The ecological and ethological significance of felid coat patterns (Felidae)

Ph.D. Thesis

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I hereby declare that this thesis has been composed by Filip Jaroš, the undersigned, with intention to acquire the degree of Ph.D. at Charles University in Prague. This thesis represents an original piece of work and has not been presented in any previous application for an academic degree.

Prague, 4th September 2012

Filip Jaroš
To Magdalena, whom I have classified as a golden cat.
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Motto:

Cats are intended to teach us that not everything in nature has a function.

Garrison Keillor (* 1942)
American broadcaster and writer
Abstract:

The presented work investigates various theories about the significance of felid coat patterns. Most of the hypotheses are based on the theory of adaptive function of animal colouration. As regards felids, it is generally believed that the coat pattern has the function of aggressive resemblance. Early testimonies about cryptic properties of colouration of cats are summarized to provide the historical perspective of the problem. Other putative adaptive functions of patterns are investigated (intraspecific communication, thermoregulation) and close attention is paid to the option that the spotted coat of the leopard (*Panthera pardus*) serves as a cue for recognition from the perspective of prey.

In the next stage, some of the hypotheses are tested by statistical means. The problem is simplified into search for association between a given category of a coat pattern (e.g. spots, stripes) and usual habitat of felid species (e.g. forest, grassland). Pagel’s test for correlated changes is employed to account for phylogenetic relationships. In addition to broadly acknowledged hypotheses, the validity of proposition that juvenile coat patterns have the function of protective resemblance is tested.

Finally, the problem of colouration of felids is linked to broader context of theoretical biology. Apart from prevailing (neo-)Darwinian perspective to the problem of animal colouration, the theory of colour conflict by Hingston and Portmann’s aesthetical morphology are discussed at great length. It is demonstrated that Portmann’s approach yields valuable insights into the problem of the colouration of felids, mainly ontogenetic colour change. Factors accounting for marginal position of Portmann’s investigations within the framework of current biology are analysed from epistemological and philosophical perspective.

Abstrakt:

Předkládaná práce zkoumá různé teorie o významu zbarvení kočkovitých šelem. Většina hypotéz je založena na teorii adaptivního zbarvení. Obecně se má za to, že vzory na kůži kočkovitých šelem plní funkci agresivní krypsy. Raná svědectví o kryptické funkci zbarvení koček poskytují přehled o historii zkoumání této problematiky. Další možné adaptivní funkce zbarvení (vnitrodruhová komunikace, termoregulace) doplňují přehled hypotéz; zvláštní pozornost je věnována výzkumu, který dokládá, že skvrnitá srst levharta (*Panthera pardus*) pravděpodobně slouží jako rozpoznávací znak pro jeho kořist.

V další fázi jsou některé z hypotéz testovány statistickými prostředky. Problém je zjednodušen na hledání korelace mezi příslušnou kategorií vzoru (např. skvrny, pruhy) a typický habitat daného druhu kočkovité šelmy (např. les, traviny). Za účelem korekce fylogenetických vztahů je použit Pagelův test pro korelované změny. Kromě obecně uznávaných hypotéz je zkoumána validita tvrzení, že zbarvení juvenilních jedinců plní funkci ochranné krypsy.

V závěrečné části je problém zbarvení kočkovitých šelem zahrnut do obecného rámce teoretické biologie. Kromě převažující (neo)darwinistické perspektivy na zbarvení živočichů je detailně diskutována Hingstonova teorie konfliktu barev a Portmannova estetická morfologie. Je ukázáno, že Portmannův přístup přináší cenné náhledy na problém zbarvení koček, zejména pak změny zbarvení během ontogeneze. Důvody, proč Portmannova zkoumání zůstala na okraji zájmu současné biologie, jsou zkoumány z epistemologické a filosofické perspektivy.
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0 INTRODUCTION

Coat patterns exhibited by individual species of wild felids raised questions about their significance and function centuries ago (the proverb “A leopard can’t change its spots” originates in Bible, Jeremiah 13:23). In terms of shapes and colours, the coat patterns displayed by the members of the Felidae family form the most variable taxon of carnivores.

Our work about the ecological and ethological significance of felid coat patterns pursues 3 main goals:

i) To provide an overview of the hypotheses about the significance of patterns;
ii) To test some of the hypotheses by statistical means;
iii) To link the problem of colouration of felids with broader theoretical biological context.

Chapter 1 introduces the main features of colouration of felids and its possible significance. Apart from the theory of adaptive function, some other perspectives (sexual selection, predator recognition) are mentioned. In respect to intraspecific variety of felids (geographical varieties, melanism), the validity of Gloger’s rule and microevolutionary approach is discussed. We also add sceptical remarks about individual hypotheses from distinguished naturalists when they promise to shed light from another angle.

Within our investigation of felid coat patterns, high attention was paid to the colouration of young individuals. Ontogenetic colour change occurs relatively often among felids and some species display remarkably different pattern during juvenile and adult stage (e.g. puma). In Chapter 2, we hypothesize that colouration of juveniles might fulfil function of protective resemblance.

After the survey into various aspects of the colouration of felids, we choose several hypotheses amenable for statistical approach. In Chapter 3, we follow previous investigations of the visibility of specific patterns in various habitats and perform statistical tests to reveal possible correlations. As the results might be biased due to the presence of phylogenetic signal, we perform Pagel’s (1994) test for correlated changes to account for shared ancestry.

Up to this stage, the attention was aimed at classical (i.e. stemming from Walace and Darwin) account of the significance of colouration. Chapters 4 and 5 focus on theoretical and philosophical reflections of this prevailing perspective. Firstly, some remarks about weak points of the theory of adaptive colouration are added. They do not have an ambition to outperform the current approach but desire to show complex issues one might face when considering interaction between felids and their prey. We believe that a health level of
scepticism can help to shed more light on the fascinating problem of animal colouration. At the end of Chapter 5, our discussion shifts to more general problems of the philosophy of science. We endeavour an attempt to illustrate the enterprise of “normal science” (Kuhn 1962) and to show the ways how neo-Darwinian paradigm has absorbed various, often contradictory phenomena.

In the two previous chapters, we have pointed out some conceptual and factual pitfalls of classical investigations of the significance of felid coat patterns. Chapters 6 and 7 introduce basic concepts of the theories of Hingston and Portmann. Hingston (1933) builds up his theory on the colour conflict between cryptic and conspicuous parts of lion’s coat and investigate coats of other felid species to prove this. Portmann (1967) links the level in rank of organization with the complexity of appearance. We follow preliminary steps in the attempt to evaluate felid coat patterns in order to provide Portmann’s insights with more general ground. Based on this endeavour, we finally search for essential differences between current biological school and Portmann’s enterprise.
From the perspective of current (neo-)Darwinism, adaptive function of the colouration of carnivores is a widely accepted hypothesis (Ewer 1973). Kitchener (1991) mentions camouflaging properties of felid coats at the very beginning of his highly respected monograph on cats:

“*The background colour of the coat is usually similar to the habitat in which the cat is normally found, and there is often a variety of spots, stripes and blotches which help to match the cat more closely to its habitat or break up its outline to make it difficult to see. (…) Many forest and woodland cats have a bold pattern of stripes, blotches and spots which seems very conspicuous to us in the artificiality of zoos. However, the dappled light falling through vegetation has a similar contrasting effect.*” (p. 2)

However, the theory of adaptive colouration is not exhausted by the remarks about camouflage. Some parts of the felid body (back of the ears, tip of the tail) are often in high contrast with adjacent regions. For this reason, one might ask about signalling function of the specific parts of the body, for example in intraspecific communication. Distinctive markings on the face (e.g. eye stripes) might also be linked to physical and physiological processes (e.g. reducing glare from the sun).

### 1.1 The theory of camouflage

In respect to felids, there are basically two types of approaches to the problem of camouflage. Firstly, one can rely on empirical research in the field and testimonies of human observers. The strength of this approach consists in the opportunity to experience the phenomenon of camouflage by one’s own senses. It should be born in mind that the effect of crypsis, disruptive colouration etc. is constituted by deceiving individual minds. We will follow mainly this type of investigation in this chapter.

The second type of investigation is driven by different epistemological belief. Modern science requires formalization of problems under question. One might first formulate a theory about colouration in a way amenable for testing. This provides the researcher with a unified theoretical framework: individual cases are investigated according to a method which is suitable within this general concept.
Since Darwin and Wallace, hypotheses about adaptive function of colouration have been mainly product of the genre of evolutionary “just so stories”. Individual observations of variable reliability often blend with hypotheses generated ad hoc for colouration of individual species. This especially applies to cats: shy animals with secretive habits are not amenable for experimental research. Caro (2005) comments on this pioneering stage of Darwinian research:

“Naturalists’ anecdotes about mammalian colouration were never put to experimental test, and the generality of these ideas—most of them formulated on the basis of only one or a handful of species—remained unexplored until very recently, except for one monumental treatise (Cott 1940).” (p. 125)

It is good to mention here that apart from Cott (1940), who mentions several felid species in respect to the theories of background matching and disruptive colouration, Mottram (1915) pays high attention to spotted species of felids which serve as good examples of his theory of obliterative shading.

Anyway, Caro refers to demands characteristic for the second type of investigation. Endler (1978) was one of the first who have asserted that the problem of animal colour patterns requires unified theoretical approach. It is important to consider all species of a given taxa and to test hypotheses considered against the entire data sample. From the methodological point of view, this approach leads to the employment of statistical tools. We will test some hypotheses about colouration of felids in Chapter 3.

1.1.1 Aggressive resemblance

Felids are known as secretive hunters and a number of naturalists have reported that their coat is surprisingly inconspicuous in natural settings. Among individual species of felids, the effect of aggressive resemblance is constituted by different means. Expressed in a simplified way, one can distinguish between cases of background matching (Poulton 1908) and disruptive colouration (Cott 1940). The phenomenon of background matching consists in the parallelism between an animal’s colour or pattern and the natural background where it lives. The effect of disruptive colouration arises as outlines of an animal are broken up by irregular markings and highly contrasting patches of colour.
1.1.1.1 Background matching

a) Uniform colouration and the open land

Poulton (1908) suggests that the colouration of the lion harmonizes with the desert. The same notion is repeated by Hingston (1933), who adds that tawny underlying hairs have a camouflaging function, whereas long guard black hairs are displayed in aggression (see Section 6.1).

Cott (1940) seeks for general rules about animal colouration and asserts that “species living in open barren country tend to be uniformly coloured, or but lightly marked” (p. 12-13). To prove his point, he mentions examples of the lion and caracal, but also less convincing cases of the Pallas’s cat (Otocolobus manul) and Pampas cat (Leopardus colocolo). The Pallas’s cat often displays slight stripes on its flanks and the Pampas cat is highly polymorphic, with spotted morph often reported (García-Perea 1994).

Further, Cott (1940) suggests that the ground colour of snow-leopard in confined to the barren highlands of Central Asia. Searle (1968) also links the colour of snow-leopard’s fur with treeless and often snow-covered highlands.

b) The tiger’s stripes and grassland

Alleged cryptic properties of the tiger’s stripes are the exemplum for aggressive camouflage among felids. Generally, it is supposed that the stripes match natural background of the habitat of the tiger. This hypothesis is dated back to Wallace (1870) who gave classical description of the function of the tiger’s stripes:

“The tiger is a jungle animal, and hides himself among tufts of grass or of bamboos, and in these positions the vertical stripes with which his body is adorned must so assimilate with the vertical stems of the bamboo, as to assist greatly in concealing him from his approaching prey.” (p. 52)

Baker (cited in Beddard 1892) links the colouration of the tiger directly with grasslands:

“The striped skin of the tiger harmonizes in a peculiar manner with dry sticks, yellowish tufts of grass, and the remains of burnt stumps, which are so frequently the family of colours that form the surroundings of the animal.” (Baker 1890, p. 191)

Mottram (1915) considered the tiger to be an excellent example of “reed-painting” (i.e. reeds being seemingly imprinted on the coat) and brought detail description of this analogy:

“(Dark stripes) are irregularly distributed, they for the most part increase in width from above, down, and on the belly they terminate in a large dark mass which, curiously enough, often shows a small white centre.” (p. 685)

The authority of Cott (1940) refers to the tiger’s stripes in a similar way:
“(…) the vertical tawny-orange and black stripes of the tiger assimilate with the tall parallel grass stems and reeds of the swamps and grassy plains where it lives.” (p. 12)

Stephenson (1946) gave a poetic account of the same scene, counting shadow into a camouflage effect:

“The fierce light striking on the tall grass or reed-stems casts vivid black stripes of colour. In such a setting it is impossible to see a crouching tiger. Only the sudden rush of attack or lightning-like spring reveals its presence.” (p. 13)

Although the original description links the tiger’s stripes with vertical stems of bamboo, it has been believed afterwards that tiger’s coat pattern is cryptic as such. Arsenjew (1924) (cited in Mazák 1980) reports that the stripes of Siberian tiger seemingly blend into brownish grey mass when the animal moves fast.

There have also been some attempts to investigate the problem of tiger’s stripes physically or mathematically with the use of computational graphic methods. Godfrey et al. (1987) paid close attention to the distribution and the size of the pattern in relation to a typical habitat, represented as a background on a photograph. The analysis was carried out on an individual walking through grassland in India. Following the notion of Endler (1978), they built on the assumption that a pattern is cryptic when it reminds a random sample of the background pattern. Because mammalian vision is based on spatial frequency analysers, both the tiger and the background were displayed on the basis of spatial frequencies. As the outline of the tiger appeared to be hardly distinguishable against the background, the conclusion arises that tiger’s stripes resemble stems of grass in the eyes of its prey.

**Sceptical remarks**

Although most authors are persuaded about camouflaging qualitites of tiger stripes, there are some who remain at least sceptical. Perry (1965) gathered a large number of reports about the tiger and his work resulted in a diminutive account of the ecology and ethology of the tiger. Importantly for our research, he dedicated a large space to the problems linked with tiger’s appearance and conditions of hunting. Perry did not work as a classical scholar and he mixed serious reports with several anecdotic stories by famous hunters (see Schaller 1967, p. 222 for comments). On the other hand, it is beyond any doubts that hunters who spent long days (and sometimes nights) in a terrain had more experience with tigers than any academicians working seriously with the literature. It is highly possible that credible field observation of a tiger brings more information than a sophisticated computational model
simulating the vision of prey. Anyway, Perry’s work is probably the most thought-provoking description of the world of the tiger currently available.

Perry firstly mentions that most hunters reported the tiger’s coat harmonizes with either reeds, grassland or forest, making him difficult to be spotted both by day and by night. Even winter land covered with snow provides some means of camouflage (bushes with dead leaves) and a tiger running on snow seems to be uniformly brownish-grey. (This is in favour with the observation by Arsenjew 1924, cited by Mazák 1980. The effect could also be attributed to Mottram’s finding that from a certain distance on, colourful objects blend into greyish mass.) As far as India is concerned, however, Perry brings a different testimony:

“(…) the predominant colour in most jungles for nine months or more of the year is in fact green; and there is no more conspicuous object than a tiger, shining like gold, walking through a sunlit jungle. Nor has the hunting tiger any guarantee that he will always be able to stalk conveniently from one concealing patch of light or shade, sunlight or shadow, to another also blending with his colour pattern (…)” (Perry 1965, p. 97-98).

It will not be amiss to highlight that Perry targets human vision here, although he is aware of the fact that a common prey, the deer, is likely to be “colour-blind” (respectively dichromatic).

Perry pinpoints a crucial aspect often omitted in other works. If the striped coat possesses camouflaging function, it has to work when a tiger is actively seeking for prey. (A tiger could also wait in ambush, but it is not probably a common form of hunt: see Schaller 1967.) Hunting is by no means static problem and the question is how well we can model it by motionless situations. Perry (1965) asserts the following:

“However perfect a tiger’s camouflage may be, its value is negative the instant he moves, because any moving object excites the suspicion of the animal he preys upon. The grasses in the foothills of the Terai are red or ochre or brown for half the year, and blend with a tiger’s colouring, but this does not prevent his slightest movement being immediately spotted by deer or monkeys.” (p. 98)

Nevertheless, tigers hunt predominantly at night. The lack of light causes impossibility to distinguish colour hues, so most animals possess probably monochromatic vision at night in effect. Camouflage could serve well under such conditions, but it is more likely tigers simply benefit of lowered level of light on the whole. Under overcast sky, it can be very difficult for some species to merely orientate in forest. (Similarly to domestic cats, tigers themselves have excellent vision ability during the night.) According to Perry, deer see much better than men at night, but his sight is challenged during crepuscular light conditions. As the following
description is again one of the most poetic and full of details at the same time, it deserves to be cited at length:

“(in twilight) only the white chest and ruff of a tiger are visible, and his stripes break up the outline of his body – as they do in deep day-shadow also – and the crazy face-markings of staring white eye-spaces with their frowning angular black markings, surmounted by black-barred forehead, produce a blurring effect.” (Perry 1965, p. 99)

Although this could be one of the best testimonies on the camouflage property of tiger’s appearance, its author concludes that even if it works under certain light conditions, the problem is of a secondary importance since deer rely mainly on the sense of smell and hearing.

1.1.1.2 **Disruptive colouration**

c) Spotted coats and forest

Besides the tiger’s stripes, flecks displayed on the coat of several felid species (e.g. leopard, clouded leopard, ocelot) attract significant curiosity of naturalists. The hypothesis about disruptive effect of this pattern was originally uttered by Wallace (1870):

“How remarkable it is that besides the lion and tiger, almost all the other large cats are arboreal in their habits, and almost all have ocellated or spotted skins, which must certainly tend to blend them with the background of foliage (...).” (p. 52-53)

Beddard (1892) suggests a disruptive effect in the case of the jaguar coat:

“The spots upon the jaguar harmonise with the oval patches of sunlight which penetrate between the leaves of the trees upon with it lives.” (p. 85)

Spotted coats of some felids are mentioned as an example of disruptive colouration by Cott (1940, 1975). The South American jaguar is mentioned in the first place:

“(its) tawny-yellow and reddish coat, broken with black spots, constitutes an effective anticryptic disguise for forest foliage” (Cott 1940, p. 12).

The leopard which inhabits wooded districts and is partly arboreal exhibits similar markings. Thoroughly arboreal species of the ocelot and clouded leopard display beautiful oblique markings (see Figure 1). Cott adds the fishing cat (*Prionailurus viverrinus*) to his account of disruptive colouration: the species is not arboreal in the strict sense, though, its elongated dark spots and stripes provide crypsis in thickets near water bodies where the cat often dwells. Disruptive colouration obliterates the shape of a whole animal although the pattern itself may be highly conspicuous (Cott 1940).
Sceptical remarks

Not all naturalists agree on the point of camouflage properties of spotted coats. Roosevelt (1910) argues that melanic morphs of leopard “thrive as well as their spotted brothers” although they are uniform in effect (p. 54). Moreover, he asserts that the spotted coat of the leopard is more visible than uniformly coloured puma. Leopards owe their hunting success almost entirely to great facility in hunting and the stealthy approach.

Species with remarkably different coat patterns (uniform lions, spotted servals, flecked leopards) hunt in precisely similar localities so some of the patterns cannot fulfil cryptic function very well. Moreover, felids usually hunt at night and it is doubtful whether their colouration contributes to successiveness under conditions of difficult visibility. Again, the ability to crouch motionless or stalk stealthily is of much greater importance. One should consider Roosevelt’s arguments very cautiously: we will analyze some of his objections closely in Chapter 4.

1.1.2 The neutralization of shadow

By the neutralization of shadow or countershading is generally conceived the principle discovered by Thayer (1909). A large number of mammals have dark backs and light undersides which account for the effect of countershading: contours of solid bodies, usually well distinguishable due to the presence of shadow, are obliterated. Poulton (1908) makes an example of carnivores, where “characteristic details are depicted on the shadowless and ghost-like surface of their general ground-colour”. Afterwards, he matches “vistas of upright stems
on the tiger” with “effects of light and shade”. In this manner the appearance of arboreal carnivores is suggested to interplay with “pin-hole images of the sun as cast by minute interstices between leaves”. We can see that this is boundary interpretation of countershading, the phenomenon could also be conceived as disruptive colouration. Poulton probably refers to the same fact that was later articulated by Cott (1975): the concealing effect of disruptive colouration is extraordinary effective when combined with countershading.

An original investigation into the principles of countershading was carried out by Mottram (1915). Because his theory is not widely known, we shall describe it in some detail. When an object is viewed, the vision conveys different perception according to the distance of the observer from the object. From a certain distance on, the object is obliterated, or more precisely, some of its visual characteristics cannot be recognized any more. This can be clearly demonstrated on chequered (i.e. consisting of black and white units) objects: the individual units are gradually blending together and forming undifferentiated grey mass. If the proportion of dark and light units is uneven, for example dark units dominating at the bottom and light at the top of the object, the perception of the object at the blending distance shows grey surface gradually darkening from the top to the bottom. In natural conditions, this provides the same effect as countershading (“obliterative shading” in Mottram’s terminology).

Mottram (1915) cites many examples of obliterative shading among felids. According to him, the effect is only slightly caused by background colour of a coat. What matters is the frequency of flecks (or rosettes), decreasing from the top to the bottom. For example, the cheetah has a lot of spots on the back, they are becoming more distant toward the ventral part, and spots on the belly are hidden by long hairs. According to Cott (1940), the same principle applies to the fishing cat. Dorsal stripes break up into spots on the flanks and become widely separated towards ventral part. Similar effect is produced by the coat of the leopard cat (*Prionailurus bengalensis*). Flecks are larger on the back, become smaller on the flanks and diminish toward the ventral part.

A bit more complex case is the jaguar. According to Mottram, black spots are frequent on the back, turning into black rings with brown central area on the flanks, and finally breaking into rosettes with a large central area which usually contains a small central black spot. An important feature is that as spots are gradually broken up into rings and rosettes, central areas (with lighter brown hue) are larger and larger. Viewed as a whole, the pattern shows decreasing quantity of black from above, which is a key factor for the effect of oblimiterative shading.

Mottram (1915) asserts similar effect applies for the serval, ocelot, and several varieties of leopard. Because patterns on felid coats blend at a relatively short distance, Mottram denies
the hypothesis that the similarity between the pattern and the background (e.g. leaf shadows) accounts for camouflage. Moreover, patterns of the felids mentioned are highly regular which is not the case of natural backgrounds. Therefore, based on Mottram’s investigation, the theory of obliterative shading must be viewed as a competitor to the concept of background matching.

As a matter of interest, not all authors are convinced that the contrast between dark backs and light undersides has a camouflaging function. Kiltie (1988) acknowledges the existence of the contrast among many terrestrial carnivores (dorsal pigmentary darkening - DPD in his words) but suggests to test whether the phenomenon accounts for the effect of three-dimensional self-shadow concealment (SSC). To be effective, SSC requires that pigmentation be graded (Thayer 1909, cited in Kiltie 1988), based on the assumption that the source of light is placed directly above and the intensity of light gradually decreases towards the underside. This assumption is problematic since direct dorsal illumination is rather rare: if we consider felids, they are active mainly at dawn and dusk. The very same objection applies to Mottram’s conception of obliterative shading. It should also be mentioned that some species have a dark dorsal stripe with sharp boundaries without a distinguishable dorso-ventral gradient in pigmentation (e.g. lynxes, the sand cat). Alternative explanations to the theory of countershading which account for the existence of DPD are discussed in Section 1.5.

### 1.1.3 The case of the king cheetah

The so-called king cheetah is a variety which was originally described as a distinct species in 1926 by Pocock. It is clear now that the king cheetah is neither a species nor a subspecies because cubs with such a patterning can be born to normally marked parents. The variety is characteristic for its peculiar shape of black markings (see Figure 2). Spots are frequently blended together and sometimes create blotches on the flanks and bold stripes on the back of the animal. The overall appearance of the king cheetah is remarkably darker in comparison to common variety. King cheetahs are frequent in the south part of Africa (South Africa, Zimbabwe, Mozambique) but can also rarely occur in central Africa (Burkina Faso) (Alderton 1998).
Figure 2: The king cheetah (a variety of *Acinonyx jubatus*). (Photograph by U. Schürer, ZOO Wuppertal)

The evolutionary significance of the king cheetah patterning remains unsolved. Across most of their range, king cheetahs inhabit wooded surroundings. There are basically two explanations: firstly, a dark pattern consisting of blotches (and stripes on the back) provides this morph with better camouflage in more shaded environment. The function of camouflage can be protective because woodlands are frequented by leopards. Secondly, it has been suggested that cheetahs have been getting used to more sedentary life in woodlands and the change is accompanied by their appearance (Kretzoi cited in Alderton 1998). It might sound disappointing but the reverse scenario is conceivable as well: the king cheetah might be a relic of a time when southern part of Africa was more wooded than nowadays.

### 1.2 Signalling function

Although felids are usually considered as cryptic in general conditions, there are few parts of their body which often contrast with the surrounding (connecting) areas. As these marks are highly conspicuous, they should serve to some special purposes. Rather than having one constant function, areas with semantic colouration might convey meaning in special encounters and situations.
1.2.1 Intraspecific communication

Among felids, the face, including the ears, and the tail are the most important organs of expression. Facial markings may serve to accentuate expressive movements of mouth, eyes, and ears (Ewer 1973). For example, open-mouthed threat of several felids is highlighted by the contrast between black gum line and white fur on the muzzle.

Special attention was paid to the “tear marks” on the face of the cheetah. They might have a signal function since the cheetah is a diurnal felid. In human eyes, the tear marks propose weepy appearance to the world’s fastest runner. Eaton (1969) suggests that the phenomenon is linked to social life of the felid (besides the lion, the cheetah is the only cat which forms groups for other than reproductive purposes). Social grooming plays a significant role in keeping cohesiveness of cheetah group and tear stripes may direct groomer’s activity in the particular region of the face. Kingdon (1977) is convinced that the facial mask composed of black eye cavity, tear stripes, muzzle, and lips margins is a reliable messenger of cheetah’s emotions. In aggressive threat, an animal lowers its head, twists the ears forward and enhances the dark outlines of the mask with black spots on the back of the ears. The visual role of a dark mask is visible from the comparison of facial expressions with the figures where facial markings have been removed (see Figure 3).

![Figure 3: Facial expressions of the cheetah. The visual role of a dark mask. (After Kingdon 1977)](image)

It is good to mention that other purposes might also explain the phenomenon. Once again, a camouflaging function is supposed by some authors. The tear stripes allegedly break up the continuity of the head and serve to detract observer’s attention mainly from the large eyes.
Potential prey (similarly to a human observer) has difficulty distinguishing the head of a predator at a distance while a cat is stalking. Kingdon (1977) also suggests that the head of the cheetah is well camouflaged at a distance but the effect is constituted by spots which cover the cheeks and the forehead. From this perspective, the spotted pattern obscures the head as well as the body (disruptive colouration). Contrary to Eaton, Kingdon believes that the tear stripes (and other parts of the expressive mask) are only visible at very close quarters.

In addition, Eaton (1979) puts forward a hypothesis that the tear stripes might serve as a glare reducing device.

Facial markings are also conspicuous on the head of the tiger. The combination of short convoluted stripes on the forehead, white eye patches and long stripes accentuating the outline of the head make up an imposing appearance of the cat. This general pattern involves a number of varieties so individuals can be recognized by differences in facial markings, as was demonstrated by Schaller (1967) in Kanha. No two individuals display the same pattern on the face. However, it is unclear whether the markings are used for individual recognition by animals themselves (Ewer 1973).

It is often impossible to reveal whether a specific organ with contrasting colour really fulfils a proposed function in intraspecific communication. We lack ethological observations for a vast number of small felids and we often rely on isolated observations of cats held in captivity (e.g. Leyhausen 1979). Caro (2009) asserts that the black-footed cat (*Felis nigripes*) exposes its black paws while walking on its toes. We have no means to directly resolve if the black paws fulfil signalling function: they might facilitate the sight of a conspecific, however, it is more likely that top parts of a body are the first ones to be exposed to sight on the distance of 10 metres and more.

There is an interesting explanation of the phenomenon usually known as countershading. Kingdon (1977) asserts there is a special function of the contrast between a dark upper part and a light underside in the case of felids. Cats often display their vulnerable underpart as a submissive signal to their conspecifics (behaviour typical namely for social felids, i.e. the lion and the cheetah). The contrast of the hues may serve well as an aggression reducing signal. However, as the phenomenon of countershading is general among mammals and the type of communication mentioned is restricted mainly to carnivores, we should be committed to other explanations if we follow the principle of Occam’s razor (see Section 1.1.2).

In the following subsections, two types of contrasting colouration often present among species of felids will be thoroughly examined.
1.2.1.1 Ears: contrasting spots on the back and tufts on the tip

White spots on the back of the ears are highly conspicuous among several felids. The most striking example might be the tiger, a contrast between the white patch and the black rest of the ear could well betray an animal from the distance. On some of the other felids (the lion), there appears a black spot against the light background of the back of the ears. Hingston (1933) stresses the fact that in the case of the lion this spot consists of a different type of hair (stiff black). Therefore, we might assume there is a significant function of the contrasting spot for the animal.

According to Ortolani and Caro (1996), the species with white spots tend to inhabit forests, whereas those with the black back of the ears are supposed to live in grasslands. These presuppositions are based on the research on the visibility of colour patterns done by Hailman (1979), asserting that light colours tend to contrast with forest vegetation, whereas dark colours are complementary to grassland habitat.

There are basically two hypotheses revealing the purpose of ear markings. Hingston (1933) puts forward a theory suggesting that the expression proposed by an ear twisted forward against a rival serves as intimidation. According to his theory of colour conflict (see Chapter 6), the patch on the back of the ears is a threatening instrument common for all representatives of the Felidae family and its presence does not depend on the habitat where a given cat occurs. (We should add that there are several species with a uniform back of the ears, e.g. *Felis nigripes* and *Puma yagouaroundi*). A notion about threatening function was later repeated by Leyhausen (1979), who asserts that ear spots are prominent during the attack threat of several felids.

