

Functional morphology and fur patterns in Recent and fossil *Panthera* species

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According to caves drawings, male specimens of ice age cave lions lacked a mane. Ethological observations of the recent subspecies showed the significance of the mane of male lions (*Panthera leo*) in intraspecific social interaction. For the Pleistocene lion, there are two possible implications; the social system was different from the modern subspecies or the cooler climate did not allow the development of manes. Whereas the former can only be discussed, the latter is supported by evidence based on infrared thermography and considerations on thermoregulation. Thermal images of the recent subspecies clearly demonstrate the significance of mane development in terms of functional morphology. Probably, manes in felids can develop in warm climate only. The mane results in considerable insulation from heat loss. In order to compensate, male lions radiate internal heat in proximal areas of the body. Pleistocene lions were probably covered by thick fur, trapping their body heat and thus limiting the biological potential to develop additional insulation such as a mane.

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Introduction

Reconstructions of fossil animals are mostly based on skeletons. In reconstructing the fauna of the Late Pleistocene, we get help from our ancestors; cave drawings provide vital clues to the appearance of the inhabitants of the mammoth steppes. Through these we know that, for example, the mammoth had small ears and a short tail to prevent heat loss. These adaptations are not surprising given the climatic conditions of the Late Pleistocene, but for other species the interpretations of the cave drawings may

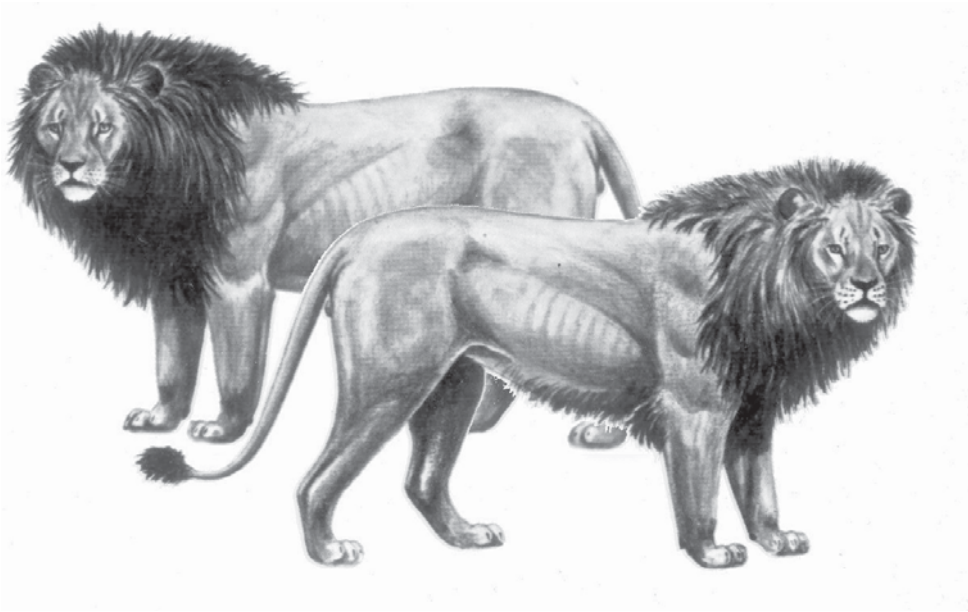


Fig. 1. Mane development in Asian (front) and African lions. (Redrawn from Mosterin, 1971, p. 276)

lead to surprising conclusions. For example, from these drawing we know that the big cave lion had, unlike its recent relatives, no mane.

The fur pattern and its development in recent and extinct large cats has been investigated by several authors (e.g., Weigel, 1961; Kingdon, 1977; Ortolani & Caro, 1996; Hemmer, 1967; Guthrie, 1990; Werdelin & Olsson, 1997; Turner & Anton, 1997). Fossilized soft tissues of the pelage of big cats have never been found. Therefore, reconstructions are based on the investigation of juvenile fur pattern, which is seen as an autapomorphic feature, or on actuopalaeontological interpretation of the adaptation to a specific environment, or - where the cave lion is concerned - on the interpretation of cave paintings.

