

Revisiting Play Elements and Self-Handicapping in Play: A Comparative Ethogram of Five Old World Monkey Species

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Play behavior has been viewed as a mixture of elements drawn from “serious” behavior, interspersed by ritualized play signals. Two other types of play behaviors have been overlooked: patterns that are dissimilar from any serious behavior and patterns with self-handicapping character, that is, those that put the animal into unnecessary disadvantageous positions or situations. Here the authors show that these 2 types of patterns can constitute a major part of play repertoire. From our own videorecordings and observations, we constructed play ethograms of 5 monkey species (*Semnopithecus entellus*, *Erythrocebus patas*, *Chlorocebus pygerythrus*, *Cercopithecus neglectus*, and *Cercopithecus diana*). The authors evaluated the self-handicapping character of each pattern and in Hanuman langurs also the (dis)similarity to serious behavior. Of the 74 patterns in the 5 species, 33 (45%) were judged to have a self-handicapping character. Of 48 patterns observed in langurs, 16 (33%) were totally dissimilar to any serious langur behavior known to us. The authors discuss the possibility that the different types of play elements may have different functions in play.

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One striking feature of animal play behavior is that it contains elements closely resembling behavioral patterns used in nonplay behavior during prey capture, food acquisition, predator avoidance, aggression, escape, and/or sexual behavior. This has led to a proposition that play may serve to train for specific skills needed

in particular serious situations later in life (Curtin, 1984; Fagen, 1981; Groos 1898; Loizos, 1967). However, not all play patterns resemble behaviors performed in serious situations. Some authors even noted that a large part of play repertoire in fact does not resemble any behaviors seen in another context (e.g., in harbor seals, Renouf, 1993). Elements that are peculiar to play (sometimes labeled as *play markers*) include, for instance, head and torso rotations (Bekoff, 1974; Byers, 1984; Donaldson, Newberry, Špinka, & Cloutier, 2002; Petrů, Špinka, Lhota, & Šípek, 2008; Sade, 1973; Wilson & Kleiman, 1974), specific body postures (Bekoff, 1995) or particular facial expressions (Pellis & Pellis, 1996, 1997; Poole, 1978). Some of them (such as the play bow in canids, Bekoff, 1995) may serve as play signals, that is, to contribute to the ultimate function of play indirectly through initiating or maintaining play interactions, but the function of others is still obscure. The distinction between elements “borrowed” from other behavioral contexts and elements that are peculiar to play is important for the understanding of the structure and function of play behavior. Yet, play elements are not usually categorized according to this criterion and therefore an assessment of the proportion of serious-like and play-specific elements has been missing in play ethograms until now.

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Some of the elements occurring during play behavior have the specific character of being self-handicapping, that is, they put the animal into unnecessarily disadvantageous positions or situations (Bauer & Smuts, 2007). Common occurrence of self-handicapping play patterns (whether they were given this label or not) has been noted in primates (Curtin, 1984; de Oliveira, Ruiz-Miranda,

Kleiman & Beck, 2003; Enomoto, 1990; Fontaine, 1994; Nishida & Wallauer, 2003) as well as for ungulates, rodents, pinnipeds, and carnivores (Bekoff, 1974; Byers, 1977; Byers, 1984; Donaldson et al., 2002; Fagen & Fagen, 2004; Gomendio, 1988; Pellis & Pellis, 1983; Wilson & Kleiman, 1974). For instance, rotational movements of head and torso that put an animal in a disadvantageously asymmetric, misbalanced, and disoriented position toward their environment have been reported in a vast number of species. Biben (1989), Watson and Croft (1996), and others suggested that playing animals self-handicap to prolong the play situation. According to this explanation, self-handicapping makes the play less harsh, aggressive, or threatening for the play partner, notably for a weaker, younger, or less motivated partner. The prominent presence of the self-handicapping elements and the fact that self-handicapping occurs also in the weaker play partners in social play and in animals engaged in solitary, nonsocial play, led Špinko, Newberry, and Bekoff's (2001) proposal that a major function of play behavior was to train for unexpected situations. The function of self-handicapping in play may be to expose the animal to unexpected situations and thus to train for general ability to regain control after the loss of control due to unexpected external events. The distinction between self-handicapping and nonself-handicapping play elements has not been treated explicitly in any published play ethogram. One reason why authors may have been reluctant to categorize play elements into self-handicapping and nonself-handicapping might be that the term *self-handicapping* may denote different things to different scientists. To define clearly what is meant by self-handicapping in each specific case is crucial for the term to be useful in play behavior research.

Thus, distinguishing between play elements that closely resemble serious behavioral patterns and those that do not, and also to differentiate between self-handicapping and nonself-handicapping patterns may prove important for our understanding of the nature and function(s) of play. Yet, play ethograms rarely have looked at these distinctions. The first aim of this study was to provide comprehensive play ethograms of five primate species. The second aim was to classify the play elements in these ethograms according to the degree and nature of their self-handicapping character and according to their resemblance to serious behavior patterns. In this way, we intend to spearhead further systematic studies into the extent and nature of self-handicapping in play behavior and on the resemblance between play and serious behavioral patterns.

Method

Videorecording

Play behavior of free-ranging Hanuman langurs (*Semnopithecus entellus*) habituated to human presence was observed and video-recorded during 12 months in Bhangarh (N 26°50', E 77°17') in Rajasthan, Northwestern India. The play behavior was video-recorded in three one-male multifemale groups. For the purpose of the ethogram the animals were not individually identified and the sex and age of the playing individuals was not systematically recorded.