The other proposed function of ear spots is quite different. Schaller (1967) suggests that conspicuous markings placed on the back of the tiger’s ears allow conspecifics to follow each other, which is extremely valuable for cubs following their mother. In this context, it is worth mentioning that the white spots are remarkable even on the ears of tiger cubs (see Figure 4).
Leyhausen (1979) believes conspicuous ear spots combine both functions. The threatening function might be phylogenetically older since the “follow-me” function is doubtful in the case of viverrids which possess ear spots (e.g. *Viverra, Genetta, Hemigalus*).

There are few species whose appearance is adorned with tufted ears: caracal (*Caracal caracal*) and four extant representatives of lynxes (*L. rufus, L. lynx, L. pardinus, L. canadensis* – see Figure 5). An ear tip is prolonged into a tassel which is black and conspicuous. According to Hingston (1933), the tassel has the same function as the ear spots: to intimidate a rival. If the ear twisted forward is additionally equipped with the tassel, the gesture of threat is more significant. Kingdon (1977) provides minute description of the ears of the caracal (see Figure 25 in Chapter 7). The ears have acquired an important communicative function and are highly mobile. Their decorative properties (contrasting light and dark areas) highlight any movement performed and thus make a whole gesture clearly visible.

**Figure 4: Contrasting white spots on back of the tiger’s ears. (Photograph by Fox Photos)**
Figure 5: Conspicuous black ear tufts of the Canadian lynx (*Lynx canadensis*). (The archive of ZOO Ostrava)

It will not be amiss to mention one more hypothesis, though not backed up by a broadly respectable author. Boyd (2005) asserts the spots on the back of ocelot’s ears can serve as false eyes tricking an attacker (an individual of another species is meant). It has the same ratio as the proposed function of eye-like spots on butterfly wings, but the hypothesis is far more difficult to verify in this case: the ocelot is primarily a nocturnal species and no one has been an eyewitness of an attack launched by larger predators (jaguar, puma) on it.

1.2.1.2 A contrasting tail tip

The position of a tail conveys aggressive or defensive intentions. Aggressive postures are often complemented with visible movements of the tail in the air, whereas in apprehensive state of mood, the tail is held down (Kiley-Worthington 1976). Generally, a contrasting tip of the tail is believed to have communicative function since it highlights its movement. Similarly to the contrasting colours of ear spots, the black tip is asserted to be visible in grasslands and plains, whereas the white tip in forests (Leyhausen 1979).

Some species of felids possess tails with repeated rings of black and white: the little spotted cat (*Leopardus tigrinus*), Geoffroy’s cat (*Leopardus geoffroyi*), cheetah (*Acinonyx jubatus*),
etc. Ringed tails are conceived as conspicuous independently on the habitat, having probably a signalling function among conspecifics (Caro 2009).

A distinct black tail tip is a trait that runs through the Felidae family (e.g. *Puma concolor*, *Felis margarita*), but the only species which possesses a tassel made of different type of hairs is the lion. According to Hingston (1933), the threatening posture of the lion is accompanied by rush movements of the tail: a black tassel swaying up and down is clearly visible. Other species of cats, with the exception of lynxes, express their emotions rather with horizontal movement of the tail. Lynxes are noticeable for extremely short tail, so called bob-tail. Hingston (1933) asserts that the way how they make the contrasting black tip visible is to lower head, elevate hindquarters and cock the tail straight up. In this position, the tail is usually moved from side to side (Ewer 1973).

A contrasting tail tip might also have a function as “follow-me” signal since kittens could easily recognize it, especially if a tail is moving. This hypothesis was asserted by Schaller (1967) and Leyhausen (1979) in the case of the Asian golden cat (*Pardofelis temminckii*) which has bright white underside of the tail tip. The last third of the tail is kept upwards and sways to and fro with the stride, a coordinated movement which strengthens the effectiveness of the signal (Leyhausen 1979, see Figure 6). Approximately the last third of the tail is kept raised also by a cheetah mother followed by cubs (Kitchener 1991). The tail is ringed and ends up with a distinct white tip. “Follow-me” signal is also observed in the case of leopards held in captivity (Leyhausen 1979).

![Figure 6: White underside of the tail tip of the Asian golden cat (*Pardofelis temminckii*). (After Leyhausen 1979)](image)
Leyhausen (1979) suggests that a contrasting tail tip alternates with ear spots: almost all species which do not have conspicuous markings on the back of the ears have a black or white tail tip. Nevertheless, he mentions three exceptions from the rule: the African golden cat (*Caracal aurata*), the caracal (*Caracal caracal*), and the flat-headed cat (*Prionailurus planiceps*).

### 1.2.2 Sexual selection

Darwin (1871) often opposes the theory of adaptive colouration worked out by Wallace. According to him, the tiger belongs to the most beautiful animals in the world and the underlying process behind the emergence of beautiful forms in animal world consists in the existence of the sense of beauty. Although Darwin asserts there is basically no difference between the coats of males and females of the tiger, he favours his concept of sexual selection to Wallace’s hypothesis of vertical stripes merging with the background. The dispute is nicely illustrated in correspondence exchange of the two great naturalists. In the letter to Wallace from 12.-13.10.1867 (Darwin Correspondence Database, letter 5648), Darwin writes:

“By the way I cannot but think that you push protection too far in some cases, as with the stripes on the tiger.”

Wallace answers by the letter from 22.10. 1867 (Darwin Correspondence Database, letter 5656) and asserts:

“I may perhaps push “protection” too far some times for it is my hobby just now,—but as the Lion & the Tiger are I think the only two non-arboreal cats, I think the Tiger stripe agreeing so well with its usual habitat is at least a probable case.”

The very first thing we must consider in relation to the existence of optically founded sexual selection is the characteristics of felid vision and the constitution of coat patterns. There are two determinants of felid coat patterns that need to be distinguished: markings and colours. Most often, markings are consisted of patches of black hairs. Black colour of these hairs is constituted by melanin and an individual hair is all-black.

Black markings are very contrasting against the underlying hairs. Therefore, they are well visible on black and white photographs, which correspond to visual representation inherent to an animal with dichromatic vision. Thus, in theory, sensory bias (Enquist and Arak 1993, cited in Flegr 2005) could lead to divergence of patterns according to specific neuropsychological preference of individual species.

On the other hand, colour hues typical for individual species might be fully recognized only by visual perception of trichromatic mammals. We do not have direct information about
colour vision of wild felids but there is a solid ground to believe that it does not differ significantly from the vision of domestic cats, which was investigated by Leyhausen (1979). Domestic cats probably have the potential to distinguish colours (their retina contains cone cells sensitive to blue light, other cone cells are sensitive to green light; see also Jacobs 1993 for discussion) but the capacity is not essential for hunting, which takes place mainly at night. It might help them for better vision by day but its real significance is not clear.

Although the sense of vision is extremely well developed among felids, it does not seem to play a crucial role during courtship. Several days before oestrus, females spray urine more often than usual and secretions are enriched with sexual hormones. Males are very responsive to the scent left by a female: they collect droplets of scent on the tongue and smell it via Jacobson’s organ. The behaviour is known as flehmening and is accompanied by turning up the muzzle and teeth baring. To conclude the course of the first stage of courtship, the sense of smell allows for non-visual contacts between potential sexual partners and announces that a female has a desire to mate.

Yet, there is another stage, when a male and a female come into visual and physical contact. The second stage may last several days. Generally said, it is now female’s turn to make her mind and accept or drive off a male. There is little known about the determinants of female’s choice and we can only speculate to which extent visual characteristics of male’s coat could be relevant.

The theory of sexual selection consists in the existence of general pattern which rules the choice and the subordination of individuals to the rules. As far as felids are concerned, we cannot be thoroughly convinced how cautious females are in their selection of a partner. We should not also preclude the possibility that females follow their individualistic choice when accepting a mate (i.e. preference does not follow a strict general rule).

An apparent exception applies in the case of lions. The lion is the only felid which displays significant sexual dimorphism. The fact that lions live in packs is another common determinant of the presence of sexual selection. A lioness is often willing to mate with several males (Alderton 1998) but her choice is not opportunistic. West and Packer (2002) suggest that a darker mane signifies a higher social status of a male and this trait constitutes preferences of lionesses in a pack.

### 1.2.3 Interspecific communication

Following his characteristic line of thoughts, Hingston (1933) asserts that a sleeping tiger reveals the white spots on the back of the ears to discourage other animals from mobbing. This
is probably hunters’ tale, nevertheless, alleged threatening function of the ear spots needs to be classified distinctively because of the suggested general effect on animals, not only on conspecifics. Hingston mentions the testimony of Beddard (without a proper citation) that ear markings resemble “a watchful and unwinking eye”. Further, Hingston is assured that a tiger sleeps deliberately in such a position that displays eye-spots: the tiger “puts his head on his fore paws and turns his ears rather forwards.” (pg. 123)

There are several hypotheses about the function of “tear stripes” of the cheetah; most of them were discussed in Section 1.2.1. One more plausible explanation consists in the means of interspecific communication. Using mounted specimens of cheetah and leopard, Eaton (1979) demonstrated that tear stripes might be important to identify the member of the species. In this perspective, tear stripes meet the definition of species-specific designative signal (Marler 1961): they have been selected for their visual distinctiveness and enable to easily discriminate between two sympatric species of felids.

1.3 Gloger’s rule and the regulation of physiological processes

In general, Gloger’s rule states that animals living in warm and humid areas are darker and possess brighter colours than those living in cold or dry regions. Gloger’s rule is often believed to operate both intra- and inter- specifically. Mazák (1979, 1980) holds that this rule also applies in the case of felids and gives examples of its intraspecific application among subspecies of the tiger and the leopard. *Panthera tigris altaica*, living in the cool region of Far East, has a light orange pelage with dull black stripes, however *Panthera tigris sumatraensis* is red-brownish with bright black stripes. Similar relation applies to leopards: individuals living in tropical forests of Africa possess brighter and darker fur than those from savannahs of East Africa or individuals from park forests in Central India. Kingdon (1977) provides further confirmation of the rule on various coats of leopards originating in Africa. The palest skin belongs to the individual from arid Horn of Africa, whereas dark skins are restrained to humid highlands of Etiopia and Kenya (Mt. Elgon). Humid mountains of Kenya and Uganda (Mt. Kenya, Rwenzori Mountains) are also home for melanistic individuals, who are seemingly all-black but show species-specific rosettes in reflected light. Kingdon reports that a melanistic form is more common in Asia than East Africa. The phenomenon of melanism will be discussed at length in Section 1.5.
Emmons (1997) asserts there is a rule which influences the distribution of two basic colour morphs of the jaguarundi (*Puma yagouaroundi*). Individuals from dryer areas tend to be yellowish-brown or red, while those inhabiting rain forest tend to be dark brown or black.

Although there is relatively good corroboration for Gloger’s rule among mammals, causes still remain unknown (Caro 2005). Some authors suggest colours obeying the rule have basic physical correlates which serve as the means of thermoregulation. Dark colours connected with hot and humid regions might enhance water evaporation (Gloger 1833, cited in Caro 2005) or protect an animal against ultraviolet radiation (Porter 1967, cited in Ortolani and Caro 1996). On the other hand, pale fur is said to reflect light, which would be of an importance in desert areas. Dark hairs impregnated with melanin are sometimes suggested to increase the durability of fur (Burtt 1981). It does not seem plausible in the case of felids, since light hairs on the lower part of the body and flanks are subject to increased contact with the undergrowth in comparison to the back (crouching, making way through thickets).

Others confirm the very same correlation between fur colour and habitats but believe that this is a matter of protective resemblance (colour harmony) in the first place. A minute account of colouration in desert animals by Cloudsley-Thompson (1979) carried out results in favour of cryptic meaning of pale colouration. Beyond the fact that animals dwelling in deserts tend to have sandy, buff or yellow backs, the hue of distinct “substrate races” resembles a local environment (colour of the soil). Although this could be caused by physiological processes as well, Cloudsley-Thompson (1979) gives an ecological account of the phenomenon, suggesting a predatory stress is very strong in deserts. As felids are commonly nocturnal hunters, it is worthy to us to account for the visibility on deserts at night. Pale colouration of desert animals is reported to keep its significance at night, as “starlight renders nearby objects visible even to the human eye, and the moon bathes the scene in a flood of silvery light” (Cloudsley-Thompson 1999, p. 128). However concentrated on preyed animals his account is, Cloudsley-Thompson extends the conclusion also to the colouration of predators. We might add that the desert cat (*Felis margarita*) with its pale fur conforms well to Gloger’s rule.

Ortolani (1999) suggests the possible means how to distinguish between physico-physiological function and camouflaging properties of patterns. Different selective pressures corresponding to adaptive functions considered affect different parts of the body. Thus, we might possibly detect the function of a pattern from its position on a body. If camouflaging properties are considered, we may suppose that the pattern covers large areas of a body (Cott 1940). Were dark colour protective against UV radiation, we might find dark areas mainly on
a dorsal part of an animal. This is true for species displaying dorsal pigmented darkening (DPD, see Kiltie 1988), e.g. the jaguar and the leopard.

Two comments may be added at this point. Firstly, many patterns allow for ambiguous explanation even if their position is considered. Facial patterns (eye contour, facial stripe: e.g. the eye stripes of the cheetah) are generally predicted to have communicative purpose (Ortolani and Caro 1996): after all, they are recognized due to their conspicuousness. But physico-physiological explanations are conceivable as well: dark eye contour might serve as antiglare devices (Eaton 1979, Ortolani 1999). Secondly, there are many doubts how selective pressures considered operate in fact. Felids possibly display their anterior parts (mainly head) to prey while on hunt, so, contrary to general belief, there is supposedly higher selective pressure for camouflaging properties of the head than of the body (back and flanks).

1.4 Colouration as the epiphenomenon of structure

Since we are primarily concerned with the ecological and ethological function of felid coat patterns, a structuralist and developmental perspective on colouration will be introduced only in basic outline.

According to Allen (1887), white markings on the head of the tiger correspond to the distribution of infra-orbital nerves (see Beddard 1892). Allen uses per analogiam argument: in the case of a hedgehog with white spites, underlying nerves and muscles for contraction of the skin were diseased. Allen’s proposition is not isolated: Tylor (1886, cited in Cott 1940) also argues that facial markings of the tiger are determined by the paths of underlying nerves.

Considering a morphological foundation of a pattern, there is no agreement which mechanisms account for the species-specific distribution of pigment cells (e.g. cell-cell or the extracellular matrix-cells interaction; see Olsson 2011). If we investigate a pattern from an ontogenetic point of view, we are inclined to prefer teleonomic account of morphogenesis: similarly to organs, patterns are “purposefully” built up by processes which go beyond incidental influence of internal structures.

In the case of felids, problems of structuralist explanation are obvious. The representatives of the Felidae family resemble one another in their morphology but differ widely in their ecology. This fact was already raised by Cott (1940), who appoints to the same anatomic plane of the cheetah, puma, leopard, and ocelot which nevertheless differ significantly in their appearance. The morph of felids undergoes small changes among individual species and the anatomy differs mainly in the apparatus of locomotion (dog-like feet of the cheetah adapted
for chasing its prey versus arboreal margay with rotating ankle joints; see Pocock 1917). There is no cue why body regions which display significant variation inter-specifically (flanks, facial area) might differ in underlying structure. As we will see in Chapter 7, similar argumentation will lead Portmann to adopt the conviction that the design of animal beings transcends adaptive functions.

In fact, there is an alternative structuralist approach which has an ambition to explain diversity of colour patterns as the result of a unified underlying mechanism (cf. Bard 1977, Gould 1984). This mechanism of morphogenesis is modelled by mathematical tools: among several different approaches (e.g. cellular automata, mechanochemical models), reaction-diffusion systems proposed by Turing (1952) and adjusted by Gierer and Meinhardt (1972) has attained most attention during the last 40 years.

Reaction-diffusion models usually consist of two partial differential equations standing for interaction of two morphogens, activator and inhibitor. Bard (1981) assumes that prepattern is formed in the areas of dermis with high concentration of a given morphogen (usually activator considered). Such a prepattern is laid down in early stages of embryogenesis so a newborn animal already possesses a pattern typical for a given species (cf. Manceau et al. 2011). Liu et al. (2006) demonstrated that reaction-diffusion model is capable of simulating coat pattern formation in the ontogeny of the leopard and jaguar. Murray (1981) shows that the variety of patterns on the body and the tail (e.g. the cheetah with spotted flanks and ringed tail) can result from different size of these areas (rings as spots blended together).

Although this approach has gained fruitful results at the intersection of theoretical and mathematical biology (Othmer et al. 2009, Murray 1981, 2003), we still need persuasive biological experiments to shed more light on the molecular and chemical nature of vertebrate pattern formation. Unfortunately, embryological studies on wild mammals are very rare (with few exceptions, e.g. Findlay 1989). Convoluted patterns are usually established at the time of birth (e.g. the tiger’s stripes) and until we have some information about their embryological formation, mathematical models must rely purely on theoretical assumptions. Further, current models involve a number of parameters with unclear connection to morphogenetic processes. Parameter fine-tuning is necessary for generation of convoluted patterns but negatively influences the robustness of proposed models (see Baker et al. 2008 for discussion). As regards felids, we may conclude that so far, reaction-diffusion models are valuable mainly for their capacity to simulate phenomenological properties of coat patterns (see Allen et al. 2011).
1.5 The case of melanism

Melanism is generally common among Carnivora and black individuals of some species of felids have obtained special attention. Among ordinary people, “black panthers” have a reputation of agile and almost demonic creatures, and only few laics know they are a variety of common leopard. Local people who share their land with leopards believe the black variety is more aggressive than the common one (Alderton 1998). That is remarkably incidental with Hingston (1933), who asserts that black leopards have a special reputation for ferocity. (At the present time of political correctness, it would be interesting to find out whether such a notion is spread through the whole range of leopard, including people with black, white and yellow colour of skin.) Inter-war period had no problem to make bold distinctions between human races, which is attested by the following anecdote:

“Black has the effect of making feline animals savage. It is certainly true that lions in zoological gardens often become restless when they see a negro or Indian.” (Hingston 1933, p. 231)

The same notion is ascribed to a melanistic form of the jaguar when compared with a common spotted form. There is probably a point in putative ferocity of melanic animals: melanin is structurally related to neurotransmitters and highly pigmented individuals are generally more active and viable than individuals with low pigment amount, albinos being an extreme example (Komárek, pers. comm.).

1.5.1 The function of melanin

The integument of animals often conveys a protective function. Feathers of birds and hairs of mammals are impregnated with several pigments (carotenoids, melanin) which react differently to individual components of light. Melanin is proposed to work as a shield against ultraviolet radiation which is extremely strong in some open habitats (e.g. deserts and polar lands possess bright surface reflecting the light).

The production of melanin is sometimes dependent on environmental (i.e. non-genetic) factors. In the case of Siamese cat, extremities and some parts of the head are dark, since they are cooler than the main part of the body. The gene responsible for this colour mutation occurs at the c (albino) locus (Searle 1968).

There are several types of colouration which are related to the occurrence of melanin in black hairs. Firstly, hairs of felid species with common spots or stripes are impregnated by black type of melanin. In this case, black pigment is present in low ratio of hairs so it does not
carry an adaptive function by its own but in the relation to an overall pattern. Secondly, dorsal pigmentary darkening (DPD) which is often present among Felidae was already discussed in respect to the neutralization of shadow (see Section 1.1.2). In the following text, we will be focusing on the phenomenon of melanism, i.e. the case when melanin is produced in (almost) all hairs of an animal.

Although there are solid experimental data showing that melanin works as an ultra-violet shield (Burtt 1979), we need to handle the hypothesis with care. Hamilton argues on several occasions (e.g. Hamilton 1979) that we do not have any persuasive proof that there is a pressure in natural conditions toward the inclusion of melanin in covering structures. Hailman (1979) points out that melanin imparts many potential advantages so that is extremely difficult to separate alternative explanations (cf. Majerus and Mundy 2003).

Indeed, there are at least three other proposed functions of melanin which have been tested experimentally on various body surfaces: abrasion resistance, thermoregulation, and camouflage.

As far as abrasion resistance is considered, Burtt (1979) shows that feathers on the wings of wood-warblers (Parulidae) exposed to the contact with airborne particles are pigmented with melanin. Unfortunately, we have little knowledge about the property of hairs in the case of felids. Theoretically, felids living in the forest (tiger, ocelot) could be exposed to high level of hair abrasion while they make their way through thick vegetation. Hairs of a black morph which are impregnated with melanin might bring selective advantage against the common form. But it is very doubtful whether hairs of non-melanistic individuals are sensitive to abrasion in levels potentially harmful to animals, so this mechanistic hypothesis remains a speculation.

The majority of authors highlight cases when melanistic individuals tend to dwell in humid or closed habitats (tropical forest). Dark pigmentation could well serve for increased water evaporation. This would be in accordance with Gloger’s rule and dark melanistic colouration thus provides an extreme example supporting the rule on intraspecific level.

Now we consider whether melanistic individuals are better equipped in terms of camouflage. Hailman (1979), who investigated conspicuous colours used for intraspecific communication, suggests that dark hues are complementary in open habitats (grassland) and light hues in closed habitats (forest). The opposite principle applies for camouflage, thus dark individuals should be cryptic in closed habitats. If we consider the habitat of tropical forest, it is hard to judge whether thermoregulation or camouflage accounts for an increased occurrence of melanistic individuals.
In our opinion, the occurrence of melanism among different species of felids does not allow for unambiguous inference about its adaptive value. There are at least 11 species with high occurrence of melanism: Geoffroyi’s cat (*Leopardus geoffroyi*), Asian golden cat (*Pardofelis temminckii*), little spotted cat (*Leopardus tigrinus*), African golden cat (*Caracal aurata*) (see Figure 7), etc. (Eizirik et al. 2003). Among them, some species inhabit mainly grasslands or savannahs (Pampas cat *Leopardus colocolo*, serval *Caracal serval*; see Kingdon 1977, Callahan and Dulaney 1997) which are open habitats. Some authors believe melanic leopards prefer to hunt in the open since it imparts challenge for cognition abilities of ungulates (Rice 1986, cited in Coss and Ramakrishnan 2000).

![Figure 7](image)

Figure 7: A skin of a semi-melanic specimen of the African golden cat (*Caracal aurata*). (Collections of National Museum in Prague, catalogue number 11965)

1.5.2 Melanism among leopards

Not all proposed functions of melanin are a good explanation for the occurrence of melanism among cats. In order to properly test the hypotheses, we would need to carry out a number of ecological studies in the first place. In the current state of knowledge, we are only able to illustrate individual hypotheses on scarce data available.

There are few field studies investigating the ecology and the distribution of melanistic individuals of the leopard. It is widely known among naturalists that “black panthers” are most frequent in southeast regions of Asia (Pocock 1929, Kingdon 1977). Kawanishi et al. (2010) confirmed general knowledge with the help of camera traps distributed in the Malay
Peninsula: from 474 samples, only 29 belonged to the spotted morph and these were without any exception taken north of the Isthmus of Kra. (However, this does not mean there are no spotted individuals south of the Isthmus – Kawanishi mentions some sporadic sightings.) Black morph is also frequent in western Java, which is generally wetter than central and eastern part of the island. The proportion of melanistic individuals to all specimens in western Java was recorded as 5/19 in the mid 20th century and 40/109 between 2000 and 2003 (Dooren 1949, respectively Foead, pers. comm., both cited in Kawanishi et al. 2010). These data might support the hypothesis that dark individuals tend to inhabit humid habitats (Gloger’s rule), though it is not clear why melanism is almost fixed in Peninsular Malaysia but not in western Java.

From the macroecological point of view, the area of the Isthmus of Kra creates an important biogeographical transition between Indochina and Sundaland. Hughes et al. (2003) assert that there is a significant difference in the composition of avifauna on either side of the transition line. The border lies in the area just north of the Isthmus of Kra and is outlined by the composition of forests: mixed moist deciduous forests in the north, and wet seasonal evergreen rain forests in the south (Richards 1996, cited in Hughes et al. 2003). Thus, the melanistic population of leopards in Peninsular Malaysia conforms well to Gloger’s rule. In this case, a black coat might facilitate the evaporation of water. It is hardly conceivable that it could act as the shield against ultra-violet radiation since leopards have enough shelter against direct sunlight in forested habitat.

Kawanishi mentions an interesting though somewhat controversial possibility that melanistic colouration might act as a protective resemblance against socially dominant tigers. Inter-generic competition between the felid species may have increased during the last 2000 years due to rapid growth of human population competing for the same habitats and species of ungulates.

However, if the theory of protective resemblance holds true, we might assume similar relations in western Java. Once densely forested highlands of wet western part of the island had been inhabited by both leopards and tigers till the half of the 20th century (the last tracks of the Javan tiger Panthera tigris sondaica were recorded in the 1970s or 1980s, see Anděra 2003 and Nowell and Jackson 1996). After the extinction of Javan population of tigers, the proportion of the spotted form of leopard might have slightly increased. In fact, the outcomes of the above mentioned studies (Dooren, Foead) carried out in the time span of 50 years testify rather for the relative increase in abundance of melanistic morph.

Nevertheless, Kawanishi and his colleagues do not support adaptive explanations in their study. They pay high attention to the theory of genetic drift, supported by the sharp division in
occurrence of spotted and black morph which is formed by the narrow Isthmus of Kra. The isthmus might create natural geographic barrier between the populations, and low rates of gene flow would be sufficient to produce largely different morphs in the separated regions. Indeed, gene flow has been found low for recent populations of tigers inhabiting the area discussed (Luo et al. 2004). To conclude, with the current stage of knowledge, any force from micro-evolutionary processes, natural selection, and physiological function (water evaporation) might account for the melanistic leopard population of the Malay Peninsula.

1.5.2.1 Genetic drift: one more theory to consider?

From the theoretical point of view, Kawanishi et al. (2010) bring a very interesting moment in context of the general problem of the significance of colour patterns. The concept of genetic drift creates the core of the theory of neutral evolution formulated by Kimura (1985) (cited in Flegr 2005). If we account for the fact that many processes on the genetic level are driven by chance, we should consequently acknowledge for similarly stochastic effects in the appearance of animals. In the case of felids, the basic question is how many loci are responsible for the change in colour pattern. The less loci code a pattern, the higher probability that genetic drift fixes the mutation of the pattern.

Other factors might contribute to the effects primarily caused by genetic drift. It would be very interesting to find out whether melanistic individuals mate preferably among themselves. If so, the role of coat colour in sexual selection should be taken into account. Unfortunately, it is hardly conceivable how to carry out a similar study in field. As regards leopards, the animals are secretive and solitary and it is likely unrealizable to trace out a significant number of pairs during mating.

The cascade of melanin production is relatively well understood for some birds and mammals (Carroll 2006). Pigment cells of skin create two kinds of melanin: eumelanin (creating blackish colouration) and pheomelanin (creating red-orange colouration). The key protein regulating the production of pigments is called the melanocortin 1 receptor (MC1R). MC1R protein binds to melanocyte stimulating hormone (MSH) which triggers the synthesis of eumelanin in the effect. Conversely, when MC1R protein is blocked by Agouti protein, pheomelanin is produced in exchange. Under usual conditions, MSH and Agouti protein are responsible for the balanced production of both pigments. But if the mutation in either MC1R or Agouti gene occurs, eumelanin is over-produced which results in melanism.

The mechanism just described accounts for most cases of melanism among felids. In the case of jaguar, melanism is a dominant trait caused by the mutation of a single gene affecting the production of MC1R protein. Five amino acids are deleted and one replaced in MC1R
protein which leads to uninterrupted production of eumelanin. Similar change in the conformation of MC1R protein is responsible for melanism among jaguarundis (*Puma yagouaroundi*).

In the case of the leopard and some other species (e.g. Geoffroy’s cat, Asian golden cat), melanism has different causes than mutations in MC1R and Agouti genes (an ancestral type of MC1R allele is present; see Eizirik 2003). As a consequence, melanism arose independently at least four times in the Felidae family.

Unfortunately, except for the case of melanism, very little is known about the genetics of colour patterns among wild felids. The only approximation available today are various patterns exhibited in distinct races of domestic cats (Eizirik et al. 2010). Until we find more about the genetics of felid coats, we shall regard the theory of genetic drift as a provoking though unproven counterpart to the selectionist theory of camouflage.
2 THE SIGNIFICANCE OF COAT PATTERNS OF YOUNG FELIDS

Although several analyses of felid coat patterns have been conducted, general attention is restricted to adult animals (Allen et al. 2011, Weigel 1961). Only few works recognized the importance of the colouration of cubs and juveniles (Werdelin and Olsson 1997). This is surprising since coats of young cats are important from several theoretical perspectives as will be demonstrated later.

In order to determine the appearance of young animals of individual species, various sources have been examined. Zoological gardens possess large collections of photographs which often document early stages of felid ontogeny. Some pictures were taken directly on the ground of ZOOs. However, this selection is restricted to species amenable for breeding in captivity. Beside direct contact to zoological gardens, some data are available from respectable zoological breeding journals such as International Zoo Yearbook. Valuable information was gathered from annual reports of Czech and Slovak associations for breeding of small and big cats (Mourek and Baghira).

Specialized journals (CATnews in the first place) are the source of the most detailed information about free-ranging felids. However, the data about young individuals are rather limited and often lack photographic documentation. Many valuable photographs are available on various internet domains (e.g. http://www.cathouse-fcc.org/cats.html, http://passion-des-felins.forum-actif.net/). There are few trustworthy addresses focused on high-quality images of wild life which serve as an excellent source of data (e.g. www.arkive.org, cathouse-fcc.org/index.html). Further, due to their cute appearance, kittens of several species mug for professional photographs as the goods designated to be sold. As regards commercial pages (e.g. http://www.superstock.com/), pictures are furnished with watermark: this disables their publication but leaves the opportunity to view important morphological features.

