ECOLOGY, SOCIAL ORGANIZATION & BEHAVIOR
OF THE FERAL DROMEDARY
Camelus dromedarius (L.1758)
in
CENTRAL AUSTRALIA

by

Birgit Dörges & Jürgen Heucke

Dedicated

to

Alex Coppock

who cares
for

cattle, horses, camels

&

feral biologists

THE TYLOPOD'S WINK

a poem by James WILCOX

In the Dead Heart, let me say for a start,
Midst the dunes, and the dust, and the flies,
Where few folks have been, there's a world to be seen,
Through the one humped dromedary's eyes.

"It's O.K. here bud. Three wives and a cud,
And a fence to keep the kids home.
We're havin' a ball, where the wild dingo calls,
And the feral biologists roam."

"For dune after dune, in their 4-wheel cocoon,
They struggle, they groan, and they grunt.
They're not to be feared, him with his beard,
And her with her humps on the front."

The camels track them around, until they have found,
A place to bed down for the night.
Then they note what they do, this car and its crew,
To fill in the time till first light.

The tylopods wink, to show what they think
Of this biological pair.
It would be hard to replace, the contempt on the face
Of a camel called Frank who lives there.

Through blood-wood tree roots, in high-heeled boots,
He skips merrily through the day.
Leaving prints in the sand, this feral brigant
Is more than a little bit gay.

There's a devil there too. He's one of the few
Gregarious kids to be found.
Black as the night, it's really a sight,
As he followes the frauline around.

Maybe one day, when they've gone away
And the camels produce their first book,
They'll record what they found, where the kangaroos bound,
And Birgit came for a look.

Acknowledgements

C O N T E N T S

1.   INTRODUCTION

The dromedary (*Camelus dromedarius*) is only known in its domesticated form; the wild ancestor already became extinct in prehistoric times (GAUTHIER-PILTERS & DAGG 1981). In Australia, dromedaries have turned feral and only there do they live in large populations today. They are the descendants of the animals that had been imported between 1840 and 1907.

Most of the more than 10.000 imported animals originally came from the north-west region of the former British-India. Three types of breeds were imported, the ones from Rajasthan, India, at the edge of the Thar desert, representing the riding camel type. The camels from the Kandahar region in Afghanistan were heavy work camels and the ones from the area of Sind, Pakistan, were rather riding camels but they were also suitable for carrying moderately heavy burdens (RAJKOWSKI 1987).

The dromedaries were essential for the exploration and the development of the central arid areas of the fifth continent. On many expeditions to the center of Australia, they proved to be superior compared with any other work or transport animal because of their modest requirements and their independence from water. They were not only used for supplying remote farms and mine fields, for the construction of the overland telegraph line from Darwin to Adelaide, and the

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construction of several railroad lines but also for the erection of the more than 2.000km of rabbit fence in Western Australia (McKNIGHT 1969).

In many places in Southern and Western Australia breeding stations for dromedaries were established. In the twenties of this century the population of the domestic Australian dromedaries reached its peak with approximately 20.000 animals. The appearance of modern means of transportation rendered the dromedaries increasingly superfluous and many of them were simply set free. Being adjusted desert dwellers they have stood their ground and their current population is being estimated at approximately 100.000 animals (CISC 1993).

When this project was begun, almost nothing was known about the Australian dromedaries. There were only the publications of McKNIGHT (1969, 1976) with the emphasis on distribution and size of population, and of NEWMAN (1975, 1979) who had primarily worked on the food spectrum on the basis of stomach analyses of shot animals. First results concerning the ecology could be obtained in 1984 during the three months long preliminary investigation (KLINGEL 1985).

The project in hand for the first time made it possible to carry out long-term studies on a larger number of individually known animals and at the same time doing comparative observations in other areas. The investigation is devided in two parts:

I. Ecology

II. Social Organization & Behavior

Part I. focussed on questions about population ecology, range utilization and habitat use, and the analysis of individual drinking habits. More than three years of studies made the recording of the seasonal food spectrum in relation to the different ecological conditions possible.

With the help of the large amount of collected data, an attempt was also made to define the impact of the dromedary on the highly sensitive ecosystem of central Australia. In addition, measurements of the body temperature of wild-living dromedaries were carried out for the first time.

Because of the heterogeneity of the subject each ecological chapter with results is discussed as complete within itself and coherent with methods and discussion.

2.   THE STUDY AREA

The investigations were carried out in central Australia in the Alice Springs District from July 1986 to September 1989.
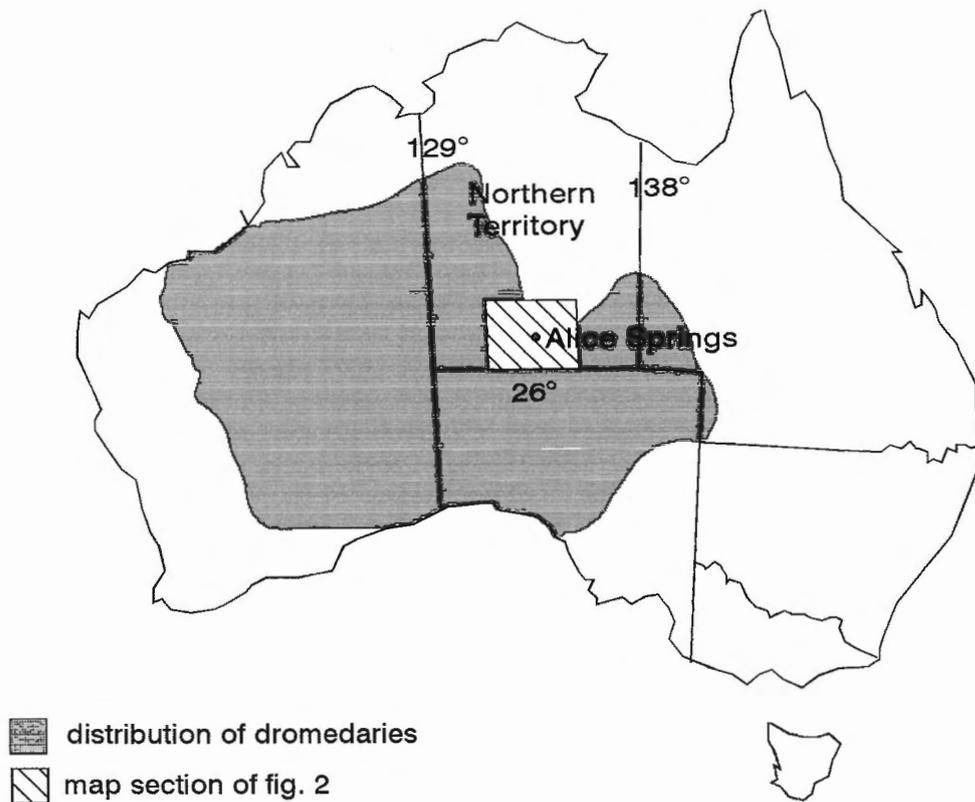
Fig. 1: Distribution of dromedaries in Australia (CISC 1993)

The station (cattle farm) Newhaven (22°50'S; 131°20'E; app. 560-580m above sea level), located 360km north-west of Alice Springs, at the edge of the Gibson desert, was the main study area. Comparative observations were performed in the border regions of the Simpson desert on the stations Allambi, Todd River, Ringwood and Horseshoe Bend, and in the Amadeus basin on the stations Kings Creek, Tempe Downs, Curtin Springs and Angas Downs (Fig. 2).
In contrast to areas not used for grazing, the stations have a certain infrastructure in the form of tracks and watering places which were useful and could be utilized for the studies.

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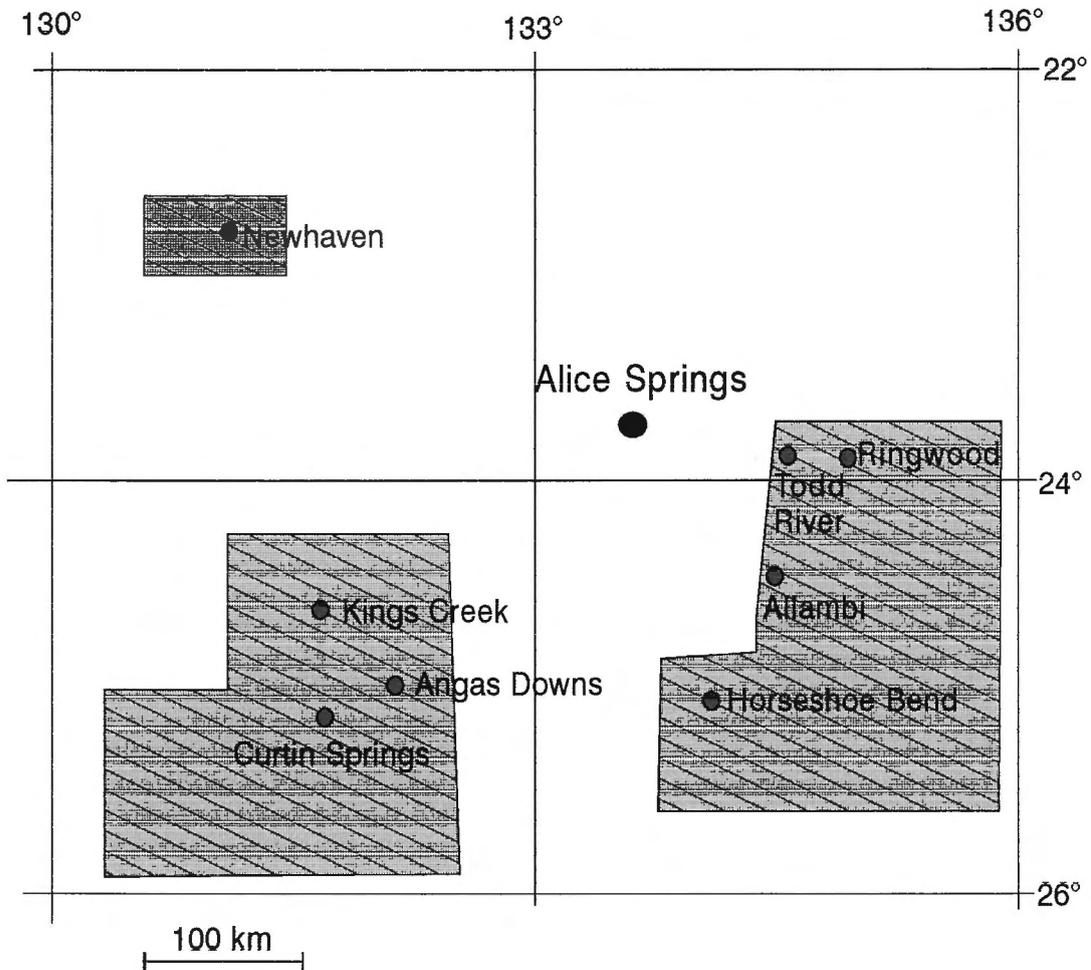
Fig. 2: Location of the study areas in the Alice Springs District

2.1   Newhaven

The station Newhaven provided the best prerequisites for a successful work. Like a peninsula, the farm stretches into extensive undeveloped aboriginal land where dromedaries are not hunted; the owner, too, tolerates the animals. That is why even at the beginning of the studies the dromedaries were less shy than in other areas, where the flight distance was often noticeably more than one kilometer. Therefore, only here systematic long-term observations regarding food selection, habitat use and population dynamics of individually known animals were possible.

The last impulse for choosing Newhaven was given by the presence of more than 40 dromedaries. In January 1986 they had intruded an $18km^2$ horse paddock and stayed there, even though the fence was no insurmountable barrier. The personal commitment of the station owner and his interest in the studies were also helpful.

Because of a density of two animals/km^2 in the Newhaven horse paddock the dromedaries could be located faster, and because of the short flight distance could be observed better than outside, where densities were at $D = 0.05$-$0.15/km^2$. The high grazing pressure, though, caused a food shortage during the extended dry season in the first year of studies. To create largely natural conditions with regard to the density, a $213km^2$ paddock was built adjacent to the existing horse paddock in July 1987. The animals from the original paddock were transferred to the new one. More than 200km of new tracks were made for better accessibility.

2.1.1.   Geology

EVANS (1972), WELLS (1972), QUINLAN (1962) and STEWARD & PERRY (1962) have described the geology of the region. The research paddock is located in the Ngalia basin, which extends from East to West. It has wide plains without drains and is composed of a thin layer of surface sediments from the Quaternary period. These consist of travertine, alluvial soils and red earths, sand and sand dunes, and stony soils. In depressions there mostly are periodically drying up salt lakes and saline pans. Tertiary ground water is probably widespread under these sediments.

2.1.2.   Land systems

In a small area the research paddock contains the most important forms of landscape and vegetation units typical for central Australia. PERRY et al. (1961) distinguish between Simpson, Singleton, Titra and Amadeus land systems.
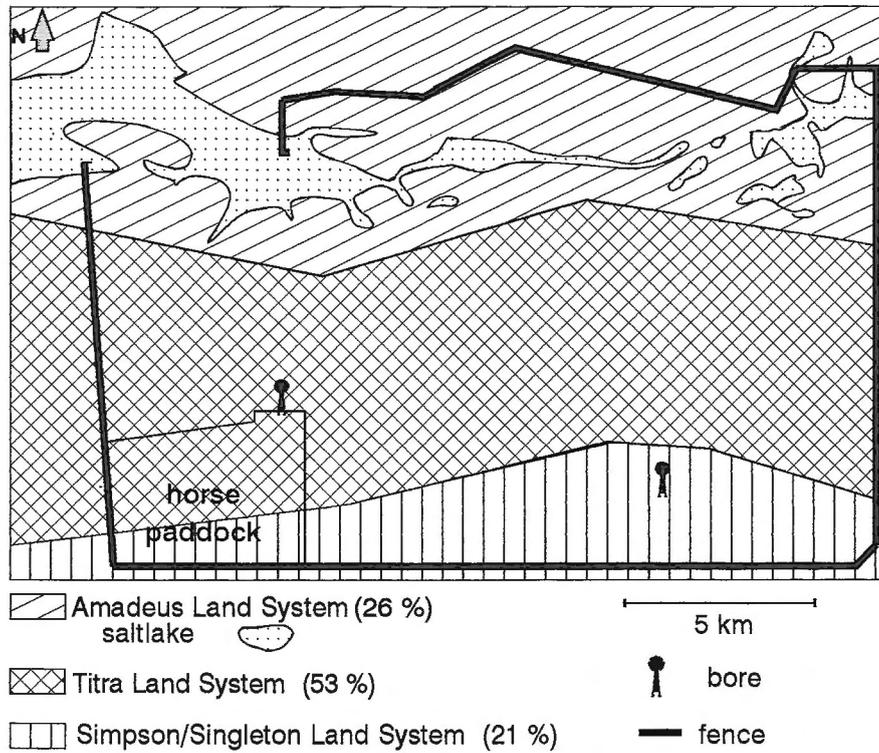
Fig. 3: The research paddock

The southern part (45km^2) is dominated by dune fields and sand plains of the Simpson and Singleton systems. The Simpson system is marked by parallel, crosswise or irregular dunes with steady flanks, few drifting sand particles, red dune sands, and red clay sands between the dunes. The Singleton system is distinguished by even or mildly undulating plains with clay sands. The characteristic plant for both land systems is the Spinifex, in this area particularly *Triodia basedowii*. Woody plants like desert oaks *Allocasuarina decaisneana* and Grevilleae *Grevillea juncifolia* characterize the vegetation of the sand or clay-sand soils. In denser vegetation units various Acacia types are to be found, mainly *Acacia ligulata* and *A. pruniocarpa*, and here and there dispersed populations of *Acacia aneura*.

The middle part of the research paddock (112km^2) is marked by elements of the Titra system. Open sand areas and loamy depressions with calcerous earths and mainly forb vegetation are to be found here. Scattered clumps of bushes of *Acacia tetragonophylla* and *A. victoriae* pass into extensive dense bushland with *Acacia-, Cassia-, Eremophila-*

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species and *Atalaya hemiglauca*. There are occasional alluvial soils with *Eucalyptus papuana*, *E. opaca* and extensive areas with Spinifex which apart from *Triodia basedowii* also include *Triodia pungens*.

The northern part of the research paddock (56km^2) is marked by the Amadeus system, characterized by saline pans with halophile *Atriplex*- and *Melaleuca*-species, salt marshes with *Halosarcia*-species, and salt lakes partly framed by red sand dunes. These are covered with *Triodia pungens*, *Acacia sessiliceps* etc. The southern border of the Amadeus system is marked by dense populations of tea-trees *Melaleuca glomerata*.

2.1.3 Water

During the study years 1986 to 1989 as well as in the years before the amount of precipitation was high compared with the longstanding average. Like on the entire station, surface water is nowhere present all year round in the paddock. During the rainy season, particularly after strong rainfalls, rainwater accumulates in the depressions which are then flooded for weeks. Even the usually dry salt lakes contain water, that can quite well be used as drinking water at first but later turns into a saturated salt solution. During the dry seasons water supply for the stock is solely available in artificial watering places. The high groundwater level a few meters below the surface allows the utilization of wind- and motor-driven pumps. The groundwater is collected in tanks and then being distributed to the troughs. The paddock had two such troughs, the Blom-bore in the southeast and the Babbler-bore in the southwest (Fig. 3), with salt concentrations of 5.000 ppm and 10.000 ppm, respectively.

2.2. Climate

The climate of the region has been described as semi arid by SLATYER (1962): about 70% of the average annual precipitation of 275mm ($\pm$ 82.5mm) are falling between November and April. The average monthly maximum of the temperature in summer is stated with >35°C the average minimum can reach 5°C in winter. Occasionally night frosts occur. The relative humidity for the region is app. 30%, the potential annual evaporation rate 3.000mm.

2.2.1 Measurements of temperature, wind and humidity

The daily extreme values of the air temperature were measured with a commercial mini-max thermometer. The measurements were done at the camp 1.5m above the ground at a place which was protected from radiation and wind. The measurement of the air temperature in the field during the studies was done with an app. 40cm long Hg-thermometer, that had been stuck in the ground upside down in the shade.

The minimum and maximum air temperature was measured in the research paddock on 540 days. In winter the average temperature of the day was 25°C (+15 - +37), the temperature at night was 9.2°C (-4 - +22). In summer the average temperature of the day was 37.9°C (+22 - +46), the temperature at night was 21.1°C (+8 - +31).

In the study area Simpson desert the extreme temperatures measured in winter went down to -10°C and in summer up to +52°C in the shade. Fig. 4 shows the average readings of the monthly maximum and minimum temperatures including their extreme values during the entire time of studies in the research paddock. The daily variations in temperatures were 16.3°C on average, or a maximum of 26°C.

＊ t min ◆ t max
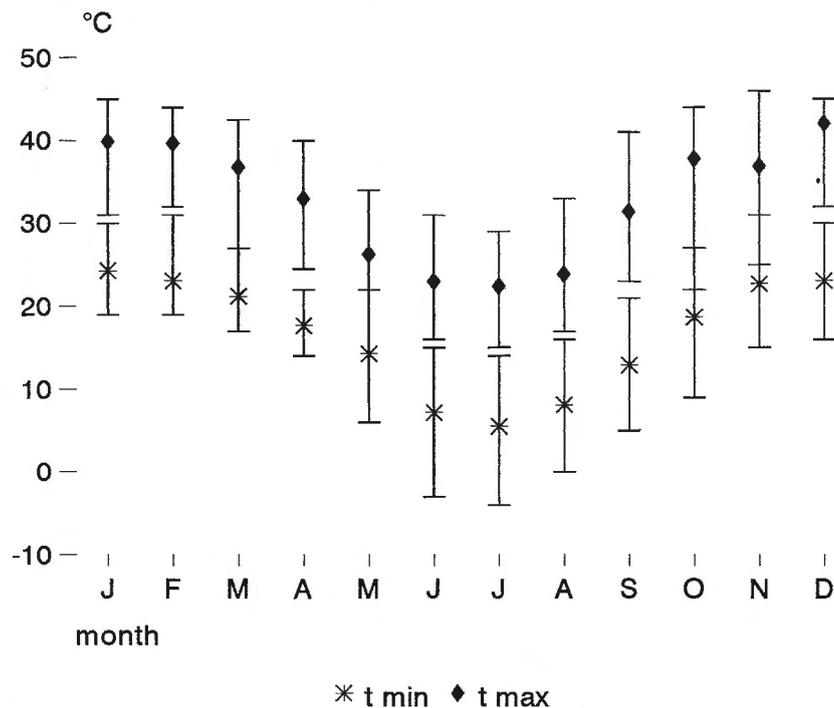
Fig. 4: Average temperatures in the research paddock during the entire time of studies from 1986 to 1989

In Fig. 5 the above values are broken down according to years. The strong variations of maximum and minimum within one month are due to suddenly setting in tropic or arctic weather situations.
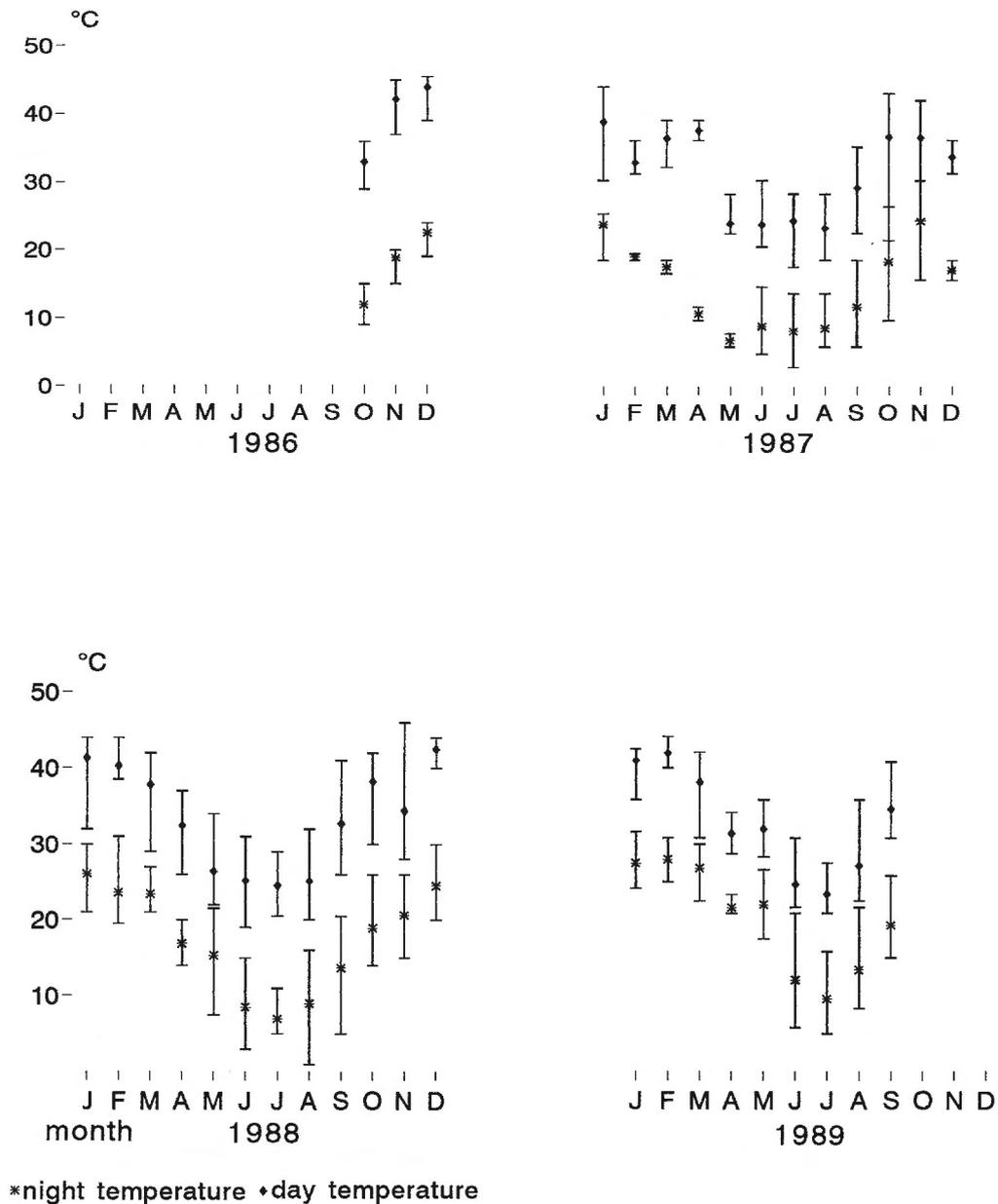
Fig. 5: Average day and night temperatures with their maximum and minimum in the research paddock from 1986 to 1989

The wind speed was determined with the help of an anemometer about 2m above the ground. Together with the beginning thermal current between 09:00 and 10:00h in the morning, wind sets in which mostly dies down between 17:00 and 18.00h when the sun activity decreases. At night it is mostly calm. The average wind speed was 3-5m/sec but maximums of up to 20m/sec were measured.

The relative humidity was measured by means of a capillary hygrometer; the measurements were done at locations that were protected from radiation and wind.

The average relative humidity in winter was 45% during the day, 66% at night. In summer it was 35% during the day and 40% at night. Fig. 6 shows the fluctuation ranges of the relative humidity with the respective average values summarized each month from 1986 to 1989. In Fig. 7 the relevant temperature and humidity values are shown according to the season.

I range ✻ average day ◆ average night

1986 -1989 N = 35360
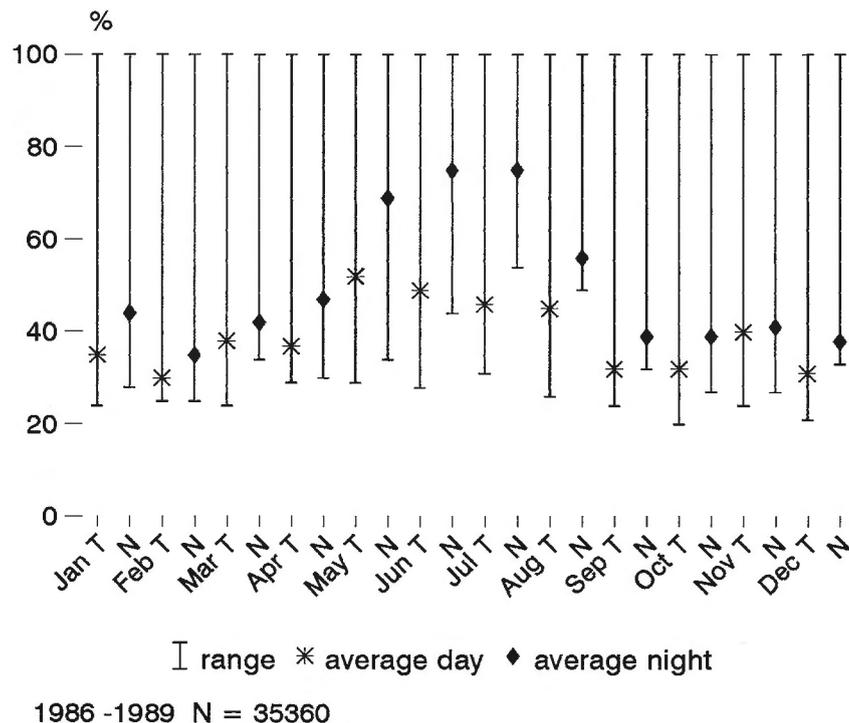
Fig. 6: Average monthly humidity readings with the respective minimum and maximum. Because it rained at least once a month during the three years, the maximums per month are always at 100%.

temperature °C   humidity %

✳ temperature ◆ humidity

1986 - 1989 N = 35360
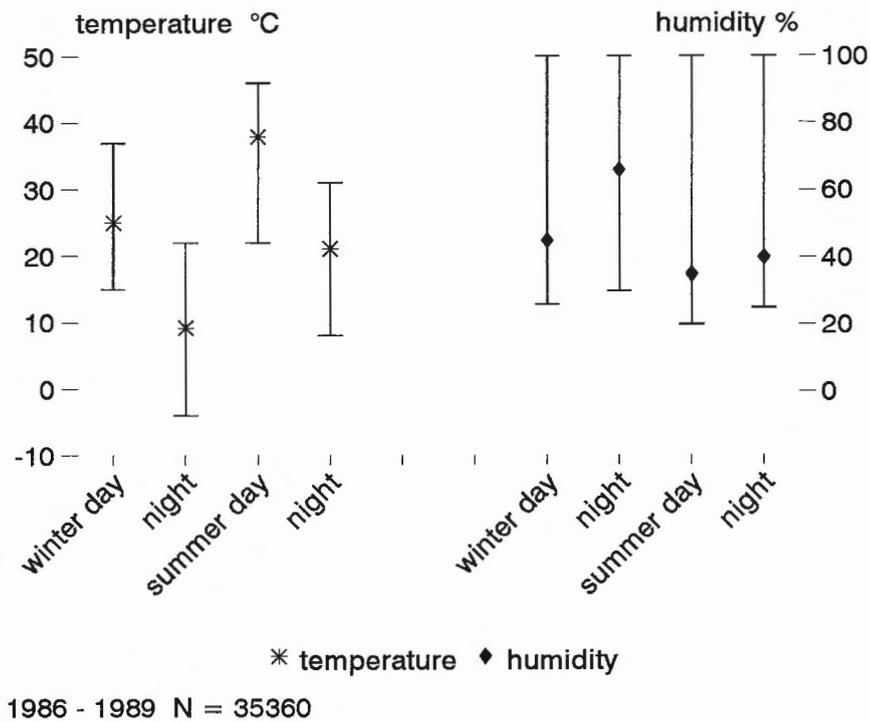
Fig. 7: Seasonal fluctuation ranges of temperature and humidity

2.2.2   Precipitation

The amounts of rain were measured with the help of simple measurement receptacles at the camp and with calibrated rain measurement devices at three more places in the study area. The data for the first six months of the year 1986 were provided by the Meteorological Institute in Alice Springs and by the station owner.

Due to local thunder storms, there was an inconsistent distribution pattern even in the relatively small research paddock. The average precipitation for each study year is shown in Fig. 8. The strong winter rains in 1986 were significant for the development of vegetation in the study area. 1987 was a relatively dry year which only by the end of the year had larger amounts of precipitation. 1988 is marked by extreme rainfalls in late summer (March). Early in 1989 it rained a lot, but subsequently until the end of the investigations it scarcely rained.