Play behavior of patas (*Erythrocebus patas*), vervet (*Chlorocebus pygerythrus*), de Brazza (*Cercopithecus neglectus*), and Diana (*Cercopithecus diana*) monkeys was observed and video-recorded in family groups living in seven zoos in Czech Republic (Ústí nad

Labem Zoo, Plzeň Zoo, Ostrava Zoo, Ohrada Zoo), Germany (Frankfurt am Main Zoo, Leipzig Zoo) and Switzerland (Basel Zoo). All these family groups were housed similarly—their indoor enclosures were equipped with tree trunks, branches, ropes, ledges, and they had access to outdoor cages with tree trunks, branches, and ropes. In Plzeň and Basel Zoo, the monkeys had instead of an outdoor cage free access to a small island with trees and at Ohrada Zoo, they had a small outdoor corral fenced with walls. All animals were individually recognized. Composition of groups and details of videorecordings are described in Table 1.

Videorecording of play behavior both in the wild and at captive settings was administered similarly. During an observation day, we focused on a single group and recorded any playful activity that was seen during the whole day. Videorecording in the wild was conducted from dawn (0600) to dusk (2000), in zoos during open hours—that is, usually between 0800 and 1800.

We used a hand-held Panasonic VHS-C camera for videotaping Hanuman langurs. They were filmed from a distance of approximately 1 to 20 m. For recording the other species we used hand-held cameras Sony DCR-TRV 110E, 160E or 730E and Panasonic NV-GS27. These were recorded from a distance of approximately 1 to 10 m from visitors' viewing areas.

Compilation of the Ethogram Table

The ethogram of all five species of monkeys was constructed on the basis of our direct experience in the field and captive settings and on repeated watching and detailed analysis of obtained videorecords of play behavior. Content of the ethogram was discussed thoroughly between all authors of this paper and with two additional students involved in research on play behavior of the same monkey subjects. Previous versions of the ethogram were adjusted until all authors reached full agreement in its composition and in definitions of all behavioral patterns. The ethogram contains patterns that were observed in any of the five monkey species. For the purpose of our study, a *pattern* was defined as a recognizable behavioral unit consisting of either a single coordinated movement or modification of body posture or of a brief sequence of such movements; a pattern was distinct from other patterns in terms of its kinematic or sequential quality or its social or physical context.

Playful patterns were distinguished from nonplayful ones by the presence of at least one of the following characteristics: (a) the movement or the body posture was awkward, exaggerated, or incomplete; (b) the speed, aiming, or accuracy of the movements were relaxed; (c) the animals used specific expressions during play (play face, play bend, play tumble, head rotations, or eyes closing); (d) the pattern consisted of a variable sequence of subpatterns, several of which had one of the characteristics of (a) through (c); and (e) the pattern had none of the criteria of (a) through (c) but was occurring regularly within sequences of playful patterns as described by (a) through (d). To a large extent, these criteria reflect the definition of play developed by Burghardt (2005, pp. 68–82). Our delimitation of play patterns had of course its weaknesses (such as the quasi-circularity of criterion (c)), but this has been a problem with all definitions of play provided so far.

Ethograms were presented differently by various authors in earlier literature. For our purpose, we followed the procedure applied for example by Dolhinow (1978); Kaufman and Rosenblum (1966); Nishida, Kano, Goodall, McGrew, and Nakamura

Table 1
Information About the Studied Groups and Videorecording

Species	Site	Period	Group composition	Videorecorded subjects	Videorecording time
<i>Semnopithecus entellus</i>	Bhangath	May to August 2002 April to June 2004 March to July 2006 September 2002	Three groups: 1 adult male, approx. 20 to 50 adult females, and approx. 15 immature individuals	Approx. 45 infants, juveniles, and subadults	>5,000 min
<i>Erythrocebus patas</i>	Frankfurt am Main Zoo	August 2007	One adult male, 2 adult females, 1 subadult female, 1 juvenile male, 1 infant male	One subadult female, 1 juvenile male, 1 infant male	700 min
	Ohrada Zoo	August 2007	One adult male, 3 adult females, 2 subadult males, 2 juvenile female, 2 juvenile males	Two juvenile females, 2 juvenile males	450 min
<i>Chlorocebus pygerythrus</i>	Basel Zoo	September 2007	One male adult, 3 adult females, 1 subadult male, 1 juvenile female, 4 juvenile males, 2 infant males	One juvenile female, 4 juvenile males, 2 infant males	612 min
<i>Cercopithecus neglectus</i>	Plzeň Zoo	March to April 2002	One adult male, 1 adult female, 1 subadult male, 1 juvenile male, 1 infant male	One subadult male, 1 juvenile male, 1 infant male	1,200 min
	Plzeň Zoo	September 2005	One adult male, 1 adult female, 1 subadult female, 1 juvenile male	One subadult female, juvenile male	480 min
	Plzeň Zoo	September 2005	One adult male, 1 adult female, 1 infant female	One infant female	240 min
	Ústí nad Labem Zoo	October to November 2001	One adult male, 2 adult females, 1 subadult male, 2 subadult females	One subadult male, 2 subadult females	300 min
<i>Cercopithecus diana</i>	Ostrava Zoo	March 2003	One adult male, 2 adult females, 1 juvenile female, 1 infant female	One juvenile female, 1 infant female	620 min
	Ostrava Zoo	November 2004	One adult male, 2 adult females, 2 subadult females, 1 infant male	Two subadult females, 1 infant male	600 min
	Leipzig Zoo	October 2005	One adult male, 2 adult females, 1 subadult female, 1 infant female	One subadult female, 1 infant female	610 min

(1999); or Thierry et al. (2000). Following these authors, our definitions were kept as brief as possible by including only truly diagnostic features of each pattern (i.e., those that served us in practice to identify the pattern and to differentiate it from other patterns). We did not include further descriptive and conceptual details as a part of the definition. We believe that pinpointing the principal features rather than diluting these in minor and possibly misleading details makes the ethogram more reliable. This differs from an approach taken for example by Vick and Conley (1976) or Pereira, Seeligson, and Macedonia (1988) who described behavior in more detail. De Waal (1988) combined both approaches in his account on communicative repertoires of bonobos and chimpanzees by listing separately definition and comments for each pattern. Our ethogram definitions correspond to the definition by de Waal.

