a playful activity with an inanimate or animate (in case of own body part) object.					

aimless manipulation	a monkey manipulates an object without any visible intention; it does not pay particular attention to it	no	+	+	+	+
object manipulation	a monkey manipulates an object or attempts to manipulate a fixed object – this includes touching, pulling, lifting with mouth, hand or foot; object manipulation may also include some patterns typical for play fighting	no	+	+	+	+
object transporting	a monkey carries an object, watches it, concentrates on the object	no	+	+	+	+
object carrying	a monkey carries an object, it doesn't watch it; the object rather makes locomotion more difficult	yes	+	+	+	+
own-body-part play	a monkey plays with a part of its own body –tail, foot, hand or fingers	no	+	+	+	+
play sitting on	a playful monkey sits on an object	no	+	+	+	+
play jumping on	a playful monkey jumps on an object and then it either stays there or continues in locomotion	no	+	+	+	+
play rubbing	a monkey rubs an object against a tree trunk or against floor as if it was food; a monkey may watch the object while rubbing it	no	-	-	+	+
EXPLORATION	Exploration is very closely related to play and often results into play. During exploration an animal is trying to gain information about its environment or an object. The behaviour is not so relaxed as during play.					
investigation	a monkey attempts to explore a place or an object by various means – examining, observing, sniffing, touching, gentle biting, licking, etc.	no	+	+	+	+
exploratory play	a monkey concentrates on an object while displaying playful behavioural patterns (i.e. exaggerated and relaxed movements, play face) and also patterns of exploration such as aimed watching, smelling, touching, mouthing, licking (often repeatedly from different sides); it may also include attempts to lift a heavy or firmly attached object, object bending, testing of a substrate by dynamic movements, disengaging of a tied or locked object, destruction	no	+	+	+	+

LOCOMOTOR PLAY	Locomotor play includes various movements and postures. Patterns from this category may occur also during other defined play categories.					
walk	basic mode of quadrupedal locomotion; at least one hand and foot is in contact with substrate in any moment; when on an arboreal substrate, forelimbs do not pull the body up	no	+	+	+	+
bipedal walk/ supported bipedal walk	a monkey rises on its hindlimbs, attempts to maintain balance and make a few steps / may support itself by placing hands on an elevated support	yes	+	+	+	+
run	fast continuous quadrupedal locomotion	no	+	+	+	+
scamper	the fastest mode of continuous quadrupedal locomotion; body may be lifted off / lose contact with the substrate during each motoric cycle	yes	+	+	+	+
play gallop	basic movement is similar to run but on take-off, forelimbs are thrown more to the sides; it is slower compared to run, exaggerated; a monkey may concurrently look backwards	yes	-	+	+	-
play jump	a monkey is jumping (usually) on all four limbs, its body is held rather horizontally; the jumps are only small, mainly stationary, with little or no moving forward – may be performed only once or more times in a sequence	no	+	+	+	+
hop	a monkey hops on its hindlimbs, the body is held rather vertically; the hops are only small, mainly stationary, with little or no moving forward – may be performed only once or more times in a sequence	yes	+	+	+	+
leap	a monkey sets off by its hindlimbs and with forelimbs outstretched forward leaps to another place – may be performed only once or more times in a sequence	no	+	+	+	+
leap up “on a wall“	a monkey leaps up on a vertical substrate where is no obvious hold and then lets itself slide down	yes	+	+	+	+
bounce	a monkey leaps up on a vertical substrate where is no obvious hold	yes	+	+	+	+

	and then bounces away vigorously					
leap “on twigs“	a monkey leaps and lands on tiny twigs or a similar support, by doing so causes the substrate to swing; then it either stays holding to the twigs and keeps swinging or continues in locomotion	yes	+	+	+	+
jump “on twigs“	a monkey repeatedly jumps up from ground on thin branches where it is not able to stay	yes	-	+	-	-
leap up „on a ledge“	a monkey leaps up on a small ledge on a vertical substrate where it is difficult to stay and attempts to hold there for a few seconds	yes	+	+	+	+
bipedal stance/ supported bipedal stance	a monkey rises on its hindlimbs, attempts to maintain balance for a few seconds and then declines back down in the original place / may secure itself by holding lightly to an elevated support (a wall, another animal, a branch, etc.)	yes	+	+	+	+
handstand/ supported handstand	a monkey sets off by its hindlimbs and for a few seconds stands only on its forelimbs, then lands with its hindlimbs back in the original place / may hold to an elevated support by its feet	yes	+	+	+	+
climbing	a quadrupedal arboreal locomotion, when a monkey firmly grasps a vertical support and its forelimbs (in tension) pull the body up with support of hindlimbs	no	+	+	+	+
play climbing	a monkey climbs by very energetic and jerky, exaggerated movements	yes	-	-	+	-
forelimb suspension	a monkey holds to a substrate only by one or both forelimbs, hindlimbs are hanging freely / it may also secure itself by lightly holding to another support by its hindlimbs	yes	+	+	+	+
hindlimbs suspension	a monkey is hanging by its hindlimbs / it may secure itself by lightly holding to another support by its forelimbs	yes	+	+	+	+
fore- and hindlimb suspension	a monkey hangs on an arboreal substrate by three or all four limbs, or by one hand and one foot	yes	+	+	+	+
brachiation/ supported brachiation	a monkey brachiates on an arboreal substrate (proceeds by swinging by its arms on an arboreal substrate); it	yes	+	+	+	+

	may support itself by stepping on a lower support to secure (at least partially) its position					
moving in quadrupedal suspension	or a monkey hangs by all its limbs on an arboreal substrate and moves forward quadrupedally	yes	+	+	+	+
swinging	a monkey wobbles or swings intentionally on a branch or a rope (arboreal substrate)	yes	+	+	+	+
bridging	a monkey stretches out its forelimbs and leans onto another arboreal support; it often has to balance to maintain this position	yes	+	+	+	+
somersault	a monkey performs a somersault forward – i.e. rolls over head or shoulders	yes	+	+	+	+
somersault in the air	a monkey performs a somersault (salto) in the air	yes	+	+	-	-
jump off by a somersault	a monkey jumps off a support placed higher above the ground by a somersault	yes	+	+	+	-
flip	a monkey performs a flip (at least one forelimb is in contact with a substrate and hindlimbs are in the air) – forwards, aside or backwards - and lands on its hindlimbs, hands may touch the ground or the partner	yes	+	+	+	+
circle	a monkey does a clear circle around an arboreal substrate – either vertical substrate and then it moves down in a spiral or horizontal circle and then it ends up in a forelimbs suspension	yes	+	+	+	+
overturn	a monkey is sitting or walking on an arboreal substrate (usually a branch), bends backwards or slides aside, and while holding to a branch by its feet, it flips backwards, head and forelimbs first, and usually ends up in a hindlimbs suspension and continues in locomotion forelimbs first	yes	+	+	+	+
unstable sitting	a monkey deliberately selects and attempts to maintain balance on a substrate which is insecure, labile, floppy or slippery	yes	+	+	+	+
demonstrative skipping	a monkey bobs or hops on a flexible substrate, by doing so produces noise and may also observe a reaction of the substrate	no	+	-	+	-
branch shaking	a monkey grapples a branch and	no	-	-	+	-

	successes it hardly by bouncing its whole body					
SOCIAL PLAY	Social play is a playful interaction between two or more animals. It is a complex behaviour, which is usually classifiable as one-sided play, inviting play, play fight, play chase or teasing. All these complex social play interactions may include any of the components mentioned below the main categories.					
ONE-SIDED PLAY	a playful monkey is using a part of another one's body for play or is using another monkey as a substrate (the other one is not actively involved in play); it resembles locomotory or object play rather than social play					
INVITING PLAY	a monkey is attempting to get involved another one in a play bout by performing various displays in proximity to the other one or by direct physical contact					
PLAY FIGHT	playful monkeys fight together but with no intention to hurt each other seriously; it resembles agonistic combats					
PLAY CHASE	a playful monkey chases another one or is being chased					
TEASING	a monkey provokes another one (usually an adult), who is not playful, in any of the following ways: touching, hopping, jumping at, kicking off, pushing away, staring, chasing; the aim of this behaviour is probably to explore limits of tolerable and intolerable behaviour towards the other one or to provoke the other one to any action					
play touch	a monkey touches or slaps another one with its hand, the touch is quite light, intended probably only to attract the other's attention	no	+	+	+	+
play tweak (rough touch)	a monkey grabs another one's tail, fur or limb and tweaks it	yes	+	+	+	+
jump on	a playful monkey jumps on another one, and either bounces away or stays and plays with the partner	yes	+	+	+	+
play attack	a playful monkey (may perform play intention movements) is waiting until	no	+	+	+	+