The Natural History Museum in London is in possession of the largest collection of felid skins and bulks in the world. With the exception of Felis bieti, the collection covers all extant felid species. In cooperation with Jakub Makal, we examined exemplars of rare species (Pardofelis badia, Pardofelis marmorata, Leopardus jacobita) and searched for young individuals among them. The result did not meet our expectation since no skins or bulks of animals younger than 6 months were available. Generally, coat patterns displayed by older subadults do not differ from typical adult form. Considering polymorphic species (Leopardus colocolo, Caracal aurata, Pardofelis temminckii, Leopardus geoffroyi), it is not possible to determine “prototypic” adult form and unambiguously decide that subadults do not undertake
change in fur pattern. However, collections are too scarce to enable statistically significant comparison between patterns of subadults and adults, so we follow the null hypothesis that individual morphs are determined before the age of 6 months also among polymorphic species.

Based on our investigation, there are 8 species which display significant change of a coat pattern on the body during ontogenesis. The list cannot be regarded as the final one since the appearance of young individuals is probably unknown for several species (e.g. *Felis bieti*, *Leopardus jacobita*, *Pardofelis badia*, *Pardofelis marmorata*; the paucity of data also challenged investigations of Jan Robovský, pers. comm.). Our search was driven by the ambition to find kittens of the possibly lowest ages. In the cases when only records of older kittens (approximately 3-4 months old) are available, there remains a possibility that the change of pattern occurs in earlier stages of ontogeny.

1.) *Felis chaus*

*Felis chaus* is usually uniform as an adult but some individuals can be faintly spotted or retain several stripes from kitten hood. Stripes are evident on the extremities but can be distinguished also on the body. Kittens around the age of 3 months display transverse stripes which can be occasionally broken up into spots (Figure 8).

![Figure 8: A three months old kitten of the jungle cat (*Felis chaus*). (Courtesy of Turovski, Tallinn ZOO, Estonia)](image)

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2.) *Felis margarita*

The body of adult specimens of *Felis margarita* is usually uniform. Seldom, insignificant spots are scattered across the flanks. In contrast, a newborn kitten of the sand cat exhibits a number of transverse stripes on the body (see Figure 9). Dark stripes sharply contrast with pale yellow ground-colour of the fur. During maturation, stripes break up into isolated spots and the whole pattern loses its intensity. However, adult animals still possess distinguished transverse stripes on the extremities.

![Figure 9: A newborn kitten of the sand cat (*Felis margarita*). (After Kondakov, Heptner and Sludskii 1992)](image)

3.) *Puma concolor*

*Puma concolor* is usually uniform as an adult without any trace of markings (Pocock 1907). (However, there is a description of 3 years old specimen with distinctive rosettes-like pattern on the flanks: see Blonk 1965.) The ground-colour of kittens is usually brownish, fading to white on the underside. The body of a newborn kitten is marked with irregular spots which are solid and dark (spots on the flanks are occasionally fainter than on the back). Although the number of spots is small compared to other felids, their big size significantly influences the appearance of an animal (see Figure 10).
4.) *Otocolobus manul*

Adult individuals of *Otocolobus manul* usually display slight vertical stripes on the posterior part of the back and loins (Pocock 1951). The body of a newborn kitten is free from any regular pattern. The back is black and the abdomen is silvery light. Since this pattern basically conforms to the dorso-ventral gradient in pigmentation, we classify it as uniform (i.e. lacking distinctive markings such as spots or stripes) (see Figure 11).

![Figure 10: Cubs of the puma (*Puma concolor*). (Photo Krchniak, courtesy of ZOO Bojnica, Slovakia)](image)

![Figure 11: Four dead newborn specimens of the manul (*Otocolobus manul*). (Photograph courtesy of Lupták, ZOO Bojnica, Slovakia)](image)
5.) *Panthera uncia*

The adult specimens of *Panthera uncia* have black rosettes or blotches on the white background. Heptner and Sludskii (1992) had an opportunity to investigate a fetus of the snow leopard a few hours before birth (Figure 12). The coat in the upper part is scattered by dark brown flecks. The flecks fuse into 3 longitudinal stripes on the croup. Some of the flecks on the back and flanks have lighter inner parts: this is a precursor to subsequent development of blotches (see also Figure 13).

![Figure 12: A fetus of the snow leopard (Panthera uncia) few hours before birth. (After Shnaposnikov, Heptner and Sludskii 1992)](image-url)
6.) *Panthera onca*

*Panthera onca* possesses a characteristic complex pattern of rosettes as an adult. On the back and flanks of the animal, the inner area of a rosette is adorned with 1-6 dots (the number may be larger). Cubs have solid black flecks up to the age of 3-4 weeks. Around the age of 5 weeks, the process of rosettes-forming is launched by lightening of the inner part of the largest flecks. After 3-4 months, there arise dots inside of the largest rosettes. The adult pattern is constituted up to the age of 10 months (see Figure 14 - Figure 16).

Figure 13: 1 month old cub of the snow leopard (*Panthera uncia*). (Courtesy of ZOO Jihlava, Czech Republic)

Figure 14: 3 weeks old cub of the jaguar (*Panthera onca*). (Photograph courtesy of Nancy Vandermey, EFBC’s Feline Conservation Center)
Figure 15: 4 months old cub of the jaguar (*Panthera onca*). (Photograph courtesy of Nancy Vandermey, EFBC’s Feline Conservation Center)

Figure 16: 7 months old cubs of the jaguar (*Panthera onca*). (Photograph courtesy of Nancy Vandermey, EFBC’s Feline Conservation Center)

7.) *Panthera pardus*

A typical adult specimen of *Panthera pardus* displays rosettes which consist of broken black margin and tawny inner area. The inner area of the rosette is darker than the basic colour of the coat (white to creamy yellow). On the head, the limbs and the tail, rosettes collapse into simple spots, respectively are not fully developed. (The significant intraspecific variability is documented in Kingdon 1977: some individuals may display the jaguar-like pattern with dots in the largest rosettes.)
Cubs of the leopard have compact black flecks up to the age of 4-6 weeks. Around the age of 8 weeks, the inner parts of rosettes begin to lighten. The adult pattern is formed already on the coat of 5 months old cubs, although their fur is still bristly and dull when compared with the coat of adults (see Figure 17 - Figure 19).

Figure 17: 4 weeks old cub of the leopard (*Panthera pardus*). (Photograph courtesy of Nancy Vandermey, EFBC’s Feline Conservation Center)

Figure 18: 8 weeks old cub of the leopard (*Panthera pardus*). (Photograph courtesy of Nancy Vandermey, EFBC’s Feline Conservation Center)
Figure 19: 5 months old cub of the leopard (*Panthera pardus*). (Photograph courtesy of Nancy Vandermey, EFBC’s Feline Conservation Center)

8.) *Panthera leo*

The body of an adult specimen of *Panthera leo* is usually uniformly tawny coloured. Sometimes (mainly on lionesses), there are rosettes exhibited on the bottom part of the flanks and the underside (Pocock 1907). On the other hand, from distance, lion cubs appear to be uniform or to exhibit transverse stripes on the whole body. In fact, the stripes consist of small rosettes or spots which are separated (see Figure 20). The pattern varies significantly in intensity with individuals. The ground-colour is tawny and fades to white on the underside but markings can be very abundant and the overall appearance rather brownish than sandy: rosettes are wider than the interspaces. Before a juvenile reaches adulthood, the markings are washed out in most cases.
2.1 Protective resemblance

Felids belong to the most effective hunters in the world. Therefore, naturalists who have been seeking for an explanation of the variety of felid coat patterns investigated their functionality for hunt. However, representatives of many felid species face considerable predation pressure. Small cats need to avoid larger predators and might seek for aggressive and protective concealment at the same time (Ewer 1973). Threats are imposed particularly on young individuals, which are vulnerable across the whole taxa of the Felidae.

There are a few species of carnivores which constitute a significant threat to felids. When they discover abandoned cubs, they do not hesitate to devour them. Eaton (1979) asserts that predation on cheetah cubs is the most important natural limiting factor for the felid. The spotted hyaena (*Crocuta crocuta*) is the deadliest enemy of the cheetah and is responsible for approximately 40% of losses to litters. Quinn and Parker (1987, cited in Kitchener 1991) report that the Canadian lynx (*Lynx canadensis*) may be predated by wolves. According to Schaller (1967), tigers are sometimes killed by the Indian wild dog (*Cuon alpinus*). Danger can arise even from herbivorous animals. The same author (Schaller 1972) witnessed deliberate deadly attacks launched by buffalos (*Syncerus caffer*) and elephants (*Loxodonta africana*) on lions.

Felids are often preyed upon by other species of the Felidae family (special case of so-called intraguild predation, see Palomares and Caro 1999). According to Abramov (1962),
Siberian tigers occasionally prey on lynxes. Even leopards were recorded to have become victims of tigers (Schaller 1967). Leopards and lions are reported to kill each other’s cubs. Cheetah cubs are especially vulnerable because an adult is not capable of defending them against larger species (leopards, lions). Leopards are readily to hunt even on adult cheetahs: although they are not able to outpace them, they can ambush them from cover (Alderton 1998).

What is significant for felid coat patterns is the fact that they are susceptible to considerable change during development. To mention two typical examples, cubs of the puma are born spotted, lion cubs are usually covered with the pattern intermediate between rosettes and stripes (Pocock 1907, Mohr 1967). Following the logic of adaptive colouration, we might therefore assume that coats of the cubs satisfy other selective demands than those of adult individuals. Generally, ontogenetic colour change correlates mainly with habitat changes (Booth 1990). As far as felids are concerned, young individuals live in the same habitat as adults so we have to look for different explanation. The first option available is that coats of young felids have the function of protective resemblance. Cubs (or kittens) before the age of 3-6 months are worthy of special attention in this regard for they are not yet capable of hunting and entirely depend on their mother’s care (juvenile lions do not kill for themselves until the age of at least 15 months; Schaller 1972).

There is also behavioural evidence suggesting the need for protective resemblance among kittens. An interesting behaviour was recorded by Leyhausen and Tonkin (1966) for the black-footed cat. When a mother is alarmed, she utters warning sounds enhancing kittens to run away from each other and remain perfectly still until she gives “all-clear” sign. The sign is accompanied by synchronous up-and-down movements of the half-flattened ears.

Having these facts in mind, it is surprising that the interpretation of felid cubs’ colouration as cryptic is quite rare. Caro (2005) shows the association between spotted coats of young artiodactyls and hider species (i.e. species that sequester their young during the first weeks after birth). Ortolani (1999) is aware of the fact that carnivores can be victims as well as hunters but predicts the function of a coat pattern (protective or aggressive resemblance) according to the size of an animal, not its age. Werdelin and Olsson (1997) believe juvenile patterns reflect the ancestral (primitive) appearance of the species. The cheetah is recognized as an exception since the cubs are less distinctively spotted than adults and have a “rug” of light hairs on the back. The significance of this appearance will be discussed separately.

The belief that the traits of young animals are very conservative and therefore valuable for the reconstruction of evolution was held by the authority no smaller than Darwin’s:
“The embryos (...) of distinct animals within the same class are often strikingly similar. (...) A trace of the law of embryonic resemblance sometimes lasts till a rather late age (...) In the cat tribe, most of the species are striped or spotted in lines; and stripes can be plainly distinguished in the whelp of the lion. (...) The points of structure, in which the embryos of widely different animals of the same class resemble each other, often have no direct relation to their conditions of existence. (...) No one will suppose that the stripes on the whelp of a lion, or the spots on the young blackbird, are of any use to these animals, or are related to the conditions to which they are exposed.” (Darwin 1859, p. 439-440)

Cott (1940) holds the same position, although he prefers adaptive accounts of colouration otherwise. To prove his point, he asserts that spotted livery is intensified in forest-dwelling species (the leopard, jaguar, serval, and ocelot), whereas spots of felids living in the open country are obliterated during ageing (the lion, puma, and lynx). Following this logic, it would mean that colouration is adaptive for adult individuals but not for young. In fact, this argument is disputable. The typical habitat of the serval is grass savannah (Kingdon 1977) and acryptic value of round markings in this environment is doubtful. All species of lynxes seem to prefer forests to the open land etc. Nevertheless, Cott has a point that uniformly coloured juveniles never acquire spots as adults.

All the same, juvenile patterns of felids demand special attention. In Section 3.3, we will investigate if colouration of kittens follows the predictive camouflaging function of coat patterns better than the design of adult individuals. To perform this task, we will assume that hypotheses suggested in Section 1.1.1 also apply for protective resemblance of juveniles. Although the limits of such an assumption are evident (worse visibility of small kittens in dense understory in comparison to the adults), we have neither sufficient data about microhabitats nor a theoretical framework suggesting a difference between patterns resulting from aggressive versus protective crypsis to allow for more elaborate analysis.

2.2 Protective mimicry

Mimetic resemblances are not very common among mammals. In the case of felids, there occurs only one phenomenon which is reported to be mimetic. The appearance of a young cheetah (up to the age of approximately 2.5 months) differs significantly from other cats: it is characteristic for a white long mantle on the back which covers short tawny hairs. Young cheetahs are the subject of the highest predatory rate among big felids (Eaton 1974, Schaller 1972). Eaton (1976) suggests that cheetah cubs resemble the honey badger or ratel (Mellivora...
*capensis*), a furious and pugnacious mustelid often living sympatrically with the cheetah. According to Eaton (1976), a white upper side of a body and a dark bottom makes an animal particularly conspicuous, constituting in fact the opposite effect to countershading. The ratel is reported to be able to drive off large predators (e.g. hyenas) and its contrasting fur is believed to carry aposematic function (Stankowich et al. 2011). Therefore, young cheetahs with a “rug” of white hairs might benefit from a (Batesian) mimetic resemblance to the ferocious mustelid.

### 2.3 Protective or aggressive resemblance?

When investigating the hypothesis of protective resemblance, we encounter an important question. How do we find out whether a specific pattern possesses qualities of aggressive or protective resemblance? Or are there properties which are camouflageing *per se*, independently on the ecological position of an animal (predator or prey)?

The author is aware of no discussion at length considering the problem mentioned. Ortolani (1999) states that aggressive and protective colouration are not mutually exclusive categories and both functions might be fulfilled in the case of small carnivores. Cott (1940) and Ewer (1973) assert that visual properties of an animal are essentially the same for a hunter and a hunted. Most of empirical tests carried out so far have investigated camouflage properties of prey, e.g. the problem of protective resemblance. There is an obvious reason for that: in the encounter of a predator and prey, a general image invokes a fast moving hunter and a fixed or very slowly moving victim. From this perspective, it is much easier to examine camouflage of prey: its model can be fixed on various backgrounds and exposed to the sight of a predator.

On the other hand, the experimental framework suitable for the investigation of a moving object is not clear. Practical limits are sometimes bridged by theoretical assumptions. Jackson et al. (1976) investigated a hypothesis that banded pattern of several snake species is responsible for the effect of flicker fusion, i.e. inability to separately perceive temporally closely spaced identical visual stimuli. When a snake escapes from a predator, its disruptive colouration virtually blends into uniform mass. Jackson and his colleagues were not able to measure escape speed experimentally but suggest that it can be derived from a relative length of the tail and circumference at midbody.

If we neglect few intuitive determinants (being carnivore versus herbivore, body size) and regard only colour pattern as such, it is problematic to predict an aggressive or protective function of a supposed camouflage. Statistical investigations of animal colouration (e.g. Ortolani and Caro 1996) regard the correspondence between a coat pattern and a habitat as an
evidence for the theory of adaptive colouration. Thus, one might assume the existence of convergence in optical design between a predator and its prey since both of them live in the same habitat. Taking into account quite volatile nature of patterns among the Felidae (consider high intraspecific variation of the Pampas cat *Leopardus colocolo*, the African golden cat *Caracal aurata*, etc.) and supposing the colouration of its main prey is adaptive, there should be a tendency for felid coat patterns to resemble those of the hunted. This is also a prediction resulting from the concept of evolutionary arm race: if other conditions remain the same, the competition between a predator and its prey seeks for the same asset, i.e. background matching in a given environment. If we consider Endler’s (1978) definition of camouflage (see the following chapter), we might bear in mind that a predator and its prey meet at a time and a place, so many factors are automatically the same (light conditions, microhabitat etc.). An objection proposing that individual species have different acuity of sight (which implies different selective pressure for cryptic properties of its prey/predator) or might be exposed to developmental constrains holds true, but merely approves of the need of theoretical framework of the problem.
3 STATISTICAL TESTS OF THE ADAPTIVE FUNCTION OF FELID COAT PATTERNS

In the previous chapters, we have introduced various assertions about the significance of felid colouration. As most authors follow the presumption that colouration has an adaptive function, we will concentrate on two general purposes of coat patterns: camouflage (background matching or disruptive colouration) and signalling function (aposematic colouration). Our attention is focused on 5 proposed associations which are amenable for testing by statistical means:

a) Spotted coats and forest;
b) Spotted coats of juveniles and forest;
c) Vertically striped coats and grassland;
d) Black/white spots on the back of the ears and grassland/forest;
e) Black tail tip and grassland.

3.1 Methods

Endler (1978) was one of the first biologists who have asserted that the problem of adaptive significance (i.e. cryptic or signalling) of animal colouration needs unified theoretical approach. In this work, he focuses on the theory of camouflage and regards a specific pattern as the result of interplay between several ecological factors, each of them working along different lines of selective force. The seven determinants of the visibility of colour patterns are the following: background matching, predation intensity and timing, predator visual acuity, colour vision, prey-to-background distance, predator flicker fusion, and sexual selection. As we can see, the determinants are proposed on the basis of the theory of protective resemblance. Nevertheless, predator-prey relation is reciprocal and we can determine analogous factors from the perspective of aggressive resemblance. It is good to mention that original testimonies about camouflage (Wallace 1870) relate almost exclusively to the factor of background matching.

Unfortunately, only few determinants have been investigated in respect to felid colour patterns. Some of Endler’s determinants are not relevant for our problem, because they are shaped mainly for different predator-prey relations (for example predator-to-background
distance is irrelevant for felids lying in ambush or crouching in undergrowth). Some informative remarks can be uttered about colour vision, hunting timing (see Section 4.2), and background matching. Sexual selection, giving growth to conspicuous patterns in theory, does not seem to be visually determined as was discussed in Section 1.2.2.

Endler (1978) states that brightly coloured animals may be well camouflaged during clear days, especially in forests with their complex mix of light and shade. These conditions make patterns with strongly contrasting patches look cryptic. This would apply perfectly to leopard and other spotted cats, but the problem is that they only rarely hunt in high sun. Most of the felids are nocturnal or are active at dawn and dusk: in crepuscular conditions, patterns with low level of contrast and brightness are predicted to be more cryptic (see also Endler 1992).

Endler (1978) further analyses what contributes for the basic determinant of crypsis: background matching. The surface of an animal can be regarded as a mosaic of patches, which differ in the size, colour, brightness and shape. These qualities of patches have to correspond with the qualities of the background (which also consists of varied “patches”) to create the phenomenon of camouflage. Endler highlights that all the variables are measurable and the concept is universal and covers special examples of general colour resemblance, disruptive colouration, and countershading. A general rule has the following form:

“A colour pattern is cryptic if it resembles a random sample of the background perceived by predators at the time and age, and in the microhabitat where the prey is most vulnerable to visually hunting predators.” (p. 321)

Endler’s approach to the problem of background matching seems to offer generally applicable methodology, at least if we investigate camouflage of prey. Can we use similar methodology to analyse felid coat patterns? The proposed function of felid coats is mainly aggressive resemblance. Accordingly, the general rule has to be reformulated as follows:

A (felid) colour pattern is cryptic if it resembles a random sample of the background perceived by prey at the time and age, and during the initial phase of pursuit which is crucial for the result of hunt.

At first sight, the ambition to investigate several optical qualities of coat patterns could bring more differentiated approach capable of generating more specific results than a general statement such as “the spotted coat of jaguar corresponds perfectly with the background in the forest”. In respect to felids, a similar task was accomplished by Godfrey et al. (1987) for a tiger and a specific grassy background. The method involves spatial frequency analysis of the animal and the background and subsequently the comparison of both. However, this approach is convenient only for the analysis of a small number of photographs and it is questionable how to select a significant set of pictures.
Moreover, there is a conceptual question if it is sensible to regard a coat of typical felid as “a mosaic of patches”. Spotted species (cheetah) and some representatives of the genus *Panthera* with rosettes (jaguar) comply better with the description such as “a wallpaper with regular pattern”. As was shown by Coss and Ramakrishnan (2000), a regular pattern can serve as a predator-recognition cue in the case of leopards, so instead of breaking the outline of a body, it might constitute its intactness from the perspective of prey (e.g. macaques).

The aim of this chapter is to test relevance of several hypotheses inferred from the theory of adaptive colouration on the whole taxa of Felidae. Felids have large areas of distribution and individual species often inhabit several habitats. Thus, for practical reasons and the lack of detailed information about determinants, we cannot undertake a complex methodology similar to that proposed by Endler for the theory of camouflage. The only convenient methodology is the one usually used in macroecology (see also Ortolani 1999 for discussion). To cover all current species of felids, we have to restrict our attention to the basic characteristics of colour patterns on one side and categorization of habitats on the other side.

To show if there is a significant association between the appearance of a given felid species and habitats it lives in, we need a statistical tool examining anticipated correlation. It is necessary to take phylogenetic history of the felids into account, since coat patterns do not depend only on ecological factors but can be determined by ancestor states. This fact was stressed by various authors (e.g. Garland 1992, 1993) and several methods have been developed to incorporate phylogenetic information into statistical analyses (e.g. Felsenstein’s (1985) phylogenetically independent contrasts, Maddison’s (1990) concentrated-changes test, Pagel’s (1994) test for correlated changes).

Considering our problem, we need to assess the relation between variables which are not suitable for quantitative approach. Felid coat patterns are usually categorized on the basis of the shape of a repeating unit: stripes (tiger), rosettes (jaguar), blotches (clouded leopard) etc. Although there are some suggestions about phylogenetic transformation between specific types of patterns (see Hemmer 1966 and his investigation of hybridization between tigers and lions) and some species display colouration which is intermediate in respect to clear categories (markings of the snow leopard are transitory between rosettes and blotches), any attempts to define transformational series or continuous array of patterns are significantly biased by the theoretical assumptions held by an author. (In this respect, discussion of the work of Weigel (1961) carried out by Werdelin and Olsson (1997) is especially instructive.)

As far as habitats are considered, it would be suitable to assess their optical characteristics, such as availability of light, geometric shapes often found among vegetation (e.g. round-
shaped leaves, vertical stems of grass), colours usually occurring in the background etc. There are some attempts to measure these qualities quantitatively (Hailman 1979) but those are restricted to a small number of habitats and therefore not amenable for our goals: felids inhabit the highest variety of environments of all carnivores.

For these reasons, our analysis is concerned with the relation between two categorical traits. Both patterns and habitats are divided into mutually exclusive categories. There are several possibilities how to perform these classifications and the results can be biased to a considerable extent. Therefore, we comprise works of several authors and perform statistical analysis for different types of categorization to check out robustness of the results.

Our investigation focuses on 38 extant felid species following a conservative taxonomy of felids: *Neofelis nebulosa* comprises Bornean variety (*Neofelis diardi*; cf. Buckley-Beason et al. 2006, Kitchener et al. 2006) and *Leopardus colocolo* subsumes three geographical races (*L. braccatus*, *L. pajeros* and *L. colocolo*; cf. García-Perea 1994). The domestic cat (*Felis catus*) is added into the analysis since its inclusion prevents the distortion of a phylogenetic tree. If a given source does not provide any data about some investigated species, character states are added according to comprehensive works about felids and carnivores (mainly Sunquist and Sunquist 2002, Sunquist and Sunquist 2009).

There have been several attempts to assess the significance of coat patterns of carnivores (Ortolani and Caro 1996, Ortolani 1999, Stankowich et al. 2011). The approach employed by this work is different in several aspects:

a) **Restriction of the analysis to felids**

Although the colouration of felids and its significance is subordinate to the problem on the level of all carnivores, there are some merits in the restriction to the taxa of the Felidae. First of all, it enables to pay closer attention to the classification of patterns and habitats. The phylogeny of felids is very well resolved (Johnson et al. 2006) and phylogenetic signal can therefore be satisfactorily incorporated into statistical analysis. In this respect, we add the banded linsang (*Prionodon linsang*) as an outgroup of the Felidae to the analysis.

b) **The use of Pagel’s (1994) test for correlated changes accounting for shared ancestry**

In their investigation of the colouration of carnivores, the concentrated-changes test (Maddison 1990) was used by Ortolani and Caro (1996) and Ortolani (1999). The results of the method can be influenced by errors in the reconstruction of ancestral character states (Maddison 2000). Here, we employ Pagel’s test for correlated changes. It is a very general method for investigating correlated evolution in two categorical traits which does not rely on the reconstruction of ancestral states (Pagel 1994). Our use of Pagel’s test is based on the implementation in MESQUITE 2.75 (Maddison and Maddison 2011). All P-values and log
likelihood differences (LD) between 8 and 4 parameter models were calculated from 200 simulations using 10 extra iterations per simulation. The significance level $\alpha$ is put equal to 0.05.

c) Detailed attention to classification of coat patterns

Together with the investigation of coat patterns among young felids, we also analysed coats of adults. From several works dedicated to the colouration of carnivores (or specifically of felids), the work of Werdelin and Olsson (1997) is adopted as a guide for our categorization of coat patterns (data sets 2.D and 3.A) (see Figure 21). Using a large number of photographic material, we believe there is a need for a new distribution of traits which differs from the data sets 2.A, 2.B and 2.C in several cases (a detailed list of sources is described in Chapter 2). The results are summarized in Appendix, Table B, data set 2.D. High attention was paid to polymorphic species (*Pardofelis temminckii, Leopardus colocolo, Leopardus jacobita, Leopardus geoffroyi*) with the intention to track down all common morphs.

![Figure 21: Categorization of coat patterns. Left column, top to the bottom: spots, rosettes, stripes; right column, top to the bottom: small blotches, blotches, uniform. (From Werdelin and Olsson 1997)](image)

d) Comparison of the results for several categorizations

As we will see, the results are very sensitive on the definition of traits and distribution of states. Namely, there are a large number of different definitions of habitats available in literature about carnivores. As habitat preference is a part of every hypothesis that will be investigated, we will perform tests according to various sources, marked as data sets 1.A, 1.B and 1.C.

1) Habitat preference

Distribution of characters for individual species is attached in Appendix, Table A.
   Habitat: 0 = temperate forest; 1 = tropical forest; 2 = grassland; 3 = arctic; 4 = riparian and aquatic; 5 = desert.

   Habitat preferences: 0 = temperate forest; 1 = tropical forest; 2 = coniferous forest; 3 = riparian habitat; 4 = grasslands and plains; 5 = mountains; 6 = desert and semideserts.

   Strong species association by habitat type: 0 = closed forest and woodland; 1 = open or interrupted woodland; 2 = settled areas (cropped, residential, commercial and associated marginal lands); 3 = grass and shrub complexes (low vegetation with few or no trees); 4 = tundra, desert and semi-desert; 6 = major wetlands.

3.2 Spotted coats and forest

A spotted coat is a compound category which subsumes flecks or spots, rosettes, various blotches, bands, etc. The hypothesis that a spotted coat serves to conceal a felid in the shade of a forest was statistically tested (the concentrated-changes test) by Ortolani and Caro (1996) and Ortolani (1999) with positive results. In addition, there is also a significant correlation between spotted coats and arboreal life. Because spots are widely excepted as an ancestral trait in colouration of felids (Werdelin and Olsson 1997), tests were sensitive to the inclusion of phylogenetic signal. Losses and gains of the trait during evolutionary history had to be taken into account. Ortolani (1999) states that spots are often lost with the switch to more open habitat, as it is the case of the lion (a common ancestor of Panthera probably possessed rosettes).
If we leave evolutionary history apart, there are some obvious exceptions from the rule: *Acinonyx jubatus* and *Caracal serval* (both spotted) inhabit mainly grasslands or woodlands, and *Puma concolor* (uniform) lives in several habitats including forests.

We will test the hypothesis that a spotted coat serves for camouflage in a forest on the data based on 3 categorizations of habitats (see above) and 4 categorizations of patterns.

2) **Adult coat pattern**

Distribution of characters for individual species is attached in Appendix, Table B.


Pattern: 0 = uniform; 1 = spots; 2 = vertical stripes; 3 = horizontal stripes; 4 = bands.


Pattern: 0 = flecks; 1 = rosettes; 2 = small blotches; 3 = blotches; 4 = vertical stripes; 5 = uniform.


Pattern: 0 = no spots or horizontal stripes; 1 = spots or blotches; 2 = horizontal stripes.


Pattern: 0 = flecks; 1 = rosettes; 2 = small blotches; 3 = blotches; 4 = vertical stripes; 5 = uniform.


Based on the data sets 2.A and 1.A (test 1.1), species with flecks (a collective category for spots and bands) are more likely to inhabit forest than other habitats (log likelihood difference (LD) = 5.269, P = 0.005). To check the robustness of the result, Pagel’s test is also performed on the data sets 2.B and 1.B (test 1.2), respectively 2.C and 1.C (test 1.3). In the former case, the positive conclusion is obtained again (LD = 3.744, P = 0.015), whereas in the latter case, the effect is not significant (LD = 1.250, P = 0.445). To find out possible biases in either data
set 2.C or 1.C, we perform additional Pagel’s test on the data sets 1.A and 2.C (test 1.4). The result shows stronger association but is not significant again (LD = 2.441, P = 0.100) so we assume that data 2.C might be substantially different from 2.A. In fact, there are only 3 species which are ascribed with different distribution of coat patterns: *Pardofelis badia*, *Leopardus jacobita* and *Prionodon linsang*. As we can see, the reason why data are in conflict does not lie only in different definition of traits but also ambiguities in distribution. This suggests that the validation of the hypothesis might be treated with caution.

Based on the investigation of specimens in the Natural History Museum in London and on photographs available on the internet, *Pardofelis badia* has a uniform coat (Figure 22). *Leopardus jacobita* is a polymorphic species: we prefer to subsume patterns into categories of flecks, small blotches or uniform colouration (Figure 23 and Figure 24). A viverrid *Prionodon linsang* is classified as spotted since its “bands” do not match a more appropriate category of patterns among felids.