To enhance the possibility for other researchers to use our ethogram or to compare it to their categorization of play behavior, we compiled a videoethogram version (see the supplement material), which includes all the patterns that were observed in play behavior of Hanuman langurs and many of the patterns observed in patas, vervet, and de Brazza monkeys.

The next two steps in our study, that is, the assessment of the (non)self-handicapping character of individual patterns and the assessment of their similarity to serious behavior was only started after the ethograms were complete and their definitions finalized.

Assessment of the Patterns' Self-Handicapping Character

Our working definition of self-handicapping is that it is a behavior that puts the animal into unnecessary disadvantageous positions or situations. To base the distinction between self-handicapping and non self-handicapping play patterns on a well-defined basis, we devised the following list of seven types of self-handicapping:

- Social self-handicapping
 1. *Effort restriction*: An animal restricts their strength, skills, or social potential while playing with a partner and does not use their full power during the play interaction. This includes role reversals in which the animal with superior abilities assumes the role of the weaker or losing partner. For instance, a stronger animal allows a weaker one to chase.
 2. *Selecting a superior partner*: An animal chooses a stronger partner for play, for example, a juvenile initiates plays with an adult.
 3. *Disadvantaged position toward a partner*: An animal adopts a position from which they cannot easily attack the partner or cannot readily defend themselves, for example, keeping their own head lower than their partner's or lying on their back in front of their partner.
- Kinematic self-handicapping
 4. *Physically demanding movements and postures*: An animal includes obviously physically demanding locomotion or postures in the play sequence, for example, they avoid quadrupedal locomotion.

5. *Selecting a demanding substrate*: An animal is playing on a substrate that demands an increased effort to keep a stable and safe posture, for example, on a weak branch.

6. *Carrying an extra object*: An animal carries an object that is not the focus of the play; therefore, the object is occupying either their hand or mouth.

- Sensory self-handicapping

7. *Restricting or deteriorating sensory perception*: An animal's behavior alters their visual, kinetic, or other sensory input in a way that may be considered demanding, which may include, for instance, eyes closing or fast head rotation.

For the purpose of this study, a behavioral pattern was considered self-handicapping if it belonged to one or more of the last five categories (three through seven). Categories 1 and 2 were not used in this study because these types of self-handicapping refer to a magnitude of expression or pattern of partner choice, which are applicable to a range of play situations, and therefore cannot be unequivocally linked to specific play patterns.

Assessment of Similarity to Serious Behavior

In the case of Hanuman langurs we assessed similarity of the play patterns to any serious behavioral patterns. As serious we consider any behavior, which does not fit our criteria of play behavior. The judgments were made on the basis of personal observation during fieldwork of two authors in India during 40 months. During this time we had the opportunity to observe the full repertoire of Hanuman langur behavior in various serious (i.e., nonplay) context and compare those to patterns occurring during play interactions. Also the published behavior repertoire of Hanuman langurs (Dolhinow, 1978) was used for comparison. We divided all elements of the ethogram into five categories. Each pattern of the Hanuman langur play ethogram was assigned to one of the following five categories.

H1. Behavioral pattern that is identical or very similar to a pattern that frequently occurs in serious repertoire.

H2. Behavioral pattern that is identical or very similar to a pattern that occurs in serious repertoire but very rarely.

H3. Behavioral pattern that is identical with or very similar to a pattern that frequently occurs in serious repertoire but on a different substrate or with a different object.

H4. Behavioral pattern that occurs in serious repertoire but in a considerably different form.

H5. Behavioral pattern very dissimilar to any serious behavior.

We did not assess the similarity of play patterns to serious behavior in the other four species because the total contact time of
(text continues on page 259)

Table 2
Ethogram of Play Behaviour of Five Monkey Species

Pattern	Definition	Self-handicap	Similarity to serious behaviour (SE)	Occurrence in species					
				SE	EP	CP	CN	CD	
<u>General play elements</u>	Elements occurring in any of the three major categories of play (object, locomotor, 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 behavior), teeth are only slightly exposed, eyes open or closed; no attempts to firmly bite	N	H5	+	+	+	+	+	
Play bend	A monkey exaggeratedly bends its neck or whole trunk backwards	4/7	NA	-	+	+	+	+	
Play tumble	A monkey lays down and welters from side to side (once or repeatedly), extensively exposing its belly	3	H5	+	+	+	+	+	
Head rotation	A monkey performs an exaggerated rotational head movement in more than one plane, that is, turning, shaking, twisting; it may be combined with play face, or eyes closing or with rotational movement of the upper part of the body	4/7	H5	+	-	-	-	-	
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	7	H5	+	-	-	+	-	
Play intention movements	A monkey performs a detectable blip of one or more of play movements defined in this ethogram but it is not fully performed	non	H5	+	+	+	+	+	
<u>Object play</u>	Object play is a playful activity with an inanimate or animate object (including own body parts)								
Aimless manipulation	A monkey manipulates an object without any visible specific intention; it does not pay concentrated attention to it	non	H4	+	+	+	+	+	
Object manipulation	A monkey manipulates an object or attempts to manipulate a fixed object with concentrated attention—this includes touching, pulling, lifting with mouth, hand, or foot; it may also include some patterns typical for play fighting	non	H4	+	+	+	+	+	
Object transporting	A monkey carries an object, steadily concentrates on the object watching it or repeatedly looking at it	non	H1	+	+	+	+	+	
Object carrying	A monkey holds or carries an object during locomotor or social play, does not steadily concentrate on the object, object is not crucial for the progression of play	6	H4	+	+	+	+	+	
Own-body-part play	A monkey plays with a part of its own body—tail, foot, hand, or fingers	non	H3	+	+	+	+	+	
Play sitting on	A playful monkey target sits on a distinct object	non	NA	-	+	+	+	-	
Play jumping on	A playful monkey target jumps on an object and then it either stays on it or continues in locomotion	non	H4	+	+	+	+	-	
Play rubbing	A monkey rubs an object with palms of its hands against a tree trunk, floor, or other substrate	non	NA	-	-	-	+	+	
<u>Exploration</u>	A monkey is intently trying to gain information about its environment or an object; the behaviour is not as relaxed compared to nonexploration play; it may occur within as well as outside the context of play								
Investigation	A monkey attempts to explore a place or an object by various means—examining, observing, sniffing, touching, gentle biting, licking, and so forth	non	H1	+	+	+	+	+	
Exploratory play	A monkey concentrates on an object while displaying playful behavioral 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 positions); it may also include attempts to lift a heavy or firmly attached object, object bending, testing the substrate by dynamic movements, disengaging of a tied or locked object, or destruction of an object	non	H4	+	+	+	+	+	