It is known from several mammalian species that fur patterns play an important role in social behaviour. This is the case in the recent African lion. Most African lions live in prides. The size of a pride varies dependant upon the available prey. In the open savannah, where it is difficult to ambush prey, better hunting success and fewer injuries are obtained through this behavioural adaptation for sociality. Two other species have developed such a social bond, Cape hunting dogs and hyenas, and both have a better-than-expected hunting success (Shipman & Walker, 1989). A further advantage is to scare off scavengers like hyenas and also other male lions, so that the kill is not lost to strangers (Alderton, 1999). A third advantage is the communal raising of offspring and, therefore, a better reproductive success. Nevertheless, small prides or even solitary lions are known, for example, from the Kalahari Gemsbok National Park (Eloff, 1973).

Coalitions (groups of male lions) may live in association with one or more prides (Schaller, 1973; Bertram 1975a, b, 1978, 1991), but still the individuals compete with

each other for prey and mating partners. Female African lions select their favourite male from the features of the mane; the longer the mane and the darker the hair (black), the more often a male is chosen by the females in mate-choice experiments conducted in the Serengeti (West & Packer, 2002). This indicates a long history of selection toward a long and dark mane as it is found in lions of the Ngorongoro Crater, Tanzania. The manes will help the males defend their territory against invaders, as the mane provides good protection during fighting (Estes, 1991). The mane is not very well developed until the male is 3 to 4 years old. At that time, they have a spurt of growth in body size and mane length (Rudnai, 1973). Furthermore, a castrated lion either does not develop a mane or, if already grown, may even lose it (Alderton, 1999; Guggisberg, 1975; Neff, 1986; Pocock, 1907).

In Asiatic lions the mane is not developed as much as in the African subspecies (Fig. 1). The mane is scantier, much lighter in the majority of the males and the hair much shorter. Asiatic lions also live solitarily or in very small groups, with only one male and one female or two females alone without a male (Bertram, 1991).

The strongly social life of lions is quite exceptional for cats and the social implications of a lion's mane are obvious. However, we must not forget the original function of mammalian fur, which is thermoregulation. Fur is an effective protection against heat loss in mammals, which allows them to be endothermic. Therefore, density and structure of fur is mainly related to thermoregulation. In big mammals metabolic heat production is often so high that it cannot be emitted properly and the mammal suffers from heat stress. Since the lion's mane is a striking fur pattern, its dense hair should not be without thermoregulatory implications. Understanding how manes affect thermoregulation is important for theories on their absence in cave lions.

The cave lion

Age and distribution — Today, most people associate lions with the open plains of the African continent south of the Sahara. In contrast, during the Pleistocene lions were found all over the Holarctic region including North America. They were also present in South America and were thus found on every continent except Australia and Antarctica. Fossil lions from Eurasia are known from many localities. From the Lower Pleistocene, the largest cave lions are known from, for example, Mauer, Mosbach and the Forest Beds. These remains are correlated with the Günz/Donau-Interglacial. The Mindel/Riss-Interglacial is documented by finds from Lunel-Viel and Swanscombe, while Steinheim and Azé are from the younger part of the Middle Pleistocene. The localities Rigabe, Grotte aux Puces and Vence are interpreted as Riss/Würm-Interglacial.

The earlier Upper Pleistocene record includes specimens from, for example, the Tornewton cave in England, Repolust cave in Austria (Schütt & Hemmer, 1978) and Binagady from Transcaucasia (Baryshnikov & Boeskorov, 2001). The Würmian area is characterised by finds from the type locality of Gailenreuth in Germany (Dietrich, 1968; Ziegler, 1994) or the Wierzchowska Gorna in Poland (Wojtusiak, 1953), and probably by specimens of a smaller member of this charismatic animal from Yakutia and Yukon (Baryshnikov & Boeskorov, 2001). Numerous cave lions were found in North Sea deposits off the Dutch coast (Deep Water Channel, Brown Bank) or in suction dredging

operations along the Dutch rivers (e.g., Aa-land near Zwolle), which probably belong to different sections of the Pleistocene (Erdbrink, 1983; Gross, 1992). Important cave lion collections can be found at, for instance, Naturalis (Leiden), The Natural History Museum (London), the Bayerische Staatssammlung (Munich), Forschungsinstitut Senckenberg (Weimar) and the Naturhistorisches Museum (Vienna).