Figure 22: A uniform coat of *Pardofelis badia*. (Collections of Natural History Museum in London)
Figure 23: *Leopardus jacobita*, a specimen with small blotches on the flanks. (Collections of Natural History Museum in London)

Figure 24: *Leopardus jacobita*, a specimen with flecks on the back and the flanks. (Collections of Natural History Museum in London)

The distribution of traits based on our investigation cannot confirm the hypothesis about camouflaging properties of spotted coats: Pagel’s test performed on the data sets 2.D and 1.A (test 1.5) is not significant (LD = 1.244, P = 0.255) (see also visualisation by the mirror tree in Appendix, Figure A). The results of test 1.1 – 1.5 are summarized in Table 1.
<table>
<thead>
<tr>
<th>Data set</th>
<th>Pattern</th>
<th>Data set</th>
<th>Habitat</th>
<th>LD</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test 1.1</td>
<td>2A &amp; 4</td>
<td>1A</td>
<td>0 &amp; 1</td>
<td>5.269</td>
<td>0.005</td>
</tr>
<tr>
<td>Test 1.2</td>
<td>2B &amp; 1 &amp; 2 &amp; 3</td>
<td>1B</td>
<td>0 &amp; 1 &amp; 2</td>
<td>3.744</td>
<td>0.015</td>
</tr>
<tr>
<td>Test 1.3</td>
<td>2C &amp; 1</td>
<td>1C</td>
<td>0</td>
<td>1.250</td>
<td>0.445</td>
</tr>
<tr>
<td>Test 1.4</td>
<td>2C &amp; 1</td>
<td>1A</td>
<td>0 &amp; 1</td>
<td>2.411</td>
<td>0.100</td>
</tr>
<tr>
<td>Test 1.5</td>
<td>2D &amp; 1 &amp; 2 &amp; 3</td>
<td>1A</td>
<td>0 &amp; 1</td>
<td>1.244</td>
<td>0.255</td>
</tr>
</tbody>
</table>

Table 1: The association between spotted coats and living in forest.

It is good to mention that our method is inclined to show positive correlations between two investigated traits if one (or two) of them has multiple states. Pagel’s methodology allows investigating relationships between two dichotomous variables (i.e. presence or absence of a given state), therefore a multiple state is analysed as the multiple occurrence of (preferably) mutually exclusive states. For example, *Leopardus colocolo* inhabits both forest and grassland and can be uniform or spotted (Ortolani and Caro 1996). If we test the hypothesis that spotted species inhabit forest, this case would contribute to confirmation (forest: present, spots: present), although a spotted morph might prefer open grassland.

Following our analysis lead by Pagel’s test for correlated changes, one must conclude that the results are very sensitive on the definition of traits and distribution of states. For example, original data by Ortolani and Caro (1996) (test 1.1) yield a persuasive confirmation of the hypothesis that spotted coats serve for camouflage in the forest. However, a slight change inherent in our classification of patterns (data set 2.D) influences the result of Pagel’s test to the extent that the same hypothesis cannot be corroborated. To sum it up, few species with a disputable type of coat pattern lower robustness of the test to the extent that the hypothesis about camouflage properties of a spotted coat remains an open question.

### 3.3 Spotted coats of juveniles and forest

3) Juvenile coat pattern

Distribution of characters for individual species is attached in Appendix, Table B.


Pattern: 0 = flecks; 1 = rosettes; 2 = small blotches; 3 = blotches; 4 = vertical stripes; 5 = uniform.

As we discussed in Section 2.3, considering patterns of coats and habitats alone, we have no means to distinguish between aggressive and protective function of resemblance. Therefore, similarly as in the previous tests, we only look for correlation between the occurrence of spots among juveniles and the presence of forest among habitats inhabited by a given species.

The implementation of Pagel’s test for correlated changes in MESQUITE 2.75 (Maddison and Maddison 2011) requires that every trait is defined for all species in the analysis. Therefore, in order to carry out the test for coat patterns of juveniles, if the appearance of young individuals of a species is unknown (e.g. Felis bieti, Leopardus jacobita, Pardofelis badia, Pardofelis marmorata), the pattern is classified as the same as if on adult. As we do not have alternative data sets classifying juvenile coat patterns, we will examine the hypothesis in respect to several definitions of habitats.

<table>
<thead>
<tr>
<th>Test</th>
<th>Data set</th>
<th>Pattern</th>
<th>Data set</th>
<th>Habitat</th>
<th>LD</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test 2.1</td>
<td>3A</td>
<td>0&amp;1&amp;2&amp;3</td>
<td>1A</td>
<td>0&amp;1</td>
<td>0.377</td>
<td>0.670</td>
</tr>
<tr>
<td>Test 2.2</td>
<td>3A</td>
<td>0&amp;1&amp;2&amp;3</td>
<td>1B</td>
<td>0&amp;1&amp;2</td>
<td>0.814</td>
<td>0.530</td>
</tr>
<tr>
<td>Test 2.3</td>
<td>3A</td>
<td>0&amp;1&amp;2&amp;3</td>
<td>1C</td>
<td>0</td>
<td>0.856</td>
<td>0.490</td>
</tr>
</tbody>
</table>

Table 2: The association between spotted coats of juveniles and living in forest.

The results of the tests 2.1, 2.2, 2.3 (see Table 2) do not give evidence of the correlation between the possession of spots among juveniles and living in the forest (see also visualisation by the mirror tree in Appendix, Figure B). Therefore, our hypothesis about camouflaging properties of spotted coat patterns of young felids cannot be corroborated. In spite of the presence of strong predatory pressure on kittens of felids, it seems that juvenile patterns reflect the ancestral (primitive) appearance of the species rather than camouflaging function.
3.4 Vertically striped coats and grassland

The hypothesis that a striped coat serves to conceal a felid in grassland was statistically tested with contradictory results. Ortolani and Caro (1996) suggest there is no significant correlation between vertically striped carnivores and living in grassland habitat. However, Ortolani (1999) found clear association between vertically striped coat and grassland habitat. Although the method used (the concentrated-changes test) was the same in both articles, Ortolani does not discuss the contradictory results. Caro (2005, p. 127) enhances confusion when citing both works and concluding that „striped species are found in grasslands, supporting the hunters’ old adage that tigers are striped to hide in tall reeds and grasses“. However, table 2 (see Caro 2005) shows clearly that there was no significant association found between striped coat pattern and grassland (or any other habitat) in felids.

There are only few felids with vertical stripes. According to Ortolani and Caro (1996), this trait is characteristic for Panthera tigris, Felis silvestris and Leopardus jacobita. (Felis margarita and Otocolobus manul are classified as horizontally striped but we find no clear justification for this characteristic.) The data set 2.A additionally includes Felis bieti and Felis libyca which are classified as vertically striped. According to our classification of patterns (data set 2.D), adult individuals of Felis margarita and Otocolobus manul also display vertical stripes on the body, whereas the markings of Leopardus jacobita might be rather related to flecks.

With the use of Pagel’s test for correlated changes and based on the original data by Ortolani and Caro (1996) with the addition of several species, we find that felids inhabiting grassland are more likely to possess stripes (see test 3.1, Table 3). However, several other tests do not show that the association is significant (tests 3.2, 3.3, 3.4 yield p-value higher than 0.05). Again, one must conclude that the results are very sensitive on the definition of traits and the distribution of states.

<table>
<thead>
<tr>
<th>Test</th>
<th>Data set</th>
<th>Pattern</th>
<th>Data set</th>
<th>Habitat</th>
<th>LD</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test 3.1</td>
<td>2A</td>
<td>2</td>
<td>1A</td>
<td>2</td>
<td>3.920</td>
<td>0.020</td>
</tr>
<tr>
<td>Test 3.2</td>
<td>2B</td>
<td>4</td>
<td>1B</td>
<td>4</td>
<td>0.945</td>
<td>0.590</td>
</tr>
<tr>
<td>Test 3.3</td>
<td>2D</td>
<td>4</td>
<td>1A</td>
<td>2</td>
<td>1.498</td>
<td>0.180</td>
</tr>
<tr>
<td>Test 3.4</td>
<td>2D</td>
<td>4</td>
<td>1B</td>
<td>4</td>
<td>1.407</td>
<td>0.145</td>
</tr>
</tbody>
</table>

Table 3: The association between vertically striped coats and living in grassland.
3.5 Black/white spots on the back of the ears and grassland/forest

4) Back of the ears

Distribution of characters for individual species is attached in Appendix, Table C.


Back of ears: 0 = darker than head; 1 = uniform; 2 = lighter than head; 3 = white spot; 4 = white tip; 5 = black tip.


We will test two hypotheses about the occurrence of distinctly coloured back of the ears: (i) species living in grassland tend to have black spots, (ii) species living in forest tend to have white spots.

Black marks on the back of the ears are a compound category which subsumes black ear tips and the back of the ears darker than the head. The hypothesis that conspicuous black marks are significant for intraspecific communication was statistically tested (the concentrated-changes test) by Ortolani and Caro (1996) with an ambiguous result.

To test the hypothesis (i) on an adjusted data set of ear marks and better resolved phylogeny by Johnson et al. (2006), we performed three tests on the data set 4.A with alternative definition of habitats 1.A, 1.B and 1.C. The results of the tests 4.1, 4.2, 4.3 (see Table 4) do not give evidence of the correlation between the possession of black marks on the back of the ears and living in grassland.

White marks on the back of the ears join white ear tips, white spots, and the back of the ears lighter than the head into one category. If we leave evolutionary history apart, there are some obvious exceptions from the hypothesis (ii): Panthera uncia has distinct white ear spots but inhabits open landscape, Caracal serval also tends to live in rather open habitats like grassland and semi-desert.

Nevertheless, according to Ortolani and Caro (1996), a white mark on the back of the ears is an ancestral state in the felids so it is necessary to include phylogenetic signal in the analysis. The concentrated-changes focused on whether the losses of the trait during evolutionary history correlate with the switch to a more open habitat (e.g. the case of Caracal caracal with black tufts on the ears and semi-desert habitat; based on the phylogenetic reconstruction used by Ortolani and Caro, its ancestor probably possessed white marks on the back of the ears) and confirmed the hypothesis (ii).
Similarly as for the hypothesis (i), we performed three tests on the data set 4.A with alternative definition of habitats 1.A, 1.B and 1.C. The results of the tests 4.4 and 4.5 (see Table 4 and also visualisation by the mirror tree in Appendix, Figure C) do corroborate the hypothesis that species with white markings on the back of the ears tend to live in a forest. An outcome of the test 4.6 is not significant.

To sum it up, there is no evidence of the correlation between the possession of the black back of the ears and living in grassland, whereas there is a strong tendency for species living in a forest to display the white back of the ears.

<table>
<thead>
<tr>
<th>Test</th>
<th>Data set</th>
<th>Back of ears</th>
<th>Data set</th>
<th>Habitat</th>
<th>LD</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test 4.1</td>
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<td>1A</td>
<td>2</td>
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<td>0.845</td>
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<tr>
<td>Test 4.2</td>
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<td>4</td>
<td>1.452</td>
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<td>1.727</td>
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<td>5.976</td>
<td>0.005</td>
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<tr>
<td>Test 4.5</td>
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<td>0&amp;1&amp;2</td>
<td>9.783</td>
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</tr>
<tr>
<td>Test 4.6</td>
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<td>1.987</td>
<td>0.310</td>
</tr>
</tbody>
</table>

Table 4: The association between the markings on the back of the ears and habitat.

3.6 Black tail tip and grassland

5) Tail tip
Distribution of characters for individual species is attached in Appendix, Table C.

Tail tip: 0 = uniform; 1 = black; 2 = white; 3 = black or light.

According to the data set 5.A, there are only 2 species with distinct white tip of the tail: *Acinonyx jubatus* and *Pardofelis temminckii*. This is very scarce occurrence which does not allow testing the hypothesis about the occurrence of white tip of the tail in forest habitat significantly. Therefore, we will focus on the correlation between the black tip of the tail and grassland habitat.
Some species of felids display intraspecific variation in tail tip markings: they can possess either white tip or black tip (e.g. *Leopardus tigrinus*, *Leopardus geoffroyi*). These species often have a ringed tail in fact so the colour of tail tip is incidental. In order to keep phylogenetic signal as clear as possible, we classify “black or white” tail tip as an additional character state (cf. Ortolani 1999).

According to Ortolani and Caro (1996), the association between the black tail tip and grassland habitat is not significant among felids. Indeed, there are a few species inhabiting the forest which possess the black tail tip at the same time: *Lynx lynx*, *Panthera onca*, *Prionailurus rubiginosus*, *Pardofelis marmorata*, *Pardofelis badia*, etc. To test whether these could be only exceptions from the rule resulting from the existence of phylogenetic signal, we employ Pagel’s test for correlated changes. Three tests based on the data set 5.A with alternative definition of habitats 1.A, 1.B and 1.C are performed. The results of the tests 5.1, 5.2, 5.3 (see Table 5) do not give evidence of the correlation between the possession of black tail tip and living in grassland.

<table>
<thead>
<tr>
<th>Test 5.1</th>
<th>Data set</th>
<th>Tail tip</th>
<th>Data set</th>
<th>Habitat</th>
<th>LD</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
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<tr>
<td>Test 5.2</td>
<td>5A</td>
<td>1</td>
<td>1B</td>
<td>0&amp;1&amp;2</td>
<td>2.003</td>
<td>0.165</td>
</tr>
<tr>
<td>Test 5.3</td>
<td>5A</td>
<td>1</td>
<td>1C</td>
<td>0</td>
<td>1.870</td>
<td>0.275</td>
</tr>
</tbody>
</table>

Table 5: The association between the black tail tip and living in grassland.
4 ADAPTIVE COLOURATION: THEORETICAL ISSUES

4.1 The tiger, scientists and hunters

In the pursuit of solving the question of the significance of tiger stripes, the most reliable method seems to be direct observation in vivo. In this respect, we might pay attention not only to scientific treatises but also to memories of hunters. Jim Corbett probably encountered far more tigers than anyone else in the history and we were eager to find out whether he made any experience with cryptic properties of tiger’s colouration. Unfortunately, as far as our knowledge goes, only indirect notions are present in his works.

“When one is looking for a tiger in heavy jungle everything red that catches the eye is immediately taken for the tiger, and here, not only could I see the red of the tiger, but I could also see his stripes. For a long minute I watched the object intently, and then, as the face you are told to look for in a freak picture suddenly resolves itself, I saw that the object I was looking at was the kill, and not the tiger; the red was blood where he had recently been eating, and the stripes were the ribs from which he had torn away the skin.” (Corbett 1959, p. 131)

According to this testimony, one might say that a reddish tone of Indian tiger (and possibly notion of stripes) makes up a conspicuous mark in the sight of an experienced hunter. If a man could train his vision to track down a tiger, it seems only natural to suppose that the vision of tiger’s prey is especially attuned to this task since an early age. But Corbett’s (1959) notes provide justification also for the opposite opinion. The following extract suggests that the colouration of the tiger does possess cryptic properties:

“(The significance of this) will be apparent when it is realized that, while the sportsman is trying to get a sight of the tiger, the tiger in all probability is trying to stalk the sportsman, or is lying up in wait for him. The contest, owing to the tiger's height, colouring, and ability to move without making a sound, would be very unequal were it not for the wind-factor operating in favour of the sportsman.” (Corbett 1959, p. 47)

(A derogative note below the line: In fact, a successful sportsman checks out whether tiger’s appearance conforms to the theory of protective resemblance, whereas a bad hunter would receive persuasive argument about the existence of aggressive resemblance few seconds before his death.)

It is beyond the scope of this work to collect enumerate encounters recorded by tiger hunters in the past. Concerning alleged cryptic appearance of tigers, it should be mentioned
that different sources bring ambiguous testimonies. Major Walford believes that the visibility of the tiger is significantly reduced by its colouration and that the same applies for the leopard. He once failed to see a wounded tiger lying in the grass under a tree at a distance of about 20 yards (app. 18 meters) of an open jungle, though the spot was shown to him by natives. He was truly amazed by what followed afterwards: “… I eventually made him out well enough to shoot him, but even then I could not see at what part of him I was aiming.” (from the correspondence between Major Walford and Wallace, cited in Cott 1940, p. 141)

On the other hand, Perry (1964) suggests that a high percentage of deer kills by the tiger are the direct result of prey’s curiosity. He mentions the hunter called “Hawkeye” (1876) who asserts that tiger’s striking colour pattern may serve to attract deer’s attention. A tiger displaying its half concealed striped body would induce deer to investigate the object: one or two inquiring steps toward a tiger can be lethal.

Schaller (1967) describes several occasions when deer displayed curious and incautious behaviour. On one occasion a lead chital doe (Axis axis), followed by 6 other animals, investigated a bush after she smelled a scent of a tiger. Similar behaviour was recorded for the barasingha (Cervus duvauceli). A herd of stags scented a tiger family which was resting after a heavy meal in a thicket (the fact known to the observer but probably not to barasinghas). Instead of dashing away, they curiously walked around and one yearling animal even entered the bush as if trying to get a better view. Nevertheless, Schaller emphasizes that typical behaviour of the deer consists in an attempt to circumvent situations when a tiger could be encountered. He illustrates this by a situation when a stag, formerly coming slowly to a trail, was rapidly alerted by the scent of a tiger and immediately trotted off.

We see that Perry supports an empirical fact (curiosity of deer) by a controversial theoretical supposition (alluring properties of the tiger’s coat). On the other hand, Schaller asserts that the deer’s curiosity is an exception from a general rule, which is to avoid a predator whenever possible. The deer may be sometimes attracted by a scent of a tiger but situations when the curiosity leads to a lethal end are without any doubts very rare.

Neither Perry nor Schaller attempted to provide a general picture of the economy of nature. Nevertheless, we might outline some tendencies inherent to their positions. Firstly, we must be aware of implicit distrust creating a barrier between academic scientists on the one hand and hunters (and amateur naturalists) on the other hand. The former are inclined to adhere to theories and have an ambition to verify them in nature, whereas the latter rely on personal experience and individual sightings.

The works of Perry (1964), who compiled the literature about the tiger and included a lot of hunters’ testimonies, and Schaller (1967), who brought out one of the first serious academic
studies of wildlife, illustrate the gap. Perry mentions a lot of observations of tiger’s behaviour and discusses the significance of tiger stripes in length. The book is full of thought provoking moments but the whole lacks a unified concept. Schaller (1967) characteristically comments on Perry’s account of the life of the tiger: “the over-all effect of the book is to emphasize the lack of knowledge about the habits of this species” (p. 222). Moreover, Schaller disregards some observations made by hunters and criticizes Perry for being uncritical in his selection of sources. Schaller himself follows a conscientious style of research and brings details about the composition of prey, feeding habits, the size of home ranges of tigers etc. Facts are often represented by quantitative data and summarized in tables. To accomplish the requirements of quantitative methods, the behaviour of the tiger is exploited thoroughly but rather indirectly: Schaller’s sporadic sightings of tiger’s hunts are outnumbered by the inferences based on the analysis of feces left by tigers and carcasses of their kills.

It is not the aim of this paragraph to judge which position is more credible, nevertheless, it will not be amiss to highlight that both have justification in the exploration of nature. Surely, many appealing observations made by amateur naturalists are probably nothing more than hunters’ tales, but it would be lamentable haughtiness to ignore rich experience that has been recorded by amateurs for at least the past 150 years. For that matter, Wallace was primarily an amateur enthusiast who succeeded to put his enumerate encounters with animals into a general theory of the adaptive function of colouration. One might speculate if the great naturalist had ever seen a tiger in a terrain, but his anecdotic story about tiger stripes blending with vertical stems of bamboo still creates the fundament of general understanding of coat patterns among the Felidae.

### 4.2 Hunting at night

Most of felids are nocturnal or crepuscular hunters. Considering that the availability of light is one of the determinants in investigations of the matter of camouflage (Mottram 1916, Endler 1978), the time of the day requires special attention. A logical objection to the theory of adaptive colouration emerges in the case of nocturnal hunters: are the details of the coat pattern important if the whole appearance of a hunter is covered by dark? Are hunted animals capable of distinguishing colours during the night? Cott (1940) addresses this objection as unreasonable for it is not colour but tone what must be assessed. Prey do not need to possess especially mighty sight to recognize contrasting areas of a predators’ body because some
habitats (e.g. deserts) are endowed with clear visibility due to starlight and nearby objects are well distinguishable even to human eyes (see also Cloudsley-Thompson 1999).

Cott’s general comments on the problem of camouflage by night should be revised in respect to felids. First of all, it will not be amiss to mention that all classical accounts of cryptic properties of felid coats, as we have reviewed them in Section 1.1.1, are based on daytime experience or mental construction. Beddard (1892) suggested that the spots of jaguar “harmonise with the oval patches of sunlight which penetrate between the leaves of the trees”. Even Cott (1940) matches whitish ground colour of snow-leopard’s fur to almost treeless highlands of Central Asia. Schaller (1972) suggests markings are not important for camouflage because their shape varies considerably among big felids and adult lions lack them completely. According to him, what matters in the case of lions is tawny colour of their pelage.

It is likely that colour is unimportant in crepuscular conditions and during the night, for even animals with normal colour vision do not see colours after the Purkyně’s shift (Walls 1942, cited in Endler 1978). Therefore, considering camouflage, we would expect that colour plays a significant role only in species usually active by day (e.g. cheetahs). General contrast of a coat (tone in Cott’s words) might be important during the night, according to the availability of light in the environment. One should also bear in mind that some habitats with dense cover (e.g. tropical forest) barely let some light through its foliage by night, leaving visual cues practically irrelevant in predator-prey encounters.

It is generally thought that felids are nocturnal or crepuscular animals, but the reality is far more complex. Most felids hunt during dawn and dusk, but they can also be active during daytime. Seidensticker (1976) detects surprisingly high daylight activity of leopards and tigers in Royal Chitawan National Park. Lions frequently hunt by day, though their activity around noon is considerably lowered by heat (Schaller 1972). Jaguars are reported to be both diurnal and nocturnal and jaguarundis are probably more active during day than night (Rosa 2000). Cheetahs hunt almost exclusively during daytime (Eaton 1974). Yet other species seem to be almost strictly nocturnal. From American species, this applies mainly to the margay (Leopardus wiedii) and the oncilla (Leopardus tigrinus). Olbricht and Sliwa (1997) state that semi-desert black-footed cat (Felis nigripes) is also strictly nocturnal. (Nevertheless, according to Leyhausen and Tonkin 1966, these cats are often active by day in captivity.)

Data comparing success rate for day and night hunts are sparse. Among lions using stalking and running, Schaller (1972) detects 21% success rate for day hunts and 33% for night hunts. When the observations are restricted to communal hunts of zebras and wildebeest, the difference is 27% to 42% in favour of night time. However, similar data only provide
argument for increased secretiveness of felids during night time and do not resolve the problem of camouflage of coat pattern (respectively coat colour).

To sum it up, we believe there is a lack of conceptual framework to include nocturnal conditions in the assessment of the theory of crypsis. There is no doubt that a stalking cat is a highly cryptic animal and this applies twice as much at night. A potential experiment is very demanding since it would have to be sensitive to slight differences in visual acuity of prey: do stripes equip a tiger with adjusted camouflage in low light conditions? Taking into account difficulties with similar experiments in daylight, one remains but sceptical about the possibilities to properly assess visual properties of felid coat patterns at night.

4.3 Colouration as a cue for recognition

Research carried out on bonnet macaques (*Macaca radiata*) (Coss and Ramakrishnan 2000) reveals an interesting perspective on the significance of the spotted coat of the leopard. It is argued that the spots have become a recognition cue for macaques during their long coexistence with the predator. This innovative approach twists the traditional concept of camouflage and leads to several theoretical reflections.

Classical accounts of the phenomenon of aggressive resemblance (Poulton 1908, Cott 1940) suggest that some animals are equipped with a very good camouflage. Although they include the notion of prey senses as vital for the concept, they still conceive the property of “being cryptic” as such, partially because we can hardly investigate the acuity of the sight of prey. But in evolutionary perspective, what matters are both sides of the relation predator-prey. If a stalking tiger was perfectly cryptic, ungulates in neighbourhood would not be able to detect it and subsequently put in danger of becoming extinct. Ungulates surely have some capacities to detect a tiger and we could assume that the better the recognition capacities are, the more fit their owners are. Now we are adopting the position of prey, and what matters are recognition cues displayed by a predator. Once a predator is detected, however “cryptic as such” it is, some of its characteristics are recognized and from now on we need to consider these characteristics as conspicuous. Therefore, we cannot strictly separate the poles of conspicuousness and camouflage. They are the outside points on the line of recognition capacities of a receiver of visual signs.

To make the matter more complex, both the appearance of a predator and the recognition capacity of prey undergo changes in the course of evolution. Theoretically, the stripes of the tiger could have become quite indistinguishable in the grassland habitat for the majority of
animals. But for the tiger’s common prey, for example the chital (*Axis axis*), the situation has to be different. With increasing selection pressure from the tiger, the chital is forced to develop a better recognition system. This is an assumption of evolutionary arms race, which in this case leads to coevolution of the tiger’s coat pattern and recognition abilities of the deer. Although arms race is generally viewed from the perspective of “improving weapons”, it has an interesting consequence: if the race has not resulted in a lethal end, there must have been a shifting-balance of power. During the evolution of a tiger-deer relation, nobody could have been a decisive winner, otherwise the second species would have become extinct. From the perspective of the recognition system of the chital, the tiger has never been positioned far from the middle of a virtual line joining the poles of conspicuousness and camouflage during their presence in a given area. In other words, the tiger has never been either too cryptic or too conspicuous for the chital.

The purpose of the thoughts in the previous paragraphs is to relativize the concept of “being cryptic” as such, regardless considering anti-predator behaviour of prey, especially the recognition properties of its visual apparatus. If a prey and a predator have shared an area for ten hundred thousand years, the prey embodied recognition cues into its neurophysiology. Following this line of thoughts, we could even assume that some morphological features of a predator’s body can serve as highly conspicuous for a particular prey. Indeed, this was proposed in the case of leopard coat pattern and the vision of bonnet macaques (*Macaca radiata*) by Coss and Ramakrishnan (2000).

Primates have trichromatic colour vision and thus are able to distinguish green and yellow colour. Visual system of bonnet macaques is attuned to yellowish hues, which could be adaptive for the need to distinguish between edible and withering leaves (Lucas et al. 1998, cited in Coss and Ramakrishnan 2000). When macaques catch sight of the spots on the tawny coat of the leopard, they elicit alarm calling. Coss and Ramakrishnan argue that a spotted coat is an inherent leopard-recognition cue because the sign alone triggers alarm even among captive-born and urban troops of bonnet macaques which have probably never seen a leopard. Instead of offering concealment, leopard’s coat is highly conspicuous for macaques and probably also for other primates with trichromatic vision. What remains a question is whether the spotted texture is also a cue for leopard recognition among ungulates, which have dichromatic vision (Neitz and Jacobs 1989, Jacobs 1993).

At this stage, it is hard to conclude whether the typical spotted texture of the leopard is not very effective camouflage generally or if macaques have acquired the property to recognize it despite its original cryptic function. Stankowich and Coss (2007) made an interesting experiment with the aim to compare deer’s reaction to models of puma, tiger and leopard, all
installed in grassland habitat. The Californian population of the black-tailed deer (*Odocoileus hemionus columbianus*) is exposed to the predation of the puma which is currently the only felid conclusively capable of killing adults in the area (according to Alderton 1998, bobcat, *Lynx rufus*, is a rather small cat to kill fit deer). Around 1.6 million years ago, the progenitors of black-tailed deer and jaguars occurred sympatrically in California: Stankowich and Coss (2007) therefore put forward the hypothesis that the deer’s perception should be sensitive to the spotted texture. The coat of the leopard is chosen as a model of early jaguars which is a bit questionable since a referential work (Werdelin and Olsson 1997) does not lead to this inference.

The deer reacted (by snorting, foot-stamping) most strongly to the model of puma, was considerably alert when it caught sight of the tiger but the majority of deer was relatively calm when the model of the leopard was exposed. Stankowich and Coss infer that relaxed selection has led to the loss of recognition of a jaguar-like spotted coat. The initial function of the spotted coat, i.e. camouflage, re-emerged. A model of the tiger revealed to be conspicuous and it is interesting to pay attention to the authors’ explanation of this phenomenon. There is no presumption that the progenitors of the black-tailed deer and the tiger shared the same area, allowing the deer to get accustomed to tiger stripes. Therefore, the deer was alerted by the felid morph as such, which was barely hidden by tiger stripes. Although this experiment shows that the tiger is not cryptic in grassland (at least at the sight of the deer), Stankowich and Coss (2007) avoid dismissing the hypothesis of camouflage as such: “background-matching properties in South Asian habitats with much thicker grass and reeds” (p. 180) might well serve as camouflage for the tiger.

The work of Stankowich and Coss is worthy of appreciation for two reasons: (i) an introduction of innovative concept (relaxed selection), and (ii) an experiment directly testing the hypothesis discussed. Despite of this, the conclusions of the study are not unambiguous. First of all, leopard-like spots are usually reported to match the background typical for forest, not for grassland (Wallace 1870, Ortolani 1999). Secondly, considering a theoretical framework of experiments, the hypothesis about camouflage of the tiger in grassland should be dismissed according to the principle of Occam’s razor. (This does not mean tiger could not be cryptic in South Asian habitats, but such an additional assumption does not follow the flow of an argument. It is also good to mention that macroecological studies aimed to statistically resolve the problem of camouflage, such as Ortolani 1999, do not distinguish different types of grassland.)

In a theoretical work carried out to predict the function of carnivore colour pattern, Ortolani (1999) mentions the significance of the head for aggressive camouflage, but patterns
on the head are investigated only in respect to intraspecific communication. Therefore, when
the function of tiger coat pattern for camouflage is discussed, the coat of the tiger is classified
as vertically striped, although there is a convoluted pattern of stripes and patches on a tiger
head. There is a good reason to assume that the head is the first part of a predator that the prey
can catch a glimpse of: the head is stretched forward and the eyes fixed on the prey in a
typical position of a stalking cat (Leyhausen 1979). In addition, Coss et al. (2005) properly
highlight the crucial role of the pair of eyes in face recognition. According to this approach, a
predator’s head is recognized in the moment when eyes are found.