(table continues)

Table 2 (continued)

Pattern	Definition	Self-handicap	Similarity to serious behaviour (SE)	Occurrence in species					
				SE	EP	CP	CN	CD	
<u>Play locomotions and postures</u>	Locomotor patterns include various movements and postures; patterns from this category may occur as a separate locomotor play or during other defined play categories								
walk	Basic mode of quadrupedal locomotion; at least two limbs are in contact with substrate at any moment; when on an arboreal substrate, forelimbs do not pull the body up	non	H1	+	+	+	+	+	
Bipedal walk/supported bipedal walk	A monkey rises on its hindlimbs, attempts to maintain balance and make a few steps; in supported bipedal walk it stabilizes its position by placing its hands on an elevated support	4	H2	+	+	+	+	+	
Run	The fastest mode of continuous quadrupedal locomotion; all limbs may be lifted off and lose contact with the substrate at one phase during each motor cycle	non	H1	+	+	+	+	+	
Play gallop	Basic movement is similar to run but less swift and on take off, the forelimbs are more spread to the sides; limb movements appear exaggerated compared to typical run; a monkey may concurrently look backwards	non	H5	+	-	+	+	-	
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	non	H5	+	+	+	+	+	
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	4	H5	+	+	+	+	+	
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	non	H1	+	+	+	+	+	
Leap backwards	A monkey leaps from ground or from an elevated place backwards; it often turns after the leap; often combined with head rotation	4/7	H5	+	-	-	-	-	
Leap up “on a wall”	A monkey leaps up on a vertical substrate where is no obvious hold and then lets itself slide down	5	NA	-	+	+	+	+	
Bounce	A monkey leaps up on a vertical substrate where is no obvious hold and then bounces away vigorously	5	H1	+	+	+	+	+	
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	5	NA	-	+	+	+	+	
Jump “on twigs”	A monkey repeatedly jumps up from ground on thin branches where it is not able to stay	5	H5	+	-	+	-	-	
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	5	NA	-	+	+	+	+	
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/in supported bipedal stance it stabilizes the posture by holding lightly to an elevated support (a wall, another animal, a branch, etc.)	4	H2	+	+	+	+	+	
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/in supported handstand, it holds to an elevated support by its feet	4/7	H5	+	+	+	+	+	
Climbing	A quadrupedal arboreal locomotion, when a monkey firmly grasps a vertical support by hands and feet and its forelimbs (in tension) pull the body up with support of hindlimbs	non	H1	+	+	+	+	+	

(table continues)

Table 2 (continued)

Pattern	Definition	Self-handicap	Similarity to serious behaviour (SE)	Occurrence in species				
				SE	EP	CP	CN	CD
Play climbing	A monkey climbs by very energetic and jerky, exaggerated movements	non	NA	-	-	-	+	-
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	4	H2	+	+	+	+	+
Hindlimbs suspension	A monkey is hanging by its hindlimbs/it may secure itself by lightly holding to another support by its forelimbs	4	NA	-	+	+	+	+
Fore- and hindlimb suspension	A monkey hangs on an arboreal substrate by three or all four limbs, or by one hand and one foot	4	H2	+	+	+	+	+
Brachiation/ supported brachiation	A monkey proceeds by swinging by its arms on an arboreal substrate/in supported brachiation, it secures (at least partly) its position by stepping on a lower support	4	NA	-	+	+	+	+
Moving in quadrupedal suspension	A monkey hangs by its fore- and hindlimbs on an arboreal substrate and moves forward quadrupedally	4	NA	-	+	+	+	+
Swinging	A monkey wobbles or swings targeted on a branch or a rope (an arboreal substrate)	non	H5	+	+	+	+	+
Bridging	A monkey stretches out its forelimbs and leans onto another arboreal support without losing grip with substrate; it often has to balance to maintain this position	4	NA	-	-	+	+	+
Somersault	A monkey performs a somersault forward—that is, rolls over head or shoulders without losing contact with substrate	4/7	H5	+	+	+	+	-
Flip	A monkey performs a flip in the air—forwards, aside or backwards—and lands on its hindlimbs, hands may touch the ground or the partner	4/7	H5	+	+	+	+	-
Circle	A monkey performs a clear circle around an arboreal support; if the support is vertical, the monkey descends in a spiral; if it is horizontal, the circle ends up in a forelimbs suspension	4/7	NA	-	+	+	+	+
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; it then grasps the support again with its forelimbs and continues in locomotion	4/7	NA	-	-	+	+	+
Unstable sitting	A monkey deliberately selects and attempts to maintain balance in sitting position on a substrate which is insecure, labile, floppy, or slippery	5	NA	-	+	+	+	+
Falling	A monkey is holding to a branch and suddenly but deliberately lets itself loose and falls down	4	NA	-	+	+	+	-
Demonstrative skipping	A monkey rhythmically bobs or hops on a flexible substrate, by doing so targeted produces noise and may also observe a reaction of the substrate	non	NA	-	+	-	+	-
Branch shaking	A monkey grapples a branch and shakes it hard by bouncing rhythmically its whole body	non	NA	-	-	-	+	-
<u>Social play</u>	Social play is an interaction between two or more individuals; it is a complex category which is generally classifiable as one-sided play, inviting play, play fight, play chase, or teasing; these general categories of social play may combine various component patterns listed below the description of the main categories	—	—	—	—	—	—	—
<u>One-sided play</u>	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 locomotor or object play rather than social play	—	—	—	—	—	—	—

