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SUMMARY

I Behaviour patterns of normal daily activity

Under daily activity are described the behaviour patterns necessary for individual self-preservation. Social aspects are also discussed.

A Patterns of locomotion and posture

The most prominent characteristics in locomotion and body posture of the grey kangaroo are its bipedality and the almost completely simultaneous and symmetrical action of its extremities. Two types of locomotion can be distinguished: the slow quadruped gait and the fast biped jumping. This is in contrast to the three types – step, trot and gallop – usual amongst fast moving Eutherians. In both forms of locomotion the tail participates, but from the functional point of view in very different ways.

B Feeding

Feeding techniques are extremely diverse. Not only the mouth but also the hand is brought into action. This is possible due to the biped posture and the special structure of the hand. The various eating methods should be interpreted as an adaptation of the species to an arid climate that produces, according to season, grass, leaves from bushes, sprouts and bark. Further components of adaptation are the ruminant-like stomach, a kind of rumination in times of rest and the preference for dry food rich in cellulose.

C Defaecation and urination

Defaecation does not seem to be ritualised nor to have any function in social communication.

Urination occurs with more or less pronounced aspects of ritualisation. The two most ritualised forms are:

1. In Basle Zoo males urinate with erect penis onto a lying treetrunk. Males and females sniff at this trunk. In addition males sometimes rub their throat and chest on it. These facts allow us to define this special treetrunk as a scentmarking post. It is not yet known whether similar posts are used by freeliving grey kangaroos.
2. Between adult males and females a scene is often observed – during oestrus of the female and otherwise – in which the male stimulates the female to urinate. The male then sniffs the female's urine. A corresponding scene with most probably similar function occurs in many ungulates, especially ruminants.

D Resting

Between resting on the one hand, and alertness and readiness to start on the other, there is a sliding transition. The resting postures indicate the degree of relaxation. In order to rest relaxedly the animals settle on resting places that ensure security as well as convenient microclimatic conditions. Resting takes place primarily during late morning and early afternoon and varies in length depending on the weather. Apart from this "midday-rest", activity and resting alternate more or less regularly throughout night and day.

In the Basle Zoo adult females tend to occupy individual resting places and when they are resting there, repulse other animals, that come too near. But otherwise they neither contend for resting places nor claim any privilege of place.

E Comfort behaviour

The Comfort behaviour of the grey kangaroo is very complex and forms an important component of daily activity; individual and social grooming occur. Depending on the part of the body, the animals scratch, nibble or lick the fur or rub it with licked areas of the arms. Each body-part except the back is in some way "combed" as well as "rubbed wet". The fur on the back is treated by wallowing and social grooming. The latter is more extensively performed by mothers for their infants than between adult animals. A special pattern of comfort behaviour, the licking of arms and legs, probably contributes to the regulation of the body temperature (cooling by evaporation).

The throat-chest-rubbing by males against objects – in the zoo observed against a lying treetrunk – has most probably a communicative function. Due to apocrine glands in the chest-region, chest-rubbing contributes to produce a scent mark. As the males also scratch at and urinate onto this treetrunk, chest-rubbing appears as part of a larger complex; skin and fur of the chest region are rubbed in with elements of secretion and urine of different age. As the chest of the male also comes into contact with the back of the female during mating, the male on this occasion possibly impregnates the female by sent.

F Avoidance of predators

In most activities at intervals a posture of alertness is adopted, a behaviour pattern with the function of detecting danger. It is temporarily absent during periods of deep rest and in males, during ritual fight and copulation. When the animals are slightly disturbed they react with alertness focussed on the cause of disturbance and with increased preparedness for locomotion, single individuals sometimes also with an exploratory approach to the source of disturbance, and the whole group occasionally with a short shift away from it.

When the animals are seriously disturbed, one or two individuals perform "signal-steps" upon which the whole group reacts with flight. When excitement is still comparatively low the ani
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is still comparatively low the animals flee in closed formation; in high excitement they at once scatter in all directions, stopping and "freezing" after a few seconds and then starting again simultaneously but without coordination of direction.

In daily activity, especially in feeding, resting, comfort behaviour, and predator avoidance the whole zoo group of grey kangaroos appears as a fairly homogenous unity. However, in certain situations integration of the individuals in social sub-groups may be more pronounced.

II Mating behaviour

The mating behaviour of the grey kangaroo shows remarkable analogies to that of ungulates, especially to eventoed ungulates of open habitat.

Amongst adult males in the zoo group mating behaviour is regulated by social hierarchy. While the female is on heat, the dominant buck claims the mating privilege and threatens any inferior attempting sexual contact with the female. The male hierarchy is evidenced in such scenes of threat during rutting; yet it is established in highly ritualised fights, which occur throughout the year when no female is in oestrus.

The adult males in the zoo seem to be able to mate at all times of the year. Pheromones in the urine of the female obviously arouse the mating mood in the male. As mentioned before, in kangaroos, as in many ruminants, the male stimulates the female to urinate and then "tests" the female's urine for oestrus pheromones. This performance is also observed when the female is not in oestrus and is then no privilege of the dominant buck. But, when the female is in oestrus, any inferior venturing to sniff at the female's genital region is immediately attacked by the dominant male.