At this point, we might recall two basic functions of disruptive colouration. Firstly,
unevenly distributed patches of different colours break the continuity of surface (pattern-
blending). The second mechanism is rather psychological: the patches tend to catch the eye of
the observer and draw his attention away from the overall shape (Cott 1940). It is this second
mechanism which we need to take into account when we think of the recognition of the eyes:
the pair of eyes could be obscured by eye patches or a stripe going across each eye. The only
experiment in respect to felids was probably carried out by Coss et al. (2005). The result does
not support the theory of disruptive colouration: from the perspective of an observer (a model
is based on the visual apparatus of macaques), leopard’s eyes are not blended with dark spots
on a face. The spotted head rather serves as an important cue for recognition.

### 4.4 Non-visual senses of prey

It is generally believed that felids approach their prey from below wind (e.g. a leopard
(1908, cited in Cott 1940) believes lions have developed a tactic of hunt consisting in
incorporation of prey’s reaction to the scent. Some individuals approach the prey deliberately
down the wind: when the antelopes or zebras get the lion’s scent, they run just toward the
other lions hidden on the opposite side.

In the detailed study of Serengeti lions, Schaller (1972) finds no justification for the belief
that lions take the direction of wind into account. From 300 hunts observed, lions stalked
upwind on 28 % of occasions, downwind on 28.3%, and with the wind from one side or the
other on 43.7 % of occasions. However, considering daytime hunts of Thomson’s gazelle,
lions were almost three times more successful when stalking upwind than downwind (18.5%
to 7% success rate in the case of a single-lion-hunt). As regards lions living in Ngorongoro,
Elliott et al. (1977) do not detect any differences in hunt success regarding upwind and
downwind stalks initiated by crouching. Serval cats and feral cats also hunt independently on the direction of wind (Kitchener 1991).

In the open plains of Serengeti, animals which are often hunted by lions rely on their sight more than on their sense of smell. Wildebeest, zebras and Thomson’s gazelle are often seen to graze in the vicinity of resting lions, watching them at the distance of about 100 meters (which exceeds the flying distance, i.e. the distance which is safe to run off at when a lion launches its pursuit). The odour of lions is so prevalent near sources of water, especially during the dry season, that hoofed animals simply get used to it. In the open terrain, they are alarmed only if they catch a glimpse of a lion at the short distance (Schaller 1972). Visual stimuli play a crucial role in the detection of the lion also in the case of prey animals living in Ngorongoro (Elliott et al. 1977).

On the other hand, Schaller (1967) describes a different scenario for tigers. A relatively low rate of successful hunts in the case of tigers inhabiting meadows of Kanha (Madhya Pradesh, central India) is supposedly caused by the fact that prey detect the predator by their senses of smell and hearing. Deer have a large number of visual and auditory channels for communication of danger (raising a tail, thumping) so if an individual becomes aware of a predator the whole herd is alerted (this applies even for mixed interspecific assemblages). Even in an abundant year, tigers were successful only once from 12 stalks accomplished.

It is good to mention that prey animals sometimes do not flee even if a predator is sensed in a dangerous distance. Schaller (1972) comments that on one occasion a stalking leopard was sensed by gazelles occurring approximately 25 metres away, but they merely snorted and stamped their forelegs and did not run away. Examples of curiosity displayed by deer which can potentially have detrimental endings were already discussed. Although such types of behaviour are probably exceptional and the psycho-motoric functions of prey are bound to enable to escape from predators, we should not restrict our thoughts of predation-prey interaction to merely physiological war of senses.

4.5 Camouflage and motion

The concept of camouflage was built upon the image of a moth resting motionlessly on the bark of a tree. All principles of camouflage (general resemblance, disruptive colouration, countershading) are demonstrated on the examples of objects which are primarily still and do not change their position against the background. The same applies naturally to pictures,
which illustrate cryptic properties of objects as a frozen momentum from the reality of never ending change and movement.

However, the principle of camouflage allegedly works also for moving animals, e.g. fleeing zebras or small songbirds flying. Cott (1940) pays attention to this problem and asserts that cryptic properties also belong to moving objects. His argument is straightforward: no one would play tennis or a similar game with a green ball, instead white or red balls are used since they have a colour complementary to green grass.

This discussion is very important in respect to camouflage properties of felids. Arsenjew (1924) (cited in Mazák 1980) testifies that the pattern of a tiger blends into indistinguishable grey mass when it moves fast. Provided a similar effect is constituted by neurophysiology of a tiger’s prey, it is not important to analyze details of the tiger’s pattern. The movement of the colour patches across the observer’s visual field is more rapid then the flicker fusion frequency and the elements of an overall pattern cannot be perceived separately (Endler 1978). Apart from this, deer (and other animals) are sensitive to moving visual stimuli and have trouble to recognise still objects.

Based on the analysis of hunting methods of some big cats (mainly tigers and lions), we suggest that there is no theoretical need for an assumption that fast moving felids are optically cryptic. There are basically three main hunting methods used by big cats which can be briefly called as ambushing, running, and stalking. Before attacking a victim from ambush, a felid is perfectly still, waiting for its prey to come as close to the cover as possible. Tigers occasionally use this method in the vicinity of water sources because prey frequents these areas relatively often. The same applies to lions: thickets along rivers and waterholes provide ideal cover near the place when prey is frequently present. Stalking and running are probably most prevalent hunting methods among big felids: Schaller (1972) detects that they are employed in 88% of lion hunts and stalking is also characteristic for the tiger (Schaller 1967). The method of running simply means that a cat is given a chance to run undetected at the start of its pursuit, for example when its prey suddenly emerges some 100 metres away, so there is no need for a hidden approach accomplished by stalking.

Schaller (1972) cautiously investigates stalks of the lion and concludes that a predator moves only when its prey is facing away from it. Otherwise it freezes in motion, sometimes having its paw raised in mid-stride. A stalking lion preferably hides behind scattered bush or protrusions in a terrain and avoids displaying in full view before it launches a final run. This behaviour is logical in the light of our knowledge of the visual acuity of ungulates which is generally rather poor (Rowland 1979). Deer have often troubles to distinguish motionless forms (e.g. chitals, see Schaller 1967). On the other hand, when the outline of a feline body is
easily recognizable and is in contrast to the background, deer exhibit alertness with a tendency to flee (see reaction to the model of puma, Stankowich and Coss 2007). In addition to this, they are very sensitive to slight movements and pay a close attention to the source of disturbance. If we use Cott’s example with a tennis ball, it might be tricky to target a flying ball made of inconspicuous colours and hit it, but the movement itself is sufficient to recognize the very presence of the ball.

According to Schaller (1972), a typical daytime hunt is employed in the areas with groundcover at least 0.4 metre high and shrubs scattered around. This does not preclude the possibility of catching prey in short grasslands: up to 25% of wildebeest and zebras were killed in the areas without a noticeable cover in the vicinity of a carcass. By far the most suitable places for hunt are the areas near water sources: the abundance of prey and the presence of thickets or erosion terraces account for more than 40% of kills of large hoofed animals. Their flight is subsequently hampered by a restricted number and narrowness of escape routes: lions are also capable of seizing the animal in a river.

To sum it up, it is crucial for a cat during a stalk to avoid making rush movements when it faces the sight of prey. If the prey looks towards the location of the felid, the predator stops moving and the image of its parts partially exhibited through vegetation come under the static view of crypsis. At the moment the cat launches an attack, the camouflage does not account for the success of the hunt. Either the prey is disturbed and tries to escape immediately after sensing the predator, or it is not aware of the attack and looks in a different direction. Visual factors were crucial for the hunted before a run was started, after that only speed and swiftness decide whether it would stay alive.

4.6 Hunting techniques

When Cott (1940) argues that optical principles accounting for camouflage apply indifferently for a predator and its prey, he pursues to show that cryptic properties of predators like felids enable them to approach close enough to launch a surprising attack on the prey. Besides colouration, he highlights other factors important for a successful hunt: the stealthy approach and the use of cover. Kirby (1896) describes the leopard’s mode of attack as follows:

“No snake in the grass moves more noiselessly; the long lithe body accommodates itself to all the intricacies of the thorny tangled bush, and the most watchful would never know of its dreaded approach.” (cited in Cott 1940, p. 143)
Cott is generally right that similar hunting technique is typical for large representatives of Felidae. We have already discussed hunting techniques of the lion and the tiger. It is good to highlight the fact that besides these typical behavioural patterns, there exist some exceptions. These can take form of individual variations (Leyhausen 1979) or they can be related to specific regions or vegetation cover types. The population of leopards from Kalahari employs stalking in less than 5% of hunts. Virtually all kills are opportunistic: this is allegedly linked to low densities of prey in semi-desert areas (Bothma and Le Riche 1986). The Canadian lynx (*Lynx canadensis*) is reported to adjust its hunting behaviour for the snowshoe hare (*Lepus americanus*) according to vegetation type: it prefers ambushing in dense spruce forest, whereas stalking is usually employed in sparse spruce. Ambushing success is 47% higher where understory cover is abundant comparing to where it is only moderate (Murray 1995).

As far as small felids are concerned, they use basically two different methods of hunting: stalking followed by a final attack (similarly to big cats) and ambushing (which can take the form of waiting near a rodent hole). Generally said, ambushing is used relatively more often among small cats in comparison to their large relatives. At the same time, we must bear in mind that cats adopt their hunting techniques primarily to natural conditions. The black-footed cat inhabits semi-deserts of Kalahari and Eastern Cape in South Africa. An animal investigates its home range the whole night and covers the distance around 15 km. The biotope does not provide many covers and a hunting style often relies on surprise and immediate catch of prey (“fast-hunt” technique, see Olbricht and Sliwa 1997).

At first sight, the cheetah seems to be an exception from the rule. The hunting technique of the cheetah is often compared to the chase adopted by pack hunters. Leyhausen (1979) points out that the similarity is only superficial, for a cheetah relies on overtaking a prey animal within short distance, whereas pack hunters such as wolves tire out the prey. The chase of the cheetah is just an outstanding form of a final run employed by other felids (e.g. lions, most small cat species). Nevertheless, there is a peculiarity about the hunting method of the cheetah which is worth considering. In the open plains of Serengeti where the cover is scarce, animals are often visible over long distances. Under these conditions, cheetahs often skip stalking and launch an attack from the distance of 150-250 metres. According to Eaton (1974), the prey is usually aware of a predator’s presence and cheetahs seem to hunt less fit individuals predominantly.

The cheetah (along with the serval) is a significant exception from the rule stating that the spotted felids inhabit mainly forests. Some animals dwell in habitats which offer some cover (wooded savannah or woodlands) and sometimes approach prey (impalas) by stalking before a final chase (Pienaar 1969, cited in Eaton 1974). However, camouflaging properties of a
spotted coat in relatively open environments are doubtful. The skin of the cheetah might be compared to a wallpaper with a regular pattern: the size and density of the spots do not resemble vegetation of grassy savannahs. (Moreover, cheetahs often share the area with lions, so either lion’s uniform colouration or the spotted coat of the cheetah does not provide its bearer with good concealment.)

Due to the transparency of savannah, cheetahs are good candidates to test Mottram’s hypothesis of obliterative shading. The tawny background of the skin of the cheetah does not display a significant contrast between upper and lower parts of the body. On the other hand, spots are more frequent and closer to each other on the back than on the bottom, which is believed to cause the effect of countershading from an appropriate distance (Mottram 1915). If the phenomenon arises within the charging distance of the felid, it would be a burden for proper recognition of the predator. Mottram based the hypothesis on geometrically idealised figures and principles: it would be revealing to carry out empirical experiments with the model of the felid and investigate the phenomenon of obliterative shading in field.

Little is known about hunting methods of secretive cats from South East Asia. The flat-headed cat inhabits mangroves and hunts small prey (often crabs) in shallow water and on muddy shores. In captivity, it has been demonstrated that the cat catches prey with its mouth or paws (Leyhausen 1979). It will not be amiss to mention that among all felids, the flat-headed cat displays the greatest contrast between the brightness of the head and the rest of the body: the light head endows an animal with ghostly appearance. If that carries an adaptive significance remains a mystery: hunting methods employed under natural conditions remain completely unknown. Considering the fishing cat, there is a surprising observation made by Breeden (1989) (cited in Kitchener 1991). A cat waited on a log overhanging the water and kept its head as near to the water surface as possible. When fish passed beneath it, a cat jumped into the water and grabbed the prey by its mouth. This method is fairly different from fishing out prey by paws which is a typical technique employed by other small cats in captivity (Leyhausen 1979). Given the fact that fish comprise more than 75% of the diet of the fishing cat (Haque and Vijayan 1993), Cott’s proposition about camouflaging properties of its coat in river-by thickets (see Section 1.1.1.2) needs to be reassessed.

To sum it up, we suggest that the combination of the hunting technique of a specific felid and optical and physical factors of the environment are crucial factors for the proper assessment of the hypothesis of the adaptive colouration of a given coat pattern. On the examples of some species and related habitats, we have attempted to show the problem in its complexity. On that basis, we believe that the detailed discussion of specificities of foraging behaviour among individual species is necessary for concluding trustworthy results about the
theory of camouflage. Naturally, such a task would demand extensive field study and goes beyond the scope of this study.

4.7 Areas with the overlap in distribution of felid species

Based on the assumption that there is a match between the type of a coat pattern and the environment, we have sought for the result that different pattern-specific species of felids live in different habitats. The analysis provided only a coarse sieve from the ecological point of view. For example, grasslands subsume both savannahs of Serengeti with thin vegetation (often under 0.5 metres of height) and tall grass areas from Nepal (to 5 metres of height, in Royal Chitawan National Park made up by *Saccharum* sp. and *Phragmites karka*, see Seidensticker 1976). It is obvious that both habitats provide significantly different conditions for the visibility of animals. However, finer distinction of habitats would bring two basic problems: Firstly, more detailed review of vegetation throughout wide ranges would be needed. Secondly, we could not use statistical methods which have been employed. A relatively small number of species (less than 40) requests maximally 5-7 separated categories, otherwise some of the groups used in the statistical test for correlated changes (Pagel 1994) would comprise a too small number of representatives.

There is another way of investigation which can be followed. This approach is more convenient in the sense that ecological studies usually cover certain geographic areas and thoroughly analyse local population of felids: feeding habits, intraspecific communication, spatial separation of different species, microhabitats in the area etc. The studies reveal a significant number of areas where two or more felid species live as sympatrics. These studies provide us with worthy comparative material: according to the theory of camouflage, one might assume that the sympatric species exhibit a similar coat pattern, for it is likely that environmental conditions are all alike (vegetation, light availability, food supply, etc.). However, we will show there are ecological constraints which act differently on individual felid species (Sunquist and Sunquist 1989). The case studies offer deeper insight into the ecology of felids than the analysis of data on a macroecological scale: in other words, there is a lower level of the loss of information in comparison to broad-scale simplifications. As an illustrative example, it is better to compare tigers and leopards from Royal Chitawan National Park than tigers from India and leopards from Central Africa. In the case of local ecological studies, the price paid is the loss of the clearness of method employed for the assessment of results. For example, if we focus on the plains of Serengeti with the population of cheetahs,
lions, and leopards alone, we have no means to take a phylogenetic signal into account, yet the colouration of the three taxa may reflect other than ecological factors.

We will undertake a brief investigation to compare ecological factors which influence the life of the tiger and the leopard. The analysis will be driven by the effort to discover some significant differences in hunted prey and habitat preferences, which would reveal behavioural patterns influenced by distinctive optical properties of coat patterns. Three localities are comprised into the analysis: Kanha in Central India (Schaller 1967), Royal Chitawan National Park in Nepal (Seidensticker 1976), and Nagarahole National Park in Southern India (Karanth and Sunquist 1995).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Habitat</th>
<th>Composition of prey (in percent)</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Tiger</td>
<td>Leopard</td>
</tr>
<tr>
<td>Kanha+</td>
<td>grass meadow, Shorea forest</td>
<td>Chital (52.2)</td>
<td>Chital (59)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sambar (10.4)</td>
<td>Langur (27)</td>
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<tr>
<td></td>
<td></td>
<td>Barasingha (8.6)</td>
<td>Porcupine (9)</td>
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<tr>
<td></td>
<td></td>
<td>Gaur (8.3)</td>
<td>Sambar (9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Langur (6.2)</td>
<td>Barasingha (4.5)</td>
</tr>
<tr>
<td>Chitawan*</td>
<td>riverine forest, tall grass areas</td>
<td>Sambar (33.3)</td>
<td>Chital (33.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hog deer (25.0)</td>
<td>Hog deer (33.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chital (16.6)</td>
<td>Sambar (25.0)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wild pig (16.6)</td>
<td>Muntjac (8.3)</td>
</tr>
<tr>
<td>Nagarahole*</td>
<td>dry deciduous forest, tropical moist deciduous forest</td>
<td>Gaur (44.8)</td>
<td>Chital (83.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sambar (28.6)</td>
<td>Sambar (9.6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wild pig (14.3)</td>
<td>Muntjac (3.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chital (10.4)</td>
<td>Langur (1.2)</td>
</tr>
</tbody>
</table>

+ Prey proportion is based on the occurrence of feces.
* Prey proportion is based on the number of kills.


In the study of carnivores living in the forests of Nagarahole, Karanth and Sunquist (1995) state that there is a high overlap of prey between tigers and leopards (Overlap Index app. 0.94, where 1.0 means the entire overlap; the definition can be found in Pianka 1973). This is against a notion inferred from the data in Table 6, where a high proportion of kills of gaur in the case of tiger makes up a significant difference in prey selection of two felids. The contra-intuitive result is probably caused by subsuming the analysis of feces into the calculation of Overlap Index. No evidence for competitive spatial exclusion of the two species was found.

There is almost an entire overlap of the prey taken by tigers and leopards in Chitawan (the value of the index could not be calculated for the paucity of data). Seidensticker (1976) asserts that tigers act as a constraint on leopards, but abundance of prey and dense vegetation...
facilitate the coexistence of two felids. Their separation is managed by different activity times and habitats used during the year. Leopards manage to successfully hunt in the areas of tall grass even after those were burned, whereas tigers exploit burns only infrequently. It is possible that a larger and less swift tiger needs more solid cover than a leopard, but the difference is hardly influenced by the distinction in coat markings.

Schaller (1967) notices a spatial ecological separation between the tiger and the leopard in Kanha. Leopards are restricted to the edges of the national park and often depend on preying on domestic livestock. According to the tracks found by Schaller on Kanha meadow during the monsoon season, tigers are much more abundant and most of leopard individuals are transient.

When we wanted to analyse data in Table 6 and to set up a framework similar to the hypotheses put forward in Chapter 1 and tested in Chapter 3, several problems would arise. First of all, including the third factor, which is the composition of prey, makes the comparisons more complex. To give an example, leopards might be conspicuous in grassland, but an insufficient visual acuity of the chital does not prevent the felid from successful hunts. Secondly, we cannot simply match the frequencies of kills of certain species with cryptic properties (or conspicuousness) of a given felid. Other ecological factors such as the size of an animal (both predators and prey) are supposed to be more important. Thirdly, ecological studies rarely mention the microhabitat of the kill-localities. In all three national parks studied, habitats are highly variable (dense forest, meadow, tall grassland, riverine forest etc.) and one might account for the possibility that tigers and leopards take advantage of different places and day times for hunting. It is paradoxical that we encounter the problem of habitat determination on this scale, whereas macroecological simplifications in the style “tiger: grassland, leopard: forest” seem to be viable.

Having these problems in mind, it will not be amiss to show some relations which can be inferred from Table 6. The purpose is merely illustrative: we seek to demonstrate troubles of the concept “more information about the ecology of a given felid leads to more data about the determinants of the theory of crypsis which finally leads to the opportunity to positively test the hypothesis”. Now three determinants (prey-pattern-habitat) will be taken into account, one of them varying while the other two remain the same: given other circumstances are stable, the change in one variable allows for anticipation that it is not the one important in presumed function of camouflage. This is somewhat a basic type of analysis, but the employment of statistics is not viable for the paucity of the data.

a) Variability in habitats
The sambar (*Cervus unicolor*) acts as an important part of tiger’s diet in all three analysed localities. The sambar prefers large tracts of forest but is not specialized in its habitat requirements (Schaller 1967). Together with the fact that grass meadow/Shorea forest of Kanha are more open that riverine forest/tall grass areas of Chitawan, we can conclude that the sambar is hunt by the tiger in varied habitats (and the tiger’s coat is not likely to be inconspicuous for sambars purely in some specific localities due to background matching).

b) Variability in felid coat patterns

There is a significant overlap between species preyed upon by the tiger and the leopard. The chital (*Axis axis*) makes up an important component of the diet of both felids. In Kanha, it inhabits forests with open canopy and prefers the transition between a forest and a meadow. It is less volatile in its habitat preferences in comparison to the sambar, and avoids dense forest (Schaller 1967). We can conclude that tigers and leopards (which possess very different coat patterns) prey upon the same species in the same environment.

c) Variability of prey

Two dominant prey animals of the leopards in Kanha are the chital and the langur (*Presbytis entellus*). They frequent the same areas and the chital often picks up the leaves and fruits dropped from langurs on a tree (Schaller 1967). Roughly expressed, chitals and langurs seem to be similarly vulnerable in the same conditions, though the physiology of their sight is supposed to be different (deer possess dichromatic and primates trichromatic vision, see Jacobs 1993).

By this analysis, we have shown that the relation between three investigated determinants (visual acuity of prey, felid coat pattern, habitat) is very loose. Field studies provide a complex picture of ecological links and data often vary from one locality to another.

In the following paragraphs, we will focus on the relative frequency of prey species in the diet of felids. From the comparison of tiger’s and leopard’s diet in the three reservations mentioned, we might infer 3 general conclusions:

i) The absence of wild pigs and gaurs in leopard’s diet;

ii) Very low frequency of muntjac kills carried out by tigers;

iii) Relatively higher frequency of the langur in the diet of leopard.

Is there a link between these facts and the optical properties of felid coat patterns and/or visual acuity of prey? It is impossible to give conclusive arguments. Generally, the size of the prey is a crucial factor for prey selection among large felids (Sunquist and Sunquist 1989). Leopards are on average 4 times lighter than tigers, so body mass is likely to be the cause of the first conclusion. The same might apply for the second conclusion: the muntjac is too light (and swift) to be hunt by the tiger. We could use the exactly same argument for the third
result, but there are some other hypotheses dealing with the relation of leopards and primates which are worthy of closer attention.

Karanth and Sunquist (1995) directly suggest langurs are relatively more preyed on by the leopard due to felid’s higher arboreality and crypticity(!) in comparison to the tiger. It is not clear whether “crypticity” means general ability of secretive hunting or if it is related to camouflaging properties of a leopard coat in arboreal habitats. Nevertheless, the verification of the suggestion would demand a detailed discussion and experimental testing. Coss and Ramakrishnan (2000) show the coat of leopards serves as a cue of recognition for bonnet macaques (*Macaca radiata*), so the question arises why a supposedly similar neurophysiology of sight (both macaques and langurs belong to the family of Old World monkeys) does not help to detect leopards in the case of langurs. Similarly to bonnet macaques, langurs are accommodated to human so the proximity of researches should not be a burden for testing. The experimental setting used by Coss and his colleagues could shed more light on the differences between the perception of tiger stripes and leopard spots but they require involvement of more testing models and controls.

As we see, it is difficult to verify the theory of crypsis from ecological studies, even if they describe the relation of two (or more) felid species in detail. Karanth (1993) (cited in Karanth and Sunquist 1995) suggests that tiger’s selectivity for gaur (*Bos gaurus*) in Nagarohole reflects the fact that the gaur grazes on open clearings in the forest, preferably in crepuscular daytime. Moreover, gaurs are supposed to have a relatively poor eyesight. This is in contrast with the findings from Kanha, where tigers selectively hunt chitals and sambars. At the same moment, the gaur is abundant in the park but prefers a closed habitat (Schaller 1967). A similarly doubtful argument is given for under-representation of chital in the diet of Nagarohole’s tigers. Johnsingh (1983) (cited in Karanth and Sunquist 1995) suggests that the cause consists in diurnal activity patterns of chital, but the animal is often active by day also in Kanha, where it comprises more than 50% of tiger’s diet (Schaller 1967).

Finally, it is good to mention a case of multiplied sympatry of cat species. Rainforests of Central America are inhabited by six different species of felids. With increasing size, these are tiger cat, jaguarundi, margay, ocelot, puma, and jaguar (jaguarundi and margay are very similar in size). There is no apparent competition between the species, although the overlap of prey species is considerable. If the theory of crypsis holds true, small spotted (respectively blotched) species (tiger cat, margay, ocelot) shall possess a less effective camouflage in a forest than the unicolor species of similar size (jaguarundi), at least from the perspective of most prey species. This would lead to a different composition of the diet between jaguarundi and the cluster of spotted species. However, Eisenberg (1990) (cited in Kitchener 1991) shows
there is a considerable overlap in the diet of ocelot and jaguarundi (small rodents, reptiles and amphibians and other prey under 1 kg in weight). Generally, it is supposed that the decisive factor in prey selection is the size of a carnivore. Kiltie (1985) (cited in Kitchener 1991) demonstrates the link between gape size (inferred from skull morphology) and the weight of neotropical felids and assumes gape size is a limiting factor for predation (prey animals are usually sized by neck). The correlation is approved in a comparative study of Emmons (1987) focused on the ecology of the jaguar, puma, and ocelot in Parque Nacional Manu in Peru. The study area is lowland evergreen tropical rainforest in the floodplain of the Manu River. There is a significant difference in the size of prey dominantly hunt by individual species: jaguars favour the prey over 10 kg of weight, pumas between 1 kg and 10 kg, and ocelots less than 1 kg of weight. Emmons (1987) also states that for a given felid, the species-specific composition of prey relates to its abundance. The only significant irregularity applies for the peccary (*Tayassu tajacu*). The peccary is overrepresented in jaguar’s diet, whereas pumas seem not to hunt the animal. This might mean the visual acuity of peccaries is insufficient to recognise the spotted coat of the jaguar, whereas pumas are not as cryptic in the rainforest. Emmons does not discuss the theory of camouflage and simply states that jaguars preferentially seek peccary, whereas pumas prefer large rodents.

One must conclude that investigation of the relative frequency of prey species in felids’ diet does not provide information which is convenient for verification of the theory of camouflage. Other factors, mainly the size of a predator and prey, seem to be decisive for the composition of their diet. Moreover, we need to reconsider whether the theory of aggressive resemblance is sensible in the case of small felids since it is doubtful that common prey species (small rodents, frogs) are capable of discriminating potential differences in their coat patterns.

### 4.8 Intraspecific variability: means to test the theory of camouflage

Typical works investigating camouflage rely on a display of models representing different morphs of a certain species of insect (e.g. moths) to an avian predator (e.g. blue jay) (Cuthill et al. 2005). Researchers have a clear idea which models should proof more cryptic and there is an anticipation that corresponding morphs are prevalent within a given environment.

There are two main problems in respect to the investigation of camouflage within felid species specifically. The first consists in the absence of theoretical assumptions about the utility of slight variations in the colouration of individual species. What is typically conceived
is the variation among different species but such a distinction is too rough. We need a hypothesis how a tiger inhabiting deciduous forest in South India should differ from the one living in the rainforests of Sumatra to match its environment best possible (within the constraints of “looking as a tiger”). Only if we have a theory about the benefits of variation in the distribution of stripes and hues of colour, we can begin to find out whether the real state corresponds to our expectations.

The second trouble consists in the fact that most felid species do not show any extraordinary variation in colouration. For example, if there were leopards with spots, stripes and blotches, we would have material with variations distinct enough to distinguish separated morphs. As far as patterns are concerned, what we have in fact is a slight intraspecific variation of a doubtful visual significance. For example, in the case of the European lynx (*Lynx lynx*), there exist spotted as well as uniform individuals, but most specimen are slightly marked and one might only guess whether camouflaging properties of such individuals are similar to that of puma (uniform) or cheetah (distinct spots).

If we take only colour variations into account, we face other problems. There are some mutations in colour which naturally occur from time to time (e.g. albinism, rufism, erythrism; cf. Mazák 1980, for a more comprehensive list of mutations see Little 1958), but nobody has discovered any geographical patterns underlying the phenomenon. The prevailing opinion is that these mutations are recessive and do not bring any benefits to differently coloured specimens. The fact that underlying genes are only rarely transmitted to next generations testifies for qualities of the prevailing forms (i.e. the mutation is swept away by natural selection) or the operation of genetic drift. Overall, mutations characteristic only for the colour of the coat seem to be too rare for a systematic investigation.

However, there are some important exceptions which are worthy of special attention. There are at least 11 species with a high occurrence of melanism (Eizirik et al. 2003) and some of them are especially promising for comparative investigation of ecological habits of different morphs. Above all, a putative ecological separation between spotted (usual) and melanic morph of the leopard calls for a detailed research (see also Section 1.5.2). Black leopards provide an ideal comparative material as they are remarkably different from normally coloured individuals: they lack a distinguishable pattern of rosettes (these are only visible in reflected light) and are very dark. If the theory of camouflage holds true, one might assume the difference between hunting methods and a favourite prey of the two morphs. Localities where both morphs normally occur (western Java) could help to shed more light on the phenomenon. So far, the exact proportion of melanic leopards has not been assessed due to cryptic habits of the felid and its low population density.
Similar applies to a blotched morph of the cheetah – so-called the king cheetah. Provided there were only few individuals with blended spots, the phenomenon could be conceived as a rarity with negative fitness, but the king cheetah is quite common in southern Africa (Alderton 1998). The king cheetah, whose overall colour is darker than the common form, is supposed to live in areas scattered with wood. This would hold together with an assumption than dark colour is cryptic in closed habitats. However, we need to check whether the occurrence of king cheetahs is restricted to sparse woodland throughout its whole range.