(table continues)

Table 2 (continued)

Pattern	Definition	Self-handicap	Similarity to serious behaviour (SE)	Occurrence in species				
				SE	EP	CP	CN	CD
<u>Inviting play</u>	A monkey is attempting to get involved another one into a play bout by performing various displays in proximity to the other one or by direct physical contact	—	—	—	—	—	—	—
<u>Play fight</u>	Playful monkeys fight together but with no obvious intention to hurt each other seriously; it resembles agonistic combats	—	—	—	—	—	—	—
<u>Play chase</u>	A playful monkey chases another one or is being chased	—	—	—	—	—	—	—
<u>Teasing</u>	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 appears to be to explore limits of tolerable and intolerable behaviour towards the other one or to provoke the other one into any action	—	—	—	—	—	—	—
Play touch	A monkey briefly but targeted touches or slaps another one with its hand; the touch is rather gentle (often only with tips of fingers), intended probably primarily to attract the other's attention (in contrast to play tweak/play attack), monkey touches the other only once (in contrast to play fencing) and does not hold the grip	non	H1	+	+	+	+	+
Play tweak (rough touch)/pulling	A monkey grabs another one's tail, fur, or limb and tweaks it; it is a single isolated tweak, not a component of a more complex pattern such as play wrestling	non	non	+	+	+	+	+
Jump on	A playful monkey target jumps on another one, and either bounces away or stays and plays with the partner	non	H1	+	+	+	+	+
Play attack	A playful monkey (may perform play intention movements) is waiting until another monkey comes closer or passes by (the other monkey is not playful); the playful monkey usually waits until the other one loses attention or is in disadvantaged position and then attacks it from a favorable 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	non	H4	+	+	+	+	+
Playful observation	A playful monkey performs play intention movements but no other playful patterns while watching its play or potential play partner	non	H5	+	+	+	+	+
Play balancing	A playful monkey jumps on another one and tries to hold on top of the other for a few seconds	5	NA	—	—	+	+	+
Play climbing on partner	An infant climbs or attempts to climb on the body of another monkey, mouthing may occur, the other monkey is usually only tolerating this but does not engage in play	non	H3	+	—	—	—	—
Swinging on tail	An animal swings on the tail of another monkey	non	H5	+	+	+	+	+
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 does not engage in play	non	H3	+	+	+	+	+
Running toward the partner	A playful monkey is running or play galloping (head rotation may also occur) toward another one from the front and then, in close proximity to the other, suddenly stops and watches the other one's reaction	non	H4	+	+	+	—	—
Quick turn	A running monkey turns quickly on the spot (approximately 180°) so that it faces its play partner who was following	non	H1	+	—	—	—	—
Mouthing/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/not resulting in injury of the partner	non	H4	+	+	+	+	+

(table continues)

Table 2 (continued)

Pattern	Definition	Self-handicap	Similarity to serious behaviour (SE)	Occurrence in species				
				SE	EP	CP	CN	CD
Dragging	A monkey grabs its play partner and attempts to drag it to another place (it may or may not be successful)	non	NA	-	+	+	+	+
Play wrestle	A playful equivalent to agonistic wrestling (the 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, for example, by pulling the other one's head away; they may be also pushing the other one away by their hindlimbs that helps them to 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	non	H4	+	+	+	+	+
Rampant pushing	A monkey is standing on its hindlimbs and pushing its play partner with the full weight of their own body in attempt to fling the partner; usually the partners hold each other by arms or shoulders	non	NA	-	+	+	+	+
Play lunge	Monkeys repeatedly hop against each other and lunge at each other by their forelimbs while slightly touching	non	H4	+	+	-	+	-
Play fencing	Standing or hopping against each other, monkeys are fencing by their forelimbs, repeatedly, physically contacting each other (but they do not hold each other as in play wrestling); fencing pair sometimes rotates	non	H4	+	+	-	+	-
Play seizure	When a play partner turns away or attempts to run away, the other one grabs it by a limb, hip, or tail and will not let go before the partner does not turn back and react (e.g., by biting, pushing, etc.)	non	NA	-	+	+	+	+
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	non	H4	+	+	+	+	+
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	non	H1	+	+	+	+	+
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)	4	NA	-	+	+	+	+
Play mounting	A monkey positions itself behind the other one as if attempting to copulate; it may perform a few pelvic thrusts; usually it lasts only for a few seconds	non	H1	+	+	+	+	+
<u>Idiosyncratic patterns</u>	This is a list of patterns, which were observed only in one or few individuals; rather than species-specific patterns, they may represent individual idiosyncrasies							
Eyes shielding	A behavioural element performed only by one subadult de Brazza monkey female in Plzeň Zoo; she shields her eyes by hand while sitting or standing but she is actually looking between her fingers	7	NA	-	-	-	+	-
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	4/7	NA	-	-	-	-	+
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 with a sackcloth hanging on a rope; either they played with it or they were shielding themselves from others while playing together (we also observed an infant patas monkey in Wrocław Zoo [Poland], to cover itself in a similar way by a towel)	7	NA	-	+	+	-	+
Whirling	A subadult de Brazza monkey in Plzeň Zoo used to perform whirling—that is, turning around (360°) on all four limbs several times in a row	4/7	NA	-	-	-	+	-

Note. Each pattern is identified as either being nonself-handicapping (non) or belonging to one of the five categories (3 to 7) as defined in the Method section. Similarity to serious behaviour (in *Semnopithecus entellus*) is identified according to the five categories (H1 to H5) defined in the Method section or as nonappropriate (NA) if the pattern does not occur in SE. SE = *Semnopithecus entellus*; EP = *Erythrocebus patas*; CP = *Chlorocebus pygerythrus*; CN = *Cercopithecus neglectus*; CD = *Cercopithecus diana*.