	another monkey comes closer or passes by (the other monkey isn't playful); the playful monkey usually waits until the other one loses attention or is in disadvantaged position and then attacks it from a favourable position; the attack is usually unexpected, attacking monkey runs and/or jumps on the other one, bites and/or grabs it firmly; the attack is usually followed by a play fight or a play chase					
playful observation	a playful monkey performs play intention movements while watching its play- or potential play-partner	no	+	+	+	+
play balancing	a playful monkey jumps on another one and tries to hold on top of the other for a few seconds	yes	+	+	+	+
swinging on tail	an animal swings on the tail of another monkey	no	+	+	+	+
play with a part of the partner's body	a monkey is playing with a part of another one's body (e.g. hand or tail), touches it, pulls it, rises it with mouth, hand or foot; the other one is tolerating this but doesn't engage in play	no	+	+	+	+
running towards the partner	a playful monkey is running or play galloping (head rotation may also occur) towards another one from the front and then, in close proximity to the other, suddenly stops and watches the other one's reaction	no	+	+	+	+
mouthng/biting	a monkey gently bites its play partner or an object, it can be only an attempt to bite, not resulting in a physical contact with mouth	no	+	+	+	+
dragging	a monkey grabs its play partner and attempts to drag it to another place (it may or may not be successful)	no	+	+	+	+
play wrestle	a playful equivalent to agonistic wrestling (its aim is not to harm the play partner); monkeys are holding each other firmly (or only one holds the other) and are attempting to mouth each other and at the same time avoid being mouthed, e.g. by pulling the other one's head away; they may be also pushing the other one away by their hindlimbs which helps them to	no	+	+	+	+

	get away from a disadvantageous position; monkeys play wrestle in different positions (standing, lying on a side or back), and these may change continuously; it is usual that monkeys rotate around each other					
rampant pushing	a monkey is standing on its hindlimbs and pushing its play partner with full weight of own body in attempt to fling the partner; usually the partners hold each other by arms or shoulders	no	+	+	+	+
play lunge	monkeys hop against each other and lunge at each other by their forelimbs while touching only slightly	no	+	-	+	-
play fencing	standing or hopping against each other, monkeys are fencing by their forelimbs (they do not hold each other as in play wrestling); fencing pair sometimes rotates	no	+	-	+	-
play seizure	when a play partner turns away or attempts to run away, the other one grabs it by a limb or tail and won't let go before the partner doesn't turn back and react (e.g., by biting, pushing, etc.)	no	+	+	+	+
play pursue	a monkey is chasing its play partner; both of them are play-galloping or running; there may or may not be occasional physical contact	no	+	+	+	+
knock over	chasing monkey knocks down its play partner by grabbing its limb and thus causing it to fall down; it might be only an attempt to do so	no	+	+	+	+
zigzag	chased monkey is unexpectedly changing its direction every so often, doubling ahead of the play partner; often bouncing off surrounding vertical substrate (walls, tree trunks, branches)	yes	+	+	+	+
ATYPICAL DISPLAYS	The term stands for atypical behaviour, which is performed only by one animal and/or only in special and rare situations.					
demonstrative hops	a diana monkey infant in Ostrava Zoo used to lift an object above its head and hop a few times in one place	yes	-	-	-	+
covering up with a sackcloth or a towel	juvenile and subadult Diana monkeys in Ostrava Zoo and juvenile vervets in Zoo Basel used to cover themselves	yes	+	+	-	+

	with a sackcloth hanging on a rope; either they played with it or they were shielding themselves from others while playing together; an infant patas monkey in Wroclaw Zoo used to cover itself in a similar way by a towel					
entangling in a rope	two juvenile de Brazza monkeys in Ústí n. L. Zoo used to repeatedly entangle themselves in a loop on a rope and then attempted to free themselves again; the process of disentangling required an intensive effort and might last up to several minutes	yes	-	-	+	-

5.2. VIDEORECORDED PLAY BEHAVIOUR

Lengths of videorecorded play behaviour of each individual is presented in Table 5.2.

Table 5.2: Lengths of videorecorded play behaviour - overall, locomotor and social play in each observed individual

Observed animal	Species	Zoo	Age (months)	Length of videorecorded play (min)		
				Overall length	Locomotor play	Social play
malá	<i>C. diana</i>	Leipzig	5	601	376	225
Fafaya	<i>C. diana</i>	Leipzig	36	390	165	225
Sulima1	<i>C. diana</i>	Ostrava	10	590	366	224
Sassandra1	<i>C. diana</i>	Ostrava	20	452	228	224
Zimmi	<i>C. diana</i>	Ostrava	6	600	348	252
Sulima2	<i>C. diana</i>	Ostrava	30	511	215	296
Sassandra2	<i>C. diana</i>	Ostrava	40	384	172	212
Prcek	<i>C. neglectus</i>	Plzeň	6	404	260	143
Miky	<i>C. neglectus</i>	Plzeň	19	995	332	663
Tomík	<i>C. neglectus</i>	Plzeň	41	785	226	559
Bart	<i>C. neglectus</i>	Plzeň	12	451	230	221
u1	<i>C. neglectus</i>	Ústí n.L.	35	250	87	163
u2	<i>C. neglectus</i>	Ústí n.L.	36	233	58	175
u3	<i>C. neglectus</i>	Ústí n.L.	36	202	47	155
infant2	<i>Ch. pygerythrus</i>	Basel	1,2	389	125	264
infant1	<i>Ch. pygerythrus</i>	Basel	3	422	104	318
Donga	<i>Ch. pygerythrus</i>	Basel	9	531	152	379
Dhababu	<i>Ch. pygerythrus</i>	Basel	13	480	182	298
Dura	<i>Ch. pygerythrus</i>	Basel	16	513	210	303
Chawa	<i>Ch. pygerythrus</i>	Basel	25	290	87	203
Chura	<i>Ch. pygerythrus</i>	Basel	26	303	104	199
Míša	<i>E. patas</i>	Ohrada	17	300	86	214
Máša	<i>E. patas</i>	Ohrada	17	312	71	241
Max	<i>E. patas</i>	Ohrada	6	364	128	236
Žofie	<i>E. patas</i>	Ohrada	6	343	146	197
fr1	<i>E. patas</i>	Frankfurt	5	357	232	126
fr2	<i>E. patas</i>	Frankfurt	17	223	106	116
Gamba	<i>E. patas</i>	Frankfurt	30	43	31	12

5.3. COMPARISONS OF OCCURENCE OF THE SELECTED SELF-HANDICAPPING ELEMENTS

5.3.1. Kendall's coefficient of concordance (Kendall's W)

All self-handicapping elements in all observed guenons

Kendall's coefficient of concordance for all studied species proved a significant concordance among all individuals in favouring or not favouring selected self-handicapping elements (Kendall's $W = 0.44$; Chi-Square = 360.28; $df = 29$; $p < 0,001$).

All self-handicapping elements in separate species

The intraspecific concordance in preferences (the results are presented in Table 5.3.1) is higher than concordance among all individuals (see above). Within each species the degree of concordance in preferences is significant, which means that the individuals belonging to each species favoured or did not favour the same self-handicapping elements.