From North America, lion-like remains were found in several sites from Alaska (e.g., Fairbanks, Lost Chicken Creek), down to Florida (Santa Fe Ichetucknee), with the most prolific site at the tar pits of Rancho la Brea. Some authors regard these large cats as fossil jaguars (Simpson, 1941; Whitmore & Foster, 1967), while others argue for a lion (Harington, 1969, Kurtén & Anderson, 1980). While Eurasia shows a west to east decline in body size, North America seems to have produced a north to south increase. Therefore, Kurtén (1985) split the Beringian lion as *P. leo spelaea* and the southern North American lion as *P. l. atrox*. Harington (1986) discussed the co-occurrence of fossil tigers that likewise ranged even to North America.

Size is the most important difference between the recent larger cats and their fossil relatives. The largest Pleistocene cave lions were about 25% larger than their recent relatives (e.g., Hemmer, 1974; Kurten, 1985; Turner 1994, Baryshnikov & Boeskorov 2001). The question remains, are there size fluctuations between warmer and cooler periods of time? The cave lions from the Middle Pleistocene seem slightly larger than the ones from the Upper Pleistocene, which lead to such names as *P. spelaea fossilis* or *P. mosbachensis* (Argant, 1988), but significant size differences between periods of different temperatures cannot be observed so far.

Size and sexual dimorphism — While we can only rely on relative dating concerning the Middle Pleistocene findings, the uranium series and radiocarbon methods allow a more precise dating of Upper Pleistocene finds and, therefore, a correlation with the Oxygen Isotopic curve. *Panthera spelaea* is known from 'warmer' periods, e.g., between 50,000 to 40,000 years BP (mean annual temperature ~6°C below today) as well as between 20,000 to 15,000 years BP (mean annual temperature ~8°C below today), the peak of the last glaciations in Europe (temperature calculations from Shackleton, 2000). A large variation in body size is co-variant with sexual dimorphism in tigers and lions (Kitchener, 1991). While sexual dimorphism can be observed in the cave lion from several sites (e.g., Wierzchowska Gorna or Yakutia), body size differences on a larger scale depending on temperature variation are not provable.

Mane or maneless — It has been a long discussed topic whether the cave lion had a mane or not (e.g., Wehrberger, 1994; Rabeder *et al.*, 2000). Our ancestors depicted these large cats in caves or as sculptures almost without any trace of a mane. The drawings from Trois Frères and Les Combarelles (both Dordogne, France; Breuil, 1952) depict a lion with some lines that may indicate a small ruff. The same can be observed in a small sculpture from Vogelherd cave (Baden-Württemberg, Germany; Wehrberger, 1994). Figures from Kostenki I (Russia), Pavlov (Tshechia) or Isturitz (Pyrenees, Spain) were carved with no mane. The little relief from La Vache (Ariège, France) is covered from head to tail with small ornaments, without any indication of a mane. Guthrie (1990) argued not for a mane, but for a small ruff and figured Les Combarelles, Trois Frères, La Vache, Kostenki I, and probably le Gabillou and three others, but only

three out of eight sites indicate longer hair around the neck.

Some say only females are depicted because they are responsible for the hunt, others argue for a cave tiger and not a lion. The cave art from Labastide, France (Fig. 2) presents a pantherine form with no mane, but the typical flehmen gesture of a male tiger or lion used to gather the scent of a female in heat. This picture was seen as a roaring lion, but Hemmer (1967) pointed out that the fangs are bared which is not usual in roaring.