Table 3
Number of Play Elements Present in Langurs and guenons

	Present in guenons?			Total
	In all species	In some species	No	
Present in langurs?				
Yes	35	9	4	48
No	12	14	0	26
Total	47	23	4	74

Note. See Table 3A in the electronic appendix for full list of elements in each cell.

the observers with the guenons was substantially shorter compared to the langurs. Furthermore, all observed guenons lived in zoos where the possibilities to fully express certain types of natural serious behavior were limited.

Results

List of Patterns

All patterns that we were able to identify in play behavior of the five monkey species, Hanuman langurs (*Semnopithecus entellus*), patas (*Erythrocebus patas*), vervet (*Chlorocebus pygerythrus*), de Brazza (*Cercopithecus neglectus*), and Diana (*Cercopithecus diana*) monkeys, and their definitions are listed in Table 2. The word *playful* is often used in definitions of the patterns. The meaning of this term in our study is defined in the Method section. Each ethogram pattern was assigned to one of five categories (double underlined in the table)—general play elements, object play, exploration, locomotor movements and postures, and social play. The social play was further divided into five subcategories (underlined rows). The categories of object play, exploration, and social play contain patterns that are exclusive to these categories, whereas general play elements or locomotor movements and postures may be combined with each other or with the former three play types.

Species Repertoire Richness and Overlap

In Table 3, the occurrence of the play patterns in the studied species is summarized. Forty-seven percent (35 out of 74) of all patterns were observed in all species. The play repertoire of any of the guenons was more extensive than that of the langurs (54 to 66 vs. 48). There were only 4 patterns that were unique for langurs, whereas 26 patterns occurred in some guenons (and 12 of them in

Table 4
Species Similarity Matrix

	SE	EP	C	CN	CD
SE — <i>Semnopithecus entellus</i>	48 (100%)	41 (85%)	41 (85%)	42 (88%)	35 (73%)
EP— <i>Erythrocebus patas</i>	41 (71%)	58 (100%)	55 (95%)	56 (97%)	49 (84%)
CP— <i>Chlorocebus pygerythrus</i>	41 (68%)	55 (92%)	60 (100%)	57 (95%)	52 (87%)
CN— <i>Cercopithecus neglectus</i>	42 (64%)	56 (85%)	57 (86%)	66 (100%)	52 (79%)
CD— <i>Cercopithecus diana</i>	35 (65%)	49 (91%)	52 (96%)	52 (96%)	54 (100%)

Note. In each column, the number of patterns (and percentage) is displayed that this species has in common with the respective species in that given column.

Table 5
Number of Self-Handicapping and Nonself-Handicapping Elements

Type of SH	No. of patterns
3	1
4	21
5	7
6	2
7	12
Non SH	41
Total	74

Note. Self-handicapping (SH) elements are split according to the type of self-handicapping.

all guenons) but not in langurs. The cross-occurrence of patterns in the species is tabulated by names in the supplement material.

Table 4 is a similarity matrix between the species, with the number of patterns in the repertoires of species appearing on the diagonal. It does seem that the guenon species were more similar to each than to the langurs. Guenons mutually shared most of their play patterns: The proportion of patterns in common between two species ranged from 79% (52 out of 66 *Cercopithecus neglectus* were shared with *Cercopithecus diana*) to 97% (56 out of 58 *Erythrocebus patas* were shared with *Cercopithecus neglectus*).

Self-Handicapping Character of the Patterns

Almost half of the registered patterns were judged to have a self-handicapping character (33 out of 74, i.e., 45%, Table 5). The self-handicapping patterns belonged mostly to Categories 4 (unnecessarily physically demanding), 7 (sensory self-handicapping), and 5 (playing on demanding substrate). Some of the patterns belonged to two self-handicapping categories, mostly Categories 4 and 7. Surprising, only one pattern (play tumble) fit into the category of disadvantageous positions toward a partner (Category 3).

Similarity to Serious Behavioral Patterns

Of the 48 patterns that were observed in langurs and therefore were evaluated for similarity to serious behavior, 13 (27%) appeared identical in form with a commonly occurring serious pattern (Category H1) while 16 (33%) were totally dissimilar to any serious langur behavior known to us (Table 6; tabulated by pattern

Table 6
Number of Langur Play Elements Belonging to Each Category of (Dis)Similarity to Serious Behavior, Crossed With the SH/Non-SH Classification

		SH?		Total
		Yes	No	
Like serious?				
H1	Identical	1	12	13
H2	Identical but rare in serious	4	0	4
H3	Similar but different substrate	0	3	3
H4	Different form in serious	1	11	12
H5	Dissimilar	9	7	16
NA	Not applicable	18	8	26
Total		33	41	74

Note. See Table 6A in the electronic appendix for full list of elements. SH = Self-handicapping; not applicable = those elements that were not present in the Langur ethogram.

name in in the supplement material). The remaining 19 patterns showed some similarity to a serious pattern and yet were different in either their form or substrate or resembled a very rare serious behavior. Thus, the langur play repertoire seems to be a balanced mixture of patterns taken from other types of behavior and patterns peculiar to play.