Table 5.3.1: Kendall's coefficient of concordance in each of the observed species

Species	n	Kendall's W	Chi-Square	df	p
<i>Cercopithecus diana</i>	7	0.74	149.86	29	< 0,001
<i>Cercopithecus neglectus</i>	7	0.64	130.45	29	< 0,001
<i>Chlorocebus a. pygerythrus</i>	7	0.78	157.89	29	< 0,001
<i>Erythrocebus patas</i>	7	0.64	129.13	29	< 0,001

In the following table (table 5.3.2) the mean ranks of self-handicapping elements (i.e. ranks of popularity of each self-handicapping element averaged from ranks of popularity of each self-handicapping element in each individual) obtained from the Kendall's coefficient of concordance test are shown for each species separately.

Table 5.3.2: Mean ranks (expressed by ordinal numbers – i.e. the lower the number, the more preferred is the element) of all self-handicapping elements in separate species:

Element	Mean rank			
	<i>Cercopithecus diana</i>	<i>Cercopithecus neglectus</i>	<i>Chlorocebus a. pygerythrus</i>	<i>Erythrocebus patas</i>
play tweak (rough touch)	1	2	3	10
play bend	5	13	12	9
play tumble	18	9	8	1
play gallop	28 - 30	12	15	30
scamper	6	15	7	7
bipedal stance	16	11	18 - 19	12
bipedal walk	19	14	24	20
brachiation	13	22	14	23 - 24
moving in quadrupedal suspension	14	20	6	11
fore- and hindlimb suspension	3	8	9	6
suspension by forelimbs	9	10	10	2
suspension by hindlimbs	25	27	18 - 19	22
swinging	8	6 - 7	20	26 - 27
unstable sitting	15	16	22	16
play jump	24	1	13	5
hop	4	3	5	3 - 4
bridging	21	17	11	28
overturn	20	23	4	8
handstand	22 - 23	24	28	26 - 27
flip	17	26	16	15
somersault	27	25	17	19
somersault in the air	28 - 30	29 - 30	30	29
jump off by a somersault	28 - 30	29 - 30	25	17
leap up "on a wall"	10	6 - 7	26	3 - 4
leap "on twigs"	11	18	1	18
leap up "on a ledge"	26	5	27	21
play jumping on	22 - 23	27	29	25
jump on	2	4	2	13
object carrying	7	21	21	23 - 24
object transporting	12	19	23	14

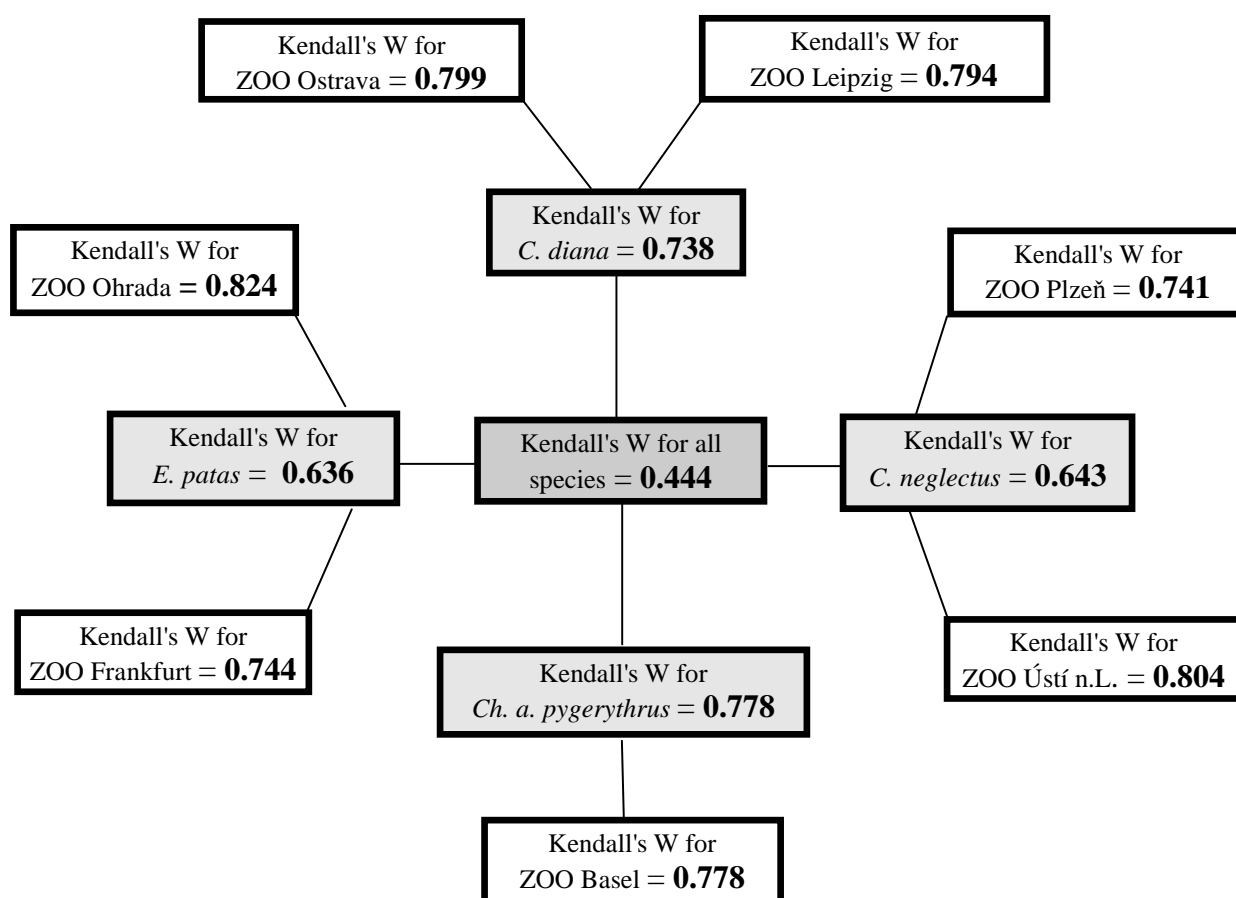
All self-handicapping elements at separate zoos:

When the preferences of individuals within each zoo were tested, it was found that the concordance in favouring or not favouring the selected self-handicapping elements is higher than within species (see Table 5.3.3 and Figure 5.3).

Table 5.3.3: Kendall's coefficient of concordance in each zoo

zoo	n	Kendall's W	Chi-Square	df	p
Leipzig	2	0.79	46.05	29	0.023
Basel	7	0.78	157.89	29	< 0.001
Frankfurt	3	0.74	64.75	29	< 0.001
Ohrada	4	0.82	95.54	29	< 0.001
Ostrava	5	0.80	115.92	29	< 0.001
Plzeň	4	0.74	85.93	29	< 0.001
Ústí n.L.	3	0.80	69.91	29	< 0.001

Figure 5.3: The degree of concordance (according to Kendall's W) in preferences increases in the following order: all individuals – species – zoo



Cercopithecus diana:

The preferences of diana monkeys in favouring selected self-handicapping elements (obtained from the Kendall's coefficient of concordance test) in each zoo are presented in Table 5.3.4.

Table 5.3.4: Mean ranks (expressed by ordinal numbers – i.e. the lower the number, the more preferred is the element) of all self-handicapping elements in diana monkeys – overall ranks and ranks in each zoo

Element	Mean rank		
	Overall	ZOO Leipzig	ZOO Ostrava
play tweak (rough touch)	1	2	1
play bend	5	3	8
play tumble	18	21	17
play gallop	28 - 30	26 - 30	27 - 30
scamper	6	6	7
bipedal stance	16	18 - 20	16
bipedal walk	19	24	18
brachiation	13	12 - 13	12
moving in quadrupedal suspension	14	10	14
fore- and hindlimb suspension	3	1	6
suspension by forelimbs	9	4	13
suspension by hindlimbs	25	25	25
swinging	8	18 - 20	4 - 5
unstable sitting	15	15 - 17	15
play jump	24	26 - 30	22
hop	4	7	3
bridging	21	27 - 30	19
overturn	20	22	20
handstand	22 - 23	15 - 17	24
flip	17	11	21
somersault	27	26 - 30	26
somersault in the air	28 - 30	26 - 30	27 - 30
jump off by a somersault	28 - 30	26 - 30	27 - 30
leap up "on a wall"	10	8	10
leap "on twigs"	11	15 - 17	9
leap up "on a ledge"	26	18 - 20	27 - 30
play jumping on	22 - 23	23	23
jump on	2	5	2
object carrying	7	9	4 - 5
object transporting	12	12 - 13	11

Cercopithecus neglectus:

The preferences of de Brazza monkeys in favouring selected self-handicapping elements (obtained from the Kendall's coefficient of concordance test) in each zoo are presented in Table 5.3.5.