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All in all the time when the studies were being carried out was characterized by extreme differences with regard to the amount and distribution of rainfalls per year.
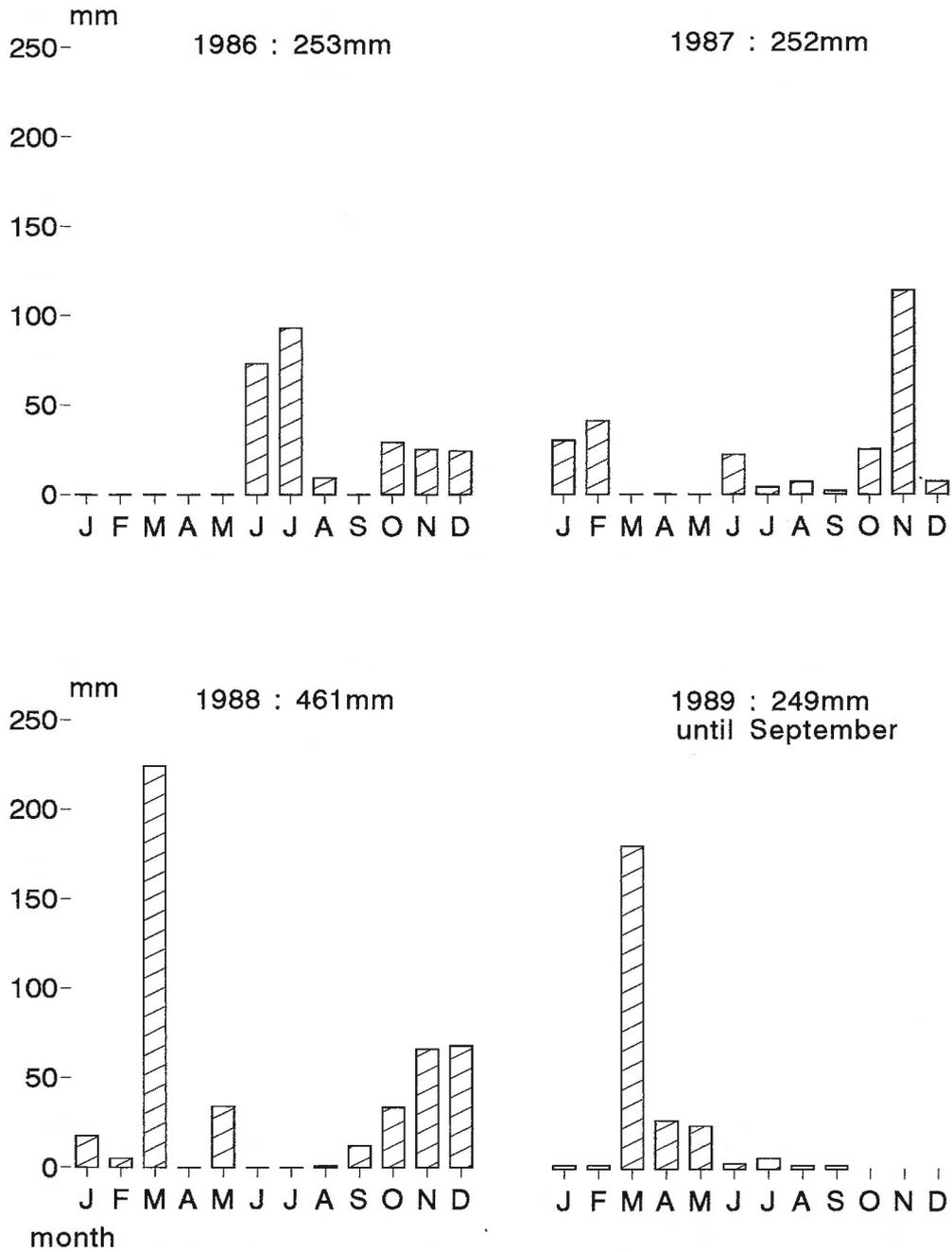
Fig. 8: Annual precipitation in the research paddock

2.3.   Vegetation

Arid zones take up almost half of the Australian continent. Even though there are rock, stony soils, gravel, sand and salt deserts, the arid center with its average annual amount of precipitation between 180 and 280mm and the potential evaporation rate of far more than 2.000mm is no defined desert (JESSOP et al. 1985). The Australian arid zone almost everywhere has at least a sparse vegetation, and the dunes, however sparsely, are vegetated, too. The most arid regions are covered with Spinifex (*Triodia* species), but the largest part of the area is taken up by shrub steppe, a partly dense, partly open bushland, composed of sclerophyllous evergreens (*Acacia-*, *Eucalyptus-*species).

Comparable regions in the northern hemisphere, like border zones of the Sahara, have much less vegetation and above all do not contain a large number of species. Precipitation there only occurs during the cold winter months, while in central Australia rainfall is irregular but mainly in summer, caused by cyclones that only occur in summer. Perennial plants in central Australia have good chances to survive because of the cool temperatures in the comparatively dry Winter. In the Sahara, though, they would wither during the hot and dry summer months, because only highly specialized Xerophytes can exist in this climate. Since in central Australia normally there is no need for adapting to longer extremely dry periods, the high diversity of species in the vegetation can be explained (app. 2.000 species, JESSOP et al. 1985). The diversity developed from a tree savannah during the Pleistocene, after the center had dried out increasingly during the last 30.000 to 50.000 years. Fire resistance is distinct with most central Australian plants. Above all there are many kinds of trees, like the desert oak (*Allocasuarina deceisnana*), which are protected by a fire resistant bark. Other species, like the Honey Grevillea (*Grevillea juncifolia*) burn down completely above the ground, but sprout again from the roots after the next rainfalls. Some plants then have adjusted to fire to the extent that their seeds only germinate after a bushfire, like Sturt's Desert Pea (*Clianthus formosus*).

Unusually long dry periods over a few years that struck Australia in the fifties and sixties of this century destroyed the tree and bush vegetation severely, a fact that does not speak for an optimal adjustment to deserts.

3.   GENERAL METHODS

3.1   Individual identification

Dromedaries can be identified individually with external features like color and condition of the coat, shape and size of the hump, and scars or other specific characteristics. Therefore, at the beginning of the investigations all animals were registered in a photographic file. Because of the coat change and other seasonal changes, mainly of the hump, a continuous supplementation or correction of the identification data was necessary. Four animals that were easily confused had to be fitted with marking collars and ear tags. These proved to be extremely durable, and they were still to be seen well towards the end of the project. Color markings of the coat were tested with some animals, but they were not to be made out well and their durability was poor. The individual identification with natural features in the region of Newhaven was granted with all animals after the end of the setting-in period.

On the stations Allambi and Horseshoe Bend at the edge of the Simpson desert five more dromedaries were marked with collars and ear tags.

In addition to the directly visible features some animals could be identified by their footprints. The footprints are individually different. The size as well as the shape were used as identification features. Some animals could be identified with the help of a photographic file of footprints of the right forefoot, including the respective lengths and widths and individual characteristics like round or oval shape, or distinct scars on the sole. This method was utilized particularly for the evaluation of tracks at the troughs.

3.2.   Catching methods

In the research paddock the animals were immobilized using a dart gun (Cap Chur system) with a combination of Rhompun^R and Ketamin^R. Only here the immobilization of the animals was possible because of the short flight distance. In the other areas the animals were chased in catching operations with cross-country vehicles and small planes or helicopters and caught with lassos. The animals were fitted with ear tags, and marking or radio collars.

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3.3   Telemetry

The radio-telemetric tracking of the animals was essential for the studies. Only by this method it was possible to locate and find the animals with transmitters together with their groups in a reasonable amount of time, at any observation phase during the day and at night, even in difficult terrain and from a larger distance (10-30km depending on the topography). Inclination switches in the transmitters produced different signal frequencies, depending on the position of the heads of the animals. Additionally to direct˙ observations these signal frequencies were evaluated for determining the activity of the animals. All in all 13 dromedaries were marked with radio transmitters, three of them in the area of the Simpson desert on the stations Allambi and Horseshoe Bend. On regular checking tours the location of these animals was determined by telemetry. After a relatively short time it became clear, though, that these animals were not be found within a justifiable time frame and at an acceptable cost.

Radio collars of the manufacturers Telonics (Mesa, AZ, USA) and Wagener (Cologne, Germany) were used. The transmitters had a frequency of about 150MHz. Yeasu receivers were adapted to the active frequency ranges of 148 - 152MHz by Wagener company. To receive signals, electronically amplifying all-around antennas mounted on the vehicles and transportable directional antennas (H-type) were utilized.

In the research paddock the animals carrying transmitters and with that their groups were recorded every day, occasionally several times a day. Animals in groups without transmitters could only be sighted irregularly but their whereabouts could often be determined by evaluating tracks.

3.4   Observation methods

In the research paddock the dromedaries were at first familiarized with the presence of the observers by visiting the individual groups regularly several times a day. With each approach an attempt was made to come closer to the animals than before. As soon as the animals became agitated another group was chosen. After six months the animals eventually allowed an observation distance of 20-30m which became even less during the course of the studies.

At each sighting the group structure, group size, the general and individual activity, and the distance of single animals to each other was recorded. When the animals were eating, the plant species they were feeding on were classified. In addition, location (coordinates, type of vegetation, plant society, openness of the area, condition of the ground) and weather conditions (air temperature, relative humidity, degree of cloudiness, wind speed) were recorded.

In monthly intervals continuous observations were done with several groups over a period of 24-48h to determine individual time-budgets according to the interval method of ALTMANN (1974), and/or continuously, using a rest-light amplifier (NOCTRON II[R]) at night. Besides the rhythm of activity, the main emphasis was put on food selection, habitat selection and the size and condition of the home range.

3.5   EDV-evaluation

The entire recorded data were evaluated with electronic data processing programs (MS-dBASE III PLUS; MS-Rbase; MS-Multiplan 3.0) after finishing the field studies. The cartographic measurements on the basis of an aerial photography on a scale of 1 : 40.000 were calculated with the help of a KONTRON VIDEOPLAN[R].

The statistical methods are described at the respective passage in the individual chapters.

4.   IMMOBILIZATION

For the realization of the studies the radio-telemetric tracking of the animals was essential. The immobilization with Rhompun^R and Ketamin^R was used to mark the animals. This method was only possible in the study area Newhaven because the animals were friendly there. Immobilizations of wild-living dromedaries were done for the first time within the scope of this study; all animals survived.

4.1.   Method

A dart gun (Cap Chur^R system) was utilized for the injection. The drugs Rhompun (Bayer) and Ketamin (Bayer) were available in crystalline form and were dissolved in distilled water. That allowed the use of highly concentrated solutions of 250mg Rhompun and 200mg Ketamin/ml, and it was possible to put the entire normal dosage in one dart gun despite the limited capacity of the 10ml tranquilizer darts. Bigger darts with a capacity of more than 10ml were not used because of poor flying characteristics and technical flaws. A list of all drug concentrations used is shown in Table 1.

To avoid an early dropping off of the injected tranquilizer darts, they were fitted with a barb at the needle. Since no practical values regarding the immobilization of wild-living dromedaries existed, the dosage was developed. Taking the estimated body weight of the dromedary to be immobilized as a basis, the dosage of both drugs was usually calculated on the basis of each 1.5 to 3mg/kg body weight.

The distance between marksman and dromedary was between 30 and 45m, depending on wind conditions. It was attempted to hit the animal in the shoulder muscles, if possible.
When the thermo-transmitters (Chapter 12) were implanted, the dosage was increased by an additional 1.000mg Ketamin which was applied intravenously following the standard immobilization.

4.2. Results

In 45 attempts 32 dromedaries were shot at, with some animals the immobilization was attempted several times. 18 animals could be immobilized successfully and subsequently be marked.

Table 1 shows the results of each immobilization attempt. Despite the strong variations which are both due to individual differences in the sensitivity of the dromedaries to drugs and to the respective situation during the immobilization, the following can be generalized:

The time interval between the injection of the sedatives and laying down of the animals is 15 to 30 minutes with one shot (immobilization No. 3,4,9,13,18,20,24,25,28,32), the time the animals remained lying is 30 minutes.

A significantly faster reaction occurred with two subadult dromedaries, a 3-year-old female (11) and a 3-year-old male (22). In both cases it cannot be excluded that the injection hit a larger blood vessel.

An old female, however, only got up after almost 6h (18).

19 shows the effect on an animal that was physically weakened by an infected wound on its ventral side; a fast reaction to the drugs occurred and the time the animal remained lying was relatively long.

13 and 23 are cases of comparatively big adult males who lived in bachelor groups at the time of the immobilization, thus were both relatively quiet. Despite the same conditions almost double the dosage of Rhompun and more than five times the dosage of Ketamin was needed for the male Ho (23). It is assumed that in male Bd (13) a vein was hit since he dropped abruptly after a relatively short time, while the male Ho (23) only sat down and had to be laid down on his side with difficulty.

In some cases the animals were sedated insufficiently which was not due to technical causes. The causes were:

7,8,16 and 17: their groups were already very nervous at the approach and constantly moved around. This restlessness was probably enhanced by driving after them.

12 and 29: both females were so distraught by the impact of the tranquilizer dart that they galloped away. This behavior was spread to the other group members and turned into turmoil during which the whole group ran away in panic.

With 2,21,26,27,30 and 31 several shots had to be fired because of the interaction of the males, but with 21,27 and 30 the immobilization was still not successful.

Table 1: Immobilization of free-ranging dromedaries

No.	Date	Camel	Dosage R(mg)	K(mg)	t_1	t_2	t_3	t_4	Success	Remarks
1	16.09.86	ad. cow	800	800	7					
		H1	1000	1000		40	11	25	+	
2		ad. cow	1000	1000	7		13			bulls disturbed
		H4	1000	1000		42	18	30	+	
3	20.12.86	ad. cow T1	1000	1000	6		28	25	+	
4		ad. cow H2	1000	1000	5		15	24	+	
5		ad. cow As	1000	1000					−	broken needle
6		sad. cow T4	1000	1000					−	broken needle
7		sad. cow T4	1000	1000					−	
8	21.12.86	subad. cow	1000	1000						no reaction
		N1/8	1000	1000		30			−	
9	09.01.87	ad. cow T2	1000	1000	3		25	25	+	
10	25.01.87	ad. cow KH	1000	1000					−	broken needle
11		sad. cow H3	1500	700	3		11	118	+	hit a vein?
12	31.01.87	ad. cow N1/9	1500	900	42				−	
13	18.02.87	ad. bull Bd	1500	1200	7		17	83	+	hit a vein?
14	05.03.87	ad. cow RT	1000	1000						broken needle
			1000	1000		60			−	broken needle

No.	Date	Camel	Dosage R(mg) K(mg)		t_1	t_2	t_3	t_4	Success	Remarks
15	11.03.87	ad. cow Pf	1000	1000					-	broken needle
16	17.03.87	ad. cow H4	1000	1000	6				-	
17	18.03.87	ad. cow H4	1500	1500	4				-	
18	04.04.87	ad. cow T3	1000	1000	12		18	358	+	old female!
19	06.04.87	ad. cow H4	1500	1500	3		11	65	+	infected wound
20	04.10.87	sad. cow T4	1000	1000	11		27	3	+	
21	30.01.88	ad. cow kW	1200	1200	10					
			1000	1000		87				broken needle
			1000	1000		13				bulls disturbed
			1000	1000		90			-	bulls disturbed
22	13.04.88	sad. bull TS	1000	1000	6		9	40	+	hit a vein? implantation
23	14.04.88	ad. bull Ho.	1800	1800	10					
			900	1900		40				
				2800		20	10	48	+	implantation
24	14.04.88	ad. cow N16	1500	1500	5		17	17	+	
25	23.04.88	ad. cow H3	1500	1500	6		17	45	+	implantation
26		ad. cow Tr	1500	1500	4					bull disturbed
			1000	1000		25	19	59	+	implantation

No.	Date	Camel	Dosage R(mg) K(mg)		t_1	t_2	t_3	t_4	Success	Remarks
27	06.08.88	ad. cow Wd	1500	1500	9					bull disturbed
			1000	1000		84			-	broken needle
28	04.10.88	ad. cow Kl	1500	2000	7		16	111	+	implantation
29	05.01.89	ad. cow RT	1500	1500	10				-	
30	06.01.89	ad. cow Lo	1500	2000	6					bull disturbed
			1500	2000		73			-	bull disturbed
31	07.01.89	ad. cow Lo	2000	3000	2					bull disturbed
			2500	2000		55	5	92	+	implantation
32	08.01.89	ad. cow N1/8	1500	2000	6		30	52	+	implantation

t_1 = time interval in minutes between the shot and the first reaction to the drugs

t_2 = only at repeated shooting; time interval in minutes after the previous shot

t_3 = time interval in minutes between the last shot and laying down

t_4 = time interval in minutes between laying down and getting up

4.3 Discussion

A successful immobilization of a dromedary - besides technical problems like breaking off of the needle or incomplete injection of the drugs - depends on the psychological and physical condition of the animals as well as on the reaction of the group members.

The animal should be in a quiet group, since nervousness has a disadvantageous effect on the success of the immobilization, especially of the Rhompun. With older or physically weakened animals the effect of the sedatives seems to be more intensive according to the observations.

The males represent a considerable disturbance when females are immobilized. Particularly during the breeding season the group holder interferes by intensive herding and copulation attempts with the female to be immobilized. On account of the effect of the drug the animals show an abnormal behavior by first walking unsteadily and later standing with their legs apart and their heads highly erected. This attracts the male's attention who at first herds the female that is staying behind and thus wakes her from the first light sleep or state of trance. As soon as the female then stands in the above mentioned "signal" position, the male tries to copulate with her which is another obstacle to the success of the immobilization. Klingel observed the same phenomenon when immobilizing plains zebras (KLINGEL 1969).

The gathered experiences showed that the immobilization of wild-living dromedaries with Rhompun and Ketamin is the method of choice. The anaesthetic is harmless and even with an overdose lethal consequences for the animals are not to be expected. According to WILLIAMS (pers. comm.) a tenfold overdose with Rhompun in cattle only caused a prolonged sleeping phase, but did not have any other consequences.

In difficult terrain, though, problems can occur because the dromedary is such a mobile animal. Due to the delayed sedating effect of the drugs the hit animal is still able to gallop away for minutes. In dense vegetation it can therefore be lost.
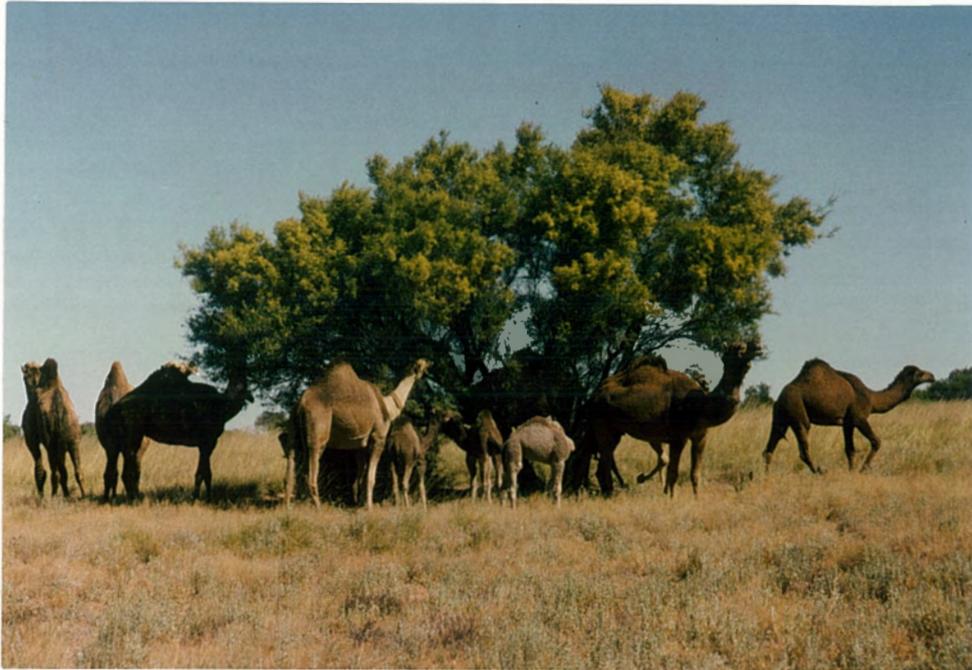
Dromedaries are mainly leaf and forb eaters with an extremely wide food spectrum. Generally they are very flexible with their food selection; they mostly use the freshest or most frequently growing plants, but also show preferences regardless of the supply. Being browsers they eat their food selectively. They mostly roam around scattered widely apart and with each step often only take in one bite. But frequently the whole group stays at one or more bushes and proceeds to the next clump of bushes together. In contrast to all the other herbivores that are native to Australia or have been imported, dromedaries because of their size are able to reach food plants up to 3.5 meters high. There are no food competitors for dromedaries in Australia. They can utilize areas that many other animals cannot reach because of their high mobility due to being largely independent from water holes and their variability regarding their food selection.
GAUTHIER-PILTERS (1961, 1965, 1969, 1974, 1975, 1977, 1980, 1981) has described the food spectrum and foraging behavior of free-ranging dromedaries in North Africa, information about food selection of dromedaries in Australia is supplied by BARKER (1964) and McKNIGHT (1969, 1976). For additional observations concerning food and analyses of stomach contents see NEWMAN (1975, 1979).

5.1 Methods

The food spectrum of the dromedaries in the research paddock was determined qualitatively and quantitatively by direct observation. In addition analyses of feces and stomach contents were done. For the research paddock a reference collection of all plants to be found was established which was continuously updated and by the end of the studies comprised 292 species. The classification of the plant species was carried out together with botanists of the Conservation Commission of the Northern Territory in Alice Springs.

The registration of potential food plants of the ground vegetation (grasses and forbs) was carried out following the method of TIDMARSH & HAVENGA (1955), after consultation with scientists of the CSIRO (ref. FRIEDEL & SHAW 1987) according to the following principle:

With the help of a 100m rope, divided into 10m segments, transects were laid; each plant which touched the rope was classified and measured. The individual 10m segments were evaluated separately, compared with each other and summarized later to analyze the spectrum of species and the extent of covering of the random sample.

The vegetation analyses were done directly in the area where the animals stayed to be able to correlate the supply with the actually consumed food plants. Furthermore, permanent transects of 100m length marked with posts were made in defined habitats. Here the ground vegetation was recorded according to the above described method to register the habitat specific vegetation spectrum seasonally.

For the registration of woody plants 25 transects were laid down altogether in all habitats in the evergreen shrub and tree vegetation. For each vegetation unit, each woody plant was classified, counted, and measured for height and width on a length of 1km. The height of tall trees was estimated.

Rectified aerial photographs on a scale of 1:40.000, photographed from a flying altitude of 6.645 m on October 24, 1988, and satellite pictures, Landsat CSIRO/MPA microBRIAN SYSTEM from August 21, 1987, were consulted to spatially divide off individual vegetation zones.

At regular intervals the food intake of the dromedaries in the different vegetation units was specifically observed. For a quantitative registration each 100 bites of one or more animals that were standing close to the observer were recorded by direct observation.

Always at the end of the month fecal samples of at least ten animals were collected and dried. In the laboratory of the Department of Primary Industries and Fisheries in Alice Springs the samples were processed and analyzed qualitatively and quantitatively under the microscope for their grass proportions according to the method of WILSON & BERTRAM (1987). Using this method the silicate-bodies of the single grasses specific for the genuses become visible. For each month four random samples were examined; the silicate-bodies found in each sample were counted and were assigned to the respective grass genuses on the basis of their shape. For the quantitative representation the average value of the four random samples was calculated. Dicotyle plants usually were so decomposed that a classification from fecal samples was not possible.

To supplement the food analyses, samples of stomach contents from the rumen of dromedaries found dead were taken and fixated in a 5% formaldehyde solution. After prior drying the samples were first analyzed macroscopically with reference collections. In addition, they were processed according to the method of WILSON & BERTRAM (1987) and examined under the microscope.

On the stations Allambi and Ringwood samples of stomach contents of dromedaries which had been shot shortly before could be taken. Furthermore samples of stomach contents were taken of animals whose date of shooting was known.

Since the food analyses outside the research paddock were only based on random observations because of the high flight distance of the animals, the food intake of tame free-ranging dromedaries was observed in addition on the stations Ringwood and Todd River. Here two more habitat types were found with accordingly different plant societies which do not exist in the research paddock: mountain ranges and river valleys. On joint "strolls" the food selection of the animals was analyzed and recorded quantitatively with the same method used in the research paddock. Furthermore feeding experiments were performed in a natural environment.

5.2   Results

5.2.1 Food plants

301 food plant species from 48 families could be identified for central Australia up to now, 262 of which by own observations. 213 species of these were new, 49 species confirmed the information of earlier authors (Table AT1 in the Appendix).

In the research paddock 292 plant species were identified. 236 of these species were definitely fed on by the dromedaries, which is proven by direct observation and equals a proportion of 80%. Of the 56 species not used here seven are at least potential food plants, which raises the total number to 243 and increases the proportion to 83%. The 236 identified food plants are divided into 148 forbs and small lignified plants, 44 shrubs and trees, 43 grasses and 1 fern. An additional 26 food plants were identified in other areas (Table AT1).

The Figures A1.1-12 in the Appendix show the food plants present in the research paddock together with the observed use during the entire study period. It was possible to identify a total of 53.038 bites as accurate as to the species level, 6.831 more as accurate as to the genus (in Figures A1.2, 5, 7 & 9-12 marked by "...species"). In 1.813 sightings grass was fed upon. Because of the difficult determination in the field these could 328 times only be determined as Gramineae (Fig. A1.5). In Figure 9 the comprehensive analysis of the food selectivity is shown.
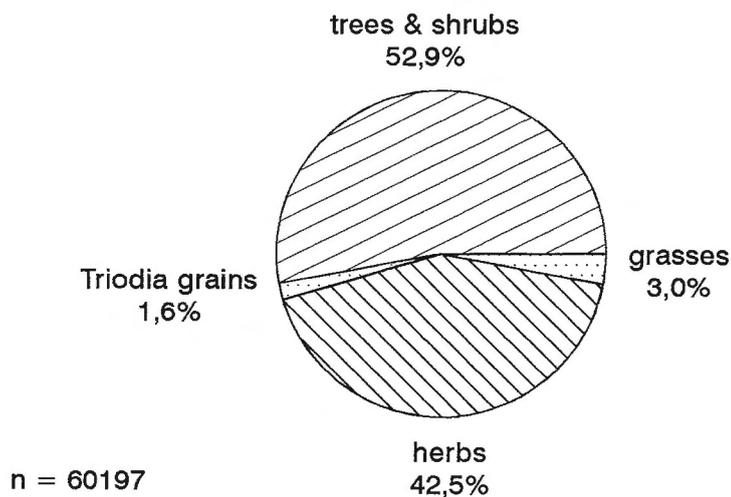
Fig. 9: Total analysis of identified food plants; determined by the individual values stated in Figures A1.1-12

For the research paddock the result is a clear preference for leafy food of shrubs and trees as well as of forbs with a total of 95.4% . Grasses are quantitatively of secondary significance since they were only eaten for short periods and only in the freshest state. The Spinifex *Triodia basedowii* was separated from the grasses, because only the fruits were used.

In the research paddock 52 plant families were identified, the number of species present is 292. Of these, 236 species were eaten; Table 2 shows the exact classification. In addition the dromedaries feed on 7 plant species that were very well present in the research paddock, but whose consumption was not observed here (marked by * in Table AT1; Fig. A1.5, 8 & 12).

A multitude of food plants the dromedaries at times fed on particularly intensively contain high concentrations of minerals and nutrients. See Table AT2 in the Appendix for an overview.

The dromedaries thus used almost the entire available food supply including some species that are poisonous for cattle or horses, like *Solanum-*, *Swainsona-*, *Zygophyllum-*, *Nicotiana-* and *Indigofera*-species. Plants with a high salt or oxalic acid content, like *Atriplex-*, *Halosarcia-* and *Calandrinia*-species were even eaten preferably. The frequent use of thorny and prickly food plants that were available in high abundance is conspicuous since cattle does not feed on them. Some species like *Acacia tetragonophylla* and *Sclerolaena* were even eaten by animals as young as a few weeks old.

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Table 2: Plant families in the research paddock

Family	species present	used species
Acanthaceae	1	-
Aizoaceae	1	-
Amaranthaceae	12	11
Asclepiadaceae	2	1
Boraginaceae	8	7
Brassicaceae	4	4
Brunoniaceae	1	-
Caesalpinaceae	6	4
Campanulaceae	2	-
Capparaceae	1	1
Casuarinaceae	1	1
Chenopodiaceae	28	26
Chloanthaceae	3	-
Compositae	24	21
Convolvulaceae	3	3
Cruciferae	2	2
Cucurbitaceae	3	-
Cyperaceae	3	3
Elatinaceae	1	-
Euphorbiaceae	11	3
Fabaceae	20	15
Frankeniaceae	1	1
Goodeniaceae	14	10
Gyrostemonaceae	2	1
Haloragaceae	1	-
Lauraceae	1	1
Liliaceae	1	-
Loranthaceae	2	2
Malvaceae	11	9
Marsileaceae	1	1
Mimosaceae	12	12
Myoporaceae	4	4
Myrtaceae	7	5
Nyctaginaceae	5	5
Pittosporacea	1	-
Poaceae	44	42
Polygonaceae	1	1
Portulacaceae	7	7
Proteaceae	9	9
Rhamnaceae	1	1
Rubiaceae	1	1
Santalaceae	2	-
Sapindaceae	1	1
Scrophulariaceae	2	-
Solanaceae	8	7
Stackhousiaceae	1	-
Sterculiaceae	2	2
Stylidiaceae	1	-
Stylobasiadaceae	1	1
Thymelaceae	1	1
Verbenaceae	1	1
Zygophyllaceae	9	9

5.2.2.   Seasonal food selection and dependency on precipitation

Due to the extremely variable precipitation pattern in central Australia and the particularly clear differences during the study period a general utilization pattern with regard to the preferred food plants cannot be put forward. But a noticeable adaptation of the food intake to the respective conditions is obvious, regardless of the season. Figures 10.a & b show the proportional comparison of the food intake "from the ground" (forbs and grasses) and "from the top" (leaves and blossoms of shrubs and trees) in relation to the precipitation. Always after rainfalls a significant change of the food spectrum can be seen which occurs with a delay. This is due to the time the forb ground vegetation needs to develop.