The outstanding drawings from the Grotte Chauvet (Chauvet *et al.*, 1995) provide further information. The depiction from this cave presents a cave lion with the typical lion tassel at the end of the tail. The indication of a scrotum identifies it as a male cave lion without a mane (Fig. 3). Had the cave lion no mane and when did it develop? The oldest cave paintings so far dated are a maximum of 38,000 yr BP. Further back in time, we cannot say anything about a cave lion's mane. Although it seems unlikely that this phenotype was reduced and survived as a genotype to be active again into recent times, the example of the cheetah proves at least the possibility.

In various archaeological finds lions are depicted. Hemmer (1963) presented different drawings and sculptures of lions from Egypt, which show features that have no expression in any African lion subspecies today. The animals portrayed are all adults. All individuals still preserve juvenile patches on their legs and females, teats well visible, carry a ruff around their neck just as in juvenile males. In Greek art, lions are presented with a recognisable, but sometimes weak, mane and never with a belly mane (Hemmer, 1966). There are two explanations. Either the lion subspecies depicted in Egypt and Greece became extinct subsequently or the mane became more dominant in the Holocene population and, in this case, developed different mane morphologies.

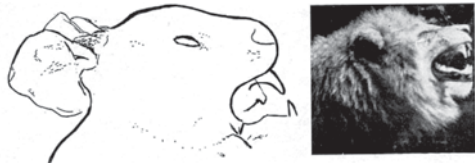


Fig. 2: A Pleistocene lion showing flehmen. In most cases, male lions display this behaviour in response to the pheromones in female urine (Bothma & Walker, 1999, p. 32)



Fig. 3. Drawing from the Chauvet cave. Male cave lion, showing scrotum and the lack of a mane.

Lion, Tiger or something else — The discussion as to whether the cave lion was a lion, a tiger or a distinct species has filled numerous papers (for detailed discussion, see Gross, 1992) and this is just a brief summary of the known facts. The latest publication concerning this question was from Sotnikova & Nikolskiy (2003), in which they listed the following characters for the cave lion in comparison to the recent lion: less inflated anterolaterally expanded bulla; less complex zygomatic-maxillary suture; V-shaped frontal-maxillary suture; P3 with less developed additional secondary cusp; small preparastyl on P4. In addition to these plesiomorphic features, some apomorphies (Sotnikova & Nikolskiy, 2003) can be distinguished as well; reduced cusp on the protocone bulge of P4 and widened nasal bones. The latter is similar to Recent tigers, which is in some respects more advanced than the lion. Grois (1996) distinguished the lion and tiger in Europe on the basis of endocranial characters. It has yet to be determined whether these characters are intraspecifically variable and whether they can be observed in the lion as well as in the tiger. The latest papers classify this animal as a separate species (e.g., Nagel, 1997; Baryshnikov & Boeskorov, 2001; Sotnikova & Nikolskiy, 2003) and therefore we refer to the large pantherine form in Eurasia as *P. spelaea*.

The large *Panthera* from North America has generated a similar discussion. Simpson (1941) and Whitmore & Foster (1967) published *P. atrox* as a giant jaguar. Harington (1969) and Kurten & Anderson (1980) regarded *P. atrox* as a lion. Herrington (1986) argued for lion and tiger in North America instead of a *P. atrox*. She classified the large fossil *Panthera* material from south of the continental ice sheet as a very large lion, while the material from the north seems to be smaller and to represent female and male tigers as well as lions. Sotnikova & Nikolskiy (2003) noted the presence of a third root in P3, a trend to a single root condition in M1, and the posterior lacerate and condylar foramina placed in one cavity in specimens from Rancho La Brea, and therefore addressed these forms as *P. atrox*.

Due to the considerable degree of variation of mane development in the Recent populations of lions and other species of big cats, such as cheetahs and perhaps even tigers (see below), the ongoing debate on the taxonomic position of the fossil relatives of the lion is not very relevant for a discussion on physiological implications of mane development. Nevertheless, it has to be taken into account that we may actually not always compare one single species when talking about fossil lions.