In the female grey kangaroo oestrus lasts 8-12 days. This includes a premating phase of 3-5 days, a main phase of 2-3 days with a total of 2-3 matings, and an end phase of 2-3 days again without mating. During the entire oestrus sexual behaviour of low intensity takes place, but only during the main phase sexual behaviour of high intensity culminating in copulation. The initiative is solely on the male's side. In sexual behaviour of *low intensity* he follows the female, sniffs at her genital region, stimulates her to urinate and sniffs at the urine. Sometimes he places himself in her way, follows at her side, smells at her pouch opening and head, embraces her from the side, and rubs his neck across her shoulders. When his excitement increases he pursues her continuously, uttering a "clucking" noise. The female's reaction to the male's initiative combines both avoidance and tolerance. Should the buck stand at her side, she may turn her head in an attempt to establish muzzle contact. The more or less ritualised behaviour pat-

terns of the male are somewhat reminiscent of infant behaviour (sniffing at the pouch opening and head of the female), of mother behaviour (clucking noises, sometimes embraces) and of male mating behaviour (neck rubbing, sometimes embraces).

In mating behaviour of *high intensity* both, the initiative taken by the male and the female's avoidance of him are intensified and manifestations of excitement frequent. Behaviour patterns resembling mother-child-behaviour disappear. Predominating activities now are the male's intensified pursuit of the female with frequent attempts to mount her, and the female's efforts to withdraw in jumping-away attempts often combined with "coughing". Finally, however, the buck succeeds in mounting. He clings firmly to the female's hips and maintains his hold even when she tries to break away. Intromission follows after a few seconds. The female soon ceases to resist or "cough". During copulation both animals show a characteristic mating face. Copulation includes active phases and 1-3 rest periods in copula, sometimes also 1-3 short interruptions of the copula. According to observations in Basle Zoo, copulation can last from 14 to 43 minutes. Already during interruptions of the premating phase as well as during mating the female usually licks her arms. After copulation licking of arms and legs is regularly observed in both partners.

III The development of the mother-child bond and of the infant's behaviour patterns

The changes in the mother-child bond and the development of the infant's behaviour patterns show many features closely connected with pouch life and therefore with no parallels in Eutherians. As a large quick-moving herbivore of half open habitat, the grey kangaroo is ecologically similar to certain antelopes e. g. impala and Grant's gazelle. These, however, give birth to highly developed offspring that follow the mother a few days after having been "set down". In the phase between birth and full ability to walk, these offspring are certainly in great danger. In the life of the grey kangaroo there is no phase similarly exposed to danger, although the offspring is born in an entirely immature state. The pouch provides safety for the infant's development and ensures the gradual maturing and functioning of its behaviour.

It appears adequate to distinguish five periods of juvenile development in accordance with the child's dependence on the mother and her pouch and, correspondingly, its confrontation with the outer environment.

In the *first period,* lasting about $6\frac{1}{2}$ months, the infant lives entirely in the pouch and is never to be seen from outside. Pouch cleaning by the mother, as well as the pouch's visible enlargement and passive movements of the pouch wall as a result of the child's activity, reveal its existence.

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In the *second period,* from 7-9 months, the young stretches more and more frequently parts of its body out of the pouch. It uses its main sense organs and develops the first patterns of feeding and comfort behaviour which bring the mouth and arms into action. The young begins to make contact, at first only muzzle contact, with its mother and its immediate environment. On sighting a "strange" conspecific or an unknown object it retreats into the pouch; later it makes muzzle contact with the former and sniffs at the latter.

In the *third period,* from 9-11 months, the infant leaves the pouch, at first only for a short time, then permanently. At the same time it develops the patterns of locomotion and the body postures characteristic of the species. It explores the surrounding in jumping-excursions and makes contact with objects and conspecifics. With its mother it indulges in play-fights and social comfort behaviour. It still flees into the mother's pouch. At the end of this period individual comfort behaviour attains "definite modality" and resting, defaecation and urination take place outside the pouch. In addition suckling from outside the pouch appears.

In the *fourth period,* lasting about 7 months, the young is still suckled. Scenes of suckling were also observed with a foster mother. When startled the child flees to the mother or directly with her, but more and more the bond to the subgroup of young animals becomes apparent in hopping-plays and play-fights as well as in collective resting and feeding.

In the *fifth period,* commencing at about 20 months, participation in youth-group activities disappears. With respect to social association the male henceforth differs from the female. The female retains a loose bond with its mother but otherwise takes increasingly part in the common activities of the adult females. The male, in contrast, looses the special relation to its mother and appears integrated into the group of adult males.

IV Social conflict

Social conflict among males differs from that among females. Antagonistic behaviour on the part of the *female* has a defensive character. It is manifested, on the one hand in "coughing" and on the other in defence threat with the arms. In females social dominance as well as conflict in such a context were never observed. In *males* the play-fighting of the youngster develops with puberty into the ritual fighting of the adult male. In ritual fights a social hierarchy is established from which sexual privileges during rutting result. Three phases of the ritual fight can be clearly distinguished: leading-up, fighting proper, and breaking-off. If one partner looses completely his fighting initiative, the scene adopts characteristics of mating behaviour. In fight over a female in oestrus, the traits of ritualisation disappear more or less completely.