In this context it is important to point out that amount and composition of the ground vegetation in central Australia depend very much on the point in time when the precipitation is falling. The Compositae *Helipterum floribundum* serves as an example: During the winter months June and July of the year 1986 rainfalls were above average which caused a sharp rise in the development of the forb ground vegetation. It was *H. floribundum* in particular which developed so strongly that it became dominant in all areas of the bushland. Until November 1986 it was used as main food plant, even though it had already been dried up at this time (Fig. A3.2 and A4.1-8). In 1987 there were almost no winter rains, thus *H. floribundum* is missing. During the years 1988 and 1989 heavy rainfalls occurred from March until May which again lead to isolated, good populations of *H. floribundum*; however for an exhaustive mass development like in 1986 the rainfalls were too early in the year.
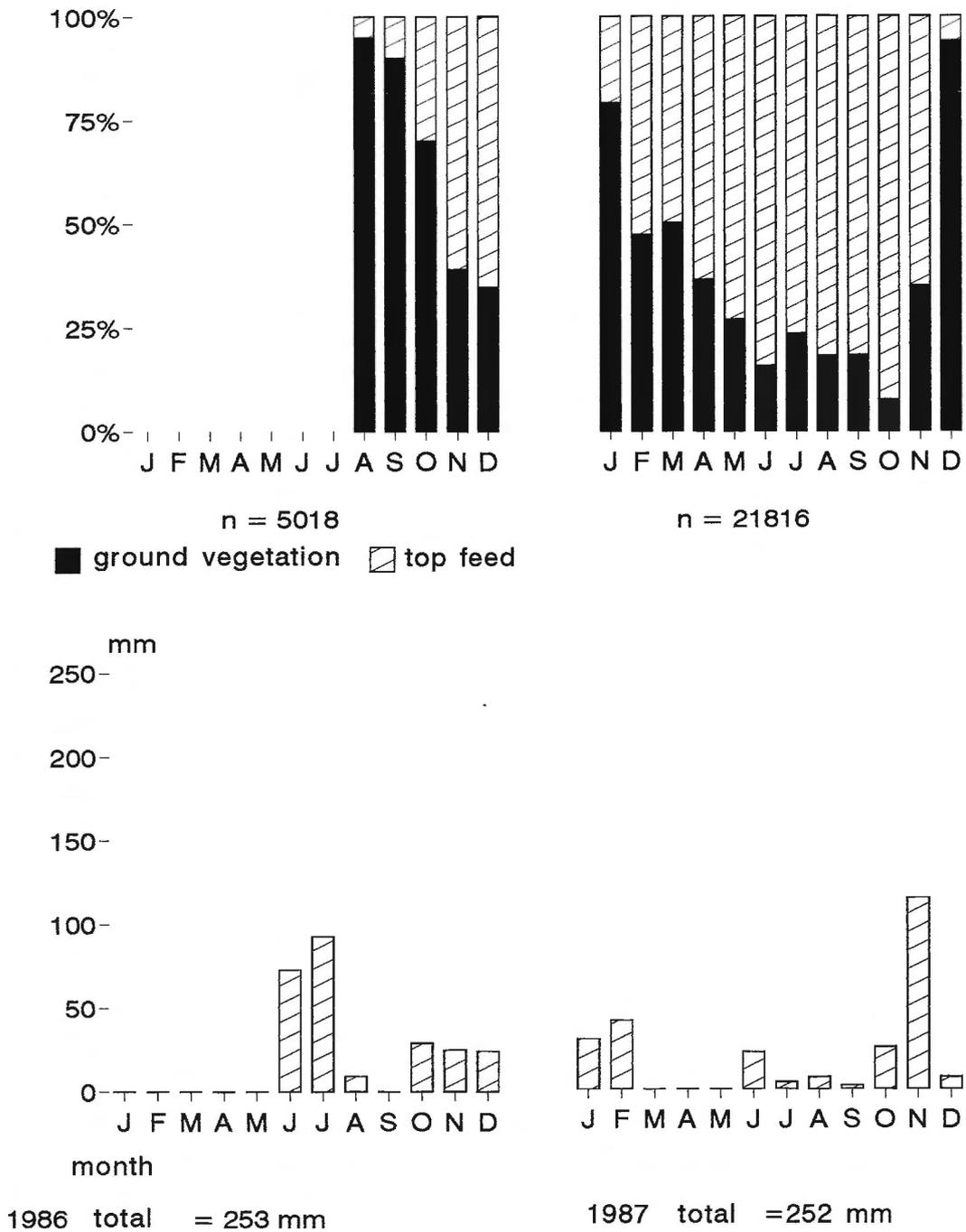
Fig. 10a: Food intake in relation to the precipitation during the
study years 1986 and 1987

Compared with 1986 the winter of 1987 (April-September) was extremely
dry with a total of 35mm precipitation. This lead to a browsing above
average of the shrub and tree vegetation compared with all other study
years.
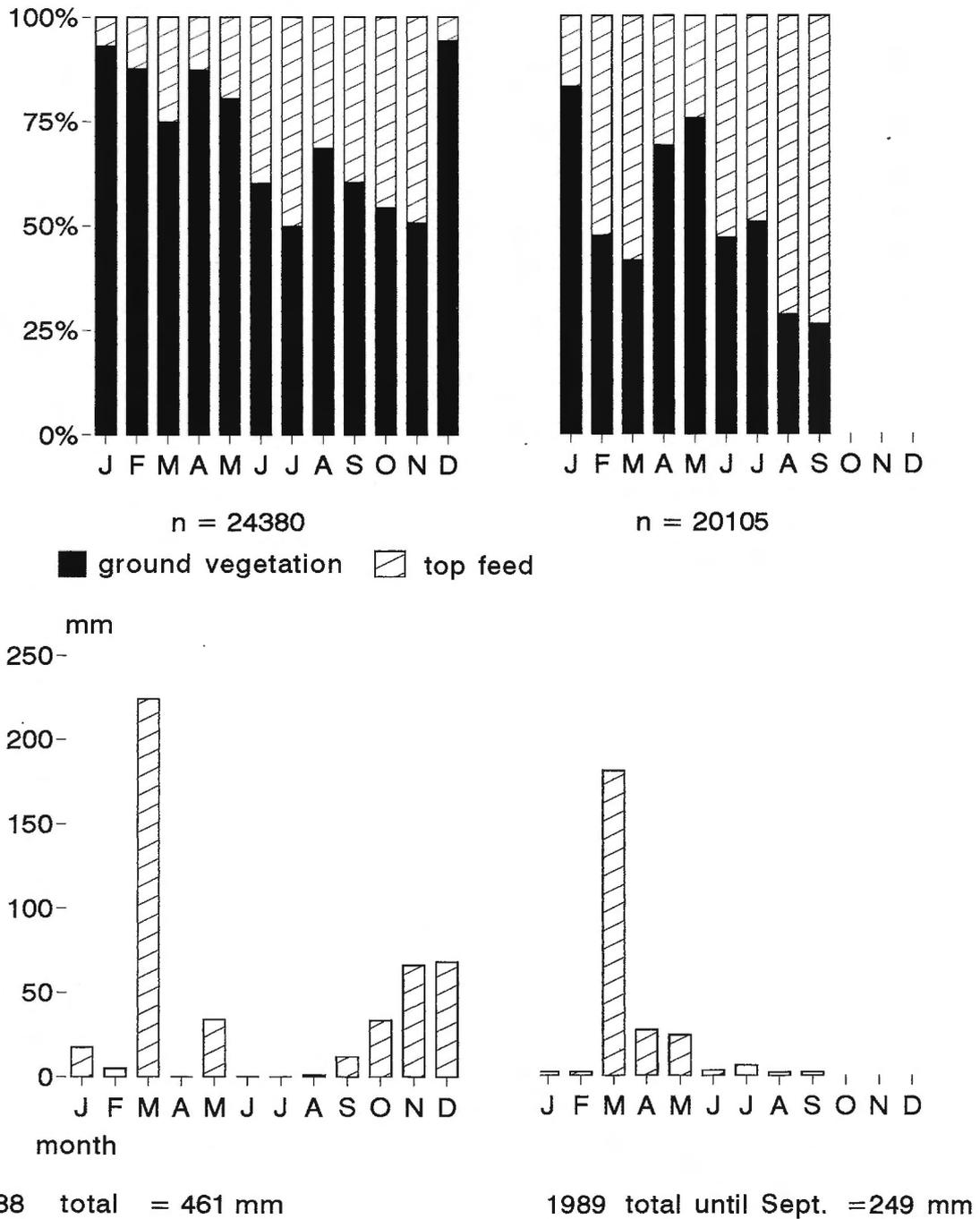
Fig. 10b: Food intake in relation to the precipitation during the
study years 1988 and 1989

To cover the results regarding the food selection in relation to the
precipitation statistically, the SPEARMAN rank correlation analysis
(LORENZ 1988) was used. The percentage of food from the ground (FG),
which was averaged over a period of two months each, was compared with
the respective amounts of rain of the month before and the first month

of the sampling to be tested. Example: Averaged feeding data of the months August/September 1986 expressed as percentage correlated with the total of precipitation from July/August 1986. This measure was necessary, since the amounts of rainfall first had to have an effect on the development of the vegetation (see above). And so 19 value pairs (Table 3) resulted over the entire study period:

Table 3: SPEARMAN rank correlation of the food selection in relation to the precipitation

Period of time	ϕ % FG	Σ rain (mm)
Aug/Sep 86	90	103
Oct/Nov 86	54	29
Dec/Jan 86/87	57	49
Feb/Mar 87	49	71
Apr/May 87	32	0
Jun/Jul 87	20	22
Aug/Sep 87	18	11
Oct/Nov 87	20	27
Dec/Jan 87/88	93	121
Feb/Mar 88	80	23
Apr/May 88	83	224
Jun/Jul 88	55	34
Aug/Sep 88	64	1
Oct/Nov 88	52	46
Dec/Jan 88/89	88	134
Feb/Mar 89	44	4
Apr/May 89	72	208
Jun/Jul 89	48	27
Aug/Sep 89	27	8

According to the formula for the SPEARMAN ranking correlation coefficient:

$$r_s = 1 - \frac{6 \cdot \sum_{i=1}^{} d_i^2}{n \cdot (n^2 - 1)}$$

n = scope of random sample
d_i = difference between both ranking numbers on the i-times test unit (i = 1,2,...,n)

equals an r_s of 0.6791 for the above series of experiments. This correlation coefficient is significant on a level of 0.004; following DIEHL/KOHR (1987) the correlation is highly significant.

By evaluation of the quantitative food analyses from random samples and continuous observations in all habitats (Fig. A2.1-93; A3.1-52) and all random observations by recording the food plants at each sighting (Fig. A4.1-35) the following utilization pattern can be derived:

Immediately after rainfalls perennial grasses were preferred (Fig. A2.40 & 70), until the forbs have grown up. Temporary mass developments of forbs are used by the dromedaries almost exclusively: in winter Fabaceae of the genus *Swainsona* (Fig. A2.89 & 90 and A3.47 & 49), the Compositae *Helipterum floribundum* (Fig. A2.29, 42 & 43) as well as Zygophyllaceae of the genuses *Tribulus* (Fig. A2.6,7 & 9 and A3.20-22) and *Zygophyllum* (Fig. A2.12 & 38 and A3.26); in summer Nyctaginaceae, mainly *Boerhavia*-species (Fig. A2.20 & 21), Portulacaceae like *Portulaca*- (Fig. A2.3 & 10) and *Calandrinia*-species (Fig. A2.56 & 57 and A3.42), and Fabaceae with *Indigofera* species (Fig. A2.16, 17, 20 & 41 and A3.37 & 38).
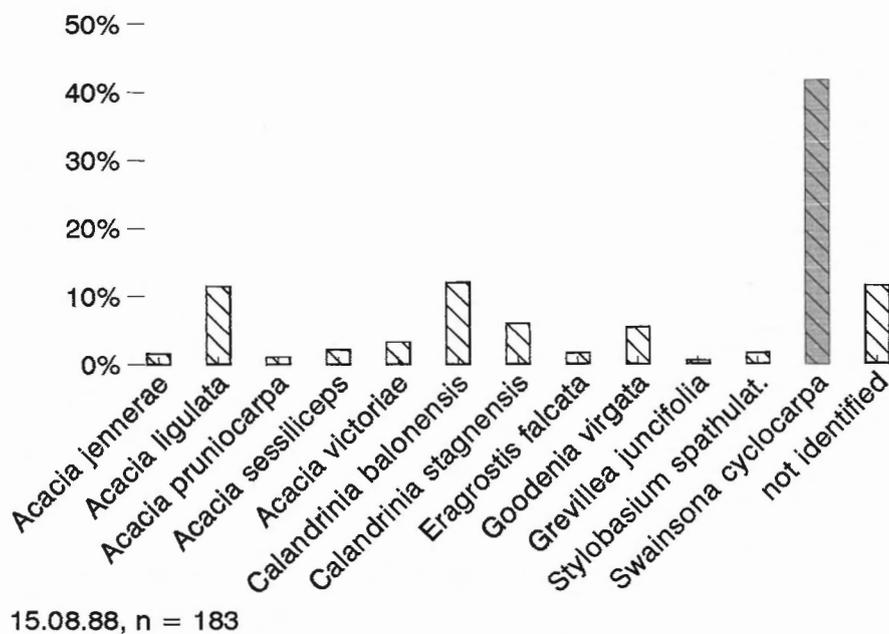
Fig. 11: Example of the food selectivity in winter for the temporary use of forbs, here *Swainsona cyclocarpa*

The Spinifex *Triodia basedowii* has a special position among the grasses. Protected by a wax-like coating the prickly blades of grass still appear relatively green even in dry periods when they are dried up completely, but they are not being eaten. During the winter months however the fruits are used selectively (Fig. A2.75, 78 & 79). Some

forbs and small herbaceous plants are being eaten by the dromedaries throughout the whole year. Succulent Chenopodiaceae like *Enchylaena tomentosa*, *Salsola kali* and various *Sclerolaena*-species are among them.

The evergreen shrub and tree vegetation is being used all year round but with varying intensity depending on the available ground vegetation, mainly in periods with low precipitation. *Acacia-*, *Atalaya-*, *Eremophila-*, *Rhagodia-* and *Eucalyptus*-species are preferred then. During flowering time and after the development of fruits these species are then eaten almost exclusively (Fig. A2.49, 54, 62, 80 and A3.14). The regular use of two Eucalyptus-species, *Eucalyptus papuana* and *E. gamophylla*, which have a high concentration of volatile oils and are therefore spurned by other animals, is unusual. In wet summer months dromedaries hardly use the woody vegetation and at times eat from the ground exclusively (Fig. A4.15 & 16 and A4.26 & 27).

5.2.3 Analyses of feces and stomach contents

The grassy particles of fecal samples examined per month in the research paddock are shown in Figure 12 relative to each other. The genuses of grasses identified in the fecal samples are shown in Table 4. A comparison of the results of the examined fecal samples with the observed grass intakes are shown in Figures 13.1-3.
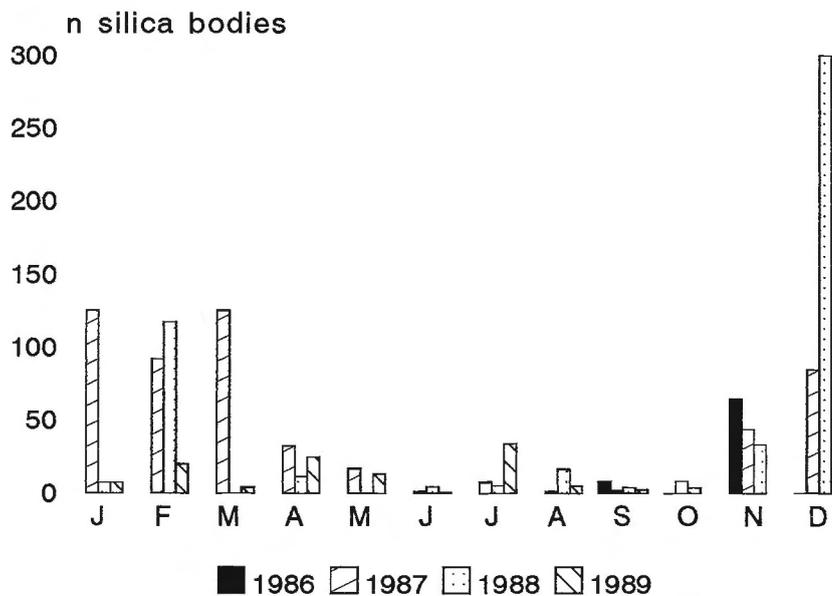
Fig. 12: Quantitative results of analyzed fecal samples per investigation month in the research paddock

35

Table 4: Qualitative results of the examined fecal samples; identified grass genuses per investigation month and year.

	J	F	M	A	M	J	J	A	S	O	N	D
1986												
Aristida											+	
Enneapogon											+	
Eragrostis									+		+	
Panicum											+	
Sporobolus									+		+	
1987												
Aristida	+	+	+	+	+	+	+		+	+	+	
Digitaria	+	+	+	+	+				+		+	+
Enneapogon	+	+	+	+	+		+				+	+
Eragrostis	+	+	+	+	+			+		+	+	
Panicum	+	+	+	+	+		+				+	+
Sporobolus	+	+	+	+	+			+		+	+	
Triodia	+	+	+	+	+				+		+	
1988												
Aristida		+		+							+	+
Dichanthium		+										
Digitaria	+			+			+	+			+	+
Enneapogon	+	+		+			+		+	+	+	+
Eragrostis		+		+			+				+	
Iseilema		+									+	
Panicum		+		+							+	+
Sporobolus		+									+	
Triodia		+				+	+	+	+			
1989												
Aristida	+	+		+	+		+	+	+			
Digitaria	+			+	+			+				
Enneapogon	+	+	+	+	+		+	+				
Enteropogon							+					
Eragrostis	+	+		+	+		+	+				
Panicum					+			+				
Sporobolus								+				
Triodia								+	+			

The qualitative results of the examined fecal samples show a quite good correspondence with the observed food intakes at the respective time.

The proportion of grass in the food only becomes important during the summer months which is verified in the study years 1987 and 1988 by the examination of fecal samples as well as by the observation data. January and February 1989 only had 4mm of precipitation, so that the proportion of grass in these two summer months can be ignored.
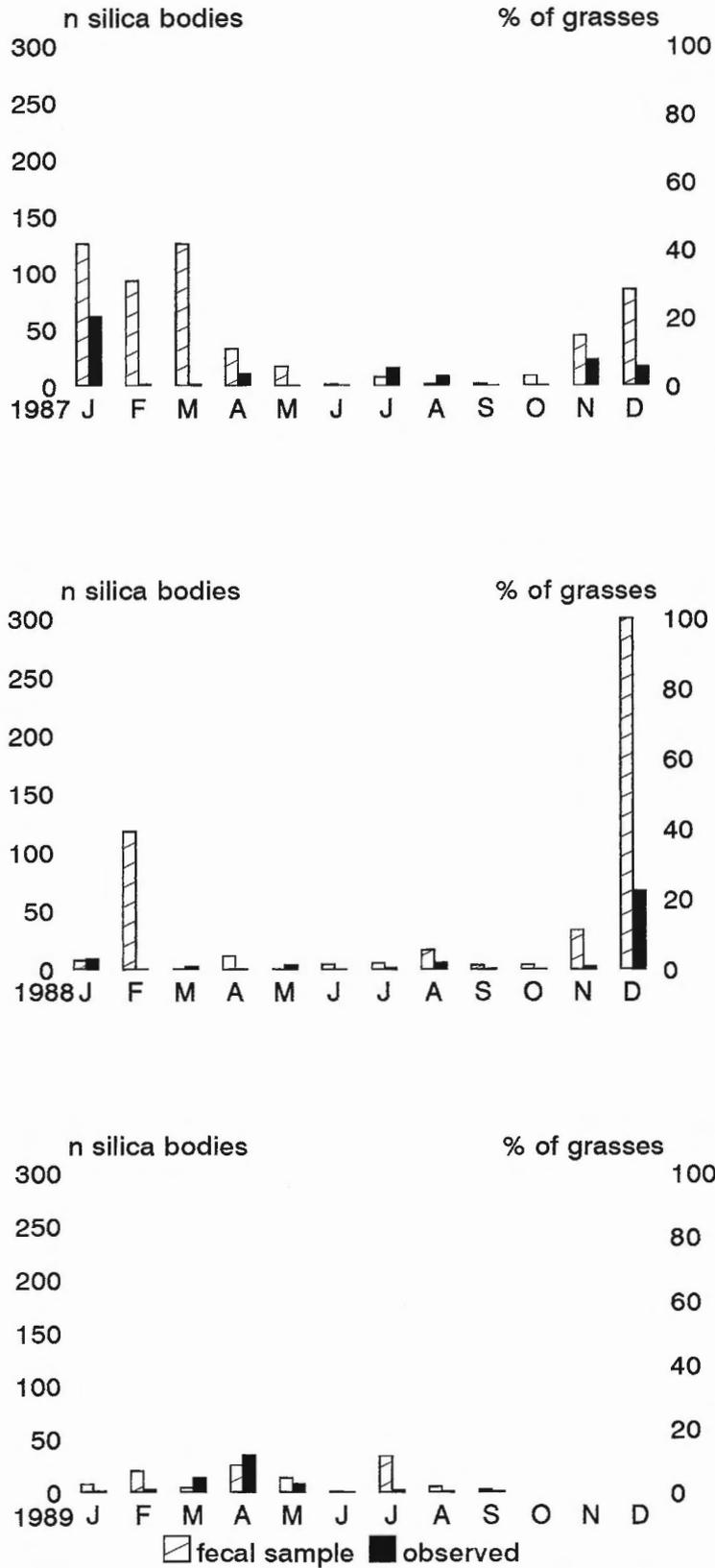
Fig. 13.1-3: Comparison of the observed grass intake with the results of the fecal sample examination in the years 1987 to 1989

In addition to the fecal samples the stomach contents of 32 animals could be examined: 8 analyses come from the research paddock; 12 dromedaries were found dead on the station Allambi, each four of which had been shot at different seasons; on the station Ringwood samples of stomach contents were taken from a group of 12 dromedaries that were shot on November 11, 1988. Except for the melon species *Citrullus lanatus* no new food plants were discovered by analyzing the stomach contents. Fig. 14 shows the results of the analysis of 8 samples of stomach contents from the research paddock.
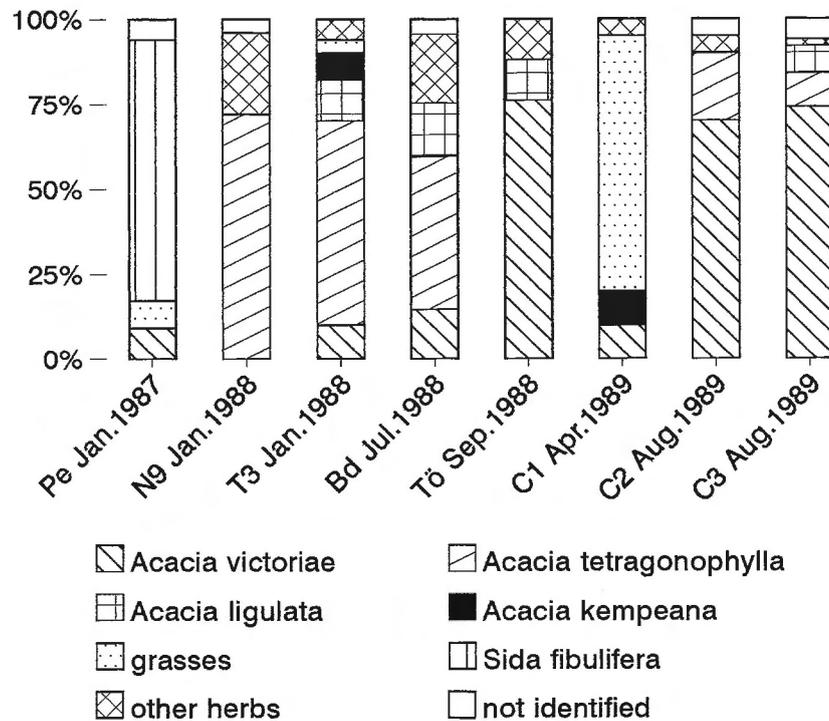
Fig. 14: Results of the examination of stomach contents of animals that died in the research paddock

The category of other herbs in the legend is made up as follows for the individual camels:

Bd:	Boerhavia schomburgkiana	8 %
	Salsola kali	4 %
	Tribulus terrestris	6 %
Tö	Salsola kali	8 %
	Zygophyllum ammophilum	4 %
N9:	Boerhavia schomburgkiana	6 %
	Cleome viscosa	5 %
	Indigofera dominii	4 %
	Portulaca oleracea	6 %
	Salsola kali	3 %
T3:	Zygophyllum ammophilum	6 %

The results of the analyses of stomach contents qualitatively and approximately quantitatively correspond to the food spectrums found by direct observation in the respective periods of time.

Fig. 15 shows the stomach contents of the animals shot on the station Allambi.
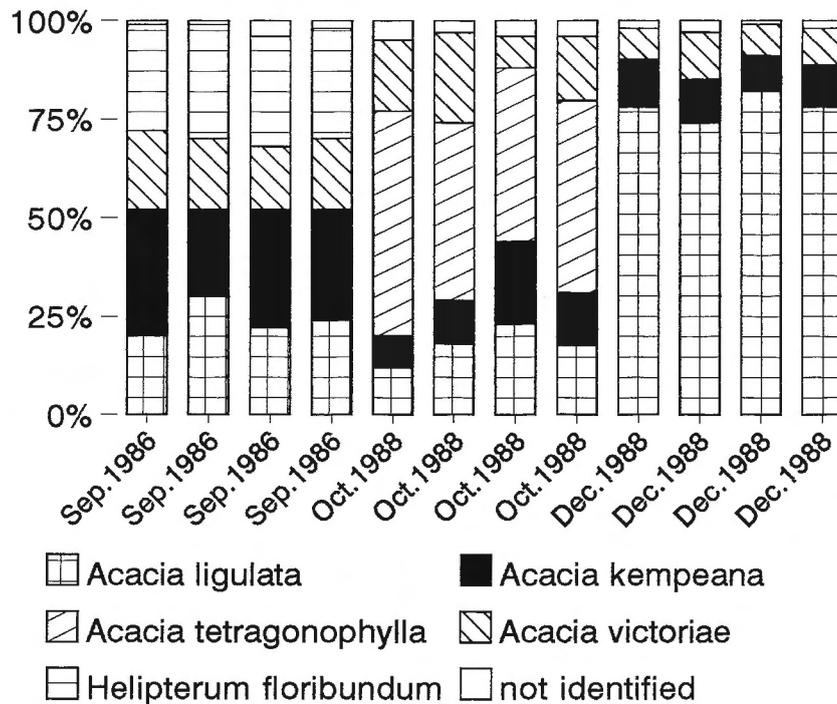
Fig. 15: Stomach contents of the animals found on the station Allambi

All animals that were shot during the same period of time showed a relatively homogenous food composition. The animals mostly fed on leafy food of some *Acacia*-species, in September 1986 they ate a lot of *Helipterum floribundum*. This corresponds to the observation data from the research paddock. The food selectivity in particular periods of time becomes even more obvious looking at the analyses of 12 animals found on the station Ringwood (Fig. 16). When they were shot this group was staying in an area with a predominant growth of *Ataläya hemiglauca*, which at this time had developed fruits which are very popular among the dromedaries. In the research paddock, too, the almost exclusive intake of *Ataläya hemiglauca* when flowering or after the development of fruits was observed (Fig. A2.1, 2 & 13).
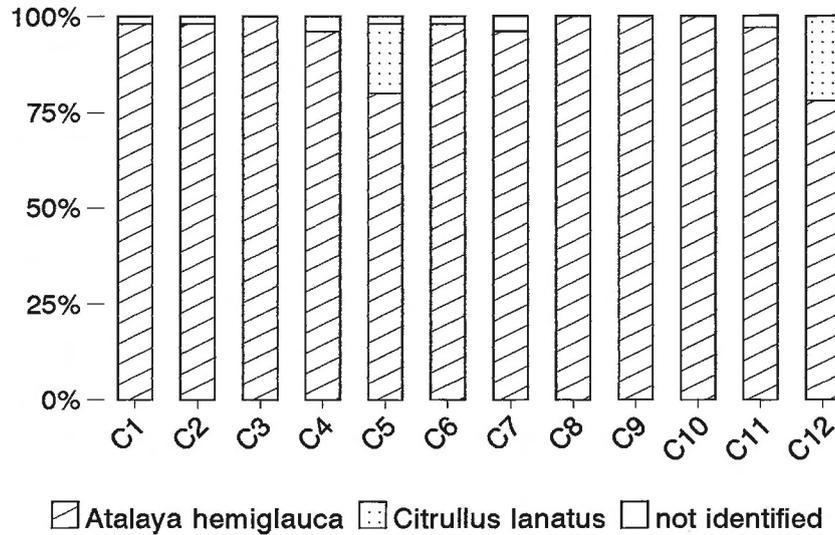
Fig. 16: Stomach contents of animals found on the station Ringwood

5.2.4 Food analyses of free-ranging tame dromedaries

The results of the quantitative food intakes which were done with the tame dromedaries on the stations Todd River and Ringwood, are shown in Figures A8.1-18 in the Appendix. In winter 1989 only the food intake of the dromedaries on Todd River could be observed. Table AT1 shows the additional food plants from both areas. The food intakes on the station Todd River showed a striking preference for *Lepidium phlebopetalum* which was eaten above all in summer as well as in winter. Even though there were other food plants that they usually liked to eat and that were available plentifully like *Acacia*- and *Eremophila*-species, the animals preferred *Lepidium phlebopetalum* even when it was dried up.

A similar trend was observed in the research paddock with the food plant *Helipterum floribundum* which still belonged to the main food plants even after it had long been dried up (Fig. A4.1-8).

5.2.5   Supply & use, impact on the vegetation

The wide variety of food plants in the research paddock made a registration of habitat specific supply and use data of the vegetation necessary in order to establish a link between supply and use qualitatively and quantitatively and eventually define the impact the dromedary has on the vegetation. The supply data are shown in Figures A5.1a-12c, A6.1-27 and A7.1-25 in the Appendix.

For a quantitative description of the food supply stating the number of individuals alone is not enough. Two plant species which were fed on preferably by the dromedaries serve as examples: *Lepidium phlebopetalum* and *Sclerolaena clelandii*. The former is a small forb with an average ground covering along the transects of about 5cm, while the latter species covers app. 60cm on average. If both were treated as equivalent in the diagram in a ratio of 1:1 starting out from the number of individuals, *L. phlebopetalum* would be overrated; even bigger discrepancies would occur in grasses that are present in high numbers of individuals, but often only have a covering of 1cm. To give small frequently occurring plant species a standardized relation compared with big rare species, the supply data were calculated from the vegetation analyses as a product of number of individuals and respective ground cover.

Apart from the general food intake of food plants with high abundance and thus intensive browsing, obvious preferences regardless of the supply were observed. Selective feeding upon rare occuring plant species like *Salsola kali* (Fig. A9.1a, 1b, 3b & 4b), *Acacia sessiliceps* (Fig. A9.2c & 2d) or particularly *Trichodesma zeylancium* (Fig. A9.2a) can have a reducing effect on their local population, even though their share in relation to the total amount of consumed food is relatively small. To illustrate this selectivity, preference indices P were calculated as abundance dependent values for the individual plant species and were shown in a percental split. These were calculated according to the following formula:

$$P = \frac{\text{use (\%)}}{\text{(no. of individuals X cover) (\%)}}$$

For a useful comparison of supply and use data the areas of the research paddock were combined to landscape types. The sandplain/dunes of the Amadeus and Simpson/Singleton land systems were treated together because of their comparable vegetation units, but the salt lakes and salt marshes of the Amadeus land system were treated separately. The areas of the Titra land system were divided up into bushland and open plains (Fig. 17).

landscape types in percent

44,5%

8,0%   6,6%

40,9%

open plain   saltlake/saltmarsh
sandplain/dunes   bushland
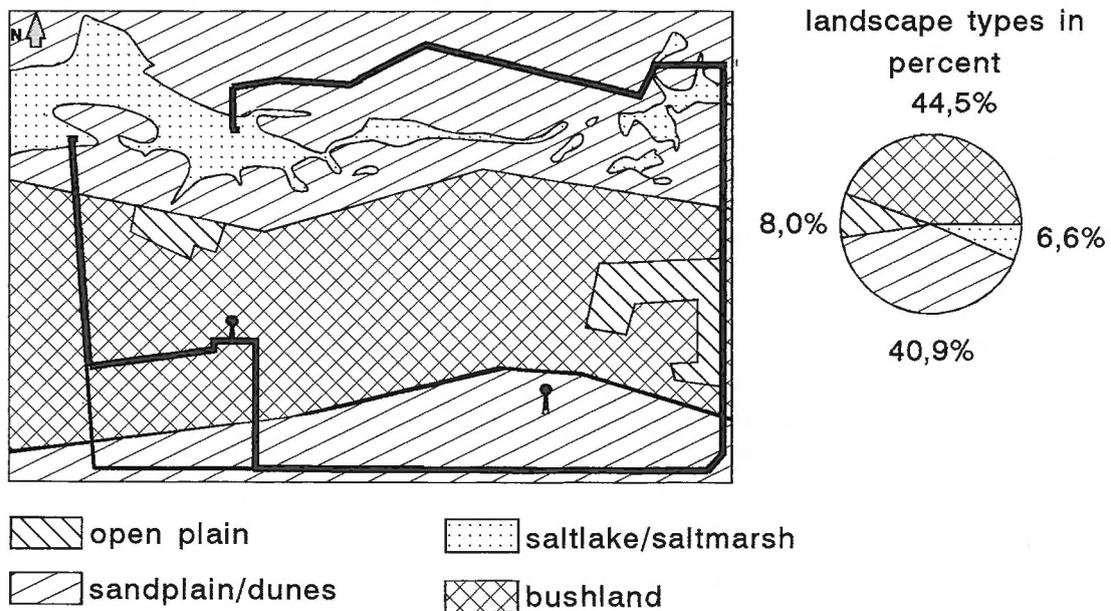
Fig. 17: Landscape types in the research paddock

All food intakes (Fig. A2.1-93; A3.1-52; A4.1-35) were compared with the vegetation supply data (Fig. A5.1a-12c, A6.1-27, A7.1-25) in the respective landscape types. They are shown in summary in Figures A9.1a-4b in the Appendix. Individual examples of the supply/use relation from all four landscape types at particular seasons are also shown in the Appendix in Figures A9.5-19.