Thermography

A promising method to study thermoregulation is infrared thermography. Apart from heat loss by conduction and convection, animals emit heat as infrared long-waves. These waves can be measured by specific infrared cameras, which give a detailed picture of the temperature distribution on the animal's surface. Even small areas with an exceptional temperature pattern can be detected. The method is used in veterinarian medicine to diagnose infections or thermic stress, but it is becoming more and more common for the biological study of thermoregulation. Since the observed animals need not to be confined, infrared thermography can be combined with locomotory and behavioural studies. Accordingly, we can use this method to get information about the influence of specific body structures and behavioural traits like running or fighting on the thermal status of an animal.

In the present study we have combined the available data on fossil and recent cats, and added infrared thermography to interpret form and function of the mane of male lions. Infrared thermographies of African lions in zoos and in East Africa (Hilsberg, 2000) are compared to thermographies of other recent cats. Using these data we test whether this comparatively new method gives us a better understanding of the fur structure of the fossil species.

Thermographic pictures were taken with infrared cameras, models Thermovision® 570 and 575 of FLIR company using a 12° lense (Pl. 1, Figs. 3-5) and a 24° lense (Pl. 1, Fig. 6). Including external sources for errors, the practical accuracy of the camera is $\pm 0.3^{\circ}\text{C}$. The data were electronically stored and analysed using the computer programme ThermaCam Reporter 2000 Basic. Ambient temperature, humidity and distance between camera and animal were included for the calculation of the absolute temperature. All temperatures are given in a false colour code that can be adjusted to the needed scale. The mean temperatures of specific areas were calculated by the programme.

Asiatic lion, *Panthera leo persica* (Pl. 1, Figs. 1, 2) — The most striking morphological character, which is always seen in Asiatic lions, but rarely in African lions, is a longitudinal fold of skin running along the lion's belly (O'Brien *et al.*, 1987). Additionally, male Asiatic lions have only moderate mane growth on the top of the head, so that their ears are always visible, while many African males develop full manes that completely obscure the ears. Finally, about 50% of Asiatic lion skulls from the Gir forest have bifurcated infraorbital foramina (small apertures which permit passage of blood vessels and nerves to the eyes). In African lions, there is only one foramen on either side (Pocock, 1939; O'Brien *et al.*, 1987).

The infrared picture of the male Asiatic lion (Pl. 1, Fig. 1) shows a distinct radiation difference between the mane-covered area, that with an average temperature of $\sim 26^{\circ}\text{C}$ is only slightly warmer than the ambient temperature of 25°C , and the rump area with an average temperature of $\sim 34^{\circ}\text{C}$. That is, there is a temperature difference of $\sim 8^{\circ}\text{C}$. Further, the area of the belly fold is significantly cooler than the surrounding belly. In contrast, the female shows a more even temperature distribution of $\sim 29^{\circ}\text{C}$ over the complete rump, which is $\sim 5^{\circ}\text{C}$ less than the male.

African lion, *Panthera leo leo* (Pl. 1, Figs. 3, 4) — The African lion is divided into twelve subspecies by many authors, including the barbary lion (*P. l. leo*) which has survived only in zoos, and the extinct Cape lion (*P. l. melanochaita*). Sometimes, the African forms are seen as one rather plastic subspecies, with a large morphological variety. For this general overview we follow the single subspecies version and refer to the African lion as *P. l. leo* in contrast to the Asiatic lion (*P. l. persica*). The subspecies *Panthera leo leo* is characterised by features such as the long and impressive mane in the male, and a slightly larger body size than the Asiatic lion.

The infrared pictures of the African male lion (Pl. 1, Fig. 3) show the same temperature distribution as in the Asiatic lion. At an ambient temperature of 5°C , the temperature difference between mane and rump is $\sim 11^{\circ}\text{C}$; once again, the mane is only slightly warmer than the ambient air. In the female and juvenile (Pl. 1, Fig. 2) this difference does not exist and both are cooler than the male.