Table 5.3.5: Mean ranks (expressed by ordinal numbers – i.e. the lower the number, the more preferred is the element) of all self-handicapping elements in diana monkeys – overall ranks and ranks in each zoo

Element	Mean rank		
	Overall	ZOO Plzeň	ZOO Ústí n.L.
play tweak (rough touch)	2	2	4
play bend	13	12	12
play tumble	9	3	20
play gallop	12	7	19
scamper	15	11	16
bipedal stance	11	18	6
bipedal walk	14	14	10 - 11
brachiation	22	19-20	23
moving in quadrupedal suspension	20	16	21
fore- and hindlimb suspension	8	9	8
suspension by forelimbs	10	5	17
suspension by hindlimbs	27	27	27
swinging	6 - 7	4	15
unstable sitting	16	19-20	9
play jump	1	1	1
hop	3	6	5
bridging	17	17	13 - 14
overturn	23	21	28
handstand	24	25	22
flip	26	26	24
somersault	25	24	25
somersault in the air	29 - 30	29 - 30	29 - 30
jump off by a somersault	29 - 30	29 - 30	29 - 30
leap up "on a wall"	6 - 7	13	3
leap "on twigs"	18	15	18
leap up "on a ledge"	5	8	7
play jumping on	27	28	26
jump on	4	10	2
object carrying	21	23	13 - 14
object transporting	19	22	10 - 11

Chlorocebus aethiops pygerythrus:

This species was observed only in one zoo so there cannot be any further details in this.

Erythrocebus patas:

The preferences of patas monkeys in favouring selected self-handicapping elements (obtained from the Kendall's coefficient of concordance test) in each zoo are presented in Table 5.3.6.

Table 5.3.6: Mean ranks (expressed by ordinal numbers – i.e. the lower the number, the more preferred is the element) of all self-handicapping elements in diana monkeys – overall ranks and ranks in each zoo

Element	Mean rank		
	Overall	ZOO Ohrada	ZOO Frankfurt
play tweak (rough touch)	10	7	12
play bend	9	14	4
play tumble	1	2	3
play gallop	30	27 - 30	29 - 30
scamper	7	6	5 - 6
bipedal stance	12	9 - 10	13 - 14
bipedal walk	20	17	21 - 22
brachiation	23 - 24	23 - 24	18
moving in quadrupedal suspension	11	12	9
fore- and hindlimb suspension	6	11	2
suspension by forelimbs	2	4	5 - 6
suspension by hindlimbs	22	26	17
swinging	26 - 27	27 - 30	19
unstable sitting	16	27 - 30	7
play jump	5	1	10
hop	3 - 4	3	8
bridging	28	25	26 - 27
overturn	8	5	11
handstand	26 - 27	23 - 24	24
flip	15	13	26 - 27
somersault	19	21	13 - 14
somersault in the air	29	27 - 30	28
jump off by a somersault	17	19	16
leap up "on a wall"	3 - 4	9 - 10	1
leap "on twigs"	18	20	15
leap up "on a ledge"	21	16	25
play jumping on	25	18	29 - 30
jump on	13	8	20
object carrying	23 - 24	22	21 - 22
object transporting	14	15	23

5.3.2. Percentages of self-handicapping elements performed on terrestrial and arboreal substrates

Each observed individual performed different proportion of selected self-handicapping on a different type of substrate as shown in Table 5.3.2.

Table 5.3.2: Percentages of self-handicapping elements performed on terrestrial or arboreal substrates by each observed individual

species	subject	terrestrial	arboreal
<i>Cercopithecus diana</i>	malá	19%	73.5%
	Fafaya	14.6%	80.6%
	Sulima1	32.7%	55.9%
	Sassandra1	25.9%	64.8%
	Zimmi	30.2%	63.9%
	Sulima2	32.4%	57%
	Sassandra2	44.6%	46.4%
<i>Cercopithecus neglectus</i>	Prcek	46.8%	42.5%
	Miky	53.3%	44.4%
	Tomík	67.2%	29.8%
	Bart	40.2%	54.7%
	u1	31.6	59.9
	u2	32%	57.7%
	u3	38.4%	55.4%
<i>Chlorocebus pygerythrus</i>	Chura	24.7%	63.8%
	Chawa	39.8%	58.7%
	Dura	33.2%	55.7%
	Dhababu	32.7%	55%
	Donga	35.1%	49.8%
	infant1	60.1%	31.9%
	infant2	50.1%	37.7%
<i>Erythrocebus patas</i>	Miša	55.2%	44.8%
	Máša	44.4%	49.4%
	Max	57.8%	36.3%
	Žofie	65.9%	27.4%
	fr1	51.6%	43.9%
	fr2	55.9%	44.1%
	Gamba	11.9%	88.1%

The remaining percentages of play were performed either on an object or on another individual, which couldn't be classified neither as a terrestrial nor as an arboreal substrate.

6. DISCUSSION

6.1. PLAY BEHAVIOUR REPERTOIRE

The behavioural repertoire of the four guenon species differs in presence/absence of many behavioural elements or patterns.

Diana (*Cercopithecus diana*) and patas (*Erythrocebus patas*) monkeys don't perform “play gallop”. According to our definition, play gallop is similar to run but on take-off, forelimbs are thrown more to the sides; it is slower compared to run, exaggerated; a monkey may concurrently look backwards. In diana monkey, this absence could be explained by the species' biology – diana monkeys spend most of their time in tree canopies, and at higher and middle forest strata (Byrne *et al.* 1983) and play gallop is a mode of locomotion performed almost exclusively on the ground (personal observation) therefore the evolution of a mode of locomotion which could be performed only rarely would be uneconomical. For patas monkey, the absence of play gallop could be explained by forelimb and pectoral girdle anatomy (Chism & Rowell 1988) which disables it to perform such movement (this may be also the cause of absence of “play gallop” in diana monkeys but there is no empirical evidence of it). Another explanation could be functional as originally proposed by Štochl (2007) – patas monkeys need to train mainly the speed and effective escaping (“physical/motor training” hypothesis - Byers 1994, Fagen 1981, Groos 1898 in Burghardt 1998, Smith 1982) while other two species which perform play gallop (de Brazza and vervet monkeys) and move between ground and arboreal environments might need to train mainly the versatility of movements (“training for the unexpected” - Špinka *et al.* 2001).

From all four species, “eyes closing” is performed only by de Brazza monkeys. This behaviour was also observed in hanuman langurs (*Semnopithecus entellus*) and some other primates (Petrů 2005). As Petrů suggests, it may be a special self-handicapping behaviour increasing the unpredictability of play and it may also be a ritualized play-signal.

“Play rubbing” was observed only in diana and de Brazza monkeys but its frequency was very low. It is possible that vervets and patas monkeys perform it as well but it was not registered in our observations.

Only vervets performed “jump on twigs” (repeatedly jumped on thin branches/twigs from the ground) but this might be simply a side-effect of different enclosures at zoos. In Basel, vervets had several bushes with tiny twigs on their island (outdoor enclosure) in contrast to the monkeys at other zoos.

“Play climbing” (climbing by very energetic and jerky, exaggerated movements) was observed only in de Brazza monkeys. This is a very uneconomical mode of locomotion and may disadvantage an animal by slowing its progression and by increasing the risk of falling down. The occurrence of this element could be explained only by the “training for the unexpected” hypothesis on the function of play (Špinka *et al.* 2001).