The figures combined according to landscape types as well as the examples picked out as random samples from the total amount of intakes

clearly show that the plant species fed on the most are not necessarily preferred in general and thus are not being affected or even damaged.
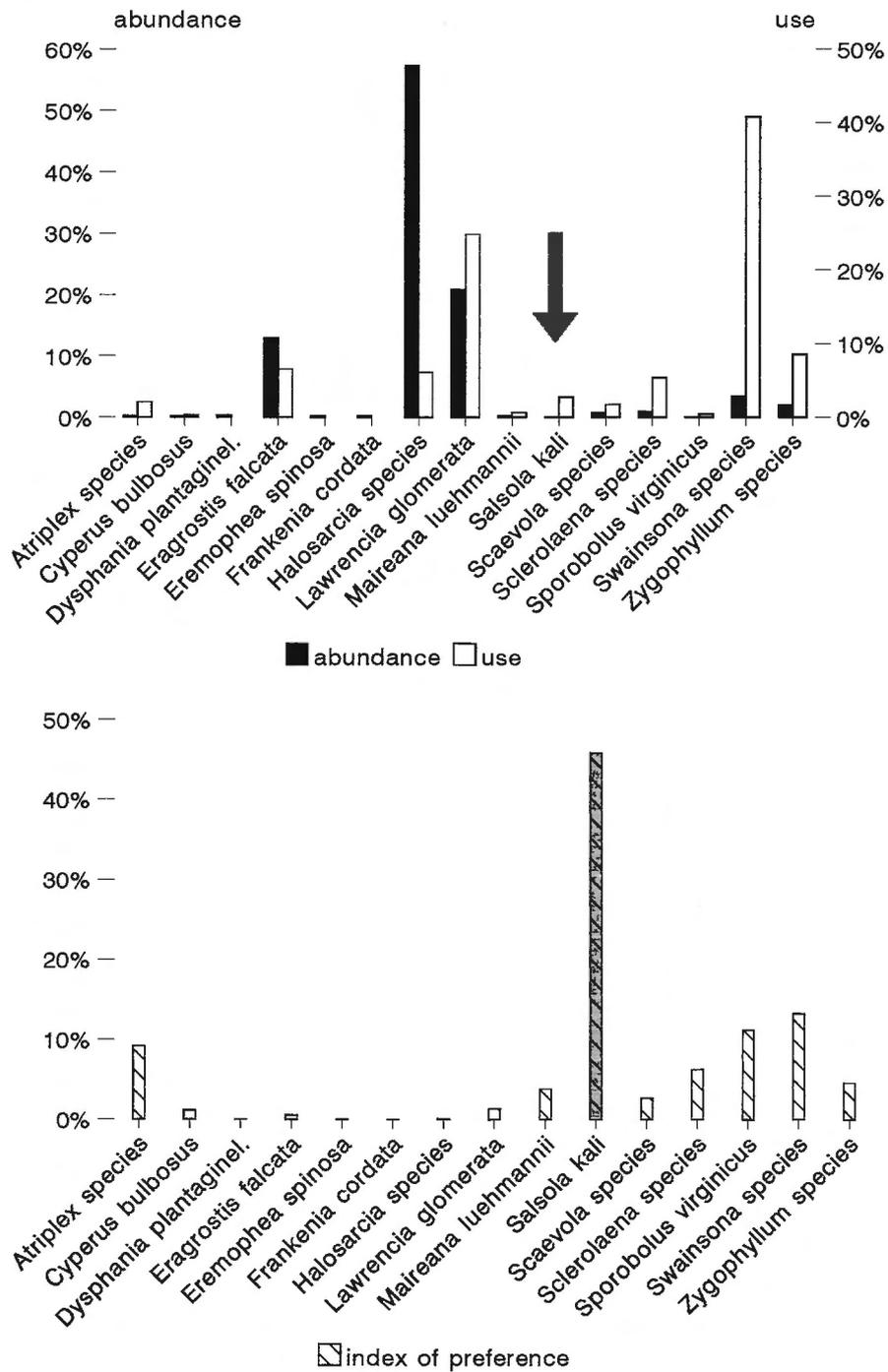
Fig. 18: Example for the supply-use relation with calculated preference indices (complete series of figures in the Appendix in Fig. A9.1-19)

In the bushland mainly leaves but also blossoms or fruits from woody plants were consumed (Fig. 19). Of the 27 species found in the transects four Acacia species were used the most both in summer and in winter: *Acacia victoriae*, *A. tetragonophylla*, *A. kempeana* and *A. aneura* (Fig. A9.1c & 1d). Because of their high abundance these species have a low preference index. *Hakea*-species and some of the Acacias rarely found here like *Acacia ligulata*, *A. pruniocarpa* and *A. sessileceps* as well as *Ventilago viminalis* have high indices because of their rare occurrence.

In winter the main food plants from the ground were *Boerhavia-*, *Helipterum-*, *Sclerolaena-*, *Tribulus-* and *Zygophyllum*-species. In summer *Boerhavia-*, *Indigofera-*, *Rhynchosia-* and *Sida*-species were eaten. The intensive use of *Salsola kali* which is only growing isolatedly, is conspicuous among the ground vegetation. It is consumed preferredly by the dromedaries in summer as well as in winter so that its preference indices are very high (Fig. A9.1a & 1b).

In the sandplain/dunes leaves, blossoms or fruits of woody plants were also eaten predominantly (Fig. 19). Here, too, the Acacia species were the most frequently consumed food plants in summer as well as in winter; particularly *Acacia ligulata* was fed on the most all year round. *Grevillea juncifolia* and *Stylobasium spathulatum* which during the flowering time were always grazed on intensively showed wider seasonal variations (Fig. A9.2c & 2d). Among the ground vegetation *Calandrinia*-species were preferred all year round, furthermore Chenopodiaceae like *Scaevola-* and *Sclerolaena*-species as well as *Salsola kali* (Fig. A9.2a & 2b) depending on the season. *Trichodesma zeylanicum* has a strikingly high preference index in summer (Fig. A9.2a). Altogether there is a supply-independent utilization pattern for the sand areas. The strong use of *Triodia basedowii* fruits in winter stands out (Fig. A9.2b).

In the open plains woody plants are missing, the ground vegetation is used. In summer shortly after rainfalls the dromedaries feed mostly on grasses, mainly *Enneapogon*-species (Fig. A9.3a), which amount to >70% of the entire supply. As soon as there are forbs, they are preferred (Fig. A9.3a). In winter mass developments of forbs like *Zygophyllum-* and *Helipterum*-species are used here at times (Fig. A9.3b).

The dromedaries visit the salt lakes/salt marshes preferredly in winter. At the beginning of the winter they almost exclusively feed on *Swainsona cyclocarpa* (Fig. A9.4b), by the end of the winter until into the summer they mostly eat *Lawrencia glomerata* (Fig. A9.4a & 4b).

trees & shrubs
84%

winter

ground vegetation
16%
bushland

trees & shrubs
70%

summer

ground vegetation
30%

trees & shrubs
69%

ground vegetation
31%
sandplain/dunes

trees & shrubs
67%

ground vegetation
33%

ground vegetation
100%

winter
&
summer

open plain

saltmarsh

winter
&
summer

ground vegetation
100%
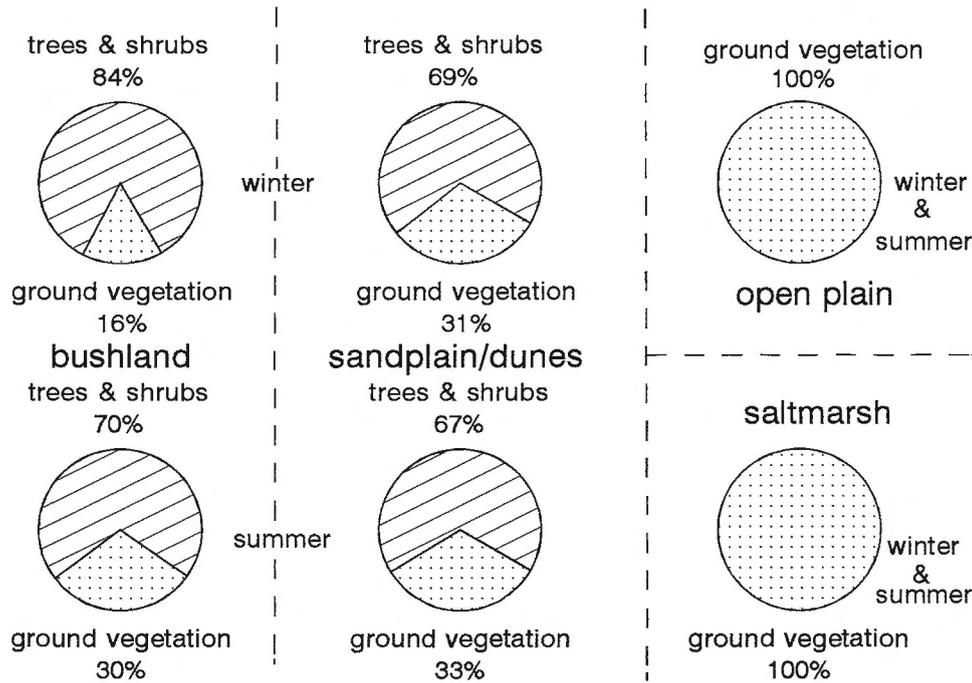
Fig. 19: Seasonal proportional utilization of woody plants and ground vegetation in the four landscape types

The summary for the entire paddock leads to the following proportional utilization (Fig. 20):

trees & shrubs
54%

ground vegetation
46%

winter

trees & shrubs
41%

ground vegetation
59%

summer
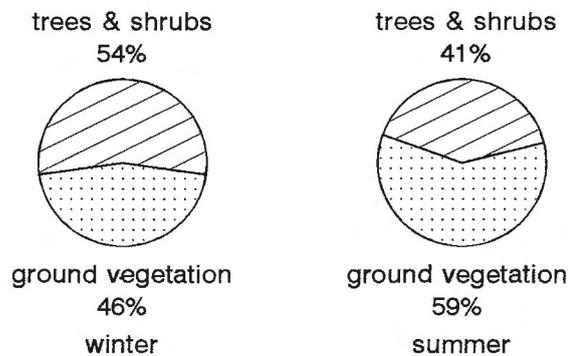
Fig. 20: Seasonal utilization pattern of the vegetation

5.3   Discussion

The vegetation of the arid zones of Australia offers a good food supply for the dromedaries all year round. The variety of food plants with their often found high abundance and a distinct food opportunism of the animals ensure an optimal nutrition for them. With the exception of extreme and persistent dry periods which also affect the evergreen shrub and tree vegetation, there are no food shortages for the dromedaries.

A comparative reflection of the results regarding the food ecology with the observations of the food intakes of dromedaries in North Africa (GAUTHIER-PILTERS 1961, 1965, 1969, 1974, 1975, 1977, 1980, 1981) is only possible to a limited extent, because there are significant differences in climate which cause extreme differences in the vegetation. The fundamental difference of the dry areas in central Australia to comparable areas in the northern hemisphere is the diversity of the flora. For central Australia app. 2.000 plant species have been identified (JESSOP 1985) in an area of 2 million km^2, the $213km^2$ research paddock had almost 300. The flora of the Sahara includes only app. 1.200 plant species on an area of about 9 million km^2 (OZENDA, 1958). The grazing areas used by the dromedaries in the Sahara that in general exceed the area of the research paddock by far often only contain between 20 to 50 plant species (GAUTHIER-PILTERS 1965, 1969, 1975) which can be reduced to 5-10 species in dry summers (GAUTHIER-PILTERS 1980). Despite the big differences in food supply there is a lot in common regarding the general pattern of food intake and the browsing behavior.

In the research paddock 83% of the available plant species belong to the food plants of the dromedaries. However, a quantitative investigation qualifies the extremely wide food spectrum considerably: 50% of all food plant species listed in Figures A1.1-12 make up only 0.5% of the total intake, while only 7% of the species constitute almost 70% of the entire amount of food. Thus it can be clearly differentiated between main food plants like *Acacia victoriae* in the research paddock, which makes up >20% of all observed food intakes, and plant species that were eaten very rarely. In North Africa GAUTHIER-PILTERS observed the same trend: almost half of the food plant species of the dromedaries identified by her together were less

than 1% of the total food intake, while the animals in most grazing areas only preferred one to two plant species, which had a share of up to 65% of the entire amount of food (GAUTHIER-PILTERS 1980).

Selective feeding on a few plant species in certain habitats and periods of time which is typical for the dromedaries becomes particularly evident when quantitative food intakes from random samples are examined (Fig. A2.1-93). In 65% of the analyses only one food plant each time was clearly favored, 17% of them only contain one food plant which accordingly was used at 100%. In 20% of the intakes two food plants are preferred, i.e. in 85% of all random samples only one or two plant species are mainly used.

The seasonal food preferences can very well be quite different from year to year. This is demonstrated by the observations in the research paddock with the Malvaceae as an example: while the perennial *Sida fibulifera* was the main food plant in January and December 1987 (Fig. A4.3 & 14) it was consumed only little, if at all, during the following years at the same time. Among other things this selective utilization pattern can be the reason that e.g. *Euphorbia tannensis* which has been described by NEWMAN (1979) as intensively browsed plant species was not eaten in the research paddock.

The grass proportion in the food spectrum of the Australian dromedaries is very small compared with the one of dromedaries in North Africa. It only amounts to 3% (Fig. 9), 43% of which are *Triepogon loliiformis*. This highly specialized desert grass already develops after a few millimeters of rainfall, grows very fast and is often available after only one day. In contrast to the observations in Australia, the animals in North Africa often even prefer dry grasses to green forbs, as long as there is sufficient drinking water (GAUTHIER-PILTERS 1980). Even though the observed animals also had enough drinking water available, they only ate the fresh grass after rainfalls for a short time and never touched the dry grass. Mainly grasses of the genuses *Aristida* and *Panicum* which belong to the most important food plants in the Sahara and in some regions temporarily represent 40-100% of the consumed food, were only eaten proportionally at 0.07%, although they occurred frequently.

A certain similarity in the preference of dry compared with other succulent plant species could also be observed in the research paddock and on the station Todd River with the forbs *Helipterum floribundum* and *Lepidium phlebopetalum*. In both cases the animals had enough water at their disposal.

The results of the nutritive analyses for the food plants were put in relation to the frequency of the intake of these plants. The plants eaten most frequently as well as the ones with high preference indices (Fig. A9.1-19) did not show significant differences regarding their contents and their digestibility in comparison with rarely eaten plants.

Dromedaries have a strong need for salt (GAUTHIER-PILTERS 1981), which explains the frequent feeding on halophile plants. Although the water in both troughs of the research paddock was very saline (Babbler-bore: 10.000 ppm; Blom-bore: 5.000 ppm) and the animals in addition regularly fed on crystalline salt in the form of saline soil, the proportion of Halophytes in the total amount of consumed food was 15.3%. GAUTHIER-PILTERS (1980) also describes a high proportion of salt plants in the food of dromedaries in the Sahara.

Among the preferred plant species of the dromedaries in the research paddock only the Fabaceae *Swainsona cyclocarpa* is rare in central Australia. In western Australia, however, it is relatively common (LATZ, pers. comm.). In the research paddock all *Swainsona*-species were eaten by the dromedaries (Fig. A1.11). Thus it seems reasonable to assume that the very rare endangered *Swainsona microcalyx*, that was not identified here, belongs to the food spectrum, too. This species only grows in a few places in central Australia along the salt lakes, one of the preferred habitats of the dromedaries in winter. The same is true for *Trichodesma* sp. A (JESSOP 1985), which is only identified in the region around Docker River. In the research paddock almost each individual of the closely related *Trichodesma zeylanicum* was nibbled at or eaten up and NEWMAN (1979) also describes a heavy browsing of this species in the Simpson desert. Therefore, an impact on *Trichodesma* sp. A, which is also among the endangered plant species in central Australia, is very likely.

Particularly the fruits of the rare tree-species Quandong (*Santalum acuminatum*), which is not to be found in the research paddock, are mentioned as preferred food of the dromedaries (LATZ, pers. comm.). The observations of the browsing even of preferred shrub- and tree-species made clear that a negative effect of the dromedary with the exception of extremely long periods of drought, is not to be expected. On the contrary, here the dromedaries can help with the distribution of seeds, as it had already been found out for the emu (*Dromaius novae-hollandiae*) (HOLLIDAY 1986).

Dromedaries feed on several plant species which are poisonous for cattle or horses, like some *Indigofera-*, *Swainsona-* or *Nicotiana-* species. Even plants like *Tribulus terrestris* (poisonous for sheep), juvenile *Salsola kali* (poisonous for sheep and cattle, oxalate) and particularly the fruits of *Atalaya hemiglauca* (lethal for horses) are preferred by the dromedaries and consequently temporarily eaten in large amounts. In central Australia there are only a few plant species that can have a lethal effect on the dromedary, two of which were present in the research paddock: *Duboisia hopwoodii* and *Gyrostemon ramulosus* (Fig. A1.4 & A1.6). Both shrub-species were growing in the research paddock in the sand areas or in the dunes and often were socialized with *Acacia ligulata* and *Stylobasium spathulatum*. While the dromedaries browsed intensively on both latter species the poisonous species standing close by were consequently avoided. The animals in the research paddock obviously knew the plants, since reports about dromedaries eating poisonous plants and subsequently dying refer to animals that came into a new area with unknown vegetation (WARBURTON 1875; GILES 1889; BARKER 1964; CISC 1993).

According to McKNIGHT (1969) *Acacia cambagei* belongs to the most widespread plant species which are poisonous for dromedaries. On the station Ringwood, though, these were regularly used as food plant. Later studies showed that the toxicity of the species varies geographically (JESSOP 1985; URBAN 1990). Since there are no analyses of *A. cambagei* from Ringwood, the contradiction remains to be clarified.

6.   DRINKING FREQUENCIES
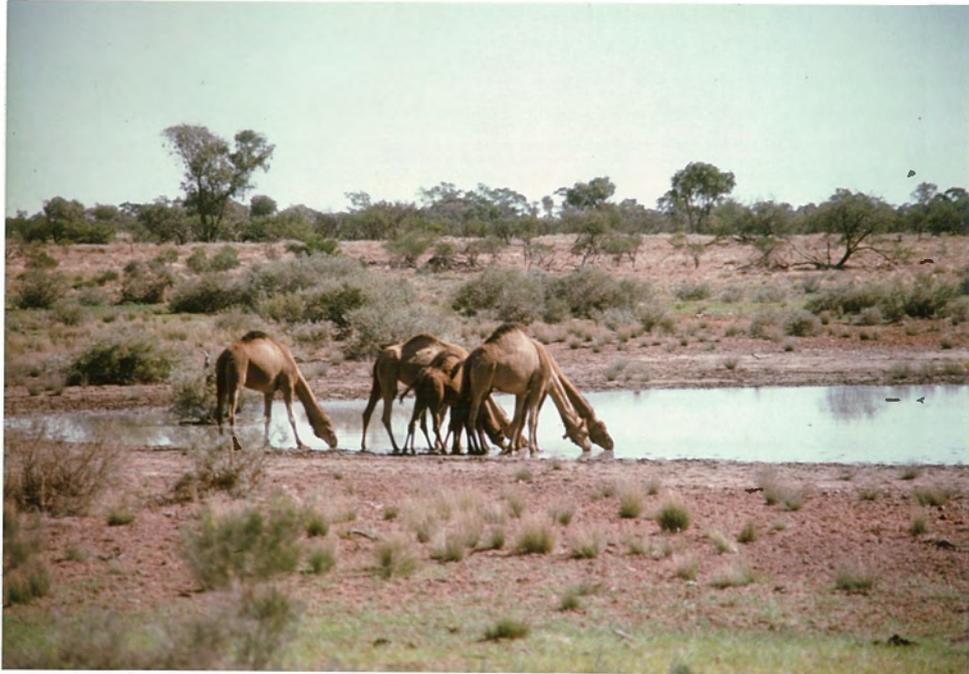
With regard to their water balance dromedaries are excellently adapted to the unpredictable conditions of the deserts and semi-deserts. Morphological and physiological adaptations make it possible for them to be largely independent from surface water. The various mechanisms for conserving water have already been known for a long time (SCHMIDT-NIELSEN 1952, 1956, 1957, 1959 and 1964).

While there are detailed data about the drinking habits of domestic dromedaries (GAUTHIER-PILTERS 1977, 1981), regarding this topic it was only known that wild-living dromedaries visit the watering places. Long-term observations concerning the drinking frequency of individually known free-ranging animals at different seasons, depending on climatic factors with the resulting food supply were completely missing.

Information on the drinking habits of domestic Australian dromedaries is to be found in BARKER (1964) and McKNIGHT (1969), occasional reports about the use of troughs by wild-living dromedaries in McKNIGHT (1976).

6.1   Methods

The drinking frequency of the dromedaries was calculated as reciprocal value of the respective drinking activity. The determination was done exclusively through the use of the troughs. Surface water was rarely available for the animals and was consequently only used for a short time, but the animals still went to the troughs during these times. When surface water was available extensively, it was not possible to record the absolute values of the drinking frequencies. Therefore, the drinking frequencies at the troughs were checked for a dependency on the precipitation.

The drinking frequency was mainly determined by evaluating tracks. The footprints are individually different and the size as well as the shape were used as identification features. A number of animals could be identified with the help of a photographic file of footprints of the right forefoot with measurements of length and width, and individual characteristics like round or oval shape, or distinct scars on the sole .

Fig. 21: Excerpt from the footprint file. Example: adult male "alter Alter" (length: 23cm, width: 22cm, shape: regular, almost round, no special features).

The two watering places in the research paddock (Fig. 3) were checked several times a day, after each checking all tracks were carefully

destroyed. Apart from evaluating foot prints the drinking frequency was determined by direct observation.

The statistical correlations between drinking frequencies and climatic factors were tested according to the SPEARMAN rank correlation (LORENZ 1988). The seasonal drinking frequencies were checked for statistical significance according to the WILCOXON test (DIEHL/KOHR 1987), the sex-specific and age-dependent drinking frequencies were checked according to the MANN-WHITNEY-U test (LORENZ 1988).

6.2   Results

The drinking frequency of the dromedaries in the research paddock was clearly different depending on the season. Since water was permanently available at the troughs and the animals were not disturbed, they got used to them and during the hot season went to the troughs regularly, even together with the stock (Fig. 22). The observed animals that originally immigrated from the dry Gibson desert needed up to six months to get used to the fenced in drinking troughs. New animals which joined old-established groups went to the trough with them right away, while others that remained isolated, needed several months to overcome their shyness.

Fig. 22: Use of a fenced in trough. Example: adult male "Fremder" uses
        the trough together with cows

Part I: Drinking Frequencies

During the summer months, the time of the strongest need for water, the troughs were used by all animals. During the winter months most animals went to the trough, though in much bigger intervals. Some did not go at all (Table 5).

Table 5: Medium interval of the average seasonal drinking frequencies of adult and subadult animals; stated in days with respective standard deviation (s.d.)

| Period of time | Interval (s.d.) | | drinking |
	males	females	
10/86-3/87	4,3 (1,5)	4,3 (1,7)	100 %
4/87-9/87	12,3 (5,2)	10,6 (3,4)	85 %
10/87-3/88	7,3 (1,9)	11,4 (5,9)	100 %
4/88-9/88	23,7 (15,9)	89,2 (44,8)	60 %
10/88-3/89	8,8 (4,1)	4 (1,8)	100 %
4/89-9/89	12,1 (6,7)	16 (22,8)	89 %

Table 5 shows the seasonal differences of the drinking frequencies. Particularly the values for the wettest periods of the early winter 1988 and 1989 spread very much as expected. To illustrate the environmental conditions present at the specific periods of time, Table 6 shows the average drinking frequency of all animals (excluding the calves) in relation to the respective medium day-, night- and average temperatures as well as the amounts of precipitation per season. In the study years 1988 and 1989 the heaviest rainfalls each time fell at the end of March. Because it was the beginning of winter, they were classified as belonging to the winter season.

Table 6: Average seasonal drinking frequencies in relation to the ambient temperature and to the precipitation

P. of time	T_{max}	T_{min}	T ϕ	rain	ϕ Int.	s.d.
10/86-3/87	39,1	20,2	29,7	149	4,3	1,6
4/87-9/87	26,9	10,5	18,7	35	11,3	4,3
10/87-3/88	38,5	23	30,8	169	9,8	5
4/88-9/88	27,6	11,3	19	271	41,3	39,2
10/88-3/89	38	21,8	29,9	172	6,5	4
4/89-9/89	24	7,9	16	245	14,1	17

Of course, the drinking frequencies are seasonal but they were very different even during the individual study years. During the first observation year 1986/87 succulent food plants were scarce from the

start because of the relative dryness. Moreover, the animals were mostly in the small 18km^2 paddock, which had less food of high moisture content available because of the high dromedary density than the research paddock in the following observation years. Accordingly the drinking frequencies are greatest for the summer 1986/87 as well as for the winter 1987. In the study year 1988 the troughs were frequented the least. With a total of 461mm of precipitation this year had the most rain with an accordingly large supply of succulent food plants. Particularly after the heavy rainfalls at the beginning of the winter the dromedaries did not go to the drinking trough very regularly. Almost 40% of the animals did not use the troughs at all that winter. During the last study year the animals used the drinking troughs more regularly again.

The drinking frequency of the dromedaries depends on several external factors: a correlation with air temperature, humidity and precipitation is obvious and was examined. For this purpose the relative drinking frequencies of all adult and subadult animals was averaged over a period of two months each. They were then correlated with the corresponding averaged data of the air temperature and the humidity as well as with the amounts of precipitation (SPEARMAN rank correlation). In all series of tests the amount of random samples was 17 value pairs, since only the data from December 1986 on were taken into account because of the above mentioned setting-in period.
As expected there was a positive correlation for the air temperature and a negative correlation for the humidity (the lower the humidity the higher the drinking frequency). There was a highly significant correlation of $r_s = 0.7107$ at a significance level of $\alpha = 0.0045$ regarding the air temperature and an also highly significant correlation of $r_s = 0.7116$ at $\alpha = 0.0044$ regarding the humidity. The correlation coefficient of the drinking frequencies with the amounts of precipitation is also negative but not significant ($r_s = 0.2642$; $\alpha = 0.2907$).

The average temperature alone is not relevant for the increase in drinking activity but the succession of several days with a relatively high air temperature. To illustrate this tendency the percentage of animals that went to the trough is listed under the respective maximum air temperatures of the day in Fig. 23 exemplary for the period of

October 1988 until September 1989. The decrease in drinking activities becomes obvious with the dropping temperature of the day (April-August). With the first hot days at the end of August the percentage of animals that went to the drinking trough rises again, even though the maximum temperature is still significantly below the values of October 1988, but has increased sharply compared with the months before.
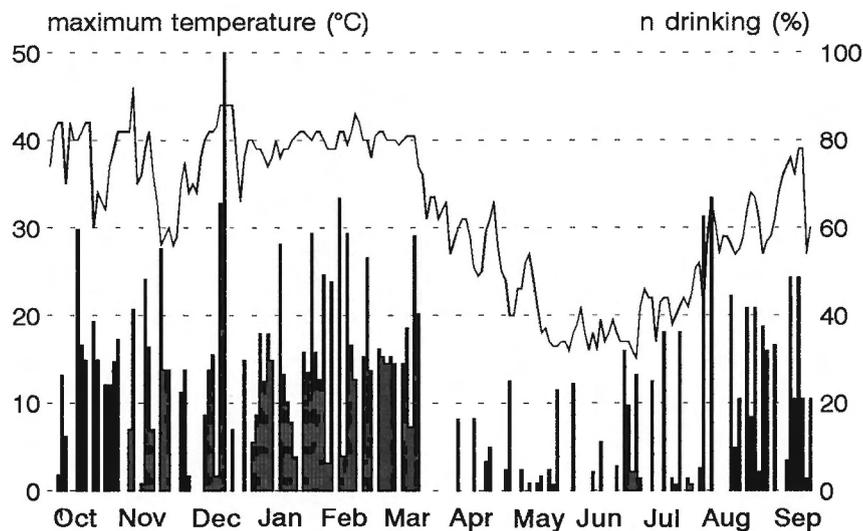
Fig. 23: Observed use of the troughs in relation to the maximum temperatures of the day (October 1988 to September 1989)

During the entire examined period individual differences were found regarding the drinking frequencies of the animals. These were affected by climatic and sociological parameters. The temperature is the deciding factor; during very hot days in summer the animals drank daily or every other day, while on cooler days the intervals became clearly longer.

But the group has an influence on the intervals of its members, too. It was never observed that a female left her group to go to the trough by herself. Each group has its own rhythm which again is determined by various factors. Groups that have females with calves e.g. go to the troughs more often than the ones without calves. If a female without a calf is living in a group of females with calves, she has the same drinking frequency as those because of the social component. When two

or more groups meet an exchange of the members can take place, among females mainly in summer, among males throughout the whole year. When this happens the actual individual frequencies are hard to be determined, i.e. after which time an animal would go to the trough of its own accord.