Amur tiger, *Panthera tigris altaica* (Pl. 1, Fig. 5) — Tigers do not possess a conspicuous mane. Pocock (1939) reported longer hair at the neck and throat from Java tigers, but in general there is a large intraspecies, sexual seasonal variation in tigers. In tigers the hair on the neck is slightly longer than on the body. The hair of tigers is further very smooth and soft, and not as coarse and hard as in lions (authors' observations). The summer fur of the Siberian tiger is about 15 to 16 mm long on the back and 25 to 20 mm long on the belly. This changes rapidly in winter, when it is about 45 to 55 mm on the back, 60 to 70 mm on the belly and the hair on its cheek is even 90 to 110 mm long (Mazak & Volf, 1967). Tigers are very well adapted to survive even under harsh conditions.

At an ambient temperature of 20°C the tiger shows an even temperature distribution over the entire body like maneless female and juvenile lions.

Cheetah, *Acinonyx jubatus* (Pl.1, Fig. 6) — Another maneless cat is the cheetah. As in female lions and the tiger temperature is evenly distributed over the complete rump. However, cheetahs demonstrate that mane development is not a character which needs a long time to evolve. Pocock (1927) reported a new species from southern Africa, *Acinonyx rex*. This cheetah was characterised by a different fur pattern; stripes mixed with blotches, and softer fur as well as longer fur around the neck (a mane?!). The name was withdrawn, when this phenotype was found in a litter of 'normal' cheetahs. Since the hunting success of a cheetah lies in its speed (Shipman & Walker, 1989), the diversification obviously did not go into social behaviour and a mane never became as important as in a lion's pride. Nevertheless, the genotypes are present as a kind of pre-adaptation. The inert possibility to change from one form to the other is well documented in *Acinonyx* and may be used as a model for other large cats.

Consequences of mane development

As shown in the infrared pictures the lions mane is an effective protection against heat loss. However, given the high temperatures in Africa combined with the metabolic heat produced by the lion, the mane is a problem for his thermoregulation. Surplus heat cannot be emitted over the complete body as in the females, but heat loss has to be concentrated on the short haired back parts of the male. Therefore, these parts radiate more heat at the same ambient temperature than the hind parts of the females and cubs. Since a distinctive temperature difference between covered and short haired areas occur in a standing lion, a running or fighting lion will be confronted with serious heat stress (Hilsberg, 2000). In the male African lion, the mane can grow so large that it covers 50% of the male's body surface. This poses a problem for thermoregulation, as now only 50% of the body surface can be used to radiate heat. These thermal windows are better developed in males than in females (see Pl. 1, Figs. 1-4). Recent lion males have significantly shorter fur in their posterior body region, compared to females. For this reason the well-developed mane of a male lion is a disadvantage, which only strong males can afford. So the selection of large, dark manes reaches an equilibrium between the advantage in the mating process and the disadvantage living in a hot environment (e.g., African savannah) (Hilsberg, 2000; Iwasa & Pomiankowski 1999). That heat-stress is indeed a limiting factor is further supported

by the observations that hunting activity in lions is positively correlated with a temperature decrease of just two degree Celsius, occurring around two o'clock in the night (Joubert & Joubert, 1999).

Implications for Pleistocene lions: Functional morphology and thermoregulation

Compared with recent lions, those living during the Late Pleistocene in the Holarctic region were confronted with a different climate. Mean annual temperature was up to $\sim 9^{\circ}\text{C}$ colder than today (Shackelton, 2000). This implies a colder winter for Middle Europe (down to -40°C), but also a quite warm summer (up to $+20^{\circ}\text{C}$) as known from the Arctic Circle. Animals had to get along with these seasonal changes.