To close the list of cases suitable for empirical investigation, we need to mention a few species which show a considerable level of polymorphism in colour of its coat. The African golden cat (*Caracal aurata*) is reported to occur in two different morphs: spotted and uniform. Van Mensch and van Bree (1969) recognized them as two races corresponding with geographical ranges (a division made up by the river Congo). However, they are intermediate grades widely distributed in the Gaboon-Cameroon area. The African golden cat is very secretive and systematic investigation into ecological significance of the phenotypic variance throughout its range seems to be beyond current possibilities. Valuable information might be collected if camera-traps were used extensively.

As regards the jaguarundi (*Puma yagouaroundi*), the hypothesis of Emmons (1997) was already mentioned in Section 1.3. According to him, the yellowish-brown morph inhabits dryer areas than the dark (or grizzled gray) morph. As regards the theory of camouflage, further research might be promising in this case: daytime habitats of the felid shall stress value of distinct colours for aggressive resemblance.

*Puma* (*Puma concolor*) displays a number of colour hues throughout its extremely wide range (Canada to Argentina). According to Rosa (2000), cinnamon, rufous brown and greyish individuals are common (a melanic morph seems to be restricted to South and Central America). Being probably least specialized from all felids in the choice of habitats and prey, one might assume that individual populations of the puma exhibit certain patterns of colouration (e.g. higher proportion of grey individuals in mountain populations, brown individuals in rainforest). Nevertheless, without detailed biogeographical study one can merely guess if the variation goes beyond accidental dispersion.

In the case of monomorphic species and in localities with uniform population, a very simple (though somewhat aesthetically cruel) experiment could be carried out: if the theory of crypsis holds true, cats sprayed with various colours and patterns should vary in hunting success according to their appearance. The asset of this experiment would consist in the fact that other factors influencing successiveness of hunts remain the same (predator’s speed, diet preferences, environment etc.).
Apart from the theory of crypsis, the experiment with a sprayed felid would provide some information about mating success of a strange-looking individual. It is of an utmost interest whether an animal turns down a potential mate because of its peculiar appearance. One might hardly conceive a better test investigating to which extent felids are driven by visual factors in sexual selection.

4.9 Conflict between cryptic and semantic colouration

Although many authors take it for granted that an overall appearance of felids is cryptic (e.g. Kitchener 1991), a number of species are known to possess conspicuous ears markings and a contrasting tail tip at the same time. Naturalists often omit to discuss potential troubles for the theory of camouflage arising from accommodation of such antagonistic principles into one body. Komárek (2011) had an opportunity to observe several Rüppell’s foxes (*Vulpes rueppelli*) in Egyptian oasis Bahríja during sunset. The whole body of animals was perfectly cryptic with the exception of a white tail tip, shining brightly through the approaching dark and revealing the very presence of every single animal. How does it happen that conspicuous parts do not betray their owner while stalking its prey? If an answer is that different parts of the body are exposed to different selective pressures (Caro 2005), we need to analyse the impacts on particular animals and to discuss whether pressures really act discriminately on related body parts.

Hingston (1933) pays a lot of attention to the tension between cryptic and conspicuous parts of animal bodies and describes this phenomenon as colour conflict. Generally said, conspicuous colours and structures are outer expressions of the emotion of anger, whereas cryptic parts are linked with the inner state of apprehension. Depending on the needs of a given situation, an animal exposes respective parts of the body. According to Hingston, obvious black-coloured hairs of a lion mane are exposed only during intraspecific fights and do not interfere with cryptic appearance of lion’s coat while an animal is stalking. (Hingston’s theory will be discussed at greater length in Chapter 6.)

The contrast between black and white areas on the back of the tiger’s ears is extremely conspicuous. Schaller (1967) testifies that white ear markings revealed tiger’s presence in the grass on two occasions: the zoologist would have probably missed an animal if the markings had been obscured. However, if a stalking animal is viewed from the front, white spots are hidden on the back of the ears. In contrast, and in good accordance with Hingston’s theory,
white spots are displayed in a threatening posture aimed in conspecific rivals, when the back of the ears are twisted forward and white spots are exposed to an enemy.

The tear stripes of the cheetah were closely discussed in Section 1.2.1. There are conflicting assertions about their function: on one hand, they seem to have signalling purpose in intraspecific communication (Kingdon 1977), on the other hand, they are supposed to make the recognition of predator’s head more difficult (Eaton 1979). There is one possible resolution of these opposing scenarios. It does not reside in different visual acuity of conspecifics and prey species but in a role of distance in which the pattern is perceived. In very close quarters, which are typical for intraspecific interactions, tear stripes might accentuate the expression of the cat, whereas in a greater distance (cheetahs launch a final run from around 200 meters), typical features of a mammalian head (eyes, muzzle, mouth) might be obliterated and a cat becomes inconspicuous.

Kingdon (1977) provides a minute description of caracal’s ears which have evolved into a highly decorative signalling structure. Elongated ears with a tuft of hairs on their tips are a very versatile and mobile structure and have a significant role in communication between conspecifics (Figure 25). Kingdon mentions that conspicuous ears make an otherwise well-camouflaged predator more visible in its (relatively open) habitat but suggests that profits in social interactions counter-balance this disadvantage. Nevertheless, in the light of a crucial role of an anterior pole during stalking, it should be cautiously assessed whether the evaluation of the felid’s general appearance as cryptic is justifiable. Similarly to other cases, the performance of visual experiments is vital to shed more light on this puzzling problem.
Figure 25: Facial expression of the caracal (*Caracal caracal*): Role of the elongated ears. (After Kingdon 1977)
5 ADAPTIVE COLOURATION: ISSUES FROM THE PHILOSOPHY OF SCIENCE

In the previous chapter, we have discussed some problems related to the theory of camouflage in respect to felids. We have expressed our concern that knowledge of felid ecology is insufficient to prove that coat patterns play a significant role for the success in hunt. In the following reflections, we will bring sceptical considerations one step further. During our theoretical research, we have come across a number of worrying paradoxes lying in the core of the concept of camouflage. It is quite obvious that some cryptic species of animals do dwell in nature but one has to question the universality of the concept. In expressing our sceptical remarks, we are not driven by an ambition to disregard the validity of the theory of camouflage as such. Instead, we would be pleased if our theoretical and philosophical reflections would lead to better understanding of presuppositions inherent in common investigations into the problem of crypsis.

5.1 The concept of camouflage

To provide motivation for our philosophical remarks on the theory of camouflage, we will illustrate related problems on the examples. Firstly, a classic case of protective camouflage consisting in predation of moths by avian predators will be discussed. In contrast, it will be shown that the alleged aggressive camouflage of the tiger’s stripes lacks empirical evidence.

If we consider the concept of protective camouflage, we must pay equal attention to both sides of the relation: prey strikes to be invisible, whereas predator attunes its sight in search for it (Endler 1984). This probably applies on two scales: individual (during life span of an animal) and species-specific (during evolutionary time scale: the concept of evolutionary arm race). A typical experimental system consists of artificial moth-like targets exposed on natural background (bark) to an avian predator, for example the blue jay (Cuthill et al. 2005). Morphs which match background best are supposed to be hardly recognizable for the blue jay: we determine them as cryptic. In this case, we can rely on our intuition which patterns generally match a certain type of bark: we assume our perception is not very different from the one of avian predators.
However, in less illustrative cases, we do not have convincing tools how to determine if “background matching” is a good description of the phenomenon observed. When viewed from the predator’s position, we might as well say that its sight is attuned to find out certain prey and it accomplishes this task with different successfulness depending on the design of individual morphs of prey species.

We assert that in the case that “background matching” is not well confirmed by human sight, we can hardly decide what accounts for the rate of predation in natural settings. Let us consider the tiger and its typical prey in India: gaur, chital, and sambar. The hypothesis is that the tiger’s stripes match the background from the perspective of some of these species (aggressive camouflage), possibly all of them, because ungulates might have evolved similar qualities of sight. We have only one option how to test the hypothesis in natural settings: to measure different rates of predatory success in respect to individual prey species. The more the tiger looks cryptic, the higher hunting success it reaches. Let say the highest rate (20%) belongs to the predation of the gaur: we conclude that this is caused by an increased level of the tiger’s camouflage in respect to the gaur. In this scenario, the tiger’s stripes prove to be “background matching”.

In fact, the previous argument is remarkably insufficient. First of all, different success rates might have several other reasons: in Kanha (Central India), gaurs inhabit areas with tall grass and it is conceivable that such a habitat provides predators with convenient cover independently of their appearance. Secondly, the gaur is a heavy animal and its escape speed is reduced in comparison to the chital and the sambar. But even if we think of colouration as a crucial determinant, we need additional reason why to call the underlying phenomenon crypsis. The same story can be viewed under opposite optics. Gaurs were able to run away in 80% of cases and one could assert that this indicates their ability to recognize the tiger’s stripes without much effort.

To make the matter more complicated, practical limitations need to be considered. Practically all field studies of the ecology of the tiger must rely solely on the number of kills of individual species (or analysis of the tiger’s faeces; see Schaller 1967). A rate of predatory success cannot be inferred from these figures. One could not even provide solid evidence for the hypothesis that small (or none) amount of muntjac kills testifies for an increased ability of the animal to escape from the tiger. The muntjac might as well be too small for the tiger to waste energy on hunting efforts (we would not say that the tiger does not prey on birds because of its imperfect camouflage but rather because they are too fast for such a big animal). Finally, there is always an option that the tiger prefers not to hunt muntjacs because meat of other ungulates tastes better.
5.1.1 Camouflage, felids and logization: a brief lecture from the philosophy of science

The theory of camouflage has been a leading interpretation of the appearance of felids since Wallace (1870). Although the formulation of governing hypotheses has scarcely been touched since (e.g. resemblance between the tiger’s stripes and stems of vegetation in the background), the means of investigation have changed considerably. In fact, this process provides a nice picture of some epistemological tendencies characteristic of a modern science. Our brief outline of the history of the problem serves to illustrate the transition from sensual observations to rationally consistent verdicts.

The theory of camouflage has its fundament in the testimony about imperfect properties of human sight. Despite the fact that big cats display contrasting patterns (black rosettes of the jaguar against tawny ground-colour), it is very difficult to catch a glimpse of an individual in natural conditions. The theory of aggressive resemblance implicitly adds the presumption that same phenomenon arises from the perspective of prey.

In order to get rid of the accusation comparing individual observations to just-so-stories, the need for the formalization of the problem arises. Scientists seek to find a conceptual framework suitable for the clearest possible formulation of a general rule. The concept of background matching and disruptive colouration is formulated and the next task is to interpret the appearance of individual felid species within this framework.

At this stage, there is the need to transparently determine crucial aspects of the objects under investigation. In the case of background matching (we will not consider disruptive colouration in the following course of thoughts), the simplification consists in the reduction of the appearance of the felid to the pattern (respectively its elements) displayed on its flanks. The counterpart to the appearance of the animal is the background, usually formalized as a typical habitat of the given species (forest, grassland, etc.).

The next phase demands lucid categorization. In Cartesian manner, one has to define distinct categories and hold the belief that these are more appropriate for the investigated problem than minute descriptions. It is highly desirable if the categories are mutually exclusive since it eases subsequent logization: individual categories can be replaced by symbols (usually numbers).

At this moment, the initial problem of background matching is encoded into a matrix of traits. With the use of statistical means, we can reliably test the association between the appearance of the animal (spots × stripes × rosettes etc.) and its usual habitat (forest × grassland × rocks etc.). The formalization of the problem gives birth to the data which are
transparently systemized in a table. The validity of the hypothesis of background matching is transmuted into the domain of mathematics: one needs to confirm a putative correlation between the two variables.

The original perspective of the phenomenon of camouflage is turned upside down. The basic problem resided in the question whether the tiger’s stripes are cryptic in grassland, i.e. whether they deceive the sight of individual animals. Now, we believe that the problem can be resolved by the result that there is (putatively) a strong association between the occurrence of striped felids and grassland habitats. However, such an association might also account for different causes or arises from side effects of the method (see the notion about traits with multiple states in Section 3.2).

A profound shift in the assessment of animal colouration is clearly visible on the currently broadly spread quantitative approach. Ortolani (1999) supposes that the function of colour pattern among carnivores can be predicted based on three factors: visibility, shape and location on the body, and their behavioural ecology correlates. At this moment, it is obvious that the formalization of the problem of camouflage replaces the original phenomenon: the value of ocula or testimony is replaced by the associations within a logically consistent framework. A crucial task in the analysis is building of a matrix of traits: the assessment relies on an extensive collection of data which need to be adjusted to fit into strictly defined categories. This type of work consists in gathering data from written sources primarily and is detached from visual aspects of the problem (which are still partially accessible e.g. on the photographs of felids in wild). The table is a crucial means of representation, characteristic for modern science (Classical episteme in Foucault’s words):

“(…) we have the area of the table. This kind of knowledge involves the allotting of a sign to all that our representation can present us with: perceptions, thoughts, desires; these signs must have a value as characters, that is, they must articulate the representation as a whole into distinct subregions, all separated from one another by assignable characteristics; in this way they authorize the establishment of a simultaneous system according to which the representations express their proximity and their distance, their adjacency and their separateness (…)” (Foucault 2002, p. 81)

The phenomenon of camouflage is constituted by the sense of sight. In order to understand the function of felid coat patterns, we believe that analyses of related factors bring valuable information only if they are carried out after the observation of cats hunting in natural conditions. The arguments should primarily ground in the depiction (photographs, videos) instead of logization of the problem. Although one must acknowledge the benefits of the comparative method (clear and universal framework, encompassment of all species), we
believe that they are outweighed by significant drawbacks (subsuming big and small cats into the same scenario of hunting, impossibility to cover the diversity of habitats and light conditions). Instead of the quantitative approach, we should restrict our attention to the few species (e.g. cheetah, leopard) which are most suitable for observation by sight. The depiction of individual hunts occurring under various conditions counterbalances the number of anonymous data originally gathered for the aims unrelated with the problem of camouflage.

5.1.2 Philosophical presumptions of the theory of camouflage

If an animal is marked as “cryptic”, we think of it as of well-hidden to the sight of other creatures. But what creatures do we bear in mind in fact? We would not say moths are cryptic toward the sight of cats, because the relation of cats to moths is quite irrelevant, they do not feed on them (at least not much). On the other hand, if we ask a question “How got the zebra its stripes?”, an anecdotic answer could be as follows: “As a camouflage against the lion, who nevertheless continues to prey on her cheerly.” One might say this example is rather spiteful, but it is very illustrative of the problems that we will discuss at greater length.

There is a surprising paradox hidden in the very concept of crypsis. When protective camouflage is considered, we suppose that the purpose of a specific design is to make its bearer invisible to predators. Yet even the exemplum for the theory of crypsis, moths resting on bark, are preyed upon by small avian predators. One might therefore ask: what substantiates us to say that resting moths are cryptic (to non-human sight)?

To some extent, it is easy to justify why “protected” animals still do have enemies. Cott (1940) accomplishes this goal in a very convincing and consistent manner (the citations which will follow are extracted from pages 167-171). Cryptic colouration conveys only “relative freedom from attack” and affords protection against some but by no means all enemies. One should not assume that some creatures display a perfect cryptic colouration. But even devices which “fall far short of perfection” have a crucial role for the fitness of species as such, for “destruction would be wholesale” without any protection.

To conclude Cott’s clarification, protective colouration of prey inflicts troubles for recognition by predators which feed on it. The same moment is present in Endler’s (1978) definition of crypsis:

“A colour pattern is cryptic if it resembles a random sample of the background perceived by predators at the time and age, and in the microhabitat where the prey is most vulnerable to visually hunting predators.” (p. 321)
Protective resemblance does not imply immunity from attack but it lowers the probability that predators potentially capable of recognizing and seizing the prey catch a glimpse of it in a crucial moment.

Weaker interpretation of the term crypsis has an ambivalent effect. Cott’s argument against naïve concept of crypsis is comprehensible: nature does not attune living beings to perfection but provides them with means to survive. On the other hand, if we assess the full consequences of the broader definition, we realize that the very concept of crypsis dissipates in effect. With the inclusion of relative measures into the thoughts about crypsis, we abandon the concept of animals “cryptic as such”. Once we say that the rate of predation is lowered by protective resemblance, we have adopted the thinking at the scale. An animal which is not perfectly cryptic is necessarily conspicuous to some extent and instead of using discrete states of crypsis versus conspicuousness, we might set up a continuous variable linking both poles. For this variable, we put forward the term visibility.

This is a very important moment in the course of our thoughts. Charm of Darwinian-Wallacian teaching about the significance of adaptive colouration resides in the reduction of animal form into two polar categories: cryptic versus conspicuous (semantic). Once we become aware of the fact that these phenomena are extreme poles of a continuous variety of forms, we begin to consider most animal species as intermediate. Portmann (1967) compares discriminative focus on cryptic and semantic form production in the study of animal colouration to “one-sidedly chosen curio cabinet” (p. 123). From the philosophical point of view, intellectual appeal involved in the belief in adaptive value of animal patterns threatens to evaporate with realization that the pair cryptic - semantic is set as polar distinctions (cf. Komárek 2009).

The following reflections are led by the concern that initial meaning of the term crypsis, i.e. optical phenomenon, is blended with broader ecological factors influencing the successfulness of hunt. Misrepresentation of the concept of crypsis in this direction is comprehensible. From the logical point of view, it is the substitution between the cause and the effect. The possession of cryptic colouration supposedly leads to the prolonged life span because the prey is less vulnerable to predators. But it is important to bear in mind that a different rate of hunting success alone does not necessarily imply distinctions in the visibility of prey, for other factors are of great importance as well (e.g. hunting technique, speed of predator, swiftness and agility of prey etc.). Theoretically, these factors could be eliminated by controlled experiments, however, it is often impossible to separate individual factors in the field. Thus, whereas implication cryptic animal → low rate of predation holds true, the opposite inference is unreasonable without further considerations.
There is another trickiness when one considers rarely hunted prey. Let us consider a cat and a moth which were mentioned at the beginning of the analysis: we cannot infer moths are cryptic from the fact that cats usually do not catch them. Thus we need to think twice which predators might serve as an example of a hunter deceived by camouflaging properties of prey: again, a number of other factors need to be considered (the prey might be too agile, disgusting or unworthy of catching in other ways). Without large empirical knowledge, it is impossible to determine suitable “candidates for camouflage” solely from the data about the diet of predators.

We have examined the case of protective resemblance because it is a basic concept within the theory of adaptive colouration. Having in mind the fact that symmetric principles apply for aggressive resemblance, we will investigate the problem of camouflage in the case of some felid species.

5.1.3 Investigation of the camouflaging properties of felids

There is a basal tension in the very concept of aggressive colouration. The theory of crypsis was induced as an empirical testimony, based on the experience of our (human) sight. But should the theory work in nature, it is the vision of prey which has to be deceived by a camouflaging pattern. Neubauer (public discussion) had an anecdotal remark: “To verify the theory of crypsis, we would have to see a tiger with the eyes of deer!” If we do not want to rely on alternated state of consciousness, science has only a rather rationalised way how to replace deer eyes: to model general conditions of crypsis and to investigate anatomy of the sight of deer.

If we try to reveal fundamentals of the tension, we find us facing a pit between empiricism and rationalism. An empiricist is bound to find out as much information as possible from the ecology of felids. He has to rely on his senses but explores the phenomenon linked with senses of different creatures: therefore, his results can be easily assaulted as having a stigma of anthropocentrism.

A rationalist might stand more firmly at the start. Having in mind pitfalls of the concept (non-human vision, light condition by dusk and night etc.), he would begin to formulate general rules concerning the conditions of crypsis. A good example can be Endler (1978), who found several optical determinants involved in the phenomenon of camouflage and formulated rules on this ground. The rules have almost physical accuracy and are generally concerned with problems on the edge of optics and the physiology of vision. In the fashion of physics, rules are formulated for ideal situations and they promise to be universally applicable.
But can these rules be successfully applied on the variety of living organisms? We must bear in mind that we are not concerned with the discipline of optics but with camouflage. Although the laws of optics are universal, the essence of camouflage consists in deceiving of individual minds. And here we get back to the problem how the senses of different species work in natural settings. To find out whose mind is deceived and whose not, we have no means but to rely on empirical inquiry of species-specific cognitive capacities.

Another theoretical approach grounds in artificial neural networks. Deceiving might be rather linked with the inability to learn how to process new settings of a familiar object than with the inaccuracy of the sight. Coss and his research group made an important step when they realized that neurophysiological system of highly predated species is likely to be attuned for the recognition of its predator. Moreover, they believe that neuroanatomical and electrophysiological research carried out on captive cats and macaques provide us with sufficient amount of information to simulate the cognition processes by artificial neural networks. Artificial neural networks are exploited in a dynamic field of artificial intelligence for its ability to learn. Following the promises of a new branch of science, Coss et al. (2005) simulate in silico whether the pair of eyes in leopard’s face is obscured by surrounding spots from the perspective of macaques inexperienced with this felid species.

One must be respectful to the impressing amount of findings and technical applications arising from artificial neural networks. Still, a bit of scepticism might enable to assess the achievements in broader context. There is some chance that other animals (mammals at least) have a similar neurophysiology of vision as we humans do: we are phylogenetically relative after all. On the other hand, as we are aware of some basic differences among the sight mammalian species (colour vision, vision by night), we have to be cautious about generalizations. But should not we pay similar attention to differences between cognitive capacities of artificial networks and living animals? How do we evaluate if an artificial model relates sufficiently to neural networks in the brain of a specific species? It might be an anthropocentric prejudice, but one would not be much surprised if our vision and its physiology relates better to mammals than virtual models of neural networks.

In fact, there is one way how to test visibility of felids from the perspective of prey and rely on empirical approach at the same time. As far as our knowledge extends, the only experiments done in a similar manner have been carried out by Coss and his colleagues. An already discussed experiment (Stankowich and Coss 2007) consisted in displaying different models of felids (puma, tiger, and leopard) to black-tailed deer (*Odocoileus hemionus columbianus*). Models were partially covered to simulate natural conditions of hunt. Shapes of the models resembled each other close enough to allow for an assumption that the deer’s
reaction was elicited only by the colour and pattern of a model (and the deer’s previous knowledge of a predator’s appearance. In similar settings, the reaction of the common prey of felids to various types of patterns and colours can be easily tested.

5.2 Maintaining the paradigm

The significance of colouration among felids has been studied mainly from the perspective of Darwinian-Wallacean theory of colouration. As the theory is an intact part of a broader paradigm of Darwinism, it has not undergone a significant shock within the last 150 years. However, it is worth examining some slight changes in opinions, for it sheds some light on much discussed topics of the history and philosophy of science: the conservative role of a paradigm in the assessment of a given class of phenomena. The tiger will serve as an exemplum for our thoughts.

At the beginning, there was a simple observation – or maybe speculation. Wallace’s account of the tiger’s stripes may be either the result of an encounter with a tiger or an artificial “just-so-story”. From the literature known to the author (Wallace 1869, 1870, The A. R. Wallace Correspondence Project website), it is not clear if Wallace had ever met a live tiger during his numerous expeditions.

Camouflaging properties of the stripes of the tiger were not postulated as a singular hypothesis, but as a part of Wallace’s (1870) general concept of animal colouration. The general theory was applied to the leopard and other felids afterwards (e.g. Beddard 1892, Poulton 1908). What is worth mentioning is the fact that this early account of the significance of felid colouration has remained unchanged in the core, regarding not only the statement of camouflage property but its occurrence in the respective habitats (e.g. tiger - grassland, leopard - forest).

Nevertheless, some problems have arisen in the course of time. Generally speaking, habitats of big felids are extremely variable and it is hardly conceivable that the tiger keeps its camouflaging properties throughout the whole area once stretching from Anatolia on the west to Far East on the north-east and Bali on the south-east.

What is a striking feature of paradigms is their conservatism. Despite the enlarging amount of findings, observations and hypotheses, there is a strong tendency to keep the original assertion. Typically, a more complex theory is developed with the aim to meet two goals. An innovated theory needs to encompass problematic facts. This leads to adding new factors (e.g. evolutionary, environmental, behavioural) and conceiving more determinants which might be
responsible for an investigated phenomenon. With the help of an enlarged set of factors, the old theory is confirmed. In the case of camouflage and felids, two main factors were considered and added: biogeographical history and the problem of the vision of prey.

Some authors (Perry 1965) challenged cryptic properties of the tiger’s stripes and asserted that the coat as such is rather conspicuous, at least in a forest during daylight. Now if we take biogeographical history into account, this cannot by any means simply reject the original theory. Mazák (1979) states that ancestors of the tiger originate in the region of northeast China. There is little known about the composition of habitats which accommodated tigers around 2 million years ago (based on genetic assessment by Johnson et al. 2006, modern tigers diverged from the common ancestor with the snow leopard 2.88 million years ago) which was the time of two major dispersals of tiger population (Mazák 1981). It can be therefore simply stated that the tiger’s stripes accomplished the camouflage function at that time, allowing the species to be fit enough to colonize other regions with different habitats.

(However, a recent analysis of mitochondrial DNA suggests that the most recent common ancestor of tigers lived 72 000 -108 000 years ago: see Luo et al. 2004.)

The inclusion of additional determinants leads very often to the violation of the principle of Occam’s razor. The tiger might have been cryptic in China during Lower Pleistocene, but it is more appropriate to reject the theory of camouflage if we do not find the coat cryptic in the current environment inhabited by the tiger.

The other factor is the vision of tiger’s usual prey. Ungulates, which are recently the most common prey throughout the whole tiger’s range, have dichromatic vision. Therefore, their ability to distinguish a tiger from its background is probably significantly lower in comparison to primates with trichromatic vision. Yellow and orange hues of the tiger’s coat can be quite conspicuous for the human observer but they blend with green foliage in the visual perception of ungulates.

There is another issue which should not be omitted regarding the coherency of paradigm. The following can be surprising for a theoretician but applies very often in the routines of (current) biology. During the stage of “normal science” (Kuhn 1962), it is not a problem if some hypotheses are rejected as long as it does not give birth to the feeling that the theory should be reconsidered as such. Normal science needs a program to follow, some findings confirm a given idea, some not: what is crucial is that new and new partial hypotheses based on the initial theory can be formulated. This process alone is maintaining the idea in the thoughts of scientists.

What is even more surprising is that a paradigm can encompass facts which contradict the empirical fundament, initially creating the theory itself. Coss and Ramakrishnan (2000) found
that leopard’s coat is highly conspicuous for bonnet macaques (*Macaca radiata*), common prey of leopards living in southern India. In fact, spotted coat seems to be a leopard-recognition cue for them. Nevertheless, Coss and his colleagues maintain the assertion that the spotted coat was originally cryptic in its function but has become a conspicuous predator-recognition cue in the course of co-evolution of the leopard and its prey. However much such an assumption violates the principle of Occam’s razor, the original theory is too precious to be abandoned.

We have pinpointed several examples how the fundament of the theory is maintained within the existing paradigm. But the matter is more complex in fact. As we have rather criticized the conservatism of the paradigm, we do not seek to formulate a meta-theory about the nature of biological enquiry in an analogously rigid fashion. Darwinian paradigm, though conservative in its nature, has developed an enormous number of branches and the entire tree of Darwinism is too complex for a comprehensive and at the same time unambiguous description. In fact, there are some works which go against the theory of camouflage properties of felid coats patterns. Their goal is not to reject the Darwinian-Wallacean theory of adaptiveness of animal colouration, but the point of view they adopt relates to another branch of Darwinian tree. Coss and his colleagues (Coss et al. 2005) later simulated the recognition process of bonnet macaques to find out whether the pair of leopard’s eyes is obscured by the spotted pattern of the face. Surprisingly, the conclusion is that even inexperienced macaques do not have troubles to identify a dangerous predator: this questions camouflaging property of leopard’s coat as such. These findings are based on methods relatively new for biology (such as face recognition, neural networks), which have recently been incorporated into Darwinian paradigm and constitute a new branch with an innovative approach.

We have demonstrated that despite of the conservative features of the Darwinian paradigm, knowledge grows along several directions. New branches do not significantly alter the message conveyed by the theory of camouflage, but considerable effort which is focused on ecological, behavioural and other factors which are related to this problem bring interesting partial information. Owing to detailed inquiries into alarm calling of primates, aspects of predator recognition, and properties of the vision of prey, we have obtained a composite picture of the problem of coat patterns’ visibility.

What matters is that the hypotheses themselves are formulated in the shape which is sensible and comprehensible for the paradigm. It is the way of thinking, the shape of questions which are asked what is characteristic for the paradigm. For Darwinian-Wallacean paradigm in biology, this means that either the colour and pattern of felid coats is cryptic for prey, or conversely, the neurophysiological system of prey is attuned to felid coats. Even the
latter option allows explaining the value of felid coats in Darwinian way: as a predator-recognition cue, it has a negative selective force for the felid. Neo-Darwinism is a whole tree of concepts, as was already mentioned, but the growth of every branch must be consistent with the rule of utility. We have not mentioned Darwinian theory of sexual selection in these reflections, because it is rarely believed to account for felid coat patterns. But even this theory, although designed as a counter-balance of natural selection, uses utilitarian language. An aesthetic display is good for attracting a sexual partner. The notion of purpose delimits the boundary of Darwinian paradigm. If a non-utilitarian approach appears, it is often perceived as hostile to Darwinism. We will show this tension in the chapter about Portmann’s aesthetic morphology and discuss options of reconciliation.
6 HINGSTON: THE THEORY OF COLOUR CONFLICT

In this section, we will focus on a theory of animal colouration worked out by a major of colonial British army R. W. G. Hingston and some of its implications to the problem of felid coat patterns. In his crucial work The meaning of animal colour and adornment (1933), Hingston proposes a highly innovative account of the significance of animal colouration and behaviour. His theory works on Wallace’s belief that the purpose of colouration is either to stress the appearance of its bearer (semantic function) or conceal it (cryptic function). In addition to the classic approach to adaptive value of colouration, Hingston pays great attention to the relation between colours (patterns, adornments) and emotions. He is convinced that continuous battle of life takes place in animal kingdom and that interactions among individual animals are orchestrated by the emotions of anger and fear. Semantic colours have the purpose to accentuate the strength and power of an animal, whereas cryptic colours express fear and apprehension. At this point, Hingston transcends mechanical view of colouration: colour design of animals is not merely an outcome of selective pressures but reflects the temper of a living being.