Only the individual drinking frequency of adult males who often live solitarily can be illustrated (Fig. 24). This and all following Figures indicate the average drinking frequency of the animals. As a reciprocal value of the respective drinking activities the theoretical value 1 means daily drinking, but this is not reached, because the drinking frequencies are seasonally averaged. 0 means the animals did not drink at all.
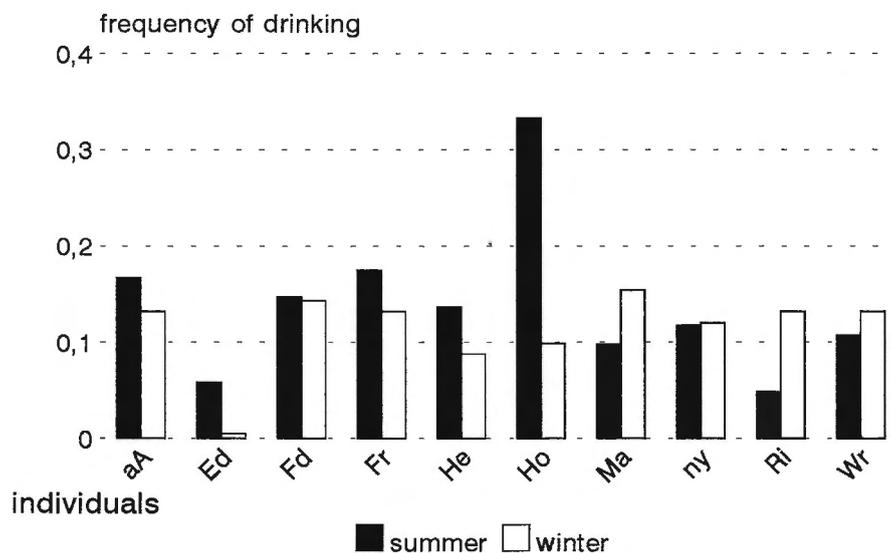
Fig. 24: Individual average drinking frequencies of 10 adult males in the study year 1989

In the following Figures the drinking frequencies of the dromedaries are summarized according to gender and age classes. The adult females are distinguished whether they nursed a calf or not.

frequency of drinking
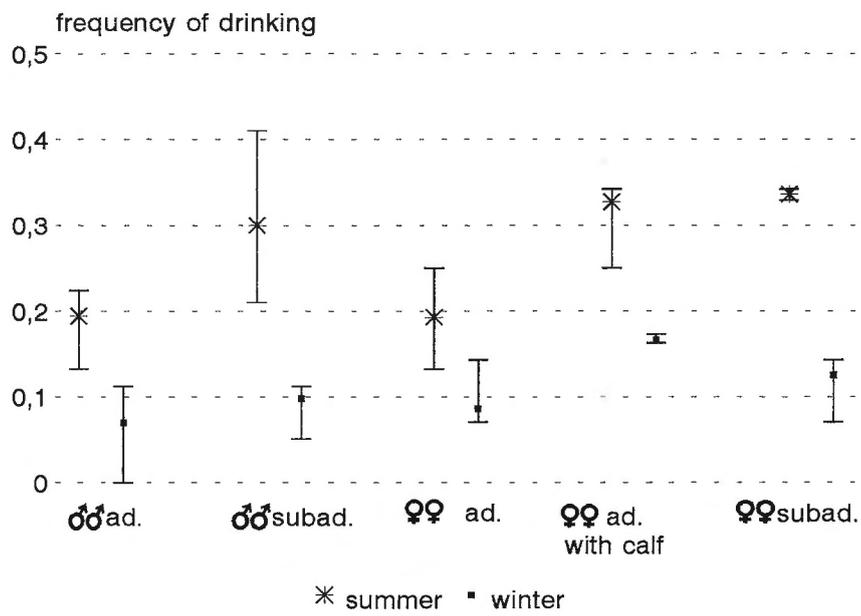
Fig. 25: Drinking frequencies in the study year 1986/87

frequency of drinking
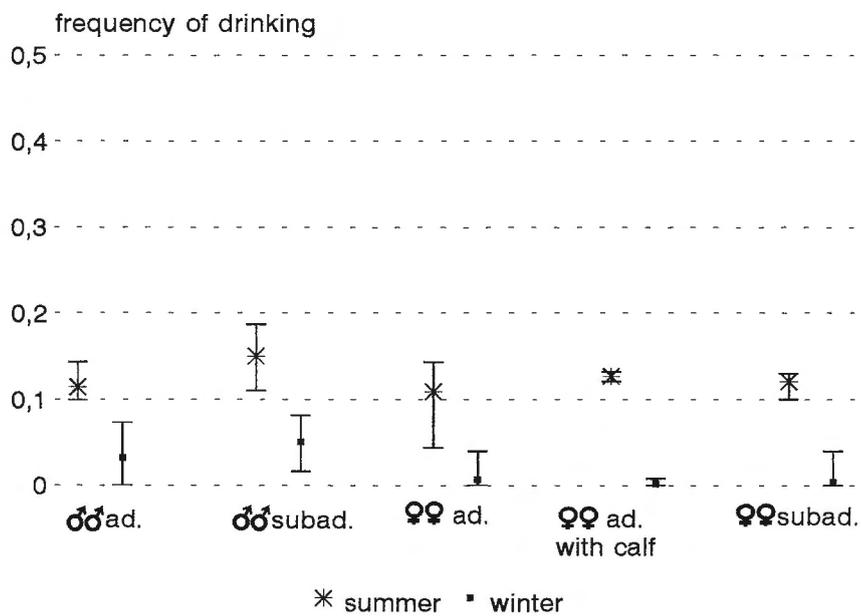
Fig. 26: Drinking frequencies in the study year 1987/88

frequency of drinking
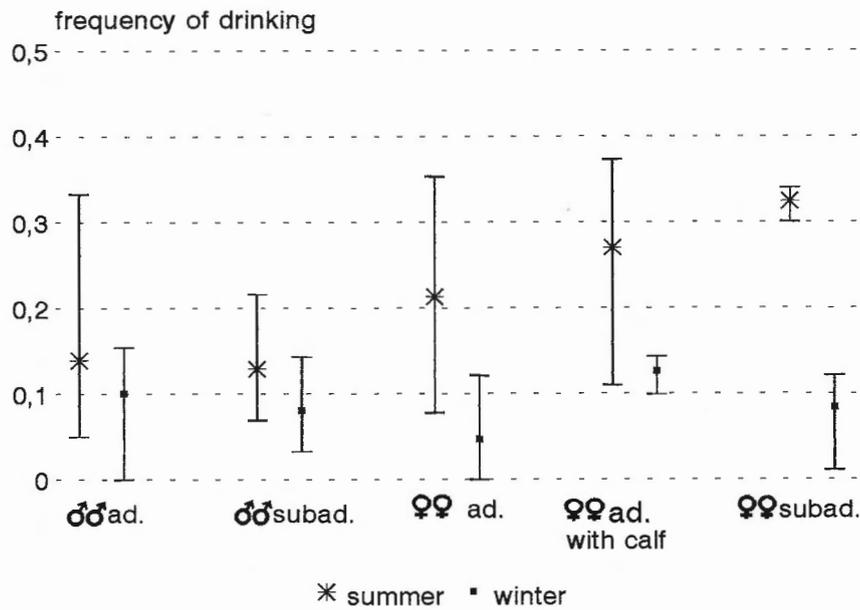
Fig. 27: Drinking frequencies in the study year 1988/89

Greater differences appear in the drinking frequencies of adult females with calves compared with those without calves. Only in the study year 1986/87 there was a group of adult females with calves and at the same time another group of adult females without calves side by side without an exchange over the entire period of time. Here the above mentioned social component does not apply, therefore this year is particularly suitable for the illustration. At the same time age-dependent differences in the drinking frequencies appear. In the research paddock subadult animals generally drank more often than adults. But the social component in subadult females is more important than in subadult males, since subadult females are always living in a group of females. The subadult males, however, frequently exchange and are often living in groups without other adult animals (DÖRGES 1995).

To ensure the above observations the differences of the gender- and age-dependent drinking frequencies were checked for statistical significance. For all significance tests the dromedaries were subdivided into classes as follows:

1. adult males
2. adult females with calves
3. adult females without calves
4. subadult males
5. subadult females

Part I: Drinking Frequencies

The test for gender- and age-dependent drinking frequencies was done as independent random samples, since the drinking frequencies of different animals were compared with each other. The MANN-WHITNEY-U-test (LORENZ 1988) was used for this purpose. The individual drinking frequencies of animals of one class were tested compared with the respective individual frequencies of the animals of all other classes. 1:2 e.g. means the examination of the drinking frequencies of all adult males compared with the ones of all adult females with calves for the respective season. For five classes 10 test series were needed, which were each done over three summers and three winters.

The drinking frequencies of the adult males are always significantly different from those of the adult females with calves. The differences are even highly significant in the summer of 1986/87 and in the summer of 1988/89. The differences in the drinking frequencies of adult females with calves are always significant compared with the ones of adult females without calves, highly significant only in the study year 1986/87. The differences in the age-dependent drinking frequencies are significant in 28 of 36 tested random samples. All individual results are shown in Table AT3.2 in the Appendix.

The seasonal drinking frequencies were also checked for statistical significance. For this purpose the frequencies of all individuals from one class were seasonally tested against each other. E.g. all drinking frequencies of adult males in summer 1986/87 were tested against the frequencies of the same males in winter 1987. Because of these dependent random samples the Wilcoxon-Test (DIEHL/KOHR 1987) was used. The seasonal drinking frequencies of all classes differ significantly, the results are shown in Table AT3.1 in the Appendix.

Due to the extremely heavy precipitation in the winter of 1988 the drinking frequency of all animals is very low compared with the other winters. On the one hand this is due to surface water that was present during the first weeks of winter. But above all the animals had food of high moisture content at their disposal in this season. In the winter of 1988 the average degree of covering of all areas in the research paddock was 50%, whereas in winter 1989 only 30% of the area was covered with grasses and forbs. In the summer of 1987/88 the average covering was 44%, in the summer of 1988/89 it was only 38% even though the amount of rain was almost the same (ref. series of Figures A5 & A6 in the Appendix).

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6.3   Discussion

The favorable climatic conditions of Australia in most years guarantee a sufficient water supply for the dromedaries via the food. Only during times of extreme and long lasting periods of drought, when even the foliage of the shrub and tree vegetation has withered up, the animals must drink. They leave the dry regions and specifically go to areas used for cattle, often hundreds of kilometers away, to drink the water from the troughs.

GAUTHIER-PILTERS (1977) also states that the dromedaries of the Sahara only drink rarely or not at all when there is a good supply of succulent food plants. She observed that free-ranging dromedaries usually do not drink during the six to seven cooler months of the year even when they were offered water (GAUTHIER-PILTERS 1977 and 1981). Even working animals manage to walk 1.000km with burdens without having to drink (MONOD 1958).

In central Australia, favored by the summer rains, dromedaries are even able to walk large distances without drinking water during the hot season: in the summer of 1883 a caravan with a burden of 350kg per animal walked 687km at very high temperatures without drinking (McKNIGHT 1969).

The wild-living dromedaries that live in the completely dry central regions of the Simpson and Gibson desert presumably do not need to drink at all during most years. That does not rule out that surface water is used, as soon as it is available.

The independence from surface water is confirmed by two more observations. An analysis of tracks on the station Allambi in the early summer of 1987 showed that a group of dromedaries moved past a freely accessible watering place without drinking. McKNIGHT (1976) describes the same situation on other stations at the edge of the Simpson desert.

Even in the research paddock where the animals were used to the troughs, the watering places were often not used for weeks in winter. One group even did not go there for months. At that time nowhere in the area surface water was available. McKNIGHT (1976) made a similar

observation in a large dry enclosure of 60km^2 where a group of dromedaries did not drink for more than ten months. In another case a single dromedary that had been kept with horses for more than a year never drank from a trough (SMITH, pers. comm.).

Reports of dromedary groups that made a real rush for the cattle troughs are without exception from extreme periods of drought in the summer months, like in December/January 1961/62 and 1965/66, when herds of hundreds of dromedaries from the Simpson desert came to the troughs on the stations (McKNIGHT 1969).

Although the dromedaries normally do not need additional drinking water in central Australia they get used to it, if it is readily available. Physiological examinations showed that dromedaries adjust their metabolism to conserving water during a water shortage (SCHMIDT-NIELSEN et al. 1956). The more dehydrated a dromedary is the more water it saves. This phenomenon was for instance used by the nomads of the Sahara by training their animals for a water shortage before a longer desert crossing. But if sufficient water is permanently available, it is not being conserved and the animals accordingly need to drink more often.

The observations showed that the dromedaries drink every two to eight days in summer, depending on the food situation and on environmental conditions. Comparable intervals were also found for the dromedaries of other continents (GAUTHIER-PILTERS 1981, WILSON 1980).

The differences in the drinking frequencies of individual animals can mostly be explained physiologically. Females nursing a calf without doubt have a higher demand for water than females without calves. This difference becomes particularly clear in the study year 1986/87, the only year without an exchange of adult females between groups of females with and without calves. In all the other study years adult females exchanged to one or the other group particularly in summer (DÖRGES 1995). Even though the group specific element could not be excluded, the drinking frequencies for females with calves (with the exception of the already atypical winter of 1988) are always significantly higher than for the adult females without calves. The drinking frequencies of subadult animals were mostly higher compared

with adult animals. In summer the drinking frequencies of subadult males were always significantly higher than the ones of adult males und adult females without calves, except for the summer of 1988/89. During this time the subadult males were almost exclusively socialized with adult males whereas in the other summers they lived more often in groups without adult males. The drinking frequency of the subadult females, however, is mostly marked by social components. Most of the subadult females in the research paddock were living in groups of females with calves and accordingly drank frequently.

GAUTHIER-PILTERS (1977 and 1981) describes an age-dependent drinking frequency of the dromedaries, but does not give information about which age-group drinks most often. Regarding the need for water, though, she states that older animals and females with calves need the most water.

Within the framework of the studies it was not possible to determine the individually consumed amount of water. With the help of the drinking frequencies it could be confirmed, though, that females with calves go to the troughs the most often. However, adult females without calves and adult males went to the trough less frequently than subadult animals. The results are not necessarily contrary to the statements of GAUTHIER-PILTERS, since subadult animals can only drink less water because of their smaller size. At the same time they have a relatively larger surface und thus larger losses of water. To compensate for these losses, they have to go to the trough more often than the adults.

At the same time the results show a pattern that was adjusted to the relevant food conditions. In the dry study year 1986/87 with very little supply of succulent food plants the drinking frequencies of all animals are the highest. In the summer of 1987/88 the drinking frequencies of the dromedaries are noticeably lower than in the summer of 1988/89 despite almost identical seasonal amounts of rain. The supply of succulent food plants was significantly larger than in the summer of 1987/88 due to the different distribution of the amounts of rain. The extremely low drinking frequencies due to food of high moisture content become even more obvious in the winter of 1988. In this season the succulent ground vegetation lasted all winter because

of the amount and distribution of the precipitation, while in the winter of 1989 most of it had already been dried up from the middle of July on. Thus, it was practically no longer relevant for the water balance of the dromedaries (ref. Chapter 5).

Regarding this topic it can finally be said that the drinking frequency of the dromedaries depends on several factors. Climatic factors are the decisive factors, mainly the temperature and the humidity. Here not only the amount of precipitation is important but also the food supply resulting from the sum of all relevant factors. That also explains the non-significant correlation of the drinking frequencies with the amounts of precipitation.

Aside from all possibilities discussed up to now, it cannot be excluded that the salt content of the drinking water (Babbler bore 10.000ppm; Blom bore 5.000ppm) is perhaps important owing to the high need of the animals for salt (GAUTHIER-PILTERS 1981). One observation supports this idea: In November 1987 everywhere in the research paddock surface water was available after a heavier rainfall; the animals still went to the Babbler bore to drink the very saline water there. Afterwards they went to the salt lakes to additionally eat saline soil.

7.   HABITAT USE

Unlike domestic or free-ranging camels in other continents the wild-living dromedaries in Australia have the unrestricted opportunity of their habitat selection. Differentiated data regarding this topic could therefore be ascertained for the first time in the framework of this study .

7.1   Methods

The dromedaries in the research paddock were visited several times a day. At each sighting the habitat type was characterized and the activity of the animals being there was recorded. Outside the research paddock the habitat type was recorded during checking flights and checking tours by car.
The four landscape types of the research paddock (Fig. 17) were further divided structurally concerning the vegetation density. With the help of rectified aerial photographs on a scale of 1:40.000 in the bushland and the sand areas or sand dunes, the denser vegetation units were separated from the more open ones. The sizes of the individual areas were determined with the help of a Kontron Videoplan$^{(R)}$ device.

The vegetation analyses (Chapter 5) were summarized specific to the habitat, and converted to random samples of equal size. By means of the program "Statistical Ecology" (LUDWIG & REYNOLDS 1988) the diversity-, richness-, and evenness-indices were calculated and correlated with the habitat use according to the SPEARMAN rank correlation (LORENZ 1988).

7.2   Results

In the research paddock six habitat types were distinguished. Three of them, the open plains, the dense and the open bushland, are in the Titra land system. The sand and dune areas with dense and open vegetation of the Amadeus and Simpson/Singleton land systems were summarized because of their almost identical morphological state, but mainly because of their similarity in plant sociology. The salt marshes are typical for the Amadeus land system. The structure of the individual land system is described in Chapter 2.1.2.
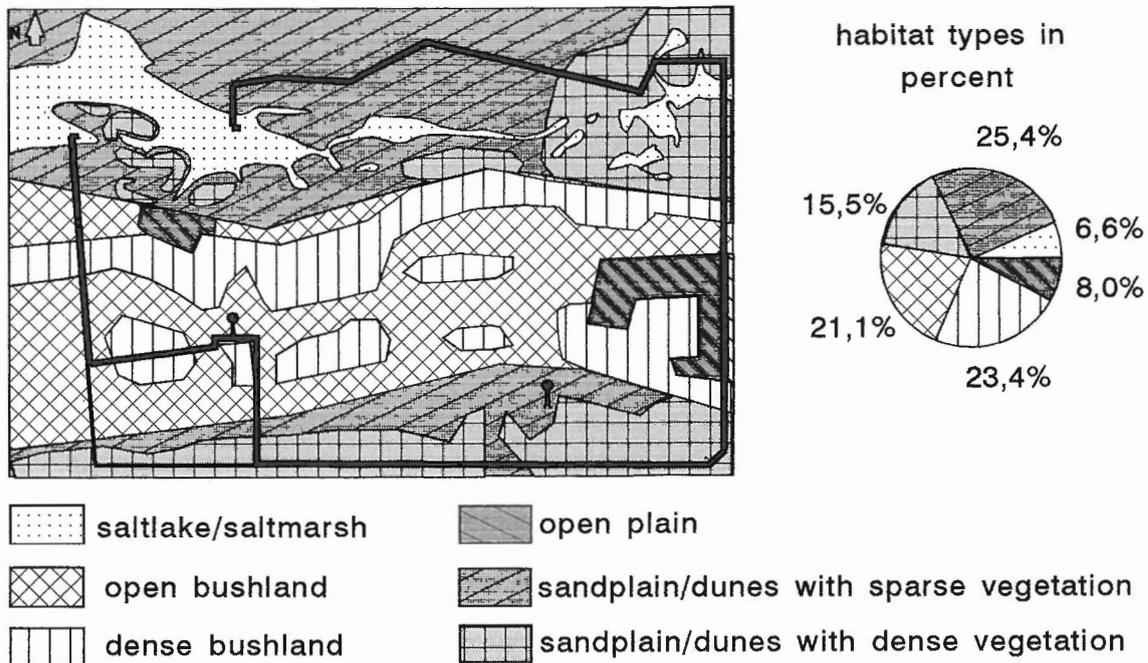
Fig. 28: Habitat distribution in the research paddock

Salt lakes and salt marshes (Fig. 29) take up 6% of the expanse of the research paddock. Woody plants do not grow in this extreme habitat type. Characteristic plants are above all *Halosarcia-*, *Eragrostis-*, *Lawrencia-* and in winter *Swainsona*-species (Fig. A5.12a-c, A6.25-27).

The open bushland (Fig. 30) takes up app. 21% of the area and is covered with woody plants between 5% and 19%. *Acacia-*, *Atalaya-* and *Eucalyptus*-species (Fig. A7.1-5, 8 & 9) are dominant here. The ground vegetation is dominated by species of the genuses *Boerhavia*, *Cleome*, *Helipterum*, *Ptilotus*, *Portulaca*, *Sida*, *Solanum* and *Tribulus* (Fig. A5.3a-c, A6.1-8).

The dense bushland (Fig. 31) takes up about 23% of the area of the research paddock and is covered with woody plants between 20% and 50%. *Acacia-*, *Cassia-*, and *Eucalyptus*-species (Fig. A7.6, 7 & 8) are predominant here. Dominant species of the ground vegetation belong to the genuses *Aristida*, *Boerhavia*, *Enneapogon*, *Indigofera* and *Tribulus* (Fig. A5.1a-c, 2a-c; A6.9).

Sandplains or dunes with open vegetation (Fig. 32) have the largest share of the area with app. 25%. The degree of covering with woody plants is between 3% and 15%. The most common woody plants are *Acacia-*, *Grevillea*, *Eucalyptus*, *Melaleuca-* and *Stylobasium*-species (Fig. A7.14-19 & 22). Dominant species of the ground vegetation belong to the genuses *Eragrostis*, *Halganea*, *Scaevola*, *Sida* and *Triodia* (Fig. A5.7a-c, 10a-c, 11a-c; A6.17-18, 20-21, 23-24).

Sandplains or dunes with dense vegetation (Fig. 33) make up about 16% of the total expanse of the research paddock. They are covered with woody plants between 20% and 40%. *Acacia-*, *Codonocarpus-*, *Eremophila-*, *Eucalyptus-*, *Melaleuca-* and *Stylobasium*-species (Fig. A7.13, 20, 21, 23-25) are prevalent here. The ground vegetation is mainly formed by species of the genuses *Aristida*, *Halganea*, *Indigofera*, *Scaevola*, *Solanum* and *Tephrosia*, but above all *Triodia* (Fig. A5.8a-c, 9a-c; A6.16, 19 & 22).

Open plains (Fig. 34) take up 8% of the area, the proportion of woody plants is between 0 and 3%. Gramineae and forbs of the genuses *Helipterum*, *Indigofera*, *Ptilotus*, *Tribulus* and *Zygophyllum* (Fig. A5.4a-c to 6a-c; A6.11-15) are dominant.

Fig. 29: Example of a salt marsh with *Halosarcia halocnemoides*

Fig. 30: Example of an open bushland with *Eucalyptus papuana, Atalaya hemiglauca* and *Acacia*-species in the background

Fig. 31: Example of a dense bushland with prevalent *Acacia*-species

Fig. 32: Example of a sand area with open vegetation with *Allocasuarina decaisneana*, *Grevillea striata* and *Triodia basedowii*.
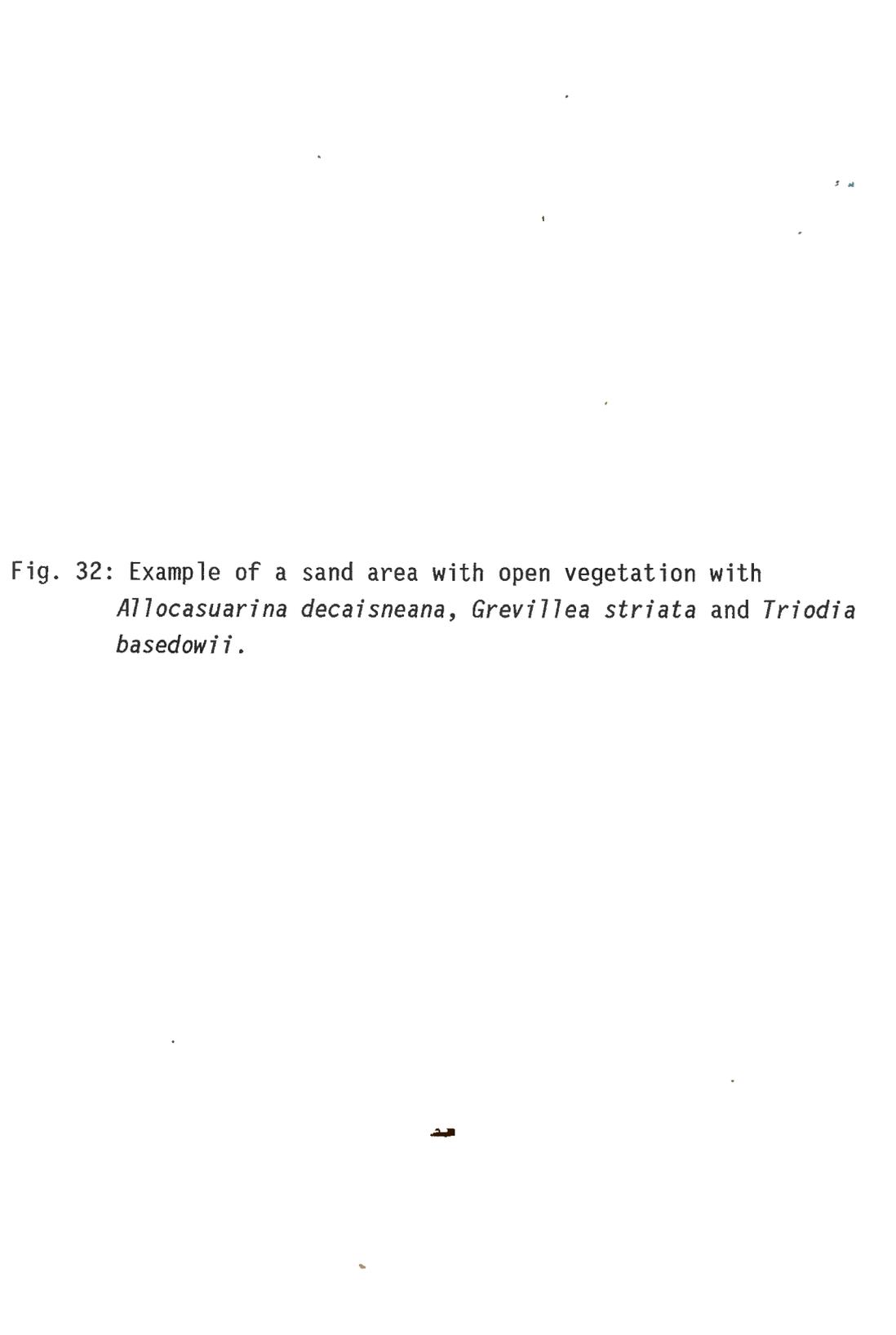
Fig. 33: Example of a sand area with dense vegetation with *Acacia-*, *Codonocarpus-* and *Grevillea*-species

Fig. 34: Example of an open area dominated by Gramineae.

The dromedaries used all habitats but with a very different distribution depending on the season. Fig. 35 shows the general habitat utilization pattern of the animals for winter and summer.
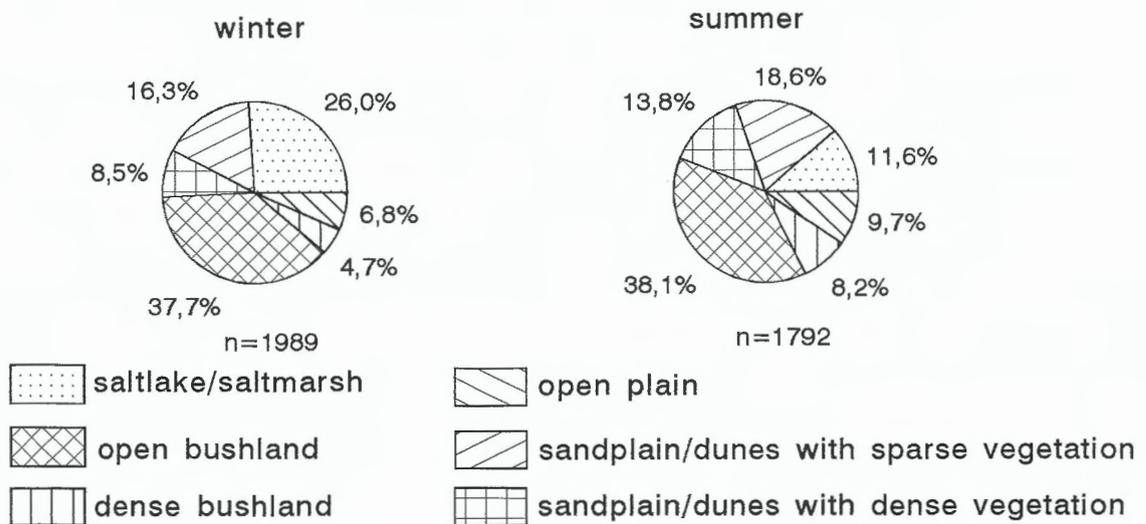
Fig. 35: Seasonal habitat use in the research paddock

The sizes of the individual habitats in the research paddock strongly differ (Fig. 28). The salt marshes as the smallest unit take up only 6.6%, while the sandplain/dunes with open vegetation form 25.4% of the total area. For the standardized evaluation of the habitat use the number of all sightings per habitat was converted to areas of equal size and they were presented proportionally to each other.

The individual monthly evaluations are to be found in the Appendix in Fig. A10.1-3.

To check a possible dependency of the habitat use on the diversity of the habitat specific vegetation, the seasonally calculated diversity indices of the individual habitats were correlated with the respective habitat use according to SPEARMAN (LORENZ 1988). A comparison of the seasonal habitat use with the indices for the general diversity of the vegetation specific to the habitat according to SHANNON is shown in Table 7:

Table 7: Seasonal habitat use (N) in relation to the diversity of the habitat type (H'= Shannon Index)

Habitat	SUMMER		WINTER	
	N (%)	H'	N (%)	H'
bushland open	38,1	3,4	37,7	3,13
bushland dense	8,2	3,07	4,7	3,21
sandpl/dunes open	18,6	3,25	16,3	3,12
sandpl/dunes dense	13,8	3,32	8,5	2,93
open plains	9,7	2,48	6,8	3,14
saltmarsh	11,6	2,02	26,0	2,15

All calculated indices (for richness according to MARGALEF (1958) and MENHINICK (1964), for diversity according to HILL (1973), SIMPSON (1949), and SHANNON and WEAVER (1949), and for evenness according to PIELOU (1975), SHELDON (1969), HEIP (1974), HILL (1973), and ALATALO (1981)) are listed in the Appendix for the individual vegetation analyses and for the summarized habitat specific vegetation analyses in Tables AT4.1-4. All calculated correlations are not significant (Table AT5). A dependency of the habitat use of the dromedaries on the diversity of the habitat could not be identified. This result becomes understandable owing to the food selectivity of the dromedaries (Chapter 5).