Occurrence of “somersault in the air” (which is performed almost exclusively on the ground) only in patas and vervet monkeys might be explained by the “physical/motor training” hypothesis (Byers 1994, Fagen 1981, Groos 1898 in Burghardt 1998, Smith 1982) - because both patas and vervet monkeys live mainly terrestrially, and they might need to train the versatility of movements to be able to outwit rivals or predators. It might be also explained by the “training for the unexpected” hypothesis of the function of play (Špinka *et al.* 2001) – by performing somersaults in the air, animals self-handicap by deteriorating their sensory perception and by deliberate use of increased effort. This element might considerably increase the unpredictability of further events.

Another element, “jump off by a somersault” when a monkey jumps off a support placed higher above the ground by a somersault, occurring in patas, vervet and de Brazza monkeys might serve probably only as a self-handicapping element increasing the unpredictability of further events. This element doesn't serve any other apparent function. Patas, vervet and de Brazza monkeys move between terrestrial and arboreal environment to certain extent but diana monkeys spend almost all time up the trees so this self-handicapping might be too risky for them.

Only in patas and de Brazza monkeys occurring “demonstrative skipping” (a monkey bobs or hops on a flexible substrate, by doing so produces noise and may also observe a reaction of the substrate) and “branch shaking” (a monkey grapples a branch and succuses it hardly by bouncing its whole body) occurring only in de Brazza monkeys may have certain function in adult life and the young might perform it purely as a training. We could not fully assess the adult behavioural repertoire at zoos.

Both, “play lunge” (monkeys hop against each other and lunge at each other by their forelimbs while touching only slightly) and “play fencing” (standing or hopping against each other, monkeys are fencing by their forelimbs) occur only in patas and de Brazza monkeys. These patterns may precede “jump on” and “play wrestle” which are quite common in diana monkeys and vervets. It is possible that diana monkeys and vervets had “play lunge” and “play fencing” in their play behaviour repertoire but that it disappeared for some reason and

only the two more harsh elements, “jump on“ and “play wrestle“, remained.

From observations at zoos, it is impossible to fully assess adult behavioural repertoire because adult animals at zoos don't express their full natural behaviour. If we cannot assess complete adult behaviour, in some elements or patterns occurring in play, we cannot decide its possible function. According to my observations, immatures are very spontaneous and driven by their nature but the adults are influenced by the stereotypic daily routine, no matter how well are their enclosures equipped. They don't forage actively (although different enrichments stimulate them to get their food at least a little bit actively), they don't need to resolve conflicts with other groups, etc. and by these restrictions, the adults inevitably don't perform all behavioural patterns as in nature and some of their instincts are suppressed. Many animals spend their days staring into the far, accustomed to the noisy behaviour of zoo visitors, not paying attention to them.

6.2. COMPARISON OF OCCURENCE OF SELF-HANDICAPPING ELEMENTS

As shown in the Tables 5.3.1 and 5.3.3., there is quite high concordance of preferences of certain self-handicapping elements within each species and even higher concordance within animals in each zoo. This shows that individuals belonging to one species tend to use the self-handicapping elements similarly. Nevertheless, we cannot exclude the possibility that the high concordance originates at zoo level due to distinct environment and group-composition.

If we look at the preferences of each species for the selected self-handicapping elements, “play tweak (rough touch)” (a monkey grabs another one's tail, fur or limb and tweaks it) is among the most favourite elements in diana, and de Brazza monkeys and in vervets. In patas monkeys the most favourite element is “play tumble”(a monkey lays down and welters from side to side, exposing its belly). Both these elements handicap a monkey in relation to its partner – in play tweak, the partner may react more vigorously or even aggressively, and in play tumble, the partner has an immediate advantage over the self-handicapping monkey. Both elements considerably increase the unpredictability of play since they:

- 1) handicap the monkey
- 2) get involved another monkey in play

“Play tumble”, which is always performed on the ground, is not very preferred in diana monkeys. This may be caused by the arboreality of this species due to which the animals don't spend much time on the ground.

“Fore- and hindlimb suspension” and “forelimb suspension” were quite abundant in all observed animals. These elements might be a good training for the unexpected – animals must balance their sensory input and after performing a suspension, animals usually attempt to get to a “normal” controlled position.

“Swinging” (a monkey wobbles or swings intentionally on a branch or a rope) is preferred by diana and de Brazza monkeys but it is not favoured very much by vervet and patas monkeys. This may reflect the prevailing terrestriality of vervet and patas monkeys and arboreality of diana and de Brazza monkeys.

Meanwhile “hop” is favoured by all observed species, “play jump” (a monkey is jumping usually on all four limbs, its body is held rather horizontally; the jumps are only small, mainly stationary, with little or no moving forward) is rather marginalized by diana monkey. As diana monkey is the only strictly arboreal species and “play jumps” are performed almost exclusively on the ground, it may be explained again by the arboreality of the species.

An element occurring in all species among most preferred is “hop” (a monkey hops on its hindlimbs, the body is held rather vertically; the hops are only small, mainly stationary, with little or no moving forward). This behavioural pattern is performed on both, terrestrial and arboreal substrates (supports) and in all types of play (locomotor, social, object). It may be favoured by the young simply because it belongs to natural primate locomotor acts and although it might be physically demanding to certain extent (body must be lifted to more or less vertical position and hindlimbs push the body up into the hop) animals may perform it as a physical training. Nevertheless, fast movement in “hop” may affect sensory input (and thus get the animal into a not fully controlled situation) and, in addition, when performed in front of the play partner, it may disadvantage the animal by slowing its potential reaction towards the partner - these features might support rather the “training for the unexpected” hypothesis (Špinka *et al.* 2001).

Among diana and de Brazza monkeys not preferred “overturn” (a monkey is sitting or walking on an arboreal substrate, e.g. a branch, bends backwards or slides aside, and while holding to a branch by its feet, it flips backwards, head and forelimbs first, and usually ends up in a hindlimbs suspension and continues in locomotion forelimbs first) belongs among

very preferred elements in vervets and patas monkeys. This is quite surprising as “overturn” would be expected to occur more in the more arboreal species.

In all studied species, except from patas monkey, “jump off by a somersault” was the least preferred or absent element. In patas monkey, it was also one of the least performed elements but it was performed more than in other species. It might serve as the versatility of movements training because terrestrially living patas monkeys might need to have a broader repertoire of acrobatic elements since they cannot always escape up the tree when endangered. Therefore they might need to outwit an intruder.

The same need (for a broader repertoire of acrobatic elements performed on the ground) may be the reason for “somersault” being preferred by patas and vervet monkeys more than by diana and de Brazza monkeys.

The abundance/absence of two elements – “leap up “on a wall”” being almost absent in vervets and “leap up “on a ledge”” being quite popular in de Brazza monkeys – may be caused by the equipment of the enclosures. In ZOO Basel, vervets spent their days mostly on a small island where no surfaces such as wall were installed. Unlike other monkeys, patas monkeys in both zoos, Ohrada and Frankfurt, had their enclosures equipped by surfaces which we can call “ledges” and this may be the reason for abundance of “leap up on a ledge” in their play.

“Jump on” (a playful monkey jumps on another one, and either bounces away or stays and plays with the partner) is among the most preferred elements in all groups except from patas monkeys at ZOO Frankfurt. This element may handicap a monkey similarly as “play tweek”. A monkey who performs it puts itself in a precarious situation as it may risk a vigorous reaction from the other one, it may also fall down or may get into a disadvantageous position.

A special type of self-handicapping, “object carrying” is not preferred very much by de Brazza, vervet and patas monkeys but is preferred by diana monkeys. For this phenomenon, we don't have a likely explanation.

Preferences of immatures may be (and very probably are) partially influenced by the age composition of a group, number of group members (especially immatures) and enclosures' equipment.