As a cautious observer, Hingston is aware of the fact that many animals possess semantic and cryptic parts within one body. To explain this phenomenon, he introduces the concept of colour conflict. Areas of bright and dull colours are unequally distributed on an individual (species-specific) body and their proportion inclines toward outer counterpart of a stronger pole within an emotional pair reaching from anger to apprehension. Moreover, the appearance of an animal is not static and postures of a body and display of semantic organs significantly change the way how it is perceived by an observer. By this means, an animal is capable of clear and highly effective expression of temporal emotions. In Hingston’s eyes, the complex of patterns and adornments constitutes a machinery which conveys a message about the temper of their bearer.

To make his theses plausible, Hingston gives many examples mainly about mammalian and avian species (e.g. stripes of the zebra, the head of the parrots of the genus Ara). He assaults a common view that a mammalian coat serves for thermoregulation purposes or physical protection: in his eyes, it is primarily a part of animal’s fighting machinery. Long stiff hairs which can be erected in the emotional state of anger provide an instrument of threat. Therefore, taxa of carnivores which are notorious for ferocious temper (according to Hingston, these are cats, dogs, civets, mongooses) all possess long guard hairs and make a
great show of hair erection. (In respect to felids, we will pay attention to this behaviour in Section 6.2.1.)

6.1 The mane of the lion

To illustrate his theory, Hingston (1933) puts forward an explanation of the colouration of the (male) lion. Basically, the lion is an animal with a tawny coat which provides him with camouflage on khaki plains where it dwells. However, there are three brown-black areas on its body which are in great contrast with the rest of the coat: the mane, the patches on the back of the ears, and the tail-tuft. The parts are not particularly visible in usual positions, but a lion fully exposes them if being angered. Intense contrast of colours signifies aggression toward a conspecific enemy. A lion spreads out its mane, twists the hind areas of the ears forward, and whisks its tail above the back. A whole “threatening machinery” serves to intimidate a rival. Hingston pays special attention to the colouration of the mane which is a crucial instrument of threat in his eyes:

“The first thing we notice about the mane is that it is not uniformly dark everywhere. It is dark on the top of the head and sides of the neck, but in front of the whole of this dark area is a fringe of pure tawny-coloured hairs. These hairs make a barrier which conceals the black area from a person standing face to face with the lion. This is true when the mane is in its normal state, but when the structure is expanded in rage, the dark hind area is spread out, and, since its hairs are much longer than those of the tawny fringe in front of it, they extend out beyond this barrier, and then become visible as a black circle around the head and neck of the lion.” (Hingston 1933, p. 12)

According to the concept of colour conflict, conspicuous areas of the lion’s body should express apprehension. Hingston discusses the issue at great length and seeks for the explanation of the following paradox: how can the tawny colour of the lion express its fear when there is nobody to be afraid of? When the lion approaches a victim, the function of its tawny coat is the same as in the case of non-aggressive animals: to be cryptic. A crouching hare is afraid of being seen from an eagle hovering overhead, whereas a crouching lion is apprehensive in anticipation of being discovered by a grazing zebra. Hingston also explains why the lion possesses short hairs which lie close along the body. According to him, all other species of cats have long stiff hairs present in the coat and are capable of erecting them when expressing ferocity. But in the case of the lion, this function is designated to the mane.
In his treatise on Serengeti lion, Schaller (1972) shares a similar view on the lion’s colouration to Hingston in some aspects. Black parts of lion’s body accentuate the vividness of its emotions: besides the black tassel on the tail and the patches on the ears, facial expressions are stressed by black lips and nose. Schaller confirms that the tail is often lashed up and down in agonistic encounters, mainly during aggressive threat.

![Division of the lion’s mane into separate areas. (After West et al. 2006)](image)

**Figure 26: Division of the lion’s mane into separate areas. (After West et al. 2006)**

As far as Hingston’s analysis of the function of the mane is considered, it is very convincing and detailed, nevertheless, it should be treated with caution. First of all, it is hard to find evidence for his suggestion that dark hairs bristle in anger. In Hingston’s description, it seems as though there were separated areas of the mane with specific colours. Based on the analysis of images of lion males, West et al. (2006) found a significant difference between the colouration of the mane on the chest (the darkest), neck (medium), and forehead (the lightest). (A schematic division of the mane to distinct areas follows Figure 26.) When a lion is in an upright position and viewed from the front, the mane on the chest is clearly visible, whereas Hingston asserts that black hairs are usually obscured with the barrier of tawny hairs (see Figure 27). Further, a black mane sometimes occurs on the belly of an animal which is the area usually linked with defensive visual signals (Kingdon 1977). Moreover, dark (black) colouration positively correlates with the age of an animal: old males often display practically all-black mane with areas of tawny hairs left only on the cheeks. It is good to mention that the tone of the mane significantly varies among subspecies (see Lupták 2009): the Barbarian lion (*Panthera leo leo*), extinct in 1942 in wild, possessed a very dark mane (with the exception of cheeks), whereas the Kruger lion (*Panthera leo krugeri*) often displays a golden yellow mane with dark hairs almost absent. Ewer (1973) points out that colouring of the mane is highly variable even among individuals living in the same habitat. As a matter of interest, there occur
completely maneless individuals among the East African lion (*Panthera leo nubica*) (see Lupták 2009).

![Image of a lion](image)

**Figure 27:** A fully developed mane of the lion (*Panthera leo*). (Internet source: www.velma.cz/lovy.html)

### 6.2 Colour conflict: a place of the theory

Hingston’s theory of colour conflict is remarkable for our topic in several ways. First of all, Hingston pays a lot of attention to felids, the lion being an exemplum for an introduction of his theory. This is quite important as original Darwinian (or “Wallacean”) account of animal colouration was built upon insects and birds in the first instance. If one may say that Wallace somewhat extended the theory of protective colouration, which worked pretty well in the realm of insects, to few mammalian species in order to make the theory universal, Hingston’s theory of colour conflict stands and falls with its credibility among mammals, carnivores and especially cats.

Further and surprisingly, Hingston was probably the first author who gave details of cats behaviour in respect to the significance of their coat. As we might have seen on Wallace’s and Darwin’s accounts of tiger stripes, their explanations are constituted by a mere statement without an attempt to discuss their appearance further. This may be caused by the already
mentioned fact that both Darwin and Wallace were primarily interested in different families of animals.

Moreover, Hingston made a considerable effort to test the hypothesis he had generated. This is one of the reasons why his theory appears to be more sophisticated than traditional accounts. For example, when he states that the mane of the lion serves as a device of threat, he discusses why other felids get away without it. As a good observer, he is sensitive to appearances of animal beings. He ingeniously finds out that displays of threat among felids are often accompanied by the elevation of the tail (e.g. lynx, lion, domestic cat).

Although Hingston’s theory as a whole has never acquired general knowledge, his particular findings are part of a contemporary zoological thesaurus. Hingston’s principle of colour conflict builds upon widely acknowledged concepts of concealing and semantic colouration. In ecological accounts of mammalian colouration, his explanation of contrasting marks on back of felid ears is valued as a solid hypothesis (cf. Schaller 1967, Caro 2005). Similarly, presumed significance of a contrasting tail tip in intraspecific communication is inferred from Hingston’s observations of felid threatening postures (see Section 1.2.1). Caro (2005) highlights the fact that different parts of the body among different species are subject to different selective pressures and mentions Hingston as the originator of the idea. But this is a switch to Hingston’s understanding of the leading power behind the scene. In his eyes, natural selection is an external force responsible for shaping various forms of life which are primarily formed by internal emotions:

“The whole tree of life is growing and spreading by one internal developing urge which for want of a better term we must call the emotional content of the tree. The channels along which that growth is proceeding are the many and varied parts of the machinery by which the emotional content is exhibited. External influences are advancing or retarding this growth, and the growth itself is predestined to a natural termination.” (Hingston 1933, p. 398)

One can see that Hingston’s original findings were incorporated into Darwinian paradigm, but the core of his teaching (relation of emotions to specific colours and patterns) was more or less abandoned and replaced with mechanistic understanding of communication in the animal kingdom. Under the current neo-Darwinian paradigm, selective pressures in the efficiency of message transmission result in the contrasting colouration of organs of communication (see Guilford and Dawkins 1991 or Endler 1992 for example).

Taking into account Hingston’s affiliation to British inter-war biological thinking, it will not be amiss to mention a surprising feature of his theory: the teaching exhibits some aspects resembling original insights of Portmann, who belongs to the continental school of biology (cf. Komarek 2003). Although Hingston’s paradigm is without any doubts of a strongly
reductive character, he does not resign in the effort to contemplate problematic and complex issues such as general meaning of colouration. As we will see in the following chapter, his search for a firm bond between colours and emotions is a direct counterpart of Portmann’s investigation into the inwardsness and laws of self-representation in the realm of animals.

6.2.1 Dymantic (startling) colouration

The insights of Major Hingston were accepted or independently re-invented by few later authors. The very concept of threatening display was familiar to Cott (1940), who cites Hingston’s observations on several occasions. Young (1957) pays attention to the specific situations when a pattern is displayed suddenly in order to startle an approaching enemy. Ghostly expression of threatening gelada baboons (*Theropithecus gelada*) serves as a prominent example. In order to distinguish this specific type of display from concealing and semantic patterns, Young puts forward the term *dymantic (startling) colouration*, but makes no reference to the theory of colour conflict.

The principle of dymantic colouration is often exploited by the representatives of the Felidae family. Hairs occurring in the coat of felids are generally of an agouti type (i.e. a hair is divided into several bands with different colours), but there are some exceptions. The most striking one is the mane of the lion: it consists of long fully-black guard-hairs. According to Searle (1968), guard-hairs on the back of domestic cats have a function of dymantic colouration: erectable guard-hairs allow the “bristling” effect making an individual seemingly bigger when facing an enemy. Fur bristled up accentuates a typical warning display which is performed by arching the back. An analogous behaviour is likely to occur in the case of other small felids. Tonkin and Kohler (1978) report that the dark stripe along the spine of the African golden cat (*Caracal aurata*) consists of hairs which are erected in excitement. Similar property of hairs along the spine was detected in the case of the Pampas cat (*Leopardus colocolo*) during play (Callahan and Dulaney 1997).
7 THE AESTHETIC MORPHOLOGY OF ADOLF PORTMANN

According to Komárek (2003), there are only three original doctrines which interpret the colouration of animals: classical Darwinism (built together by Darwin and Wallace), the theory of major Hingston and the aesthetic morphology of Portmann.

A Swiss biologist Adolf Portmann (1897-1982) established very specific and highly thought-provoking biological teaching. He asserts that there is a clear distinction between two parts of animal bodies: internal organs and the surface of the body. Internal organs are the centre for vital metabolic, locomotive, and neural faculties of an organism but do not establish its specificity and identity. Only a specialized anatomist is capable of distinguishing a lion from a tiger by examining their viscera or skulls. On the other hand, the surface of the animal body is displayed to all observers and even a child at the ZOO can learn to distinguish the two cats without a considerable effort. Their outer structure “impresses itself easily upon our memory” and our eyes and brains prove to be excellent organs of reception when dealing with external manifestation (Selbstdarstellung) of living beings (Portmann 1967, p. 33). In contrast, when the attention is focused to the realm of the hidden, the shapes and outlines of internal organs always threaten to desert the preserve of active knowledge of a researcher.

Portmann strives for an erudite description of the inner life of organisms. An animal interacts with the outer world through its inwardness (Innerlichkeit), a species-specific aggregate of sensual and neurophysiological faculties. The characteristics of inwardness are manifested by outer organs. This representation can take two forms: firstly, there are species-specific patterns and colours which go far beyond adaptive value. Secondly, on the level of individual life form, inner conditions are immediately manifested in external appearance. Cats provide a nice example: a moving tail expresses uncertainty or excitation, tilted ears fear, baring teeth threat etc. (see Figure 28)
Figure 28: Latine square illustrating the variety of facial expressions of the felid. (After Leyhausen 1979)

The more complex inwardness, the higher position of an organism in the rank of animal organization. Portmann seeks to prove that rank is an objective category which reflects the complexity of organisms within a given taxa and can be properly measured with appropriate tools. Roughly expressed, phylogenetically older forms (more “primitive”) which are closer to a common ancestor belong to the low ranking level (e.g. the tapir in comparison to the horse). The structure of the brain and the advancement in sense organs development is asserted to be the best criterion for determining the level in rank. Moreover, there is a correlation between the level in rank and the complexity (and the level of differentiation) of the organ of the head (Portmann 1967). In comparison to rodent-like animals (see Figure 29), the head of felids is detached from the general outline of the whole form (see Figure 30). The head is an actual organ of display: facial muscles enable to express a whole morphospace of emotions. In the case of felids, emotions are marked with other parts of the head: the position of ears, the shape of eye pupils, the conformation of lips-teeth-mystacial whiskers system etc.

Figure 29: From left to right: the head of pouched mouse, tree shrew, rat. (After Portmann 1967)
Portmann implicitly works with the idea of higher and lower forms of organismal organization and illustrates the differences on pairs of species belonging to the same taxa. For example, among ruminants, the giraffe (*Giraffa camelopardalis*) belongs to a higher level in rank than the Chinese water deer (*Hydropotes inermis inermis*) (Portmann 1967). The difference between indeces of their cerebral cortex (29.5 for the giraffe - 12 for the Chinese water deer) only illustrates an apparent scope between the two forms, the level of their organization being visible by an experienced eye. The Chinese water deer has some archaic anatomical features (e.g. short stature) and gives birth to a number of offspring, a feature typical of all primitive mammals. In contrast, limbs and neck of the giraffe are extremely elongated. (In a substantial number of cases, Portmann values higher the forms which are somehow liberated from the ground and benefits primarily from optical orientation.) An outstanding length of the neck is caused by the elongated seven vertebrae, the length of legs is brought about by the elongation of the middle toes. In accordance with the advanced organization of the animal, the surface of the giraffe’s body is beautifully designed: the visible parts are dotted with ochre spots of irregular shape separated by white lines, the head is adorned with two knobs and the neck is accentuated with short mane.

7.1 The tiger’s stripes: preliminary thoughts about Portmann's approach

“How elaborately is the tiger’s body divided up by the arrangement of stripes! The transverse markings around the limbs and body have their various directions unified by cleverly arranged gussets where the legs leave the trunk. In the magnificent pattern on the
head, the most beautiful figuring is reserved for the purpose of bringing eyes and ears into relief. For all its free rhythm, the pattern nevertheless still follows strictly the arrangement of the particular parts. It emphasizes the leading pole, it frames and accentuates the important sense organs. This correlation between internal structure and outward appearance creates a unity of the visible form which appeals to us clearly in its powerful impression.” (Portmann 1967, p. 75)

Figure 31: The tiger and its stripes. (Illustration by Lucie Čermáková)

This beautiful description of the tiger’s appearance provokes several reflections. First of all, one might hardly avoid being moved by the stylistics of the author. It goes far beyond descriptive scientific language, though metaphors are virtually absent. The main aim is to depict the unity of the animal’s form, the means consist in the integration of details into a whole picture. To reach such an effect, Portmann uses expressions and phrases typical mainly for aesthetical disciplines (e.g. “free rhythm”, various adjectives etc.).

However, without further considerations, this does not mean that Portmann’s approach should be linked with “aesthetics” and not with “biology”. It is rather typical for influential biological theories that they are promoted with language that is as much poetical as factual. Dawkins (1976) is probably the most illustrative example of the power of scientific poetry (his effort is directly opposite to Portmann and one might say his poetry in anti-aesthetical, highlighting the virtuality of animal bodies in contrast to the ontological primacy of genes).
Portmann is moreover very “biological” in his sense for the details of design of animal surface. This clearly arises in the comparison with Wallace, a classic of the theory of concealment, who spends only a short time with the description of individual animals. The reasoning of Wallace is very straightforward and his evaluation unproblematically determined by his belief in the privilege value of adaptiveness. Let us recall his account of the tiger’s stripes (Wallace 1870):

“The tiger is a jungle animal, and hides himself among tufts of grass or of bamboos, and in these positions the vertical stripes with which his body is adorned must so assimilate with the vertical stems of the bamboo, as to assist greatly in concealing him from his approaching prey.” (p.52)

The appearance of the tiger is reduced to the possession of stripes, taking no account of a convoluted pattern displayed on its head. The reduction reaches the level of simplified geometric appropriation: the tiger’s stripes and stems of bamboo are described as vertical lines.

A typical modern neo-Darwinian approach to the problem of animal colouration can be illustrated by the work of Ortolani and Caro (1996). A body of a (general) carnivore is separated into mutually exclusive areas (head, back, tail, etc.) and each area is characterized according to a list of categories of patterns. An additional list encompasses several ecological characteristics of species (activity patterns, habitat, etc.). The interconnection of the two lists enables to test predictions about the adaptive value of the specific phenomena displayed by carnivores with the use of statistics. We exploited this method to test several hypotheses (e.g. camouflage property of spotted coats in the forest) in Chapter 3.

However, the contrast does not reside merely in the fact that Darwinism is a reductive theory and Portmann seeks for eidetic understanding (cf. Neubauer 2002). Portmann holds his own theses and strives to verify them on examples from the animal kingdom: one might say that being holistic in description, Portmann is reductive in intentions. For the most important epistemological aim is not to praise the beauty of living beings but to show that organisms with a higher level of anatomic (and sensual) constitution (the higher level in rank in Portmann’s words) display a more sophisticated design of the surface. This is a very important moment since it provides the form of order and measurement: according to Foucault (2002), these means belong to characteristic features of Classical episteme, i.e. modern science.

Indeed, Portmann quantifies brain indices for several taxa of organisms (mainly birds) and determines the types of colouration reflecting the level in rank. In low ranking forms, the head is not accentuated by specific colouration or design. If a facial stripe is present, it simply resembles stripes displayed on the body (e.g. the striped possum, Dactylopsila trivirgata, see
Typically, the pattern does not match any division of the body and it seems as if it was printed on the surface *en bloc* (e.g. *Holacanthus* fish, see Figure 33). In contrast, high ranking forms are characteristic of special design of an anterior part (as we have seen on the example of the tiger). Individual organs often exhibit different varieties of patterns and the body is sometimes adorned with aesthetically valuable structures (e.g. the mane of the lion or the horse).

Figure 32: Examples of striped marsupials. From left to right: banded hare-wallaby (*Lagostrophus fasciatus*), striped possum (*Dactylopsila trivirgata*), banded anteater (*Myrmecobius fasciatus*). (After Portmann 1967)

Figure 33: Total design of *Holacanthus* fish. (After Portmann 1967)

There are several moments where Portmann conceptualizes same peculiarities as current biologists. For example, intriguing patterns found on the heads of the African guenons (*Cercopithecinae*) are compared to (species-specific) coat of arms (Portmann 1967). The same notion can be applied to the variability of coat patterns exhibited by individual felid species.
What creates the identity of a leopard in the eyes of an observer is its spotted “coat of arms”. Marler (1961) uses a category of species-specific designative signal for similar phenomena. The individuals of either the same or other species are able to identify a leopard at the moment they distinguish its characteristic coat. According to experimental findings, cognitive abilities of leopard’s prey are attuned for recognition of spots scattered on a tawny field (Coss and Ramakrishnan 2000).

7.2 Felid coat patterns, aesthetic morphology and the level in rank

At this place, we will give some insights into the outward design of felids which follow Portmann’s way of thinking. The stunning appearance of the lion (Panthera leo) was discussed at great length by Hingston (1933). In his view, the possession of the mane has the function of expressing intimidation. The same applies to a black tassel of hairs on the tip of the tail. Under the prism of aesthetical morphology, the identical phenomena are conceived to be purely semantic, without direct effects in intraspecific interactions (fights, recognition, etc.), though these could have been subsequently acquired. The mane boldly accentuates the outline of head and when viewed from the front, its long guard black hairs give an impression as if the head was one and a half times larger. As the only cat living in packs with a high degree of hierarchical organization, the superior position of males is expressed by a significant difference in body weight and the fact that females completely lack mane or have it only insignificantly outlined (Lupták 2009). Further, the scrotum of a male is pushed posteriorly as far as possible and is only partially hidden by the tail. The conspicuous design of an anal pole is a characteristic feature among several groups of mammals (e.g. primates, ungulates) and Portmann (1967) determines it as a benchmark of a high level in rank.

Another species worth of special consideration is the caracal (Caracal caracal). Similarly to the lion, the caracal’s body is not covered by any pattern but the whole appearance of the cat is pleasing to an eye. Although this species of felid is inconspicuous when compared to its relatives with beautiful markings, it precisely approves of the notion of Portmann (1960) that not only flamboyant forms of life deserve appreciation for its design. (In this respect, the question of the level in rank is not raised by Portmann.) The constitution of the caracal is very athletic but not as robust as in the case of its larger relatives and balanced proportions of the individual parts of the body suggests that its bearer is a very agile cat. Indeed, caracals are frequent hunters of birds, swift enough to grab them with both forepaws. The most conspicuous part of the felid is its head. The head of the caracal is relatively small and is held
by a distinguishable neck so the animal keeps it elevated from the rest of the body (when compared to the tiger for example). It is decorated with a pair of elongated ears with tuft of hairs growing from its tips; the ears are as long as the height of the rest of the head. Ewer (1973) witnessed a pair of animals exchanging ear twitches, one individual evoking an answer from the other. “The ears are lined with long white hairs within but are black behind and, although this colour is sometimes modified by grey flecking, both the rims of the ear and their bases have crisp black margins which serve to isolate the ears visually, making them stand out from their background like a black butterfly settled on the palm of one’s hand.” (Kingdon 1977, p. 331)

Moreover, there are three transverse stripes on the forehead, optically linking the eyes with the ears: two of them are black, short but relatively bold if viewed from the front. The third one is a narrow but clearly distinguishable ridge of hairs which virtually cuts the forehead into two symmetric halves. The forehead stripes, together with outstanding ears, accentuate facial expressions of this elegant semi-desert felid.

Figure 34: The head of the caracal (*Caracal caracal*). (Internet source: en.wikipedia.org)

Attentive description can reveal important morphological details of individual species and show their meaning within the unity of form. However, isolated insights do not match the requirement of the verification of universal laws. Since we have shown that Portmann’s conception of rank is quantifiable, we have an ambition to test some of his hypotheses statistically. If we determined rank of individual species within the taxa and we had a clear order of patterns ranging from “primitive” towards “advanced”, we would be able to test
whether the level in rank of animal organization correlates with the semantic (aesthetical) value of the displayed patterns.

In the case of felids, we are challenged with practical limitations. First of all, cerebral indeces have been determined only for few representatives of the Felidae. Further, individual species of felids display a rich variety of patterns (spots, stripes, blotches, rosettes, etc.) and Portmann’s work does not provide a clear clue for their evaluation (related to the level of organization).

The only available source of data about cerebral indeces of several species of felids is Mangold-Wirz (1966). Our attention will be limited to the index for total brain (Totalhirnindices, TI). TI is defined by the following way: for a given body-weight in the group of animals under consideration, we take species with the lowest weight of remnant of the stem. TI is calculated as a ratio of the weight of total brain and this elementary nervous mass. Table 7 displays values for nine species investigated by Mangold-Wirz (1966).

<table>
<thead>
<tr>
<th>Species</th>
<th>Total brain index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Panthera onca</td>
<td>28.0</td>
</tr>
<tr>
<td>Panthera pardus</td>
<td>28.2</td>
</tr>
<tr>
<td>Panthera leo</td>
<td>27.1</td>
</tr>
<tr>
<td>Panthera tigris</td>
<td>28.2</td>
</tr>
<tr>
<td>Acinonyx jubatus</td>
<td>28.4</td>
</tr>
<tr>
<td>Puma concolor</td>
<td>27.5</td>
</tr>
<tr>
<td>Leopardus pardalis</td>
<td>27.5</td>
</tr>
<tr>
<td>Lynx lynx</td>
<td>28.9</td>
</tr>
<tr>
<td>Felis silvestris</td>
<td>22.9</td>
</tr>
</tbody>
</table>

Table 7: The values of total brain index for several felid species. (After Mangold-Wirz 1966)

A task to order specific patterns of individual species is a delicate one. Portmann did not have the ambition to systematically classify patterns and did not attempt to determine distinct categories. Therefore, he made only dual comparisons between the selected species (e.g. giraffe versus Chinese water deer). Expressed in a simplified way, if attention is restricted to the body, one can say that more convoluted patterns belong to the manifestation of higher rank.

Moreover, to evaluate the value of patterns, we need to distinguish among separate parts of an animal body since they participate on display by different proportions. The usual categorization of felid coat patterns (e.g. Werdelin and Olsson 1997) is based on markings
occurring on flanks, but this can be misleading from the perspective of Portmann. When we take semantic properties into account, there are two prominently important parts of a mammalian body: the head and the anal pole (Portmann 1960). The anal pole of a felid body gets a specific design due to the existence of a distinct tail, which can comprise around one half of the whole body length (in the case of the marbled cat, *Pardofelis marmorata*). The position of the tail toward the body (together with its movements) expresses emotions of an animal and the outline of the tail can be accentuated by a specific pattern (Baxa 2011). The end of the tail is often marked by a distinct tip: this trait probably highlights its movements.

At this stage, we need to assign a rule for the relative importance of individual body parts on the composition of a total design. We follow the method used for the computation of salience in Stankowich et al. (2011). Since the importance of a specific body part in display does not directly reflect the relative proportion to the total body area, we need to adjust scores for their supposed semantic value (see Table 8). The sum of the resulting scores gives a full score of 1. The “semantic scores” are subjective but not arbitrary and the results are robust to slight changes in point values.

<table>
<thead>
<tr>
<th>Part of the felid body</th>
<th>Semantic score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body (flanks)</td>
<td>0.3</td>
</tr>
<tr>
<td>Forehead</td>
<td>0.5</td>
</tr>
<tr>
<td>Tail base</td>
<td>0.05</td>
</tr>
<tr>
<td>Tail tip</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Table 8: Semantic value of individual body parts of felids.

In the following paragraphs, we will discuss pattern categorizations for individual body parts. As far as the body (flanks) is considered, there is a great diversity in contrast between markings and the underlying colour of the coat. We suppose that more contrasting markings reflect a higher level in rank than those scarcely visible by an eye. Subtle spots are often irregularly distributed on the body (e.g. rusty-spotted cat, *Prionailurus rubiginosus*), whereas distinctly contrasting spots are seemingly ordered and a coat resembles a tapetum (e.g. cheetah, *Acinonyx jubatus*). Rosettes and blotches are valuated higher than spots for two reasons: there are geometrically more complex and the hairs which make up their inside are often distinctly coloured (e.g. the inner area of leopard’s rosettes or ocelot’s blotches is darker than the underlying colour between individual rosettes/blotches). The transversal stripes of the tiger are structurally convoluted: moreover, given the tiger has a prominent place as an exemplum of a high ranking form (Portmann 1967), we constitute a singular category for
them. The highest score belongs to large blotches (marbled cat *Pardofelis marmorata*, clouded leopard *Neofelis nebulosa*), undoubtedly the most complex pattern displayed among felids which is made up by hairs of three distinct colours. The categorization used is original and the distribution of types among individual species is based on the analysis of photographs from various sources (see also Section 3.1) (Table 9).

<table>
<thead>
<tr>
<th>Category</th>
<th>Pattern</th>
<th>Pattern score</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>uniform</td>
<td>0.0</td>
</tr>
<tr>
<td>1</td>
<td>simple transverse stripes</td>
<td>0.1</td>
</tr>
<tr>
<td>2</td>
<td>subtle spots</td>
<td>0.2</td>
</tr>
<tr>
<td>3</td>
<td>distinct spots</td>
<td>0.5</td>
</tr>
<tr>
<td>4</td>
<td>rosettes or small botches</td>
<td>0.7</td>
</tr>
<tr>
<td>5</td>
<td>distinct convoluted stripes</td>
<td>0.9</td>
</tr>
<tr>
<td>6</td>
<td>large blotches</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Table 9: Scores for individual type of patterns displayed on the body of felids.

The categorization of patterns on the head follows a precise morphological work of Weigel (1961). For most felid species, markings are especially visible on the forehead, which is also the largest area of a felid face. To classify patterns on the forehead, we distinguish several simple categories: uniform, spots, and stripes (or spot lines). We assert that this order also reflects the raising level in the complexity of patterns. If a given species shows the characteristics of two categories, mediate value of pattern score is ascribed (see Table 10). The margay (*Leopardus wiedii*) is not recognized as a separate species by Weigel and its forehead pattern is classified as stripes.
Figure 35: Skins of the margay (*Leopardus wiedii*). (Internet source: www.nex.org.br)

<table>
<thead>
<tr>
<th>Category</th>
<th>Pattern</th>
<th>Pattern score</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>uniform</td>
<td>0.0</td>
</tr>
<tr>
<td>1</td>
<td>small spots</td>
<td>0.5</td>
</tr>
<tr>
<td>2</td>
<td>stripes (or spot lines)</td>
<td>1.0</td>
</tr>
<tr>
<td>0&amp;1</td>
<td>polymorphic</td>
<td>0.2</td>
</tr>
<tr>
<td>1&amp;2</td>
<td>polymorphic</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Table 10: Scores for individual type of patterns displayed on the head of felids.

Categorization of patterns on the tail base follows the same procedure. A detailed morphological description by Weigel (1961) allows defining three distinguished categories: uniform, spots, and stripes (or rings). We suppose that this order reflects the raising level in the complexity of patterns. Pattern scores are derived similarly as for the forehead, the tail base of *Leopardus wiedii* is classified as spots (Table 11).

<table>
<thead>
<tr>
<th>Category</th>
<th>Pattern</th>
<th>Pattern score</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>uniform</td>
<td>0.0</td>
</tr>
<tr>
<td>1</td>
<td>spots</td>
<td>0.5</td>
</tr>
<tr>
<td>2</td>
<td>stripes (or rings)</td>
<td>1.0</td>
</tr>
<tr>
<td>0&amp;1</td>
<td>polymorphic</td>
<td>0.2</td>
</tr>
<tr>
<td>1&amp;2</td>
<td>polymorphic</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Table 11: Scores for individual type of patterns displayed on the tail base of felids.
The categorization of the tail tip colour follows Ortolani and Caro (1996). The tail tip was included into our analysis due to its possible signalling function: therefore, we are interested in contrast rather than in colour. We prescribe zero pattern score to undistinguished and full score to white or black (i.e. contrasting) tail tip. Species which possess black or white tail tip (ringed tail) are scored medially (Table 12).