Some characteristic examples of the monthly categorized distributions demonstrate the high variability of the habitat preferences (Fig. 36).
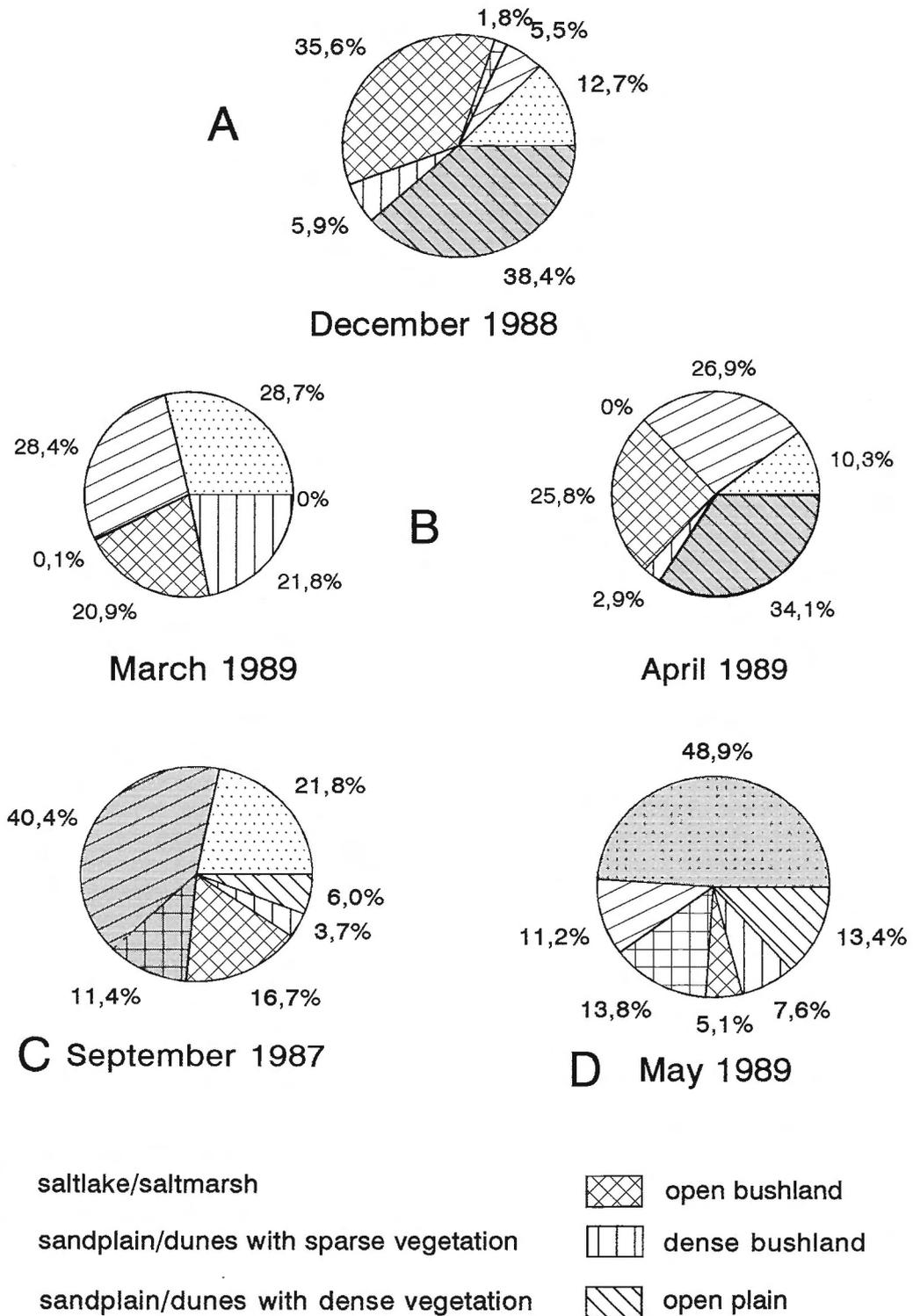
Fig. 36: Characteristic examples of the habitat use; habitats that are preferred because of the food selectivity of the dromedaries are highlighted in grey.

Due to the heavy summer rainfalls of a total of 168mm in the months of October to December 1988 a variety of grasses and forbs developed in the open plains. This attractive food supply was used here by the dromedaries (Fig. A2.37 & 38). In December 1988 the animals stayed in the open plains at nearly 40% of the time. For resting they moved into the open bushland with large shady trees. During this month all other habitats hardly had any significance (Fig. 36 A).

In the following summer months the situation changed:
In January and February of 1989 there were only 4mm of precipitation. Consequently the use of open areas decreased extremely down to zero in March. At the same time the use of the dense vegetation units continuously increased, from 6% in December to 22% in March. The torrential rains of 181mm within two days at the end of March crucially changed the habitat preferences in April. The use of the dense bushland went down to 3%, while the animals stayed in the open plains at 34% (Fig. 36 B).

In September of 1987 sandplains with dense and open vegetation were used by the animals at 52%. This preference had its reason in the development of *Calandrinia balonensis*, a Portulacaceae the dromedaries particularly liked to eat (Fig. A2.41; A3.42) and that only grows in sand areas (Fig. 36 C).

In May of 1989 salt lakes and salt marshes were used at almost 50% because *Swainsona*- and *Zygophyllum*-species were growing there (Fig. 36 D).

A general group specific preference of certain habitats could not be found. However, the dense vegetation units, in the bushland as well as in the sand areas, provide good hiding places from potential enemies for individual animals. In 67% of all observations of mothers with newborns or with calves the age of up to three weeks they were in habitats with dense vegetation.

7.3 Discussion

The open bushland is preferred all year round by the dromedaries in contrast to all other habitats. This habitat type provides a rich and varied food supply regardless of the season. The open bush and tree vegetation ensures a good openness of the surrounding area. In addition there are bigger shady trees, under which the animals rest in summer.

The dromedaries relatively seldom stay in the dense bushland. Although this habitat type also offers a rich food supply, mainly leaves of shrubs and trees, the proportion of which after all is 53% of the total amount of food, the animals do not prefer it. This is probably due to the insufficient openness of the area. Potential predators, although they do not exist in Australia, could stalk unnoticed in this habitat. It was never observed that groups stayed overnight in the dense bushland. However, this habitat type is attractive for single animals because of the hiding places, above all for mothers with very young calves.

The increase in use of the denser vegetation units in summer can be due to microclimatic differences. In the denser vegetation zones the humidity lasted longer because of reduced evaporation by wind and temperature. For a long time after rainfalls the ground vegetation here was still clearly more green than in the open areas. A similar tendency can be seen with the use of the sand areas with dense vegetation which was also more frequent in summer.

The sandplains and sand dunes with open as well as with dense vegetation also offer a rich food supply for the dromedaries with their shrub and tree vegetation, above all the succulent plants. Because of the soft sandy soil these two habitats are particularly attractive as resting places and places to sleep. In the evening hours groups often move from other habitats to the sand areas to stay there overnight. In summer the widely sweeping tops of the desert oaks offer ideal resting places in the shade even for large groups at the hottest time of the day. High sand dunes are especially popular since on the one hand they allow a good overview and on the other hand in summer they provide the dromedaries with additional cooling because of the wind exposure.

The biggest seasonal fluctuations were found for the salt lakes and salt marshes. With 26% this habitat type is the second most frequented in the winter months. This strong frequenting of the salt lake in winter is due to the presence of *Swainsona*-species (Chapter 5). In summer the dromedaries avoid the salt marshes during the hot time of day. Apart from the intensive direct sun radiation, extreme heat occurs here due to strong reflection. Furthermore the food supply of the salt marshes is clearly lower in summer than in winter.

The dromedaries relatively seldom stayed in open plains. But after rainfalls these areas for a short time become the habitat type used the most because of the readily available food supply of forbs and grasses. In the open plains the ground vegetation mostly develops faster than in the other habitats, but because of the stronger exposition to wind and sun it withers up faster, too.

The habitat selection of the dromedaries does not depend on the diversity of the vegetation (Table 7, AT5). It is primarily determined by the seasonally preferred food plants whose attractiveness does not become clear via the different diversity indices, though. Besides, nearly all preferred food plants are mostly abundant in several habitat types at the same time and are picked specifically by the dromedaries. The potentially available habitat specific spectrum which also includes plant species which are never or only rarely fed upon, is obviously not relevant.

In addition, the openness and condition of the area is important. The habitat selection of the dromedaries can therefore rather be classified in a functional context, in which the habitats with the freshest or widest supply of preferred food plants are chosen. Habitats with soft grounds and with big shady trees are preferred for resting, particularly during the day in summer. Before the birth of a calf and within the first weeks with the calf dromedary females prefer habitats with dense vegetation (DÖRGES 1995), which offer sufficient hiding places compared to the more open areas.

8.   RANGE UTILIZATION PATTERNS

Dromedaries live in groups. They are not territorial and therefore do not monopolize any particular areas (DÖRGES 1995). The flexibility regarding the range and their high mobility enable the animals to move long distances in a short time. Satellite-telemetric studies showed that individual groups move up to 70km per day (GRIGG 1987; CISC 1993). However, so far nothing was known about the seasonal range utilization patterns of free-ranging dromedaries.

8.1   Methods

A detailed map of the area was a prerequisite for a systematic recording of the changes of location of the dromedaries in the research paddock. At the beginning of the studies it was drawn up with rectified aerial photographs and divided up into 1km^2 grids. Each group had one mapsheet per month on which each sighting was recorded. The data acquisition was done by visiting the individual groups several times a day. When doing continuous observations all changes of places were recorded. On top of that more data regarding this topic were acquired by telemetric tracking and analyses of tracks.

Supplementary parallel studies at the edge of the Simpson desert with animals equipped with transmitters were evaluated for extensive migration activities.

8.2   Results

Although the dromedaries are not territorial, a clear avoidance of the individual groups among each other can be seen which is differently distinct depending on the season. In the research paddock the following differences in the range utilization could be determined:

In the summer months, outside of the rutting season, the various groups often used home ranges for weeks which were sometimes smaller than 20km^2. From these grazing areas they regularly went to the trough, moving up to 15km and passing through areas where other groups stayed. After a short rest at the watering place they returned directly to the same area.
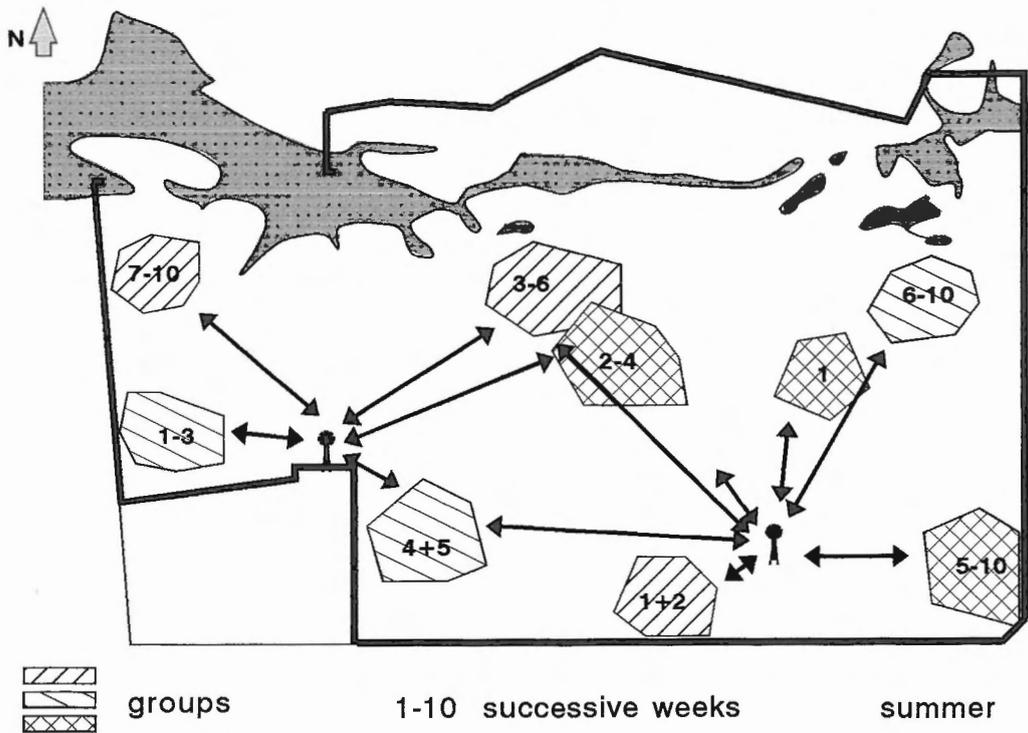
Fig. 37: General range utilization pattern of the dromedaries in
        summer

From time to time, without discernible external reason, the groups
changed their short-term home ranges and moved to another area to stay
there for some weeks. The individual groups mostly had home ranges far
apart from each other, but sometimes they overlapped. Sometimes in
summer two or more groups would join together for a short period of
time.

During the winter months, in the rutting season, there was a
completely different pattern. The groups showed a clear restlessness:
especially the males roved around the area in irregular patterns in
search for females. As soon as they encountered groups of females with
a male they initiated intensive migrating activities. While the stay
in the individual home ranges lasted several weeks in summer, the
stays are mostly short-term in the winter months due to permanent
disturbances of the groups among each other. This way the entire
available area (213km^2) was used by all groups, and they attempted
more clearly than in summer to keep their distance. Isolated groups
that were not disturbed by other dromedaries stayed in the same range
for weeks.
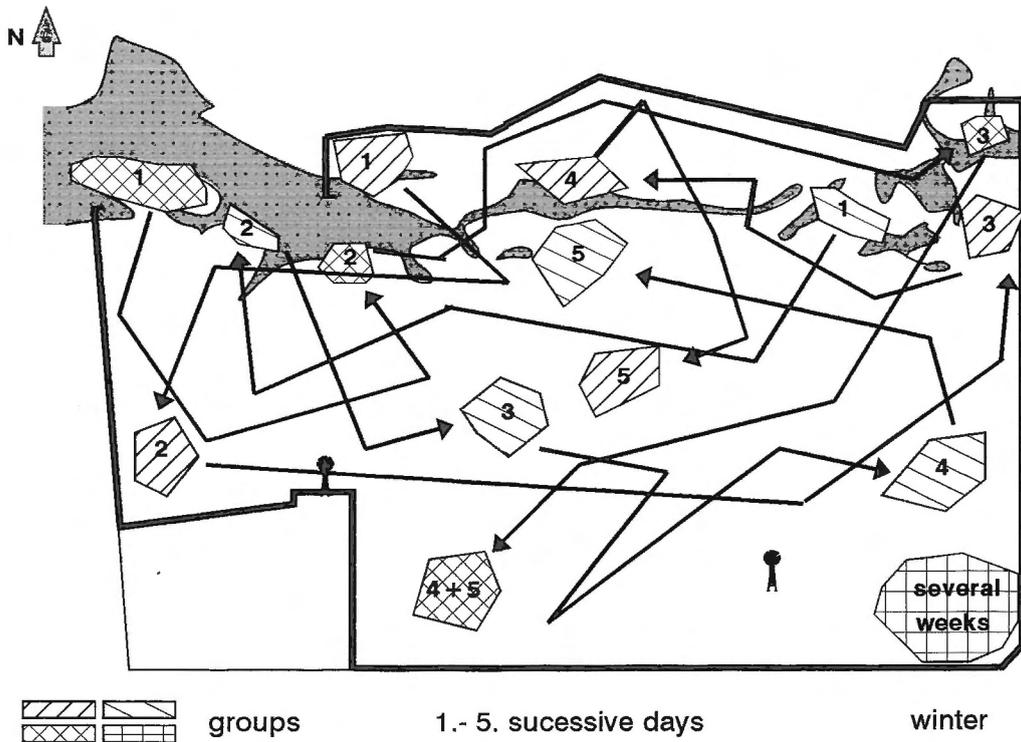
Fig. 38: General range utilization pattern of the dromedaries in
        winter

These movements throughout the research paddock were restricted by the fence. Observations outside the research paddock and at the edge of the Simpson desert confirm the general pattern.

The range utilization pattern for winter and summer was established with the monthly analyzed data for each group, some of which are shown exemplary in the Appendix (Fig. A11.1-18). In order to clarify the seasonally different range utilization the factors that trigger the migrations of individual groups at the respective point in time are described in detail with five original examples:

During one month in summer, one group of bachelors stayed in an only $10km^2$ home range. The structure of this area is marked by sand dunes, sand plains and salt marshes. The rich food supply of *Calandrinia-*, *Sclerolaena-*, *Acacia-* and *Grevillea*-species and large shady desert oaks (*Allocasuarina decaisneana*) were ideal for the animals in this season. From here they regularly wandered to the trough and always returned almost without a detour (Fig. 39).
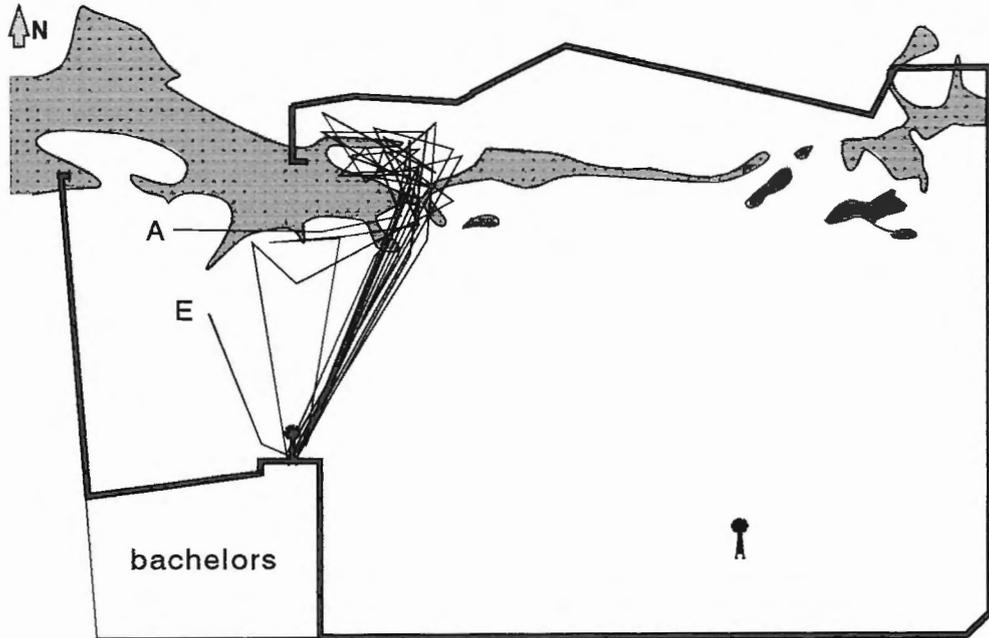
15.11. - 15.12.88

Fig. 39: Range utilization of a group of bachelors in summer

During the winter months the same bachelors had a completely different migration pattern.
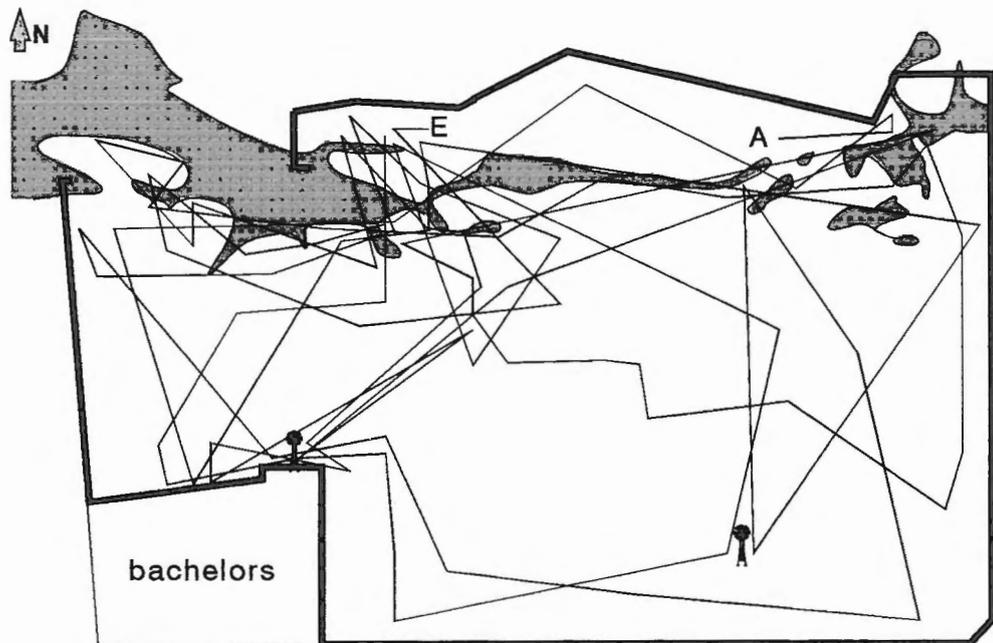
03.08. - 24.08.88

Fig. 40: Range utilization of a group of bachelors in winter

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They now roamed about the entire area restlessly, always looking for females. As soon as they encountered a group of females with a herding male their migration activities increased, either because the group holder chased away the rivals vehemently and extensively or, with a weaker male, because the bachelors permanently followed the group. The regular stay along the salt lakes is typical, since at this time of the year the salt marshes provide an attractive food supply.

The seasonal differences in the range utilization of a particular group of females (here N22) are shown in Figures 41 and 42.

18.12.88 - 14.01.89
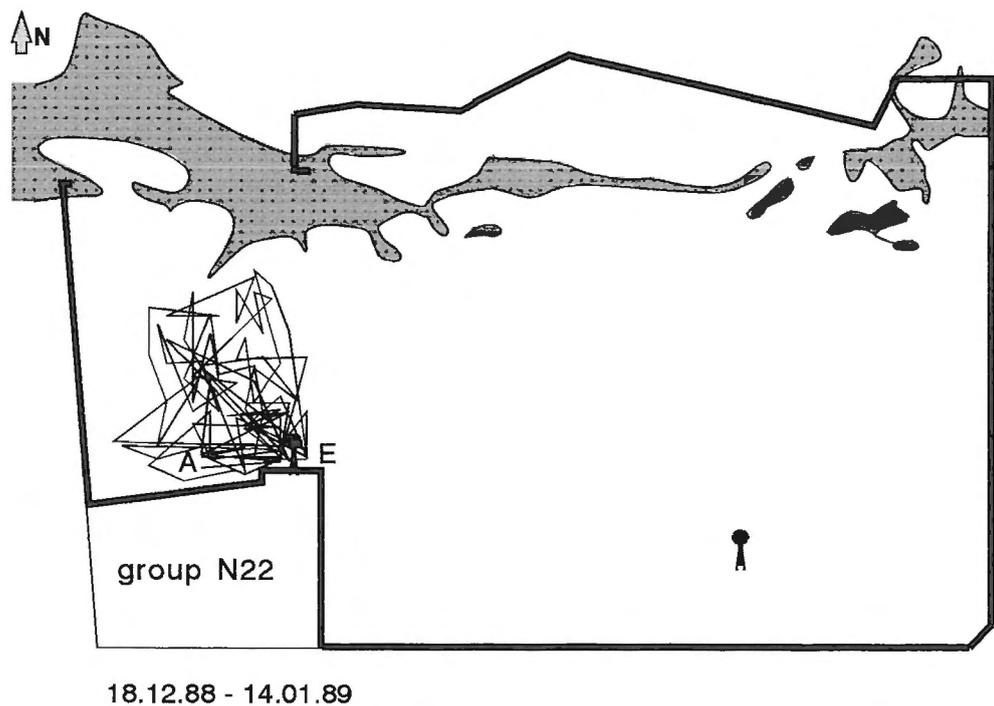
Fig. 41: Range utilization of the group N22 in summer

In summer, the group used a home range in the area of the trough for several weeks which was smaller than 20km^2. The animals only stayed in the open to dense bushland which provided a rich food supply - particularly in the depressions - because of the rainfalls in November/December. Scattered large *Eucalyptus*- and *Atalaya*-trees gave plenty of shade during the daily resting phases. The animals regularly went to the nearby trough.

group N22

11.07. - 29.07.88
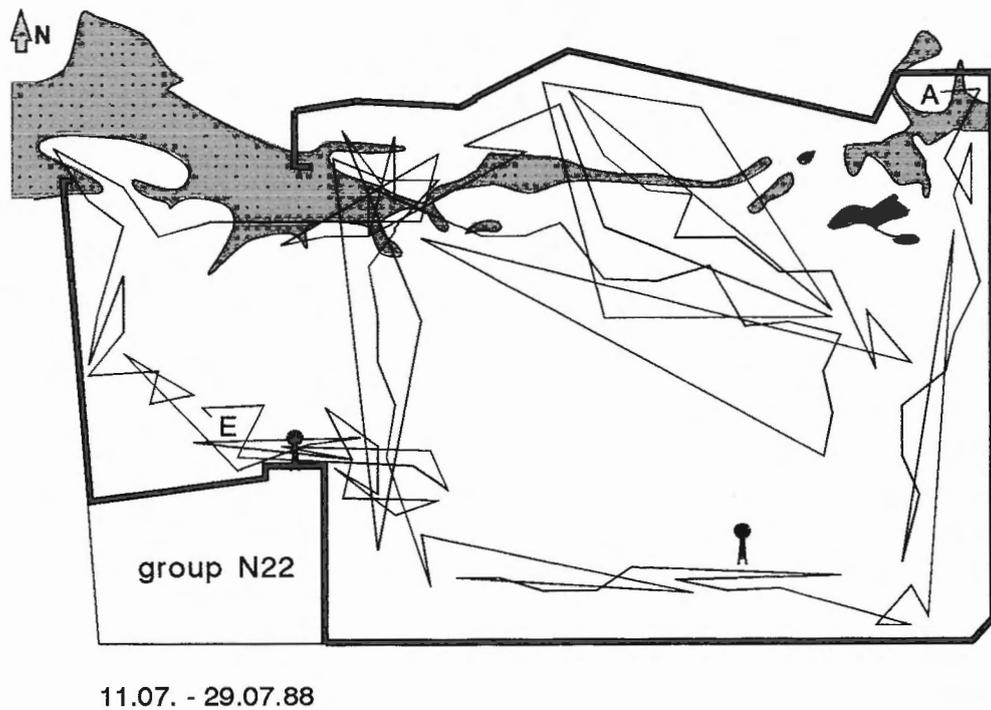
Fig. 42: Range utilization of the group N22 in winter

In winter, the group N22 had contact with conspecifics at least ten times, particularly with bachelors, within the described period of time of 19 days. These initiated intensive migrating activities that extended across the entire research paddock.

According to the observations the restlessness in winter can only be explained by the frequent interactions of individual groups among each other. Groups that had no contact with others, remained in a relatively small range for weeks, even during the main reproduction time. Group Nk5 is a very good example for this explanation. For five weeks it stayed in a home range of about 15km^2 in the sandplain/dunes. Here the animals mainly used fruits of *Triodia basedowii*, but also *Acacia ligulata*, that was blooming at this time. On July 17, 1989, the group was tracked down by 16 bachelors and chased for days because of the relative weakness of the group holder. The strongest male among the bachelors took over the group of females that eventually returned to the original range after seven days.

— A-E$_1$ 12.06.-17.07.89 undisturbed
— — E$_1$- E$_2$ 17.07.-24.07.89
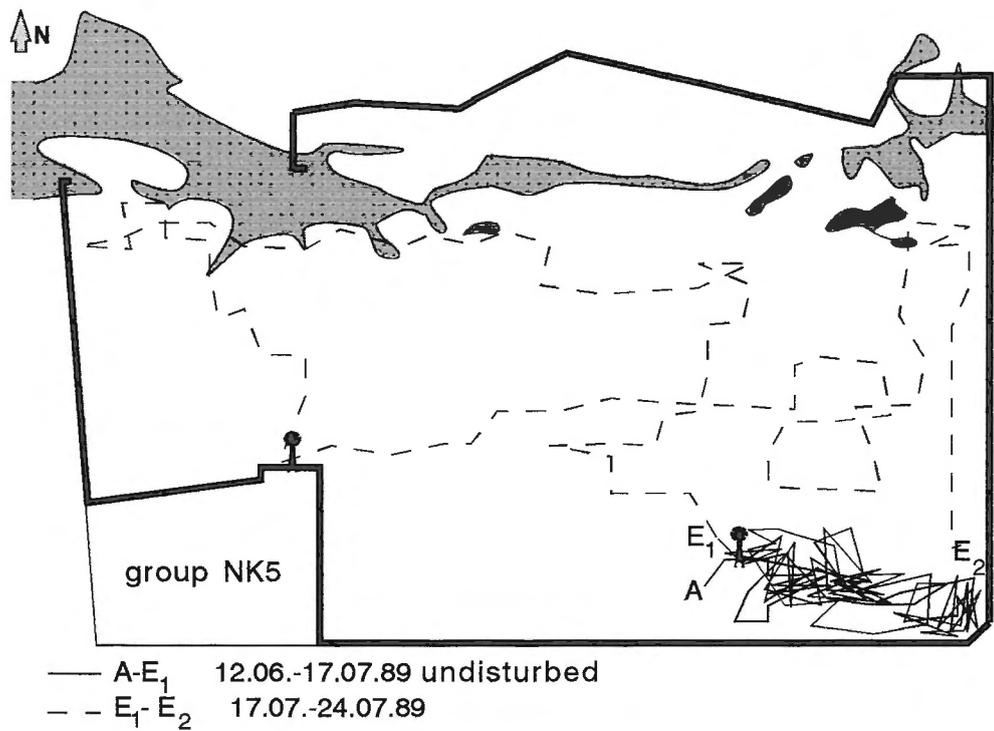
Fig. 43: Range utilization of the group NK5 in winter

By contrast an undisturbed group had a closed range of about 35km^2 at the main reproduction time in winter (Fig. 44).

08.08. - 08.09.87
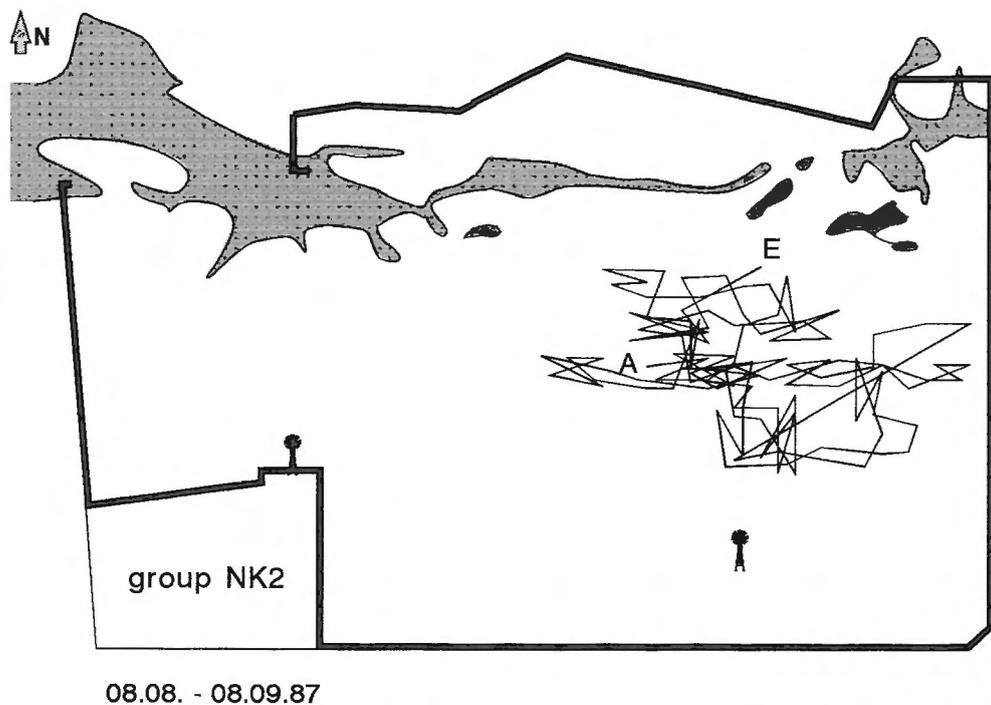
Fig. 44: Range utilization of an undisturbed group (Nk2) in winter

The additional observations regarding the range utilization patterns of the dromedaries on the stations at the edge of the Simpson desert showed small home ranges as well as extensive migration activities. Some marked animals that were found again indicated the repeated use of certain ranges:

One dromedary female fitted with a collar in September 1984 on the Allambi station at the edge of the Simpson desert was shot in May 1986 by the station owner, almost at the same place where she was marked. In the meantime the animal had not been seen in the regularly and very thoroughly checked areas.

One male who as a calf had been marked with an ear tag by the same station owner in the spring of 1978, only stayed some kilometers away from the place where he had been marked in September 1986. This animal, too, had not been seen by the station owner in the meantime (SMITH, pers. comm.).