6.3. PERCENTAGES OF SELF-HANDICAPPING ELEMENTS PERFORMED ON TERRESTRIAL AND ARBOREAL SUBSTRATES

All diana monkey immatures performed more self-handicapping elements on arboreal substrates which corresponds with the lifestyle of adult diana monkeys.

In de Brazza monkeys from Zoo Plzeň, the selected elements were performed quite equally on both types of substrate except from Tomík, who performed more of them on the terrestrial substrate. In Zoo Plzeň, the outdoor enclosures constitutes a small island with trees where the animals spend much time on the ground. All de Brazza monkeys from Zoo Ústí n.L. performed more self-handicapping elements on arboreal substrate. In nature, de Brazza monkeys are terrestrial but forage often on the ground (Oswald & Lockard 1980) so, with regard to the fact, that at Zoo Plzeň, terrestrial substrate was more attractive for the immatures than at Zoo Ústí n.L., these results also correspond roughly with the biology of the species.

Young vervets observed at Zoo Basel spent almost all days outside, on a small island where they performed more of the self-handicapping elements on arboreal substrate except from the two youngest males who performed more of these elements on terrestrial substrate. This is natural because the two were very young (2 and 3 months) and thus more confident on the ground. These two juveniles were very active and during the day they spent only minimum of time with their mothers (personal observation). The older individuals performed more of the self-handicapping elements on arboreal substrate but mainly at lower strata which also corresponds with their biology since they inhabit savannah and riverine woodlands (Chism and Rowell 1988).

Patas monkey immatures performed more of the self-handicapping elements on terrestrial substrates except from Máša (but in this case the difference was only small) and Gamba. The length of videorecorded play behaviour of the latter was only 43 min so we cannot judge from this. Although observed patas monkeys performed more of the self-handicapping elements on the ground or storey, they also performed considerable proportion of these elements on arboreal substrates. This may be in accordance with their biology (they inhabit grass and woodland savannahs - Chism & Rowell 1988; Nakagawa 2000) but it may be also a side effect of enclosure equipment. In zoos where these animals were observed the areas of enclosures could not provide enough space and opportunities for self-realization of the immatures on the ground and a variety of arboreal supports could be quite stimulating for performing more elements on them.

6.4. FURTHER ANALYSES

This study will have a continuation where frequencies of self-handicapping will be assessed and compared and the “training for the unexpected” hypothesis (Špinka *et al.* 2001) will be tested further.

7.CONCLUSIONS

According to this study, the young of the four studied species differ in modes of self-handicapping which appears to correspond with their biology. By preferring and performing self-handicapping elements that are the most relevant for preparation for the unexpected situations in their lives, they may be well prepared and trained for situations which they cannot fully control and this may have immediate as well as long-term benefits.

Each pattern appearing in the ethogram may serve a different function (motor training, self-assessment, training for the unexpected situations, training of social skills, establishing social relationships, etc.) but as shown in this study all the observed animals belonging to one species self-handicap in a distinct way and on the basis of these findings we cannot deny that one of the functions of play may be training for the unexpected.

8. REFERENCES

- Aldis, O. (1975): Play fighting. *Academic press, New York*.
- Altmann, S.A. (1962): A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Science*, 102, 338-435
- Baldwin, J.D., Baldwin, J.I. (1974): Exploration and social play in squirrel monkeys (*Saimiri*). *American Zoologist* 14: 303-315
- Baldwin, J.D., Baldwin, J.I. (1973): The role of play in social organization: comparative observations on squirrel monkeys (*Saimiri*). *Primates* 14: 369-381
- Barber, N. (1991): Play and Energy Regulation in Mammals, *The Quarterly Review of Biology* 66 (2): 129-147
- Bauer, E.B., Smuts, B.B. (2007): Cooperation and competition during dyadic play in domestic dogs, *Canis familiaris*. *Animal Behaviour* 73: 489 – 499
- Bekoff, M. (2001): Social Play Behaviour, *Journal of Consciousness Studies* 8 (2): 81-90
- Bekoff, M. (1984): Social Play Behavior. *BioScience* 34(4): 228-233
- Bekoff, M. (1977): Social communication in canids: Evidence for the evolution of a stereotyped mammalian display. *Science* 197: 1097-1099
- Bekoff, M. (1976): Animal play: problems and perspectives. *In: Perspectives in Ethology*, edited by Bateson, P.P.G. and Klopfer, P.H., Plenum Publishing, New York. 165 – 188
- Bekoff, M. (1974): Social play and play-soliciting by infants canids. *American Zoologist* 14: 323-340
- Bekoff, M., Allen, C. (1998): Intentional communication and social play: how and why animals negotiate and agree to play, *In: Animal Play (ed. by Bekoff, M. & Byers, J.A.)*, Cambridge University Press, Cambridge, 97-113
- Bekoff, M. & Byers, J.A. [editors] (1998): Animal Play: Evolutionary, Comparative, and Ecological Perspectives. *Cambridge University Press, Cambridge*.
- Bekoff, M. & Byers, J.A. (1981): A critical reanalysis of the ontogeny of mammalian social and locomotor play: an ethological hornet's nest. *In: Behavioral Development: The Bielefeld Interdisciplinary Project*, edited by Immelmann, I. Et al., Cambridge University Press, Cambridge. 196 - 337
- Biben, M. (1998): Squirrel monkey playfighting: making the case for a cognitive training function for play. *In: Animal Play (ed. by Bekoff, M. & Byers, J.A.)*, Cambridge University Press, Cambridge, 161-179
- Booth, A. (1958): The zoogeography of West African primates: A review. *Bulletin de l'I.F.A.N.*

20 (sér. A): 587–622

Brennan, E.J. (1985): De Brazza's Monkeys (*Cercopithecus neglectus*) in Kenya: Census, Distribution and Conservation, *American Journal of Primatology* 8: 269-277

Breuggeman, J.A. (1978): The function of adult play in free-ranging *Macaca mulatta*. In: *Social Play in Primates*, edited by Smith, E.O., Academic Press, New York. 169-191

Burghardt, G.M. (2005): The Genesis of Animal Play: Testing the Limits. MIT Press, Cambridge, MA.

Burghardt, G.M. (1999): Conceptions of play and the evolution of animal minds. *Evolution and Cognition* 5: 115 – 123

Burghardt, G.M. (1998): Play. In: *Comparative Psychology: A Handbook*, edited by Greenberg, G. and Haraway, M.M., Garland Publishing, New York. 725 - 735

Butynski, T.M. (2002): The Guenons: An overview of Diversity and Taxonomy. *The Guenons: Diversity and Adaptation in African Monkeys*, edited by Glenn and Cords, Plenum Publishers, New York.

Byers, J.A. (1998): Biological effects of locomotor play: getting into shape, or something more specific? In: *Animal Play* (ed. by Bekoff, M. & Byers, J.A.), Cambridge University Press, Cambridge, 205-219

Byers, J.A. (1984): Play in Ungulates. *Play in Animals and Humans*, edited Smith, P.K., Basil Blackwell, Oxford. 43-65

Byers, J.A., Walker, C. (1995): Refining the Motor Training Hypothesis for the Evolution of Play, *The American Naturalist* 146 (1): 25-40

Byrne, R.W., Conning, A.M., Young, J. (1983): Social Relationships in a Captive Group of Diana Monkeys (*Cercopithecus diana*), *Primates* 24 (3): 360-370

Chalmers, N.R. (1980): The ontogeny of play in feral olive baboons (*Papio anubis*). *Animal Behaviour* 28: 570-585

Chism J. & Rowell T.E. (1988): The Natural History of Patas Monkey. In: *A Primate Radiation: Evolutionary Biology of the African Guenons* (edited by Gautier-Hion, A., Bourliere, F., Gautier J.P., Kingdon, J.), Cambridge University Press, Cambridge, 412-438.