The frequencies in Table 6 also indicate a link between the self-handicapping nature of a pattern and its (dis)similarity to serious patterns. Taking Categories H1 versus H5 and categories of self-handicapping and nonself-handicapping patterns, we get a 2 × 2 frequency table that proves (two-sided Fisher’s exact test, $p = .0084$) that serious-behavior-identical play patterns prevailingly were not self-handicapping, whereas serious-behavior-unlike play patterns were mainly self-handicapping (Table 7.)

Discussion

In this study we present play ethograms of five monkey species, Hanuman langurs and guenons, which included patas, vervet, de Brazza and Diana monkeys. The ethograms include brief diagnostic descriptions of all patterns that we identified during extensive videorecording and direct observation of play in the five species. Using this extensive material, we assess two questions that have echoed in the research on play behavior: the apparent self-

handicapping nature of many play elements and the question of similarity or dissimilarity to movements used in other serious contexts.

Self-handicapping patterns (according to our definition) were common in play situations of all five species, contributing to about half of all observed patterns. The prominent presence of the self-handicapping elements fits well with the hypothesis that a major function of play behavior is to train for unexpected situations (Špinka et al., 2001).

To our knowledge this is the first study to explicitly examine how many of the play elements in primates possess a self-handicapping character. We identified seven different ways in which animals can put themselves into a disadvantageous position or situation. We believe that this classification may help to dispel confusion arising from diverse understanding of the term self-handicapping. For instance, Bauer and Smuts (2007) defined self-handicapping as cooperative tactics during play through which participants actively make themselves more vulnerable to attacks by their opponents. Their delineation restricts self-handicapping to social play in its agonistic form and is identical to Category 3 self-handicapping in our study. In our study, most of the patterns belonged to Categories 4 (physically demanding) and 7 (sensory self-handicapping), whereas only one example of social self-handicapping (play tumble) was identified in the ethograms. However, it does not mean that social self-handicapping is rare in the five species. Several elements of social play (e.g., play touch, play attack, or jumping on) can attain a self-handicapping character classifiable into our Categories 1 and 2 depending on how and with whom they are performed rather than on characteristics of the pattern itself. Also the fact that only one element falls in our Category 3 (disadvantageous positions toward the partner) may reflect limitations of the ethogram approach. It is possible that there are various slight and rather irregular self-handicapping positional adjustments toward the play partner, which cannot be defined as readily identifiable ethogram patterns. A more detailed kinematic analysis of body maneuvers during social play and tracking of the choice of play partners would be necessary to discern the self-handicapping of Categories 1, 2, and 3. For instance, Foroud and Pellis (2003) were able to show that domestic rats at a juvenile age often used a less stable variant of pinning down the play partner and in this way offset the advantage that they gained from their preceding maneuvers.

Table 7
Putative Function of Play Elements as Dependent of Their SH/non-SH Character and Their (Dis)Similarity to Serious Behavior

	Is the element similar to patterns used in serious contents?	
	Yes	No
Has the element a self-handicapping nature?	Yes	Training handicap-based Zahavian ($n = 1$)
	No	Practice: training specific skills ($n = 12$)
		Training for the unexpected: training the general ability to regain control or: play signals ($n = 9$)
		Play signals: communicate playful intentions ($n = 7$)

Note. The number of elements falling into each category in our ethogram is given in parentheses.

Play behavior has been traditionally viewed as being composed of a mixture of elements predominantly drawn from various other contexts such as agonistic behavior, predation, antipredatory behavior, and sex (Cordoni & Palagi, 2007). In Hanuman langurs we found instead that a third of the play repertoire consists of patterns that are unique to play. Because they have no counterpart in other types of behavior, either in adulthood or other stage of ontogeny, they cannot serve to train specific skills needed in serious behavior. Some of them may have a signaling function, as is probably the case of play face and eyes closing. Thus, they do not have a function beyond the boundary of play, but rather serve to keep the play going and thus allow other play elements to be performed and fulfill their function. However, signaling is unlikely to be the sole function for all the patterns in this array. First, for signaling a playful intention, a few displays in the repertoire would be sufficient but we have a set of 16 patterns that are dissimilar to any nonplay behavioral element. Second, specialized signals are usually encoded in rather stereotypic movements to transmit information reliably (Braestrup, 1966; Hinde, 1982; McFarland, 1987; Morris, 1966; Zahavi, 1979). In contrast, we observed that several patterns in the Category H5 (very dissimilar to any serious behavior) were very variable, for example, play tumble, somersault, and swinging. In a previous study on langurs, Petrů et al. (2008) showed that head rotation, a typical and frequent pattern for this category, is extremely variable in duration, composition of head positions and sequencing. Third, if the patterns served only for signaling play intention, they should be present in social but not in solitary locomotor play. In Petrů et al. head rotations were present both in social and in solitary play, and this was what we also observed for other Category H5 patterns such as play tumble, swinging, and eyes closing in the present study. Thus we suggest that self-handicapping play elements serve either to promote further play or to train for the unexpected, or both functions. For instance, Palagi (2008) found that pirouettes/somersaults in bonobos that we would propose to have the training for the unexpected function, also increased the probability that solitary play will turn into a social one.

In our study there was a wide overlap between self-handicapping patterns and patterns dissimilar to serious behaviors. A 2×2 predictions table can be constructed (see Table 7) relating the character of a play element to its possible function. Nonself-handicapping patterns similar to serious behavior (e.g., object transporting, climbing, quick turn) may most likely serve for practicing important specific kinematic skills (Chalmers & Locke-Haydon, 1984; Groos 1898; Smith, 1982). The self-handicapping, serious-behavior-unlike elements (e.g., play tumble, head rotation, eyes closing) might either serve for training of the unexpected (Špinková et al., 2001) or for promoting further play. Third, elements that are not self-handicapping but different from serious patterns (e.g., play face or play gallop) are the most likely candidates for play signaling function. Finally, patterns of self-handicapping character that also occur in serious behaviors (only one element in our langurs, namely bounce) might have the function to practice handicap-based displays utilized outside the play in social signaling (Zahavi & Zahavi, 1997). This variety in kinematic and ontogenetic characteristics of the play elements supports the view that different patterns serve different functions during play.