One female, that had been fitted with a collar in August 1986 on the station Horseshoe Bend, was found dead in November 1988 75km away from the place where she had been marked.

Of the three females that had each been marked with a radio transmitter in August and September 1986 on the stations Allambi and Horseshoe Bend, the location of two animals could after all be determined telemetrically over one month and six months, respectively. The third female was not found despite an intensive search.

The first female was marked on September 9, 1986. On September 21, 1986, she was about 5km away from the place where she had been marked and on October 11 and 12, 1986, she was located for the last time 25km southeast of the area where she was caught in the direction of the Simpson desert.

The second female was marked on August 24, 1986, and on the following day set free in a 60km^2 paddock, the doors of which were opened. On October 9 and 10, 1986, this animal was still or again in the paddock. On November 20, 1986, it was located outside the paddock 20km north-west of the place where it was marked. On February 23, 1987, this female was seen for the last time in the paddock.

Even though in the following months until the middle of 1988 all marked animals were regularly searched for extensively, none could be found again.

8.3   Discussion

Dromedaries are opportunists with regard to their range utilization; they use the habitats that are most favorable for them concerning structure and food supply. As excellently adapted desert dwellers they are not territorial, they have no investment in particular places and, because of their high mobility, they are always able to move to other areas without any loss of investment should the conditions change for the worse.

The seasonal range utilization pattern of the dromedaries mainly depends on social factors. Above all during the rutting season interactions are considerably more frequent, triggered by the hormonally caused restlessness of the males. Because of the low tolerance of rutting males among each other, the resulting avoidance or chasing away leads to a real chain reaction in the migration pattern of individual groups. These mechanisms were naturally the most obvious in the comparatively small research paddock, since interactions occurred more often because of the relatively high density of the animals. As soon as different groups encountered each other in winter serious changes of the home ranges took place. Often both groups would even practically burst away in opposite directions and run away from each other for kilometers. By contrast groups that were not tracked down by other dromedaries had a range utilization pattern like in summer with relatively small long-term home ranges.

Observations outside the research paddock indicate that the seasonal range utilization patterns are universally applicable. For example 68% of all direct observations of dromedaries on the station Newhaven outside the research paddock were done in the winter months. Further analyses of tracks and the experience of the station owners based on many years of observations correspond to the results regarding range utilization that have been established in the research paddock.

The annual home ranges of the dromedaries outside the research paddock are estimated at several thousand to 10.000km^2. They depend on the respective ecological situation.

Satellite-telemetric studies with two dromedary females proved extensive migration activities. Both females, whose local movements

could be followed in the years 1986 and 1987 for almost 12 months, used annual home ranges of at least 7.800 and 7.200km^2, respectively (GRIGG 1987). Preliminary data of six more dromedaries that were fitted with satellite transmitters in 1993 by the Conservation Commission of the Northern Territory confirmed the order of magnitude. For these animals migration distances of up to 170km within one week were determined (COPPOCK, pers. comm.).

Observations at the edge of the Simpson desert showed seasonal migration patterns of the camel population there. In winter 20-30 groups of camels regularly stayed on the station Allambi and they disappeared without trace with the beginning of the summer. Obviously the animals had moved to the more central regions of the Simpson desert, where a rich ground vegetation, mainly the succulent *Calandrinia*-species, develops due to the summer rains. Because of dwindling food resources due to the nearly dry winter months the animals leave the Simpson desert at the beginning of the winter and return to areas with cattle farming which provide more food. The precipitation in the peripheral areas of the Simpson desert is around 200mm p.a. (e.g. Finke station with 195mm). In contrast to that there are only 70mm p.a. in the central Simpson (GIBSON & COLE 1988). These observations were confirmed by the owner of Allambi, too, who on regular checking flights in summer found almost no dromedaries on his station (SMITH, pers. comm.).

According to the observations the water that is available in cattle troughs on the stations during the winter months is only of secondary importance for the dromedaries (Chapter 6). It is assumed that a relative restlessness and the intensive hunting on the adjacent stations is the reason for the seasonal migration activities of the dromedaries in the region of the Simpson desert. The animals can avoid this pressure because of the more favorable food supply in summer by moving to the Simpson desert.

9. ACTIVITY PATTERN

Dromedaries are mainly diurnal, but can also make use of the night depending on the environmental conditions. The general activity pattern is controlled by various factors, external factors like daylight and air temperature having a crucial effect besides the hormonal situation of the animals.

In this chapter only the ecologically relevant activities are taken into account. Lying and standing describe inactive, walking and feeding describe active patterns. More detailed categorizations and specific characteristics and individual activities are described in DÖRGES (1995).

9.1 Methods

At each sighting the individual and general activity of the dromedaries was recorded, considering external factors like time of the day, intensity of the light and air temperature.
In monthly intervals continuous observations were done with several groups over a period of 24-48h according to the interval method by ALTMANN (1974), and/or continuously to determine individual time-budgets.
The listing of the general seasonal activity patterns was performed by an hourly summary of all relevant data regarding the activity in the summer and winter months. The transition months April and September were not considered. The examples of the activity patterns in relation to the air temperature are taken from the respective continuous observations.

9.2 Results

The activity rhythm of the dromedaries is subject to strong seasonal fluctuations. A general pattern can nevertheless be described: at sunrise the activity phase begins. Depending on the air temperature it is interrupted by differently long resting phases around midday and continues on until early or late in the evening. At night the animals mainly rest. A correlation of the night activity to the lighting conditions could not be found.

In the summer months October to March the morning activity phase
generally already begins before sunrise between 05:00 and 06:00h.
Depending on the air temperature the animals stay active into the late
morning while they are mainly busy feeding. After the daily resting
phase the afternoon activity phase is continued until late in the
evening.

winter   n = 51132
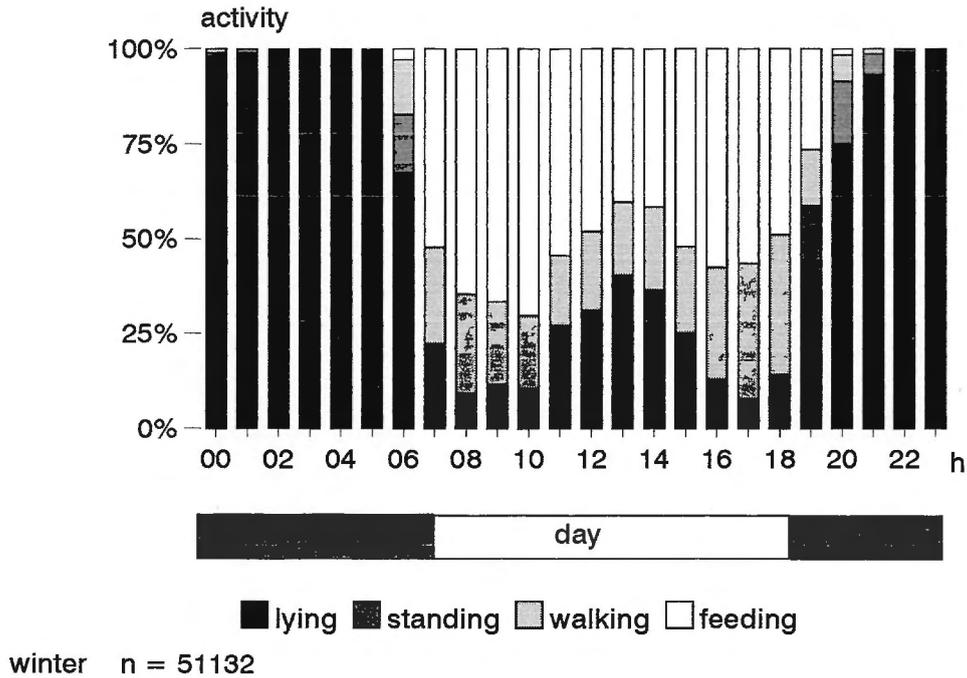
Fig. 45: General activity pattern in summer

summer   n = 68139
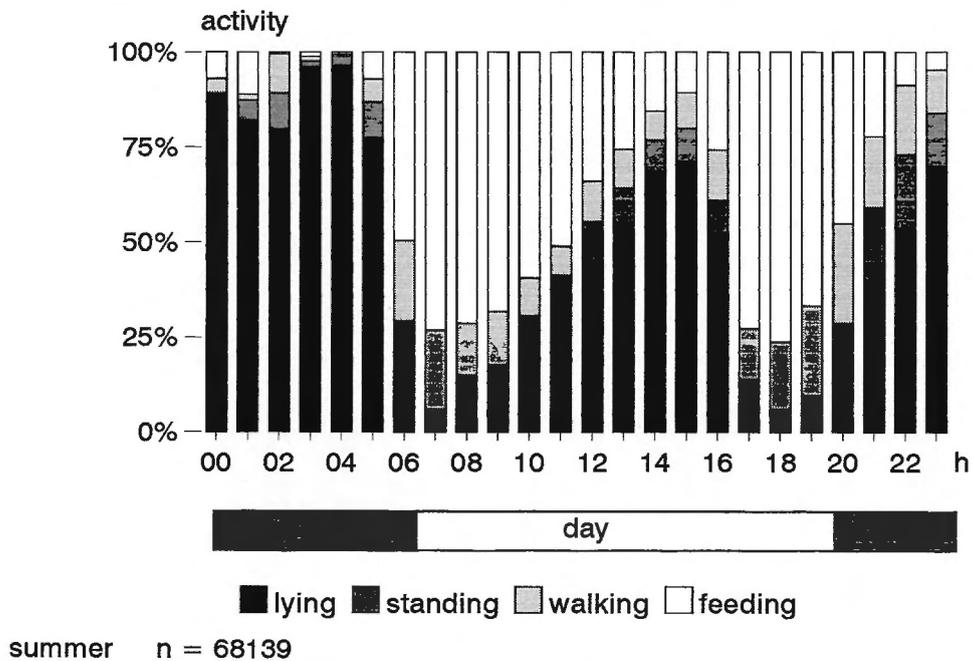
Fig. 46: General activity pattern in winter

During the winter months May to August the pattern changes: the activity phase only begins after sunrise and continues over the entire day, interrupted only by short resting phases. The animals already become inactive relatively early in the evening and in contrast to the summer months they rest nearly exclusively at night. The increased walking activity in the winter months is due to the general restlessness of the animals during this season (Chapter 8).

Temperature dependent variations were observed which differed from the seasonal basic patterns. They are shown in Figures 47 and 48 as examples for a cold and a hot summer day:
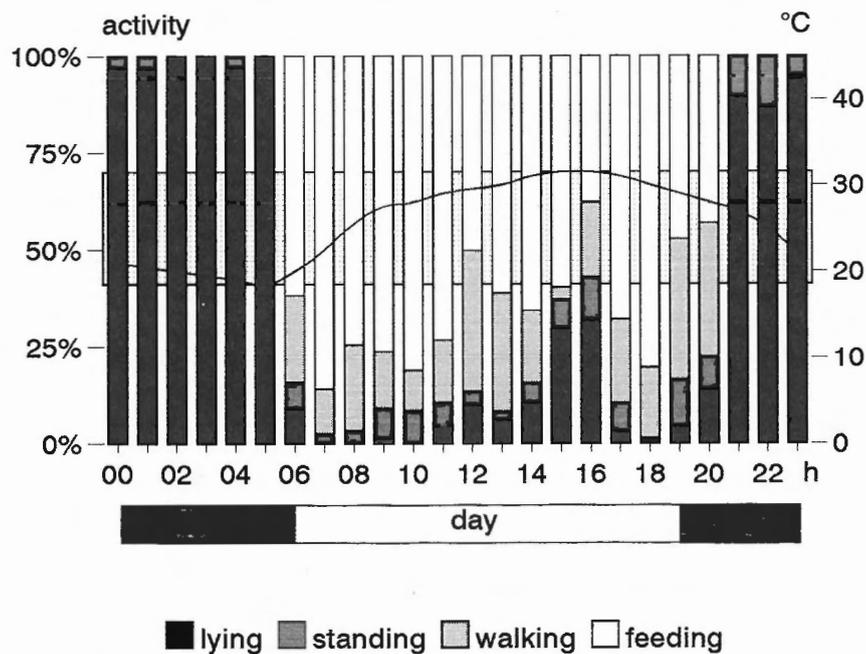
Fig. 47: Example of the activity pattern for a cool summer day

On cooler summer days the dromedaries show an activity pattern which is comparable with that in winter. They are active nearly all day and they only rest for a short time or less often during the day. The night resting phase begins relatively early compared with the general activity pattern of the summer. However, compared with the winter it begins clearly later.

On hot summer days the animals are inactive between 11:00 and 16:00h. They lie or stand in the shade, and only from 16:00h on they show signs of activity. In contrast to cooler summer days they are then much longer active in the evening (Fig. 48).
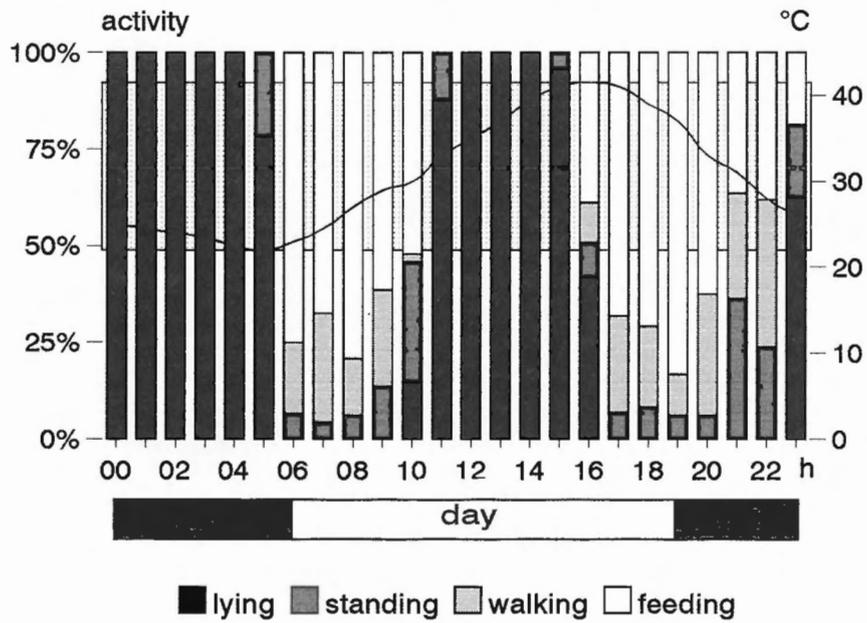
Fig. 48: Example of the activity pattern for a hot summer day

Comparable variations were observed for a cooler and a warmer winter day (Fig. 49 and 50).
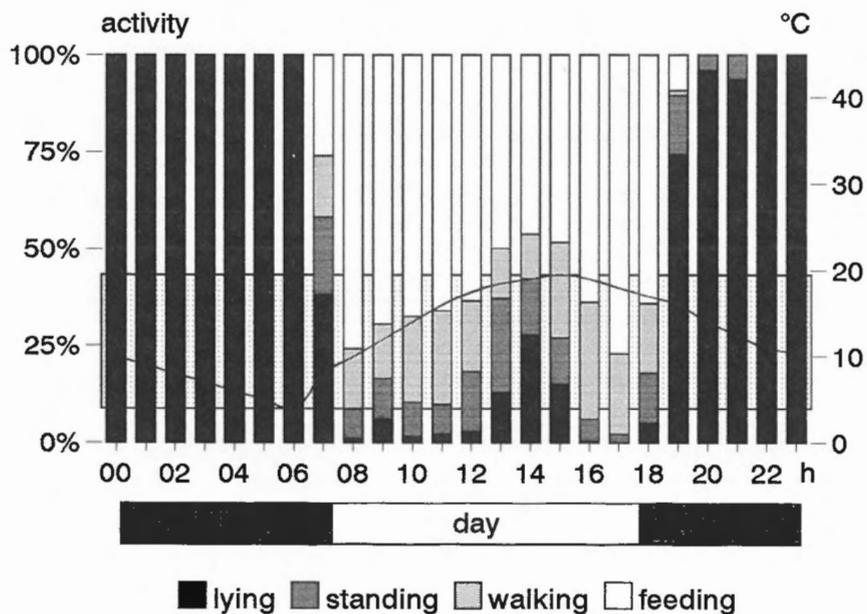
Fig. 49: Example of the activity pattern for a cool winter day

Despite the low air temperature a short resting phase could be observed at noon. In contrast to the observations in summer the animals are now lying in the sun.

Although the air temperature of the warm winter day is in the range of the air temperature of a cool summer day, the dromedaries show a clearly different activity pattern. On a warm winter day they follow the pattern which is characteristic for the summer, with long resting phases around noon that are extended until the afternoon. Only the early night resting phase indicates that these are winter activities.
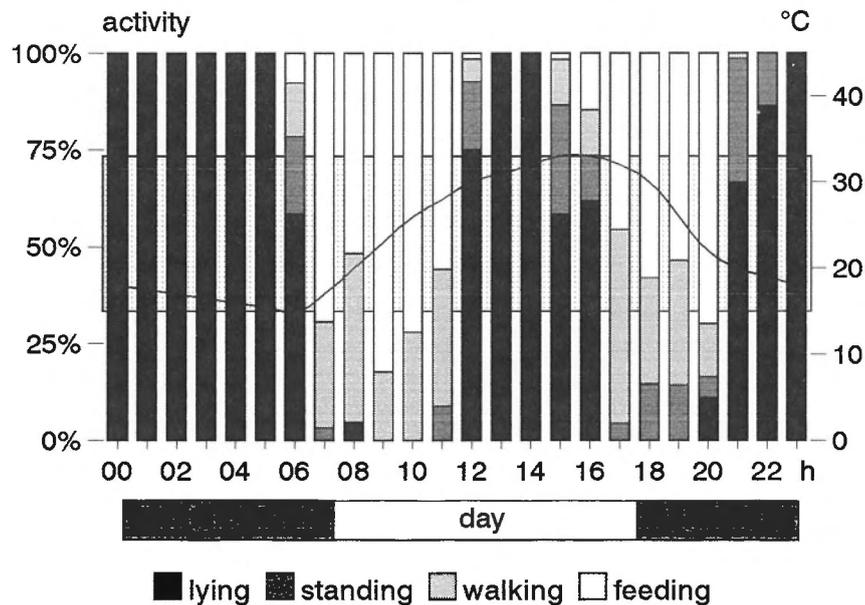
Fig. 50: Example of the activity pattern for a warm winter day

The exemplary chosen Figures A12.1-12 in the Appendix show an overview of the activity patterns from the monthly time-budgets in relation to the air temperature. Here, too, an adaptation of the activity pattern to the respective conditions can be seen. It cannot be left out of consideration that apart from the air temperature other factors like social components are important which were not considered in this study. For the individual activity patterns and analyses see DÖRGES (1995).

Within the studied period of time the daily feeding time lasted between 5½ and 9 hours. It is dependent on the quality and quantity of the food supply. In times of a rich food supply the feeding times are significantly shorter. This connection becomes particularly obvious in the following examples: In the very dry winter of 1987 there was only extremely little food available in the horse paddock because of the high population density of the dromedaries, while in the adjacent

research paddock there was plenty of food. The animals in the horse paddock had to expend 9 hours a day for eating, whereas the ones in the research paddock only needed 6½ hours and consequently could allow significantly longer resting phases for themselves. In Fig. 51 the activity patterns between 07:00 and 19:00h of each six females in the horse paddock and in the research paddock are shown for the months of August and September 1987.
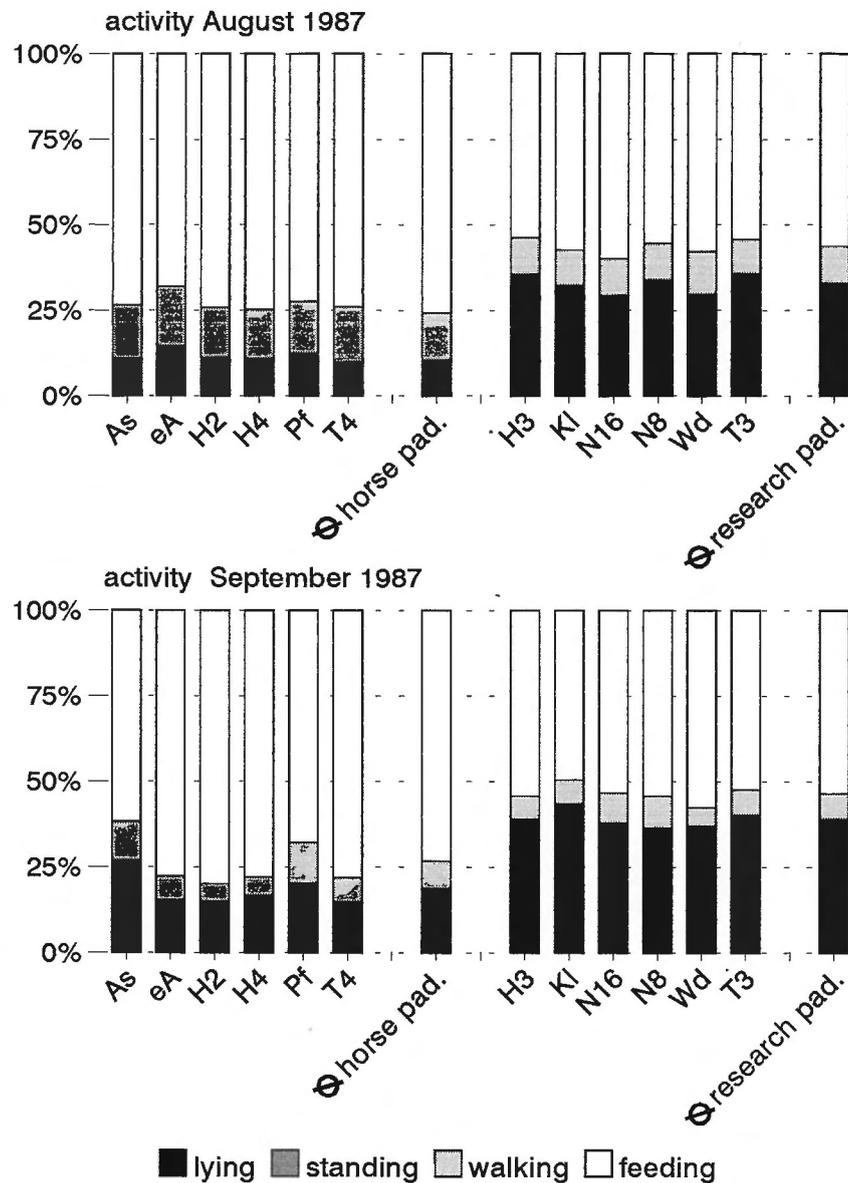
Fig. 51: Day activity pattern of six females in the horse paddock and six females in the research paddock for the months of August and September 1987

In May 1988 the vegetation in the horse paddock had recovered due to the extremely heavy rains in March. At the same time the density of dromedaries had decreased from 2.0 to 0.4, since most of the population could already be dismissed into the research paddock. Horse paddock and research paddock at this time corresponded with each other regarding food supply and density of dromedaries. A comparison of the day activity pattern of each five females in the horse paddock and in the research paddock showed similar patterns with daily eating times of app. six hours for both test groups (Fig. 52).
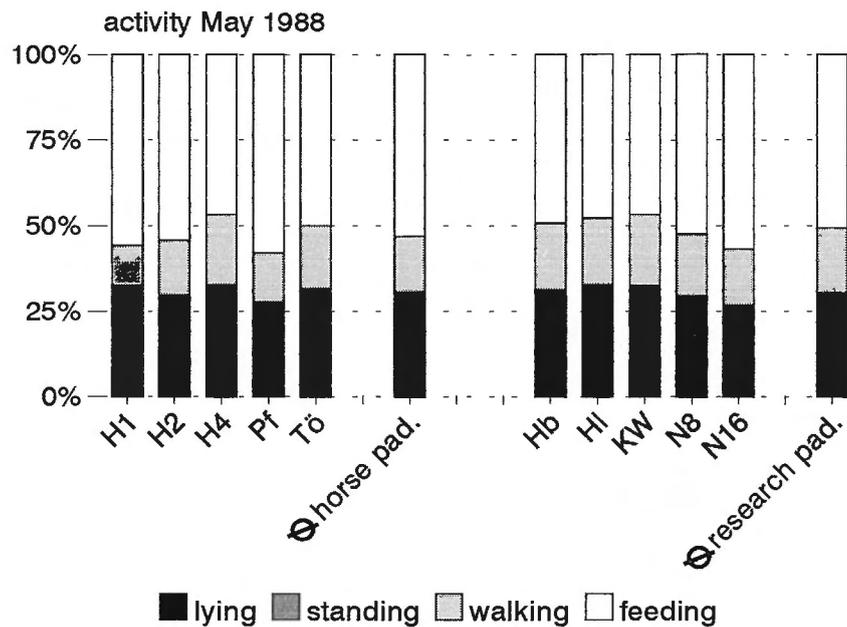
Fig. 52: Day activity pattern of five females in the horse paddock and in the research paddock in May 1988

9.3   Discussion

The activity patterns of the dromedaries are very variable but mainly show temperature-dependent distributions. It is conspicuous that the seasonal patterns on warm days in winter and hot days in summer are very similar and those on cold days in winter and on cool days in summer. A significant adaptation of the activity pattern to the relevant conditions can be determined. However, the absolute value of the air temperature is not the decisive factor but the relation of the air temperatures of successive days to each other.

Therefore, no typical summer or winter pattern of activity can be assumed but an activity pattern which is adapted to the respective situation. Since in winter there are more cool and in summer there are more hot days the seasonal basic pattern shown in Figures 45 and 46 develops.

Accordingly the animals in winter generally lie longer at night than in summer, while in summer they rest more during the day and are consequently active longer in the evening. In winter they almost exclusively rest at night, while the night in summer is used for feeding and walking, too. While the intensity of the night activity depends on the day temperatures which last for longer periods of time, it is almost independent from lighting conditions. Mainly inactive phases in bright nights as well as mainly active phases in dark nights were observed.

The grazing pattern depends on the quality and quantity of the food plants. On average the dromedaries feed 5½-7h per day with good grazing conditions, with poor or more inferior food up to 9h a day. GAUTHIER-PILTERS (1980) describes a grazing pattern of 8-12h a day for the dromedaries of the Sahara which is independent from the food supply. The differences in the measured daily feeding times with good and bad pasture were a maximum of 3½h with the observed dromedaries. In contrast to the studies by GAUTHIER-PILTERS the authors had the opportunity to study the feeding behavior of two separate groups within the same time frame under extremely different food conditions. The significantly shorter feeding times of the Australian dromedaries are due to the richer food supply compared with that in the Sahara.

Up to now there have not been any limits for the growth of the dromedary populations in Australia with regard to space, food and water. Diseases which in other continents cause serious losses of dromedary populations are unknown in Australia. Natural enemies that could decimate the population do not exist; only man has an impact on the development of population by specific shooting of the animals.

So far there have not been any soundly analyzed models or models which are calculated in detail about the development of the population of feral dromedaries. Only a rough estimate of the population numbers of 100.000 animals at the moment exists (CISC 1993).
The data collected in the research paddock were taken as a basis for the calculations concerning the population ecology to establish a universally applicable model of the population development of feral dromedaries in central Australia. The evaluation has to take into consideration that these data were obtained in an optimal period of time for the dromedaries, when food was almost always in plentiful supply. The observed mortality rate can therefore rather be considered too little. Periods of drought over several years certainly have a negative impact on the population development by decreasing the birthrate and increasing the mortality.

In the research paddock a total of 99 individually known dromedaries were observed. In August 1986 32 dromedaries were in the horse paddock. 36 animals immigrated during the course of the studies, 11 left the area; nine animals older than two years died, 43 calves were born, 31 of which survived. When the studies were finished in September 1989 79 animals were in the research paddock.

Table 8: Population structure in the research paddock

Study year	1986	1987	1988	1989
n total	38	53	68	82
n males	18	23	35	40
n adult (>5J.)	6	6	12	11
n subadult (2-5J.)	6	10	18	19
n foals	6	7	5	10
n females	20	30	33	42
n adult (>5J.)	16	21	23	28
n subadult (2-5J.)	2	3	2	7
n foals	2	6	8	7

Causes of death of animals >2 years:

1. Old age: 1 adult female

2. Nematode infection: 1 adult female

3. Snake bite: 1 adult male

4. Sepsis after an injury from a fight: 1 adult male

5. Stress after capturing: 1 subadult female

6. Unknown: 1 adult male (skeleton was only found after two years)

7. Unknown, probably old age: 1 adult female (was clearly weak at last sighting)

8.-9. Unknown: 2 adult females were not found during the last study months despite intensive search; they probably died, since migration is out of the question

The actual lifespan of the wild-living dromedaries is not known. In the author's estimation the average lifespan of the one-year-olds (LE) is around 30 years. This estimate is based on the favorable situation in central Australia with plenty of food, no predatory enemies plus the irrelevance of diseases, and takes into consideration information about maximum ages of dromedaries in BARKER (1964) and KRUMBIEGEL (1952). Camel females are reproductive up until this age (NOVOA 1970). In the research paddock a female certainly died of old age; her teeth were visibly worn out. Incisors and molars were reduced to tiny stumps. She left behind a still nursing 16-month-old young.

Sexual maturity in females starts off at three to four years (WILLIAMSON & PAYNE 1978). The gestation period is 389.9 ± 2.1 days according to bibliographical reference (MEHTA et al. 1962), 370 days (±5) according to own observations. At an age of five to six the females have their first calf (SPENCER 1973). Births take place throughout the whole year but with a distinct increase of 93% in the six months of June to November.
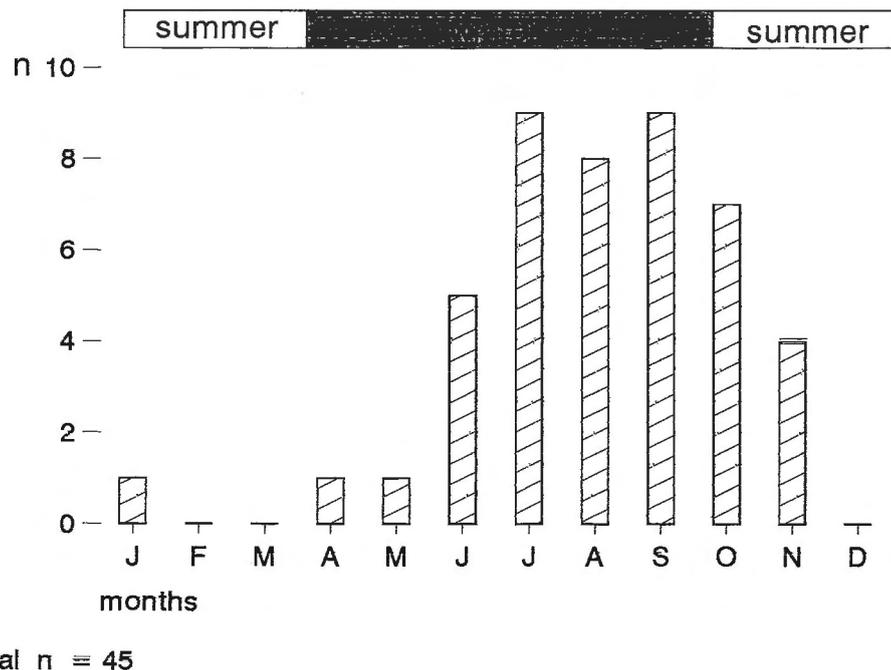
Fig. 53: Distribution of births in the research paddock

The birth intervals were 22.2 months on average, if the previous calf survived, but only 14.4 months if the previous calf died (Fig. 54).