Decker, J.S. (1995): Survey of deBrazza's Monkey (*Cercopithecus neglectus schlegeli*) in the Tororo District of Eastern Uganda and Trans-Nzoia and West Pokot Districts of Western Kenya, *Journal of East African Natural History* 84: 25-34

Dolhinow, P. (1999): Play: a critical process in the developmental system. In: *The Non-Human Primates* (edited by Dolhinow, P. & Fuentes, A.), Mayfield Publishing Co., Mountain View, CA. 231-236.

- Dugatkin, L. A. and M. Bekoff (2003): Play and the Evolution of Fairness: A Game Theory Model. *Behavioural Processes* 60: 209–14.
- Fagen, R. (1981): *Animal Play Behavior*. Oxford University Press, New York.
- Gautier-Hion, A. & Gautier, J.P. (1978): Le singe de Brazza: une strategie originale. *Z.Tierpsych.* 46: 86-104
- Groves, C.P. (2001): *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.
- Gomendio, M. (1988): The development of different types of play in gazelles: implications for the nature and functions of play, *Animal Behaviour* 36: 825-836
- Groos, K. (1898): *The play of Animals*(translated by E.L.Baldwin). D.Appleton & Co., London
- Hinde, R. (1970): *Animal Behavior: A Synthesis of Ethology and Comparative Psychology*. 2nd edition, New York, McGraw-Hill.
- Holmes, W.G. (1994): The development of littermate preferences in juvenile Belding's ground squirrels. *Animal Behaviour* 48: 1071-1084
- Kozlová, A. (2002): Ethogram of play behaviour of de Brazza monkey (*Cercopithecus neglectus*). BSc. thesis. University of South Bohemia, České Budějovice
- Lee, P. (1981): Ecological and social influences on development of vervet monkeys. *PhD thesis, Cambridge University, Cambridge*
- Levy, J.S. (1979): Play behaviour and its decline during development in rhesus monkeys (*Macaca mulatta*). *PhD thesis, Chicago University*
- Lozois, C. (1967): Play Behaviour in Higher Primates: a Review. In: *Primate Ethology* (ed. By Morris, D.), Anchor books, Chicago, 226-282.
- Maestriperi, D., Ross. S.R. (2004): Sex Differences in Play Among Western Lowland Gorilla (*Gorilla gorilla gorilla*) Infants: Implications for Adult Behavior and Social Structure. *American Journal of Physical Anthropology* 123: 52–61
- Martin, P. (1984): The time and energy costs of play behaviour in the cat. *Z. Tierpsychologia* 64: 298-312
- Martin, P., Caro, T.M. (1985): On the Functions of Play and Its Role in Behavioral Development, *Advances in the Study of Behavior* 15: 59-103
- McGraw, W.S. (1998): Comparative Locomotion and Habitat Use of Six Monkeys in the Tai Forest, Ivory Coast, *American Journal of Physical Anthropology* 105: 493-510
- Mendoza-Granados, D. (1995): Play in Chimpanzees of the Arnhem Zoo: Self-serving Compromises, *Primates* 36 (1): 57-68

- Nagakawa, N. (2000): Foraging Energetics in Patas Monkeys (*Erythrocebus patas*) and Tantalus Monkeys (*Cercopithecus aethiops tantalus*): Implications for Reproductive Seasonality. *American Journal of Primatology* 52: 169-185
- Napier, J.R. & Napier, P.H. (1967): A Handbook of Living Primates. *Academic Press, London.*
- Nowak, R.M. (1991): Walker's Mammals of the World, 5th Edition, Vol.I, The Johns Hopkins University Press, Baltimore and London
- Nunes, S. *et al.* (2004): Functions and consequences of play behaviour in juvenile Belding's ground squirrels, *Animal Behaviour* 68: 27-37
- Oshawa, H. (2003): Long term study of the social Dynamics of Patas Monkeys (*Erythrocebus patas*): Group Male Supplanting and Changes to the Multi-male Situation. *Primates* 44: 99-107
- Oswald, M., Lockard, J.S. (1980): Ethogram of the deBrazza's Guenon (*Cercopithecus neglectus*) in captivity, *Applied Animal Ethology* 6(1980): 285-296
- Palagi E. (2006): Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implications for natural social systems and inter-individual relationships. *American Journal of Physical Anthropology* 129: 418-426
- Palagi, E., Cordoni, G., Borgognini Tarli, S.M. (2004): Immediate and Delayed Benefits of Play Behaviour: New Evidence from Chimpanzees (*Pan troglodytes*). *Ethology* 110: 940-962
- Palagi, E., Paoli, T., & Borgognini Tarli, S. (2006). Short-term benefits of play behavior: conflict prevention in captive bonobos (*Pan paniscus*). *International Journal of Primatology*, 27: 1257-1270
- Paquette, D. (1994): Fighting and Playfighting in Captive Adolescent Chimpanzees. *Aggressive Behaviour* 20: 49-65
- Pellis, S.M., Pellis, V.C. (1996): On Knowing It's Only Play: the Role of Play Signals in Play Fighting. *Aggression and Violent Behaviour* 1(3): 249-268
- Pellis, S.M. & Iwaniuk, A.N. (2000). Comparative analysis of the roles of postnatal development in the expression of play fighting in juveniles and adults. *Developmental Psychobiology* 36: 136-147
- Pellis, S.M., Iwaniuk, A.N. (1999): The Problem of Adult Play Fighting: A Comparative Analysis of Play and Courtship in Primates, *Ethology* 105: 783-806
- Pereira, M.E., Preisser, M.C. (1998): Do Strong Primate Players 'Self-Handicap' during Competitive Social Play? *Folia Primatologica* 69: 177-180
- Petrů, M. (2005): Self-handicapping in play behaviour of Hanuman langur (*Semnopithecus entellus*). *Diploma thesis [in Czech]. Charles University, Prague.*

- Poirier, F.E., Bellisari, A. & Haines, L. (1978): Functions of Primate Play Behavior. In: *Social Play in Primates* edited by Smith, E.O., Academic Press, New York, 143-168.
- Power, T.G. (2000): Play and exploration in children and animals. *Mahwah, New Jersey: Lawrence Erlbaum and Associates*
- Refisch, J., Koné, I. (2005): Impact of Commercial Hunting on Monkey Populations in the Taï region, Côte d'Ivoire, *Biotropica* 37 (1): 136-144
- Rowe, N. (1996): The Pictorial Guide to the Living Primates. *Pogonias Press*
- Sharpe, L.L. (2005a): Frequency of social play does not affect dispersal partnerships in wild meerkats. *Animal Behaviour* 70: 559-569
- Sharpe, L.L. (2005b): Play does not enhance social cohesion in a cooperative mammal. *Animal Behaviour* 70: 551-558
- Shimada, M. (2006): Social object play among young Japanese macaques (*Macaca fuscata*) in Arashiyama, Japan. *Primates* 47: 342-349
- Smith, P.K. (1982): Does play matter? Functional and evolutionary aspects of animal and human play. *Behavioral and Brain Sciences* 5: 139-184
- Špinka, M., Newberry, R.C., Bekoff, M. (2001): Mammalian Play: Training for the unexpected. *The Quarterly Review of Biology, University of Chicago* 76 (2): 141 - 168
- Symons, D. (1974): Aggressive play and communication in rhesus monkeys (*Macaca mulatta*). *American Zoology* 14: 317-322
- Symons, D. (1978): Play and aggression: A study of rhesus monkeys. *Columbia University Press, New York*.
- Thompson, K.V. (1998): Self assessment in juvenile play. In: *Animal Play* (ed. by Bekoff, M. & Byers, J.A.), *Cambridge University Press, Cambridge*. 183-201
- Thompson, K.V. (1996): Play partner preferences and the function of social play in infant sable antelope, *Hippotragus niger*. *Animal Behaviour* 52: 1143-1155
- Vick, L.G., Conley, J.M. (1976): An Ethogram for *Lemur fulvus*. *Primates* 17(2): 125-144
- Wahome, J.M., Rowell, T.E., Tsingalia, H.M. (1993): The Natural History of de Brazza's Monkey in Kenya. *International Journal of Primatology* 14(3): 445-466
- Watson, D.M., Croft, D.B. (1996): Age related differences in playfighting strategies of captive male red necked wallabies (*Macropus rufogriseus banksianus*). *Ethology* 102: 336-346

9. APPENDICES

Appendix I – details of zoos and group compositions

ZOO OSTRAVA - *Cercopithecus diana*

Michálkovická 197, 710 00 Ostrava, Czech Republic

Periods: March 8 – 20, 2003
November 11 – 22, 2004

Indoor enclosure:

- 2-storeys, tiled, equipped with tree trunks with branches, ropes, ledges, sackcloths suspended on ropes, fresh branches with twigs given several times a week, wooden straw on the floor
- front part (facing to the visitor's area) and ceiling – metal bars (cage)

Outdoor enclosure:

- equipped similarly as the indoor enclosure
- walls, ceiling and front parts – cage

Both in- and outdoor enclosure were fully accessible for animals all day long except from approx. 20-30 min when one of the enclosures was being cleaned.