In terms of methodology of this study, we admit that the total numbers of items in the species' repertoires and in the subcatego-

ries are somewhat arbitrary. Some patterns could be further subdivided (for instance, by considering bipedal walk and supported bipedal walk as two different patterns) or, on the opposite, lumped into more widely defined items (e.g., by pooling bounce and leap-up on a wall). This arbitrariness is an inherent limitation present in any category-based scoring system and therefore the absolute numbers of elements reported in this study should be taken with caution. Nevertheless, we believe neither the question of how detailed the ethogram is nor any doubts about (non)distinction between two specific elements invalidate our main conclusion that a substantial proportion of play elements in the monkeys' repertoires are self-handicapping and dissimilar to serious behaviors. Any categorization of behavior can be seen as a sampling that simplifies the richness and fluidity of the stream of behavior. So far as the sampling has been done independently of the ultimate question, it remains an unbiased representation of the real behavior. We first finalized the ethograms of the five species and only then started the assessment of the self-handicapping and similarity to serious pattern and we therefore believe that our current contribution quantifies correctly, even if roughly, the extent of self-handicapping in play and the similarity of play patterns to behaviors used in other contexts.

Our comprehensive ethograms also may provide helpful basis for further studies of play behavior in other primate species because they are more detailed than previously published ethograms such as that of Dolhinow (1978). The extensive list of kinematically described elements also enabled us to compare the repertoires of the five species.

Play ethograms of the species under our study were similar to each other, with almost a half of the patterns detected in all five species. However there were also differences in play repertoires. Some of the interspecies differences may have resulted from different environments. The occurrence of jumping on twigs only in vervet monkeys and in wild Hanuman langurs may be explained by the fact that no other guenons had bushes with tiny twigs available in their enclosures. Differences related to substrate availability can be also expected to occur between wild Hanuman langurs on one side and all captive guenons on the other. It could be argued that the captive environment with less space allowance and limited access to play objects, substrates, and often also play partners, will lead to reduction of play behavior (Jensen, Vestergaard, & Krohn, 1998; Renouf, 1993). Several studies on primates and other mammals have documented quantitatively more play in richer environments (Hoff, Forthman, & Maple, 1994; Jensen & Kyhn, 2000; Johnson, Morrow-Tesch, & McGlone, 2001; Marashi, Barnekow, & Sachser, 2004), but effects on the broadness of play repertoire are less clear. In kangaroos, for example, captive studies showed more increase in the play repertory as the function of the observation time compared to the field studies (Watson, 1998). We found more play elements in captive guenons than in free-ranging langurs. Absence of numerous elements in langur as opposed to guenon play cannot be explained by absence of relevant locomotor skills or by absence of similar behaviors in the adult behavioral repertory in langurs but not guenons. The causes of broadening of play repertory in captive conditions could be manifold and may include more time available due to reduced foraging demands and predator pressures or, as in harbor seals, better observation opportunities (Renouf, 1993). However, we suggest that main factor in the case of our study was the limited

opportunities to select play objects, substrates, and partners in captive monkeys, which lead to an intensified concentration on the available opportunities to play and may in turn result in emergence of additional play components. This was also shown by historical observations by de Haan on a 5-year old chimpanzee housed singly in an empty cage, where the chimpanzee was still able to develop more than a dozen distinct ways of play (Loizos, 1967).

There are, however, dissimilarities in ethograms that are unlikely to be caused by different environments, but may rather represent true interspecific differences related to divergent general locomotor styles. Absence of play gallop in patas monkeys may be attributable to the emphasis on practicing speed rather than versatility of locomotion in this terrestrial and cursorial species. Run, which is the fastest locomotor mode, may be more appropriate than gallop in the patas monkeys play. However this would not apply to the absence of play gallop in Diana monkeys, a species that spends most of the time at higher and middle forest strata (Byrne, Conning, & Young, 1983). Play gallop possibly did not occur in this species, as it is performed almost exclusively on the ground and therefore is not relevant to its locomotor style. Similarly somersault, which is performed almost exclusively on the ground is absent from play behavior of Diana monkeys. Another pattern of locomotor play, play climbing, was observed only in de Brazza monkeys, which can be characterized by arboreal climbing and walking rather than leaping.

Surprisingly, head rotations were found only in Hanuman langurs, although this is a pattern commonly described for other mammals, including primates (Bekoff, 1974; Byers, 1984; Wilson & Kleiman, 1974). Petrů et al. (2008) documented that Hanuman langur's head rotations are highly variable and fast in angular speed, indicating that they may serve for sensory self-handicapping. The most similar elements of the guenons play, play bends, are according to our observations restricted to the sagittal plane and involve not only the neck but also the thoracic region. Thus they are exaggerated yet relatively invariant movements, suggesting that their function may be different from that of the more variable play head rotations.

In conclusion, we found a suite of differences in the play behavior of the five species. Some of those differences seem to match the differences in adult locomotion or habitat use, although others are difficult to explain. Despite these interspecies differences, self-handicapping elements make up about half of the patterns in all five play ethograms and the elements without an analogy in serious behaviors contribute with about a third in Hanuman langurs. Notwithstanding certain arbitrariness inherent to any definition-based categorization, our study persuasively documents the prominent presence of elements differing substantially in their kinematic character and in likeness to serious behaviors indicates in the play of the five monkey species. These findings support the idea that play may have multiple functions, and that the constituent play patterns may be specialized to fulfill solely, or predominantly, one of these functions, but not the other.

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