Longer, denser fur would have been an advantage during the harsh winters and a mane would decrease heat loss even further. However, during the warmer summers, because of the larger body size, Pleistocene lions would loose less heat than their recent relatives, thus adding an element of thermal stress in the life of these animals. This has some implications for the thermal system; if we assume a winter fur comparable in length to that of Amur tigers, agitated movement would result in rapid overheating. Therefore, the harsh winter and warm summer conditions did not allow the development of skin regions into a big mane and short-haired areas for heat radiation because the energetic disadvantages would have been too great due to the cave lions greater body size. From the remains of the cave lion we have some evidence of this predator hunting in prides. Indicators are sexual dimorphism (Turner, 1994), the Wierzchowska cave in Poland (Kurten, 1976) with numerous cave lion remains and paintings from the Grotte Chauvet (Chauvet *et al.*, 1995). It is doubtful that even a pride system similar to the one of today would have made up for the thermoregulatory disadvantage of a mane.

Discussion

It has often been reported that in Serengeti lions, the females do most of the hunting and in more than 70% of all observed kills, the male will come and join the females to feed after the kill was made. The females will make way for the males and allow him to eat his share first (Schaller, 1973). The prejudice that male lions are 'lazy' while the females do most of the work probably has a logical explanation. We have reason to assume that this remarkable social system of lions is linked to the interaction between enhanced reproductive success and the drawback in thermoregulation. Other social carnivores such as hyena have developed a totally different approach to this problem in producing 'feisty' females and 'meek' males (Holekamp & Smale, 2000). Therefore, an impressive element like the mane has not been necessary. Both groups profit from the advantage of a higher reproductive success and an easier control of the territory.

The Pleistocene lion was interpreted as a social animal by Turner (1994) because of its sexual dimorphism, which is only known from pack animals. This theory is further supported by the paintings of "le panneau des Lions" in the Grotte Chauvet (Clottes, 2001; Chauvet *et al.* 1995). Guthrie (1990) argued for Pleistocene lions hunting in small groups with a maximum of three individuals per pride, well supported by actuopalaeontological observations from Van Orsdol *et al.* (1985), who plotted lion pride size ver-

sus prey density. The crucial argument is how large was the prey density in the periglacial area. In North America it was large enough to sustain two different kinds of top predators; modern felids such as lion-like forms, jaguars, the American cheetah, and sabre-toothed cats, beside bears, wolves, wolverines and foxes. Even in Europe, where sabre-tooth cats were believed extinct at a much earlier stratigraphical stage, new evidence from the North Sea area of the Netherlands now indicates the very same situation as in North America (Reumer *et al.*, 2003). It is likely that Pleistocene lions were flexible in forming prides of different size correlated to the amount of available prey, just as lions do today.

Conclusions

Mane development, especially dark mane, in male lions has advantages in mating (West & Packer, 2002). This is linked to disadvantages in thermoregulation and restricted activity for male lions. As to the cave lion, this animal had to be able to cope with cold winters and comparatively warm summers. Although a change of winter and summer fur is normal for many cats, it is doubtful that the necessary extreme adaptation in the pelage each year was economically.

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Plate 1: Infrared Images

Figs. 1, 2

Asian lions (*Panthera leo persica*). Summer, ambient temperature 25.2 °C. Indoor enclosure.

Figs. 3, 4

African lions (*Panthera leo leo*). Winter, ambient temperature 5.0°C.

Fig. 5

Amur tiger (*Panthera tigris altaica*). Summer, ambient temperature 20.0°C.

Fig. 6

Cheetah (*Acinonyx jubatus*). Summer, ambient temperature 23.5°C, with caretaker.

In the cheetah two artifacts are visible: the caretaker had stroked this cheetah intensely, hence the warm areas over the ribs and on the shoulder.

Pl. 1, Figs. 1 and 2 were taken in an indoor enclosure in "Tierpark Berlin-Friedrichsfelde", Germany; Pl. 1, Figs. 3 and 4 in Berlin Zoo, Germany (see Hilsberg, 2000); Pl. 1, Fig. 5 in "Tierpark Hagenbeck", Hamburg, Germany; and Pl. 1, Fig. 6 in Krefeld Zoo, Germany. All animals were adapted to the ambient temperature.