Feeding: 3 times a day

Animals:

animal	sex	age – March 2003	age – November 2004
Dan	♂	19 years	20 years 6 months
Adéla	♀	13 years 2 months	14 years 9 months
Krista	♀	13 years	14 years 7 months
Sassandra	♀	1 year 8 months	3 years 4 months
Sulima	♀	10 months	2 years 6 months
Zimmi	♂	---	6 months

* animals written in bold are the observed youngs

Length of videorecording of play behaviour: March 2003 – 700 min
November 2004 – 680 min

ZOO LEIPZIG - *Cercopithecus diana*

Pfaffendorfer Str. 29, 04105 Leipzig, Germany

Period: October 14- 23, 2005

Indoor enclosure:

- 2-storeys, tiled, equipped with tree trunks with branches, ropes, ledges, fresh branches with twigs and wire-balls with straw given several times a week, wooden straw on the floor
- front part (facing to the visitor's area) – lower part – glass; upper part - metal bars (cage)

Outdoor enclosure:

- equipped similarly as the indoor enclosure
- walls, ceiling and front parts – cage

Both in- and outdoor enclosure were fully accessible for animals all day long except from approx. 20-30 min when one of the enclosures was being cleaned.

Feeding: 3 times a day

Animals:

animal	sex	age
Rhabo	♂	17 years
Oka	♀	23 years
Fafaya	♀	3 years
malá	♀	5 months

* animals written in bold are the observed youngs

Lenght of videorecording of play behaviour: 710 min

ZOO ÚSTÍ NAD LABEM – Cercopithecus neglectus

Drážďanská 23

400 07 Ústí nad Labem

Czech Republic

Period: October, November 2002 (continuously)

Indoor enclosure:

- tiled, equipped with tree trunks with branches, ropes, ledges, sackcloths suspended on ropes, fresh branches with twigs given several times a week, wooden straw on the floor
- front part (facing to the visitor's area) – glass

Outdoor enclosure:

- equipped similarly as the indoor enclosure
- front part - glass and metal bars

Both in- and outdoor enclosure were fully accessible for animals all day long except from approx. 20-30 min when one of the enclosures was being cleaned.

Feeding: 3 times a day

Animals:

animal	sex	age
male1	♂	8 years
female 1	♀	unknown (adult)
female 2	♀	10 years
u1	♂	3 years
u2	♀	3 years
u3	♀	3 years

* animals written in bold are the observed youngs

Lenght of videorecording of play behaviour: 320 min

ZOO PLZEŇ– *Cercopithecus neglectus*

Pod vinicemi 9, 301 16 Plzeň, Czech Republic

Periods: March, April 2002 (continuously); September 1 – 15, 2005

Indoor enclosure:

- wooden, equipped with tree trunks with branches, ropes, ledges, fresh branches with twigs given several times a week
- front part (facing to visitor's area) – glass

Outdoor enclosure:

- small island with trees
- separated from other grounds by a brook

Both in- and outdoor enclosure were fully accessible for animals all day long except from approx. 20-30 min when the indoor enclosure was being cleaned.

Feeding: 3 times a day

Animals:

March, April 2002

animal	sex	age
Ťulda	♂	22 years 4 months
Beruška	♀	5 years
Tomík	♂	3 years 5 months
Miky	♂	1 year 6 months
Prcek	♂	6 months

September 1-15, 2005

animal	sex	age
Ťulda	♂	25 years 9 months
Beruška	♀	8 years 1 month
Líza	♀	3 years 10 months
Bart	♂	12 months

* animals written in bold are the observed youngs

Length of videorecording of play behaviour: **March, April 2002 – 1200 min**
September 2005 – 510 min

ZOO BASEL – *Chlorocebus pygerythrus*

Binningerstrasse 40, Postfach, CH-4011 Basel, Switzerland

Period: September 16 – 28, 2007

Indoor enclosure:

- wooden, equipped with tree trunks with branches, ropes, ledges
- not accessible for visitors

Outdoor enclosure:

- small island with trees and bushes, tree trunks on the ground, ropes and sackcloths suspended on ropes
- separated from other grounds by a brook

Both in- and outdoor enclosure were fully accessible for animals all day long except from approx. 20-30 min when the indoor enclosure was being cleaned.

Feeding: 3 times a day

Animals:

animal	sex	age
Zawadi	♂	5 years
Fibi	♀	10 years
Kisiwa	♀	8 years
Nafasi	♀	6 years
Tumbili	♂	3 years
Chura	♂	2 years 2 months
Chawa	♀	2 years 1 month
Dura	♂	1 year 4 months
Dhababu	♂	1 year 2 months
Donga	♂	9 months
infant 1	♂	3 months
infant 2	♂	2 months

* animals written in bold are the observed youngs

Length of videorecording of play behaviour: 670 min

ZOO OHRADA - *Erythrocebus patas*

373 41 Hluboká nad Vltavou, Czech Republic

Period: August 2007, continuously

Indoor enclosure:

- tiled, equipped with tree trunks with branches, ropes, ledges
- front part (facing to visitor's area) – glass

Outdoor enclosure:

- outdoor run surrounded by a wall with big windows
- equipped with tree trunks with branches, ledges, fresh branches with twigs given several times a week

Both in- and outdoor enclosure were fully accessible for animals all day long except from approx. 20-30 min when the indoor enclosure was being cleaned.

Feeding: 3 times a day

Animals:

animal	sex	age
male	♂	15 years 7 months
Ekita	♀	8 years 4 months
Gamba	♀	7 years 2 months
Bára	♀	3 years 5 months
male1	♂	2 years 5 months
male2	♂	2 years 4 months
Míša	♂	1 year 5 months
Máša	♀	1 year 5 months
Max	♂	6 months
Žofie	♀	6 months

* animals written in bold are the observed youngs

Lenght of videorecording of play behaviour: 450 min

ZOO FRANKFURT - *Erythrocebus patas*

Alfred Brehm Platz 16, 603 16 Frankfurt am Main, Germany

Period: September 13- 25, 2002

Indoor enclosure:

- 2 interconnected enclosures
- 2-storeys, tiled, equipped with tree trunks with branches, ropes, ledges
- the ceiling and the front part (facing to the visitor's area) - metal bars (cage)

Outdoor enclosure:

- 3 interconnected enclosures
- equipped similarly as the indoor enclosures
- walls, ceiling and front parts – cage

Both in- and outdoor enclosure were fully accessible for animals all day long except from approx. 20-30 min when one of the enclosures was being cleaned.

Feeding: 3 times a day

Animals:

animal	sex	age
Nisnas	♂	13 years
Karla	♀	21 years
Ekita	♀	4 years 3 months
Gamba	♀	2 years 6 months
fr2	♂	1 year 5 months
fr1	♂	5 months

* animals written in bold are the observed youngs

Lenght of videorecording of play behaviour: 700 min

Appendix II – photographs of studied species

diana monkey (*Cercopithecus diana*)



de Brazza monkey (*Cercopithecus neglectus*)



vervet (*Chlorocebus pygerythrus*)



patas monkey (*Erythrocebus patas*)