<table>
<thead>
<tr>
<th>Category</th>
<th>Pattern</th>
<th>Pattern score</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>uniform</td>
<td>0.0</td>
</tr>
<tr>
<td>1</td>
<td>black</td>
<td>1.0</td>
</tr>
<tr>
<td>2</td>
<td>white</td>
<td>1.0</td>
</tr>
<tr>
<td>3</td>
<td>black or white</td>
<td>0.5</td>
</tr>
</tbody>
</table>

Table 12: Scores for individual type of patterns displayed on the tail tip of felids.

In this place, it is appropriate to mention a method leading to the determination of pattern scores. Scores are chosen to cover a whole scale between 0.0 and 1.0. Once there is basic approval of the order of patterns values, the exact number standing for pattern score is not crucial since the results are robust to slight changes in point values. This means that the relative order of comprehensive species-specific pattern scores is consistent when individual pattern scores are altered slightly up or down.

Comprehensive species-specific pattern score is computed by the following equation:

\[ S_c = \alpha_1 S_1 + \alpha_2 S_2 + \alpha_3 S_3 + \alpha_4 S_4, \]

where \( \alpha_i \) stands for semantic score of a given body part (see Table 8), \( S_i \) for corresponding pattern score, \( i = 1,2,3,4 \) denotes individual body parts in the following order: body (flanks), forehead, tail base, and tail tip.

If we restrict our attention to the species with determined total brain index \((TI)\), the resulting comprehensive species-specific pattern scores are displayed in Table 13. (A table encompassing values of \( S_c \) for all felid species can be found in Appendix, Table D.) Graphical representation of two investigated variables \( TI \) and \( S_c \) is depicted in Figure 36.

<table>
<thead>
<tr>
<th>Species</th>
<th>Comprehensive species-specific pattern score ( S_c )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Panthera onca</td>
<td>0.71</td>
</tr>
<tr>
<td>Panthera pardus</td>
<td>0.56</td>
</tr>
<tr>
<td>Panthera leo</td>
<td>0.43</td>
</tr>
<tr>
<td>Panthera tigris</td>
<td>0.95</td>
</tr>
<tr>
<td>Species</td>
<td>Score</td>
</tr>
<tr>
<td>--------------------------</td>
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<tr>
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<tr>
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<tr>
<td>Leopardus pardalis</td>
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<td>0.38</td>
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Table 13: Comprehensive species-specific pattern score for selected felid species.

**Figure 36: Scatterplot matching the values of comprehensive pattern score and total brain index for selected felid species**

Based on intuition following graphical representation, we have no clues to assume that TI is correlated with $S_c$ in any manner. If we leave aside the case of *Felis silvestris*, all TI values are clustered between 27.1 (*Panthera leo*) and 28.9 (*Lynx lynx*). On the other hand, $S_c$ values are scattered within the whole scale in a seemingly random manner.

To test this heuristic result with statistical tools, we employ Spearman’s rank correlation test ($n = 9$) in STATISTICA 8.0 (2007). The critical value for $n = 9$ and significance level $\alpha = 0.05$ is equal to 0.683. Since Spearman’s correlation coefficient $r_s = 0.345$, the null hypothesis (independence of TI and $S_c$) cannot be rejected.

To sum it up, the correlation between total brain index and comprehensive pattern score was not demonstrated.
7.3 Coat patterns of juvenile felids

Portmann holds interesting thoughts about the coats of juvenile individuals. He asserts that juveniles display a colouration and patterns of a lower level in rank (Portmann 1967). It means that the pattern is not constituted by a sharp contrast and typically consists of longitudinal stripes (piglets of the bush pig *Potamochoerus larvatus*), transverse stripes (kittens of *Felis chaus* - see Figure 8, *Felis margarita*, and the arrangement of marks on cubs of the lion) or irregular spots (cubs of *Puma concolor*, Figure 10). In theory, the head is usually free from pattern or displays markings quite unrelated with its structure. Among felids, this holds true in the case of the puma: the head of young individuals is marked with spots of similar shape and unclear boundaries as those scattered on the body. Analogous situation takes place with the lion: if kittens display any pattern at all, it spreads continuously from the body on the head. Markings on lion cubs subsequently disappear as they get older. (Some animals possess juvenile markings even in their adulthood: does it mean that they keep youngish temperament in their nature?)

Sand cats (*Felis margarita*) confirm Portmann’s idea of a typical juvenile coat very well. Spots, linked to 4 to 8 dark longitudinal stripes, often extend from the upper portion of the neck towards the forehead of very young kittens (Heptner and Sludskii 1992, Figure 9). By that means, the head of a blind and helpless kitten is optically indifferent from the rest of the body. The spots disappear with maturation (between 6 and 9 months of age), sometimes leaving hardly distinguishable traces on the top of the head. In contrast, stripes which posteriorly extend from a lateral corner of the eye and highlight facial expressions of the cat remain throughout aging.

Nevertheless, there are also cases contradictory to Portmann’s belief: convoluted markings on the head of the tiger are present from the birth. In this case, however, we might state that the stripes of adults are brighter and more contrasting than the ones of young individuals. (This is in accordance with the general observation that the age of an animal can be estimated by brightness and “freshness” of its coat - cf. Pavliska 2010.) Characteristic facial markings of the Asian golden cat (*Pardofelis temminckii*) are already present on a kitten around the age of 3 months (see Figure 37).
In addition to the examples already mentioned, there are a few cases of significant ontogenetic change of coat patterns displayed on the body of felids. The jungle cat (*Felis chaus*) possesses spots or slight vertical stripes as a juvenile but is usually uniform as an adult. Pallas's cat (*Otocolobus manul*) is uniform after birth, whereas slight vertical stripes are visible on adult specimens. The jaguar (*Panthera onca*) and the leopard (*Panthera pardus*) are distinctly spotted immediately after birth (Figure 14 and Figure 17) but the shape of markings changes during their ontogenesis: spots break up into rosettes. In the case of the snow leopard (*Panthera uncia*), a similar process takes place but the resulting pattern consists of small blotches (markings of the snow leopard are transitory between rosettes and blotches and different authors prefer different categories; compare the upper part of the forelegs and the body on Figure 38). Young individuals of the cheetah (*Acinonyx jubatus*) have a “rug” of light coloured hairs on the back which subsequently disappears during maturation. However, the spotted pattern of a coat, partially covered by light long hairs, remains the same during ontogenesis.
Based on these facts, it is problematic to corroborate Portmann’s hypothesis that adult animals display a colouration of a higher rank. If we do not consider the case of Pallas's cat (stripes are not particularly distinct), we can conclude that uniform pattern is derived from the spotted or striped pattern of kittens. However, we are reluctant to say that a uniform coat belongs to an animal with a higher differentiation of design. Portmann does not precisely discuss the problem of uniform animals: based on some of his notions, it is unlikely that a simple design necessarily correlates with a lower complexity of sensual world. Generally, he warns against underestimation of animals which do not catch the eye either due to its technical form, design, or camouflage properties (Portmann 1960). Not only flamboyant forms of life deserve our appreciation and forms indifferent in design often prevail within a given taxa.

On the other hand, the ontogeny of coat pattern of the jaguar and leopard seems to follow Portmann’s insights. As far as the jaguar and leopard are considered, rosettes of adults are geometrically far more complex than juvenile spots and the transition (i.e. break up of spots) is not a mere epiphenomenon of growth, since the inner area of rosettes has a different colour (dark ochre) (Figure 39). The rosettes create a morphological unit of doubtful importance for viability of an animal: we are not aware of possible adaptive value in comparison to simple spots. In the case of the jaguar, some rosettes are even supplemented with dark spots in the inner area. Although decline in popularity of the skins of both felids was terminated with the commencement of environmental movement, the patterns are still highly appreciated by designers and artists. For a human eye, the jaguar and the leopard are aesthetic animals par
excellence and serve as examples of animal forms whose investment into outward design transcends the necessity implied by the struggle for life and reproduction.

Figure 39: Detail of the rosettes on the skin of the leopard (*Panthera pardus*, left) and the jaguar (*Panthera onca*, right).

### 7.4 Portmann’s place in biological enterprise

Portmann’s position within a modern biological science is very ambiguous. A crucial question shall be asked: does Portmann’s teaching represent a solitary position, independent or even opposing to neo-Darwinism, or is it only, though specific, a part of Darwin’s universal heritage in biology?

The problem does not have a simple solution (cf. Jaroš 2010). From the theoretical point of view, Portmann has a vigilant opinion on the strength of natural selection. He does not contradict the very concept of the process but argues that its capability of forming adaptive traits is limited. Taking colouration into account, a selective process can start only after it has acquired a meaning in the eyes (and neurophysiological organs) of an animal which operates as a selective factor. The cause and the effect are switched: a new form arises before the process of natural selection modulates it into a resulting shape.

It is probably his fascination in morphology what keeps Portmann aside from evolutionary explanations based on population dynamics. He supposes that forces involved in the formation of *Gestalt* (appearance) are more or less autonomous, independent from the environment. Various patterns and striking colours are manifestations of inwardness and only secondarily acquire a role in intra- and inter- specific interactions. An animal is interpreted primarily as an autonomous being with inherent laws of self-construction.
Grene, a Dutch-American philosopher of science, asserts that Portmann not only opposes Darwinian biology but a whole paradigm of the modern science (Grene 1974). With a keen interest in primarily optic perception of animal form, Portmann ignores a mechanical approach typical for Cartesian philosophical foundation of modern science. Indeed, there are a number of places where he explicitly formulates his position as nonparallel (if not hostile) to Cartesian programme (Portmann 2008). Animals should not be compared with mechanical inventions of the mankind, since there is a vast difference in the structure of internal organs and external form. (Portmann seeks to delimit his position against the mechanomorphic understanding of living beings. However, it is also possible to regard human technical inventions as specific extension of evolution. According to this view, mechanical devices such as cars, clocks, etc. are biomorphic; cf. Komárek 2009).

On the other hand, Portmann was primarily a biologist by education and occupation and thus could not stand in opposition to the whole scientific milieu. Kleisner acknowledges originality of Portmann’s insights but highlights their affiliation to German (semiotic) teaching about umwelt (i.e. environment or surrounding world) (Kleisner 2006). In his view, Portmann is primarily a Darwinian, who pays intensified attention to the appearance of forms (see an interview with Kleisner in Náhlíková 2011). Portmann’s teaching is more or less compatible with current standard biological prism and some of his remarks can be fruitfully elaborated in neo-Darwinian terms. In this view, there is no significant difference between Portmann’s description of mandril’s head (Portmann 1967) as the manifestation of complex inwardness and a role of the head in intraspecific communication accentuated by (neoclassic) Darwinians.

In our opinion, Portmann has a unique position in the biological science of the second half of the 20th century. No doubt he acknowledged Darwin as a formative light of biological teaching, but he stood out of the stream of knowledge practices which formed neo-Darwinian research program (knowledge practice is a term used by Turnbull in the context of the sociology of scientific knowledge, cf. Turnbull 1993). The title of his crucial book speaks alone: Neue Wege der Biologie (i.e. New paths of biology; Portmann 1960). The paths which shall be taken by those who wish to appreciate visual richness displayed by animal bodies and investigate the significance of intriguing decorations, colours and patterns. As an inheritor of Goethean tradition, Portmann believes that the play of life is predominantly visible and human eyes are exclusive organs of sense. This does not mean that biology on molecular level, a dynamic and promising branch of biological enterprise established in late 1950s, should be dismissed (cf. Portmann 1990). Portmann was (legitimately, as we could say now) driven by a
fear that his alternative biological paths would not be trod out by a number of scientific-minded explorers.
8 CONCLUSIONS

In the presented work, we have studied the colouration of wild felid species from 3 perspectives: the theory of adaptive colouration, Hingston’s concept of colour conflict and Portmann’s prism of aesthetical morphology. Hingston’s findings of various displays of emotions among felids were incorporated into (neo-)Darwinian framework: a threatening function of spots on the back of the ears and the significance of a contrasting tail tip in communication belong to widely acknowledged facts in contemporary ethology. In contrast, some ideas of Portmann follow ways nonparallel to current biological enterprise. We seek to show that Portmann’s insights (e.g. specific value of juvenile coat patterns) shed some light on the peculiarities of felid colouration. For his teaching occupies a unique position in theoretical biology, it will not be amiss to reflect its status from the perspective of the philosophy of science at the end of our treatise.

8.1 The adaptive significance of colouration of felids

Following the theory of adaptive colouration, there are two main functions of felid coat patterns: aggressive resemblance and intraspecific communication. Spotted coats in wider sense (e.g. leopard, ocelot, clouded leopard) are reported to be cryptic in the forest, whereas striped coats (e.g. tiger, wildcat) supposedly match the background in grassland habitats. Markings which are exposed in an intraspecific communication (spots on the back of the ears, movements of tail tip) are supposed to be conspicuous in the natural habitat of a given cat. Accordingly, white markings are theoretically associated with closed habitats (e.g. the tail tip of the Asian golden cat inhabiting the forest) and black markings with open habitats (e.g. ear spots and tail tassel of the lion). Considering a high predation rate of juveniles (mainly cheetah), we evaluate the hypothesis of protective resemblance of coats in juvenile stages of the life cycle of felids. In the light of general belief in the adaptive significance of colouration of felids, cryptic value of juvenile coats is surprisingly underestimated by contemporary researchers. Since coat patterns among juveniles are not sufficiently described in literature, we conduct basic empirical research of ontogenetic pattern change.

The main hypotheses about the adaptive significance of coat patterns were tested with statistical means. Several data sets containing characteristics of colouration and habitats of extant felid species were investigated. After having performed Pagel’s (1994) test for
correlated changes which accounts for shared ancestry, most hypotheses could not be corroborated. The only significant results were obtained for the association between spotted coats and forests and white spots on the back of the ears and forests. However, even these results are not unambiguous since Pagel’s test based on alternative data sets did not yield significant results. One has to conclude that statistical results are influenced by the definition and distribution of states (e.g. classification of patterns on the felid body) to a considerable extent.

The strength of the statistical approach resides in a unified methodology and clarity of statements which are tested. Nevertheless, we refuse to acknowledge the superiority of quantitative approach to individual observations in the field. In our opinion, statistics provides an elegant way how to comprise macroecological data about all extant species of felids. However, one might cautiously assess a number of variables which might account for camouflage or conspicuousness in natural settings.

In fact, there are several problems in respect to the aggressive resemblance of felids. First of all, one must bear in mind that supposed (aggressive) camouflaging properties of patterns are significant only during the initial phase of attack. To understand the interaction between a predator and its prey, we need more information about the importance of vision for the detection of danger. Most felids are nocturnal hunters and one can only speculate about the visibility of a given pattern (e.g. the tiger’s stripes) from the perspective of common prey (e.g. deer) at night. Further, there is no clear concept which would explain why several species possessing supposedly cryptic coats (e.g. leopard, tiger, puma, jaguar) inhabit a high variability of habitats with completely different optical conditions (availability of light, composition of vegetation, etc.). Until ecological research of individual species of felids is carried out with regards to these conceptual problems, we remain sceptical about the value of the tested hypotheses.

There is one highly innovative approach in the investigation of the role of coat patterns for visual detection of the predator. Coss and Ramakrishnan (2000) turn the usual perspective on aggressive camouflage upside down and show that the spotted coat of leopards serves as a cue for recognition in the eyes of the bonnet macaque (Macaca radiata): putting it in another way, the spots are conspicuous for prey. The authors suppose that the cognitive system of macaques has been shaped to evaluate appropriately the danger resulting from the presence of a tawny coat with a regular distribution of spots. In contrast to the somewhat mechanical investigation of the relation coat pattern – habitat, this point of view takes into account cognitive processes involved in predator – prey interaction. As the result, we believe there is a need to substantially reconsider the theoretical framework of the theory of camouflage.
Our theoretical investigation of the theory of camouflage can be concluded into three remarks:

a) It is almost impossible to distinguish the role which the colour pattern plays from other factors present in hunting. On the part of the cat, these are various determinants, e.g. skilfulness at stalking, speed of attack, selectivity for size, etc. From the point of view of the prey, the decisive factors are the ability to catch a glimpse of movement, escape speed, and familiarity with a predator. The problem of intertwine factors would remain even if we could theoretically possess a full record of both successful and unsuccessful hunts.

b) If we assume that the concept of crypsis holds true, there is an option to focus on field research of polymorphism. Most felid species are not very convenient for such an investigation, but some exceptions occur. Primarily, species frequently exhibiting a melanic coat (leopard) might provide some data about the differences in ecological habits. The same applies in the case of the so-called king cheetah. Further, some other polymorphic species (jaguarundi, puma) might be suitable for valuable results, although practical limitations (low population density, large ranges) should be considered with caution.

c) Apart from the exemplary examples (e.g. moths resting on bark), we cannot persuasively distinguish between crypsis and conspicuousness, for they are only two poles of one variable (visibility). Therefore, there is only little chance to find more appealing facts than a quantitative comparison. For example, the investigation of a tiger – gaur (Bos gaurus) relation in some localities of Indian subcontinent indicates the following results: tiger hunts the gaur with the ease in deciduous forest (Nagarahole), with some effort in grass meadows (Kanha), and with troubles in riverine forest (Chitawan). Although we might say that the tiger is conspicuous in riverine forest and cryptic in deciduous forest, it is nevertheless capable of catching the gaur in all these environments and its appearance is of a questionable importance for fitness.

8.2 The position of Portmann’s aesthetical biology: general laws versus revealing insights

Within current neo-Darwinian paradigm, Hingston’s or Portmann’s concepts are not considered as a challenge for the theory of adaptive significance of animal colouration. Biologists are living in a period of Kuhnian normal science and it is the very first characteristic of this stage that it has no ambition (and intellectual property) to challenge its foundations. Zrzavý (2006) is probably right that we (i.e. current neo-Darwinian biologists)
are not able to think in other contexts. Hingston is cited from time to time by current zoologists but only superficial aspects of his approach are considered. When Caro (2005) mentions him it looks as though Hingston was just one of Darwinian thinkers who enhanced the theory of adaptive colouration with colour conflict, i.e. the existence of different selective pressures affecting distinct parts of animal bodies. But Hingston’s concept of colour conflict was rooted much deeper: in his eyes, the individual parts of the body express antagonistic emotions struggling within an individual animal being.

Portmann’s findings have a rather marginal position in the current biological thesaurus. He is occasionally mentioned as an exceptional authority in the field of animal colouration (Murray 2003). However, the acknowledgment is reserved for the number (and peculiarity) of the phenomena described and considered by Portmann but not for an underlying concept which creates the genuine core of his studies. One of few exceptions owes to be ascribed to an outstanding work about cultural perception of crows and ravens and the history of mutual interaction between the birds and humans (Marzluff and Angell 2005). Here, Portmann is mentioned as “the pioneering Swiss zoologist (who) measured the brains of hundreds of birds in the 1940s” (p. 40). He is reported to have found out that corvids (Corvidae) possess larger brains relative to their body size than any other taxa of birds. Compared to similar occasional references to his crucial biological studies, Portmann’s philosophical anthropology is currently much more influential.

On the current map of biological studies, there is only one place where Portmann’s heritage is fruitfully developed. Kleisner (Charles University in Prague) holds the position that Portmann is a Darwinian biologist who focuses on the autonomy of organismal form and asserts that its function is not fully comprehendible as a means of survival (Náhlíková 2011). His ambition is to put Portmann’s insights into context of current (neo-Darwinian) biology and a new scientific branch of biosemiotics (studying life phenomena as the result of processes of interpretation on several scales). A semantic role of the mammalian scrotum in the design of anal pole (Portmann 1967) is contextualized with the recent phylogeny of mammals (Kleisner 2010). The question how semantic organs have acquired a specific meaning during evolutionary process is analyzed on several occasions (Kleisner 2008, Kleisner and Markoš 2005). From this perspective, the reconciliation between neo-Darwinism and “Portmannism” is feasible. For example, highly decorative ears of the caracal surely manifest inwardness of the animal and represent semantic organs par excellence, yet fulfil an important communicative function at the same time: their conspicuousness perfectly confirms presuppositions about contrasting colour of organs of communication. After all, Kingdon’s
wonderful description of the ears of the caracal (see Section 7.2) is situated in the theoretical framework of adaptive function.

Portmann holds the conviction that “there exists a connection between level in rank and the appearance of an animal; one which follows definite laws and can be comprehended objectively.” (Portmann 1967, p. 76) Our attempt to test the hypothesis about the association between the level in rank and the complexity of colouration did not yield positive results. The values of total brain index ($TI$) are documented only for a small number of felid species and they do not show the desired variance: statistically significant correlation between total brain index and comprehensive pattern score was not found.

Coat patterns displayed by juveniles of felid species generally confirm Portmann’s assertion about the association between lower rank and basic types of coat patterns. Most significantly, the pattern of juveniles of the puma ($Puma concolor$) and the lion ($Panthera leo$) indiscriminately covers head and body and undergoes a distinct change during maturation. During the first months, accidental and irregular distribution of the spots marks juvenile appearance of the cubs.

Generally, Portmann’s thoughts are rather problematic when developmental aberrations are considered. Colour mutations often have a dramatic effect on the appearance of an animal but it is doubtful whether they are linked with a corresponding shift in inwardness. (At this place, we might recall Hingston’s conviction that a melanic form of the leopard is more ferocious than a spotted one: until we do not put similar propositions into conceptual framework, they are hardly distinguishable from hunters’ tales.) Anyway, the occurrence of polymorphism on the intraspecific level requires some other types of explanation since the terms of inwardness and rank primarily refer to the interspecific level. We lack reliable means to compare the richness of emotions or temper among individuals of the same species.

Do these problems of Portmann’s teaching push his insights away from science into the area of “mere” aesthetical biology? In other words, if Portmann is right only with some special cases cautiously taken out from the richness of animal kingdom but can be contradicted in the light of more analytic approach, should his position be abandoned as metaphysical (i.e. unsustainable when clashed with concrete facts)?

At this moment, one might recall several negative results linked to the adaptive significance of felid coat patterns. Based on these findings, one would not surely reject the theory of camouflage as non-legitimate. Komárek (2009) convincingly argues that every biological theory relies on the selection of convenient phenomena and place them on the pedestal of the related paradigm. Moreover, due to maintaining a leading role in theoretical biology, Darwinism has developed diverse tools how to subsume phenomena which are even
opposing the core paradigmatic principles. In the light of the philosophy of science, Darwinism meets the definition of scientific research programme (Lakatos 1978). Expressed in a simplified way, such a programme yields testable hypotheses but cannot be falsified as the whole: additional points of views are available and all of them have been embraced by the governing stream of scientific research. As far as the theory of camouflage is considered, we presented specific examples in Section 5.2.

We have shown that Portmann’s aesthetical morphology determines rank very precisely. Therefore, several propositions about the association between rank and colouration are amenable for testing. There is no epistemological obstacle for an attempt to establish a research programme stemming from Portmann’s way of thinking. Reasons accounting for marginal position of aesthetical morphology probably reside in the history of biological enterprise and sociology of science (cf. Komárek 2008, Zrzavý 2010). First of all, one must be aware of a winning campaign of Anglo-American school of functionalism and the fact that German biological school wafted away.

Portmann’s work is sometimes perceived as the branch of aesthetical biology (Stibral 2006, 2009). It is interesting to discuss whether aesthetical dimension of Portmann’s work push it beyond the borders of Darwinism. Aesthetical considerations are biased by human sense of beauty and are likely to differ from the taste of individual species. Therefore, if we evaluate the animal form with an aesthetic eye, we skip the Cartesian space of objective quantities. But there is a wholly Darwinian counterargument to similar allegations. Our human sense of beauty is a special case of mammalian preferences and is likely to be akin to considerations of relative species (especially those optically oriented). Darwin more or less implicitly ascribes human-like sense of beauty to birds and constitutes the phenomenon of sexual selection: there is an aesthetically valuable object (a male peacock) on one side and a subject endowed with the sense of beauty for such a form on the other side (Darwin 1871).

Komárek (2009) points out that the descriptive method of Portmann resembles the work of an art historian: here only, the nature stands at the place of an artist. But in the context of post-Darwinian age, Portmann was not the only biologist who has believed that the creations of nature are gifted with artistically valuable forms. Kunstformen der Natur (Haeckel 1904), a lithographic eulogy of the richness and peculiarities of animal forms, served to highlight the power of Nature and to acknowledge Darwinism as its reliable interpreter. Haeckel, who was fascinated by symmetries of geometrical forms, took a position of an art historian of the nature upon himself. In his effort to fully appreciate minute details of living forms, Haeckel created an aesthetical canon of its own (cf. Breidbach 2005).
By this reflection, we have meant to demonstrate that Darwinism (in its broad sense) is not hostile to aesthetically gifted spirits. The branch of aesthetical biology had been discarded both by biology and philosophy (or aesthetics) on a higher level of (academic) hierarchy. This process was not directly linked with a global dominance of neo-Darwinism but with more general process inherent in the flow of (Western) knowledge. Adorno’s words about natural beauty also refer to the almost forgotten world of aesthetical biology:

“Since Schelling, whose aesthetics is entitled the Philosophy of Art, aesthetic interest has centered on artworks. Natural beauty, which was still the occasion of the most penetrating insights in the Critique of Judgment, is now scarcely even a topic of theory. The reason for this is not natural beauty was dialectically transcended, both negated and maintained on a higher plane, as Hegel’s theory had propounded, but, rather, that it was repressed.” (Adorno 1997, p.61)

Despite all critical remarks, we cannot get rid of the conviction that the manifestation of inwardness which takes place on the surface of animal bodies is a crucial law of the animal form design. On the other hand, Portmann’s programme of biology seems to be unsuitable for detailed analytic tasks. His thoughts stem from the unity of form whereas the established biological science relies on a categorization providing clear analytical tools. Therefore, Portmann’s biology provides excellent heuristics but fails to stand firm criteria of the exact science on the scale of statistical analysis. This tense is typical for a situation of several branches of modern science and philosophers and scientists have made few (and according to Kratochvíl 1994 unsuccessful) attempts to reconcile (sensual) experience and logic (phenomenology) or provide an alternative modelling basis of science (structuralism).

Zeman (2012) conceptualizes the gap between “wild” (popular, subjective) cognitive methods and scientific process of reductive analysis. “Wild” cognitive methods lack the rigorousness of the exact science but enable basic orientation in the network of complex phenomena and are capable of revealing important facts (e.g. the use of traditional medicine is acknowledged in modern anthropology, classification of fauna carried out by “ primitives” is surprisingly rational etc.). On the other hand, contemporary science brings inexhaustible amount of information which is generated in accordance with strict methods. The price we pay resides in an incompatibility of distinct branches of science and a limited opportunity to implement new concepts.

Zeman asserts that the problem can be bridged by so-called middle horizons. To explain the concept, a following optic metaphor is used: the highest magnification does not necessarily reveal a meaningful shape and contour of an object. A star cluster of Pleiades is a
significant object on the night sky visible by the naked eye. To fully appreciate twinkling light of the stars, our sight needs to be extended by field glasses. If a telescope with needlessly high magnification is focused on the cluster, beauty of a compact shape evaporates. Field glasses mediate middle horizon between the naked eye and the telescope.

On the scale of middle horizons, it is enabled to switch between the level of conceptual framework and isolated insights. They can often mediate holistic pictures which are not accessible by usual scientific methods. Zeman (2012) illustrates that middle horizons are often used for the description of phenomena like national sports, esprit of a given country or impression from mid-term visit of a new town. (Komárek 2008b, in a master book of travel essays, praises the significance of first impressions and their relevance for grasping the spirit of foreign countries.) If one might depict the nature of Argentinian football, he has to regard peculiarities of Argentinian national identity and self-perception of men (both players and supporters) living there (see Archetti 1995). It would be possible to scrutinize the pace of a game and defensive/offensive tactics and compare them with football played in Brasil, Germany, etc. Such an analytic approach is methodically reliable but would deprive us of a meaningful context and the opportunity to comprehend the phenomenon of Argentinian football.

In our personal opinion, the magic of Portmann’s approach resides in the art to reveal the principles of life on the scale of middle horizons. It brings precious insights into the design of living beings and the creation of animal form. It might not be applicable on specific cases and not very amenable for statistical testing due to its eidetic approach, but this does not disprove its heuristic cogency. Similarly to the description of newly visited towns, the strength of Portmann’s thoughts grounds in the deep insight of a gifted spirit with the sense for a detail and the ability to incorporate it into a frame of general concept.
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Table B: Coat patterns of juvenile and adult felids. For sources of definition of categories and distribution of traits see Section 3.2 and 3.3.
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Table C: Coat patterns on the back of the ears and tail tip. For sources of definition of categories and distribution of traits see Section 3.5 and 3.6.
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Table D: Species-specific comprehensive pattern scores and coat patterns on individual body parts. For sources of definition of categories and distribution of traits see Section 7.2.
Figure A: The association between spotted coat pattern and forest habitat, results of test 1.5 (see Section 3.2). Black colour of branches signifies the presence of spots (tree on the left) and forest (tree on the right) after reconstruction based on maximum parsimony. Phylogenetic relations follow Johnson et al. 2006.
Figure B: The association between spotted coat pattern of juveniles and forest habitat, results of test 2.3 (see Section 3.3). Black colour of branches signifies the presence of spots (tree on the left) and forest (tree on the right) after reconstruction based on maximum parsimony. Phylogenetic relationships follow Johnson et al. 2006.
Figure C: The association between white spots on the back of the ears and forest habitat, results of test 4.5 (see Section 3.5). Black colour of branches signifies the presence of white spots (tree on the left) and forest (tree on the right) after reconstruction based on maximum parsimony. Phylogenetic relations follow Johnson et al. 2006.