Despite the absence of predatory enemies the losses among the newborns are high: during the study time 29% of the calves in the research paddock died during the first week of life (Fig. 55), with the socio-biological infanticide being the main cause of mortality (DÖRGES 1995).
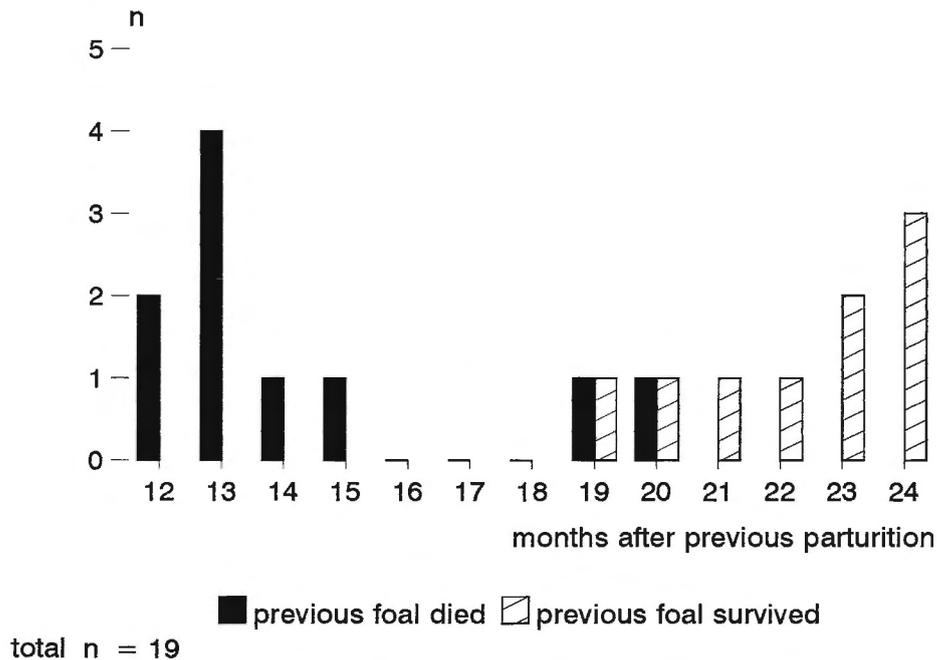
Fig. 54: Observed birth intervals
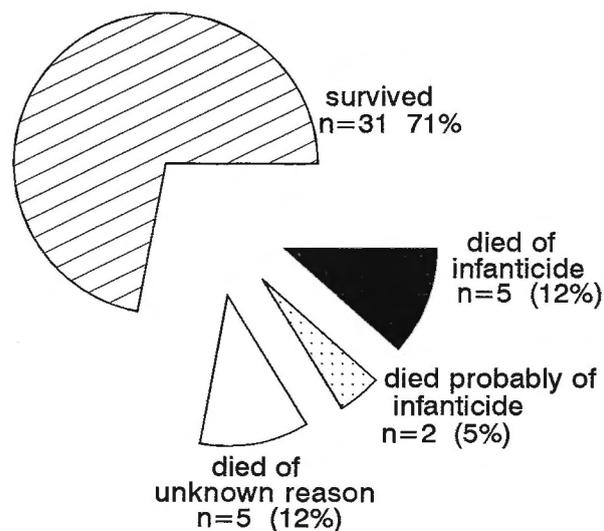
Fig. 55: Survival rate of calves and causes of mortality in newborns

The mortality rate and the birthrate are of crucial importance for the development of the survival curve and the calculation of the growth curve of the population.

The mortality rate (M) in the research paddock is calculated by taking the observed mortality by accidents and diseases (M_U) plus the purely statistical mortality on grounds of age (M_A) which depends on the average lifespan.

$$M = M_U + M_A$$

To calculate the term M_U all deaths in the research paddock with the exception of the ones on grounds of age were taken into consideration. Here the original population sizes are important. The number of animals observed in the research paddock per study year is shown in Table 9.

Table 9: Number of observed animals in the research paddock

period of time	Total
October 1986 – September 1987	52
October 1987 – September 1988	69
October 1988 – September 1989	82

The average is a total of 67.7 animals, seven of which died of diseases and accidents in the entire study time, an equivalent of 2.33 per year, i.e. 3.45%.

The above calculation of the mortality did not take into consideration the deaths which resulted from tearing down the barbed wire fences. This factor is hard to determine and very different from region to region depending on the fence density, but still occurs relatively often (five cases in the research paddock). It is estimated with reservation at 0.5% p.a.; this equals a total mortality by external influences (M_U) of 3.95% p.a.

In addition there is the purely statistical mortality on grounds of age (M_A) that depends on the average lifespan (Table 10).

Table 10: Calculated total mortality rates dependent on the average
         lifespan of the one-year-olds (LE) with a mortality by
         accidents and diseases of 3.95%

⌀ LE	M_A			M_U			M	
20 years	5	%	+	3,95	%	=	8,95	%
25 "	4	%	+	3,95	%	=	7,95	%
30 "	3,33	%	+	3,95	%	=	7,28	%
35 "	2,86	%	+	3,95	%	=	6,8	%
40 "	2,5	%	+	3,95	%	=	6,45	%

As expected the actual mortality rate strongly depends on the
estimated lifespan and varies between 6.5 and 9%.
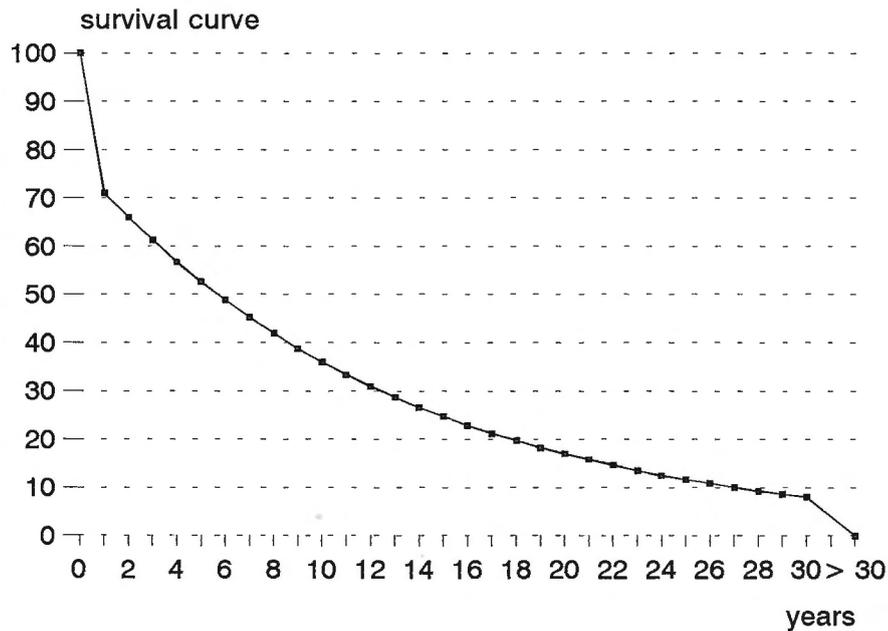
Fig. 56: Survival curve of a dromedary population with a 29% calf
         mortality occurring in the research paddock and an average
         mortality rate of 7.28% with an estimated lifespan of 30
         years.

The birthrate is determined by:

$$\frac{\text{proportion of reproductive ♀♀}}{⌀ \text{ birth intervals}}$$

The proportion of reproductive females in the adult population again depends on the average lifespan. It can be expressed by the simple following formula:

$$\text{proportion of reproductive } \female\female = S \times \left(1 - \frac{5}{LE}\right)$$

The term S indicates the proportion of females in the population at the gender ratio 1:1; therefore, the mathematical value is 0.5. The fertility rate of the females in the research paddock was 100%; all adult females observed for more than 1.5 years had at least one calf. This model is based on the assumption that the observed fertility rate applies to the entire population.

LE is the average lifespan and 5 stands for the age of the females at the birth of their first calves. With a lifespan of 30 years the proportion of reproductive females within the population equals 0.5 x (1-5/30) equivalent to 0.5 x 5/6, or 0.42 rounded up. With an average lifespan of 20 years the proportion of reproductive females is reduced to 0.5 x (1-5/20), i.e. 0.5 x 3/4, to only 0.375.

For the calculation of the birthrate the assessed mean value of the average birth intervals is needed first. This depends on the frequency of the normal (B_{In}) and the reduced birth intervals (B_{Ir}), if the previous calf had died. In the research paddock 71% of the young animals survived (Fig. 55). The normal birth intervals thus occurred in 71% of all observed cases. The statistical birth intervals are calculated as the product of time and relative frequency: normally the birth intervals are 22.2 months, i.e. 1.85 years, consequently:

$$B_{In} = 1.85 \times 0.71 = 1.314$$

For shorter birth intervals of 14.4 months on average (= 1.2 years), which occurred in 29% of all cases, the following applies:

$$B_{Ir} = 1.2 \times 0.29 = 0.348$$

Since these are 100% of all cases, the sum of B_{In} and B_{Ir} leads to the assessed mean value for the average birth intervals B_{Ia} of 1.662 years.

The calculated birthrate does not correspond to the reproduction rate. The average intervals for a successful reproduction B_{Is} are needed. Since only 71% of all calves survived, the assessed mean value for the average birth intervals has to be divided by the survival rate:

$$B_{Is} = B_{Ia}/0.71$$

Thus, the average interval for a successful reproduction B_{Is} is 2.34 years.

The Malthusian parameter or the specific reproduction rate r is calculated by the difference of birthrate and mortality rate. Both parameters strongly depend on the average lifespan and they are shown in some examples in Table 11.

Table 11: Growth rate of dromedary populations dependent on the varying average lifespan (LE) of 20 to 40 years

ϕ LE	BR	MR		r	Growth p.a.
20	0,160-	0,0895	=	0,0705	7,1 %
25	0,171-	0,0795	=	0,0915	9,2 %
30	0,178-	0,0728	=	0,1052	10,5 %
35	0,183-	0,068	=	0,115	11,5 %
40	0,187-	0,0645	=	0,1225	12,3 %

BR = Birthrate considering the calf mortality
MR = Mortality rate regardless of the calf mortality

According to the general formula for the determination of the population size at a certain point in time (REMMERT 1980):

$$N_t = N_0 (1 - r)^t$$

with $\qquad N_t$ = Population size after the time t

$\qquad\qquad N_0$ = Original size of the population

the respective growth curves in relation to the average lifespan can be calculated (Fig. 57).
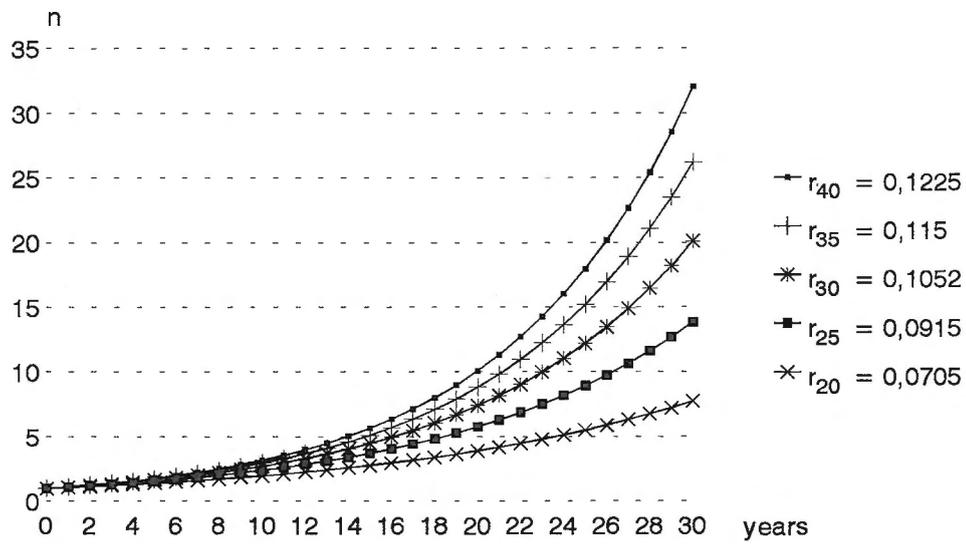
Fig. 57: Growth curves in relation to the average lifespan: 20 years
(r = 0,0705) to 40 years (r = 0,1225)
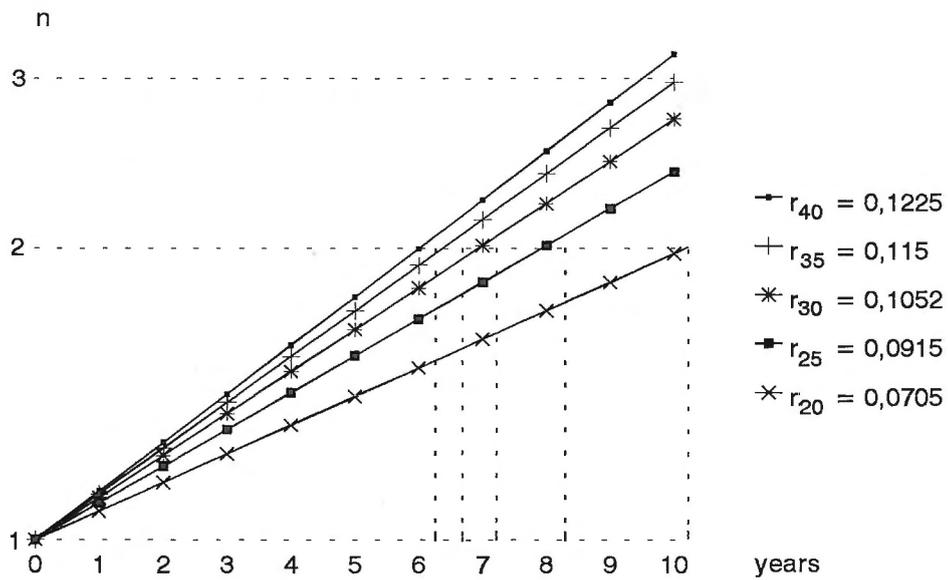
Fig. 58: Doubling periods of the dromedary population in relation to
the average lifespan: 20 years equal r = 0,0705; 40 years
equal r = 0,1225 (Table 11)

The doubling period of an undisturbed dromedary population is 6 to 10 years depending on the average lifespan (Fig. 58). With a mortality rate between 16 and 18.7% and an assumed lifespan of 20-40 years the population remains stable, there is no growth ($r = 0$).

For the Northern Territory in 1984 a dromedary population of 31.570 animals was calculated (GRAHAM et al. 1986) within the scope of an aerial survey for feral horses and other large mammals. With an undisturbed development of the population as well as with an annual shooting rate of 5% the following numbers could be expected for 1994:

Table 12: Calculated growth of the dromedary population for the Northern Territory on the basis of the population numbers of 1984 (GRAHAM et al. 1986)

ϕ LE	N 1984	N 1994	N (5% shot p.a.)
20	31.570	62.394	38.673
25	31.570	75.773	47.410
30	31.570	85.839	54.028
35	31.570	93.761	59.261
40	31.570	100.262	63.569

Of course, well-founded predictions regarding the expected development of the dromedary population in Australia are only possible with reservation after only 3½ years of observations. For instance, reliable data regarding the fertility rate of the females in Australia, the reproduction intervals during long lasting periods of drought and particularly the actual average lifespan of free-ranging camels are lacking. On the other hand, the collected and calculated data provide an absolutely realistic trend for the development of the population under normal conditions.

In contrast to all other wild animal populations, the dromedaries in Australia at present do not have limiting factors like predatory enemies and epidemics.

Except for man, adult animals do not have enemies. The dingo (*Canis lupus* f. dingo) would be the only possibility as potential predator of newborns. But only in exceptional circumstances, if the mother is not with the calf, the dingo has the chance to kill a calf.

Diseases have so far not been relevant for wild-living dromedaries. When the animals were imported, *Trypanosoma evansi*, the cause for camel Trypanosomiasis or "Surra", had already been ruled out by quarantine measures. Agents of pathogenic far-reaching epidemics like Brucellosis (*Brucella abortus*), Tuberculosis (*Mycobacterium tuberculosis*) or Camel-smallpocks (*Orthopox virus cameli*) were not found in central Australian dromedaries (WILLIAMS 1992). Nematodes like *Nematodirella dromedarii* and *Cooperia pectinata*, only have a minimal impact under natural conditions. Within 3½ years only one animal died of a nematode infection in the research paddock. Abscesses of the lymph nodes caused by *Corynebacterium pyogenes* are frequent diseases, that were found in 90% of all examined camels (WILLIAMS 1992). In the research paddock, too, several animals with abscesses of the lymph nodes were observed, but without lethal effects. In some parts of Australia Scabies (*Sarcoptes scabei var cameli*) can have an effect on weakened animals. In the Simpson desert and in the Amadeus basin dromedaries strongly infected with Scabies were often observed, but not in the study area Newhaven. Relatively harmless ectoparasites of the dromedaries are the camel bot fly *Cephaloptina titillator* and, particularly in young animals, dermatophytes of the genus *Trichophyton* which cause ringworm (WILLIAMS 1992).

Table 12 can only give clues about the expected growth of the dromedary population under natural conditions, because neither the actual average lifespan nor the shooting rates are known.

According to KRUMBIEGEL (1952), dromedaries in the zoological gardens can reach an age of 50 years and more. BARKER (1964) states a lifespan of up to 40 years for the Australian dromedaries. His animals were used as working animals. At night they were set free hobbled and searched for their food by themselves. Because of the rich vegetation they were not given supplementary food in periods of drought, i.e. they ate like wild-living dromedaries. According to McKNIGHT (1969), the dromedaries in Australia were trained at an age between three and five years and subsequently served for up to 30 years as working animals. The estimated average lifespan of 30 years is therefore realistic.

The living conditions for dromedaries are ideal in central Australia. The food supply is always sufficient despite possible local shortages, there are neither natural enemies nor do diseases have a serious impact. An excessive development like the one which occurred with other imported animals in Australia, is not possible because of the reproduction characteristics of the dromedaries. The sexual maturity only starts late, at an age of five years, the birth intervals are 2.34 years with a successful reproduction. Apart from that, in a denser population the likelihood increases that females with newborn calves are discovered by rutting males that roam around, which causes a rise in the calf mortality due to infanticide.

11. IMPACT OF THE DROMEDARIES ON THEIR ENVIRONMENT IN AUSTRALIA

Changes in the fauna caused by released exotic animals or by species which have turned feral is a big problem worldwide. Particularly highly specialized island ecosystems are often severely disturbed by the presence of introduced species, whether by predation or by food competition with the original fauna. The consequence in the end often is the extinction of the native animals.

The Australian continent can be considered a large island where except for some rodent and chiroptera species only marsupials were at home (STRAHAN 1983).

The ecological niche of the large leaf-eaters was occupied by giant marsupials until about 10.000 years ago, who then became extinct after a change in climate (ARCHER 1985). This free niche was recently taken by the feral dromedary that still occupies it today without any competition.

Apart from a few escaped animals at the end of the last century, dromedaries only turned feral in the twenties of this century. There are no detailed figures about the actual number of free-living dromedaries in Australia today; latest estimates state 100.000 animals (CISC 1993).

The calculated population densities in various areas of central Australia are around $0.05-0.15/km^2$. GRAHAM et al. (1986) on transect flights determined densities between <0.1 and >0.4 dromedaries/km^2 for the Northern Territory; SHORT et al. (1988) calculated densities between 0.01 and 0.5/km^2 according to the same method for the same area.

A damaging impact of the dromedaries on the vegetation cannot be seen with the current population densities in central Australia. That applies to the comparatively high density of 0.3 in the research paddock, too.

However, with a density of two dromedaries/km^2 over a period of 13 months in the 18km^2 horse paddock (Fig. 3), considerable damage to the shrub and tree vegetation could be observed.

With only 184mm of rainfall during this period of time it was relatively dry (average of several years = 270mm ± 30%). Increasingly

the dromedaries pulled down branches of up to 10cm in diameter and broke them off, especially with *Acacia aneura*, *A. pruniocarpa*, *Eucalyptus papuana* and *E. opaca*.

Fig. 59: Damage by breaking off branches of *Acacia aneura*

Fig. 60: Density-dependent impact of the dromedary on the vegetation, here blooming *Acacia victoriae*; left D = 2/km, right natural population density of D = 0.05-0.1/km^2

Nearly all bushes were bitten, mainly preferred species like *Acacia kempeana, A. ligulata, A. tetragonophylla* and *A. victoriae.* Due to strong browsing the latter species was not even able to develop blossoms (Fig. 60). Because of the drought the ground vegetation did not grow again and was virtually not present any more after some months. After the dromedaries had been released from the horse paddock into the research paddock, the severely bitten species recovered after the next rainfalls, though.

The effect of the dromedary on endangered plant species has already been described in Chapter 5. At this point it has to be considered that dromedaries in some areas damage species that are not endangered like *Crotalaria cunninghammii* and *Trichodesma zeylanicum.* Almost each individual of these two species was nibbled at or eaten up in the research paddock. Because of the high abundance of both species in central Australia this effect can be ignored, though (LATZ pers. comm.).

The foraging behavior of the dromedaries is adapted to desert conditions. The animals continually walk while eating food and mostly take one bite every few steps. Unlike cattle and sheep that eat their food, mainly grass, down to the root, dromedaries only use parts of the food plants. The less food is available the bigger are the distances of the animals to each other. This way the areas are never overgrazed. Because of their independence from water they only rest seldom and then for a short time near watering places. Thus, they do not contribute to overgrazing of these areas.

Some of the main food plants of the dromedaries are also used by small native marsupials and birds. *Amyema maidenii, Amyema preissii, Cassytha filiformis, Cuscuta victoriana, Glycine falcata* and *Leichhardtia australis* belong to this category (LATZ pers. comm.). Because of the grazing behavior of the dromedaries - not to eat up the available food completely - it can be assumed that the dromedaries do not take away this food resource from these native animals. In periods of drought a competition with some bigger kangaroo species can occur, since they have to turn to the remaining bush vegetation in place of the grass they otherwise mostly feed on. A food competition could occur mainly with *Acacia kempeana, Atalaya hemiglauca, Eremophila*

longifolia, *Rhagodia eremaea*, *Rhagodia spinescens* and *Santalum lanceolatum* (LATZ pers. comm.).

In the course of the evolution no animals with hard hooves have developed in Australia and correspondingly the vegetation is not adapted to them. The import of domestic animals like cattle, sheep and horses had a devastating effect on the vegetation in some areas because plants were trampled on and the structure of the soil was damaged. Being a tylopode, the dromedary has comparatively large feet with soft soles and therefore has no damaging effect on the structure of the soil or the vegetation. Unlike all other ungulates the dromedaries hardly affect the very sensitive structure of the sand dunes because of the large supporting surface of their feet and the reduction of weight per cm^2. A comparison of foot prints of dromedary and cattle in soft sandy soil is shown in Fig. 61.

Fig. 61: Comparison of foot prints; left: cattle; right: dromedary

Compared with other ungulates it is thus not as likely that dromedaries trample down sensitive vegetation areas.

All in all the impact of the dromedary on its environment can be rated as rather insignificant. Even though the dromedary originally does not belong here, as an adjusted desert animal it does not have negative effects on the biocenosis of Australia. In 1925 the Australian government rated the dromedary as a pest. The "Camel destruction act" gave everybody the right to shoot dromedaries on their land (McKNIGHT 1969). Today this attitude has clearly been put into perspective for instance by the Conservation Commission of the Northern Territory which considers the dromedary to be a valuable addition to the fauna for a planned National Park Simpson Desert (GIBSON & COLE 1988).

12. MEASURING THE BODY TEMPERATURE

Being inhabitants of hot dry areas it is essential for dromedaries to conserve water. Morphological and physiological adaptations lead to a minimization of water losses. The physiological performances of the dromedary, particularly the mechanisms for thermoregulation, have been known since the studies of SCHMIDT-NIELSEN on domestic dromedaries (SCHMIDT-NIELSEN 1959, 1964; SCHMIDT-NIELSEN et al. 1952, 1956, 1957, 1967). However, measurements of the body temperature of free-ranging camels have so far not been done.

12.1 Methods

From April 1988 to March 1989 telemetric measurements to determine the body temperature were done with seven animals in the research paddock. For this purpose Austec (Canada) transmitters (148 MHz) embedded in wax were implanted intraperitoneally (Fig. 62).
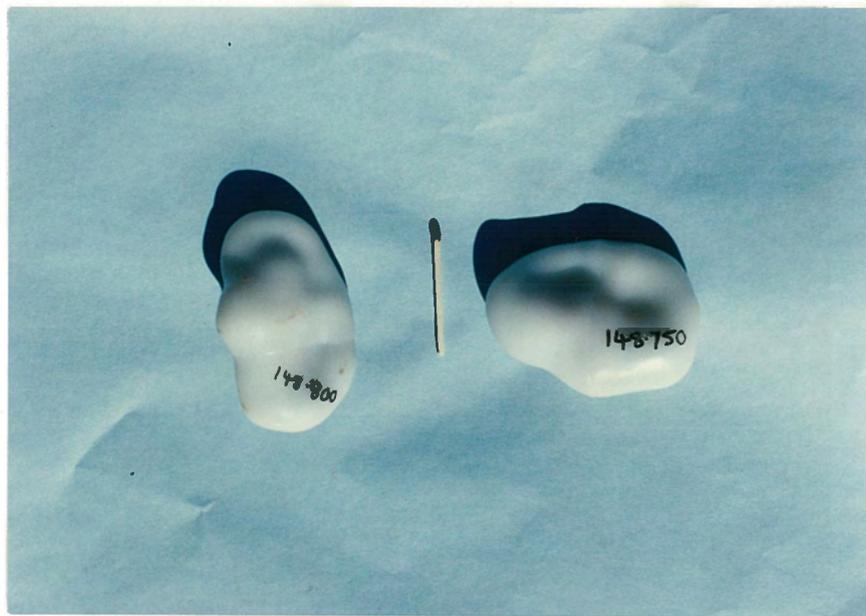
Fig. 62: Transmitter for the measurement of the core temperature

The implantations were performed in the field under conditions as sterile as possible; all animals survived the operation without complications. The dosages for the drugs for the preceding immobilization can be seen in Table 1 in Chapter 4.

The pulse intervals of the transmitters were correlated with the temperature to ± 0.1 °C. For the determination of the body temperature the time of 10 consecutive impulses was measured three times each with a stop watch. The resulting average value on the calibration characteristic of the respective transmitter indicated the body temperature.

At each measurement of the body temperature the behavior of the respective animal and the abiotic factors at the time of the measurement were noted (temperature in the shade, relative humidity, wind velocity, degree of cloudiness).

From January 21, 1989, until February 2, 1989, dehydration experiments were performed by denying the animals access to the troughs. After two weeks, however, the dromedaries succeeded in walking around the barriers, so that the experiment had to be broken off early.

Methodical problems arose with the locating of the first experimental animals who were not fitted with additional collar transmitters (Ho, TS). When the transmitters were tested the range was 1.5-2km and thus seemed to be sufficient for finding the animals in the research paddock. But after the implantation the range was reduced to about 20-50 m. The body temperature of these first animals could therefore only be measured very irregularly, when they were found by chance.

Because of the peristaltic the position of the implanted transmitters in the peritoneum changed and with this the range, too. Much stronger problems with telemetric reception arose in dependency to the height. The body temperature therefore could not even be measured from a distance of 10-15m when the animals were lying down.

The rather poor life of the transmitters turned out to be an additional problem; some only worked for a very short time (ref. Table 13). Because of this fact, seasonal comparisons of the body temperature of the same animals were not possible.

To support the telemetric measurements of the body temperature of the animals in the research paddock, the rectal temperature of some tame dromedaries was taken with a fever thermometer in summer.

12.2 Results

Seven animals could be examined in all: four in winter and three in summer. A summary of the respective measurement data are shown in Table 13.

Table 13: Study time and total measurement data per animal

Individual	Σ data	N days	period
subad. male TS	62	41	13.04.88-21.07.88
adult. male Ho	133	77	14.04.88-26.10.88
adulte cow H3	8	4	23.04.88-28.04.88
adulte cow Tr	93	40	23.04.88-26.06.88
adulte cow Kl	239	82	04.10.88-29.03.89
adulte cow Lo	50	21	07.01.89-03.02.89
adulte cow N8	158	43	08.01.89-29.03.89

The summarized results for six dromedaries are shown in relation to the air temperature in Fig. A13.1-6 in the Appendix. For the seventh dromedary, the adult female H3, there are not enough data for a useful graphical presentation.

The average measured body temperature is shown in Fig. 63. The graph of the variation ranges of the measurements of all examined animals is shown in Fig. A13.8 in the Appendix.
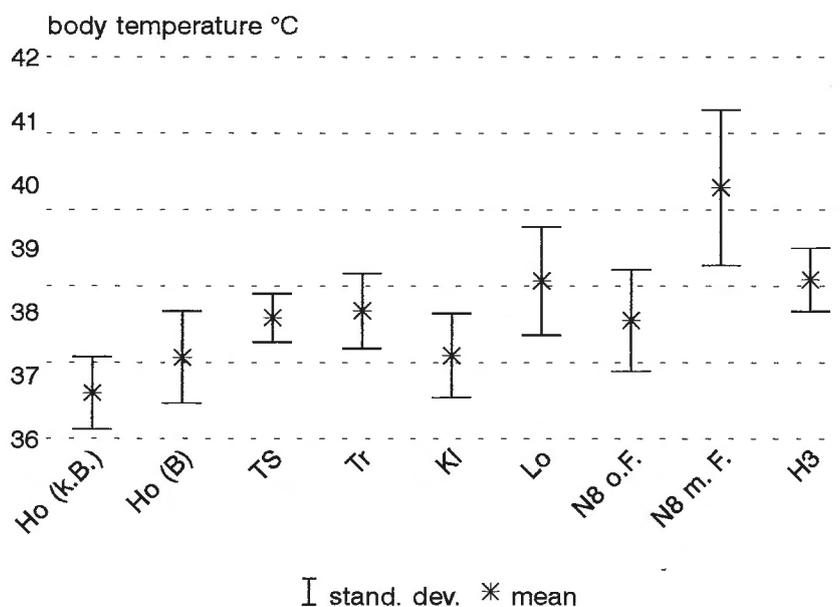
Fig. 63: Average body temperature with standard deviation

The average daily difference in temperature of all animals examined in winter was 1°C, in summer 1.5°C, and 2.3°C with dehydration in summer. Individual values are shown in Table 14.

Table 14:   Average daily differences in body-temperature of the animals examined in the research paddock at the respective seasons

	camel	a.t.r.	diff.	mean
winter: hydrated	Ho*	36,3-37,4	1,1	1,0°C
	TS	37,7-38,5	0,8	
	Tr	37,4-38,4	1,0	
winter:	Ho**	36,6-38,4	1,8	
summer: hydrated	N8	37,3-38,5	1,2	1,5°C
	Kl	36,6-38,1	1,5	
	Lo	38,0-39,9	1,9	
summer dehydrated	N8	37,4-39,3	1,9	2,3°C
	Kl	36,2-38,7	2,5	
	Lo	37,5-39,9	2,4	

a.t.r = average temperature range
*   = data of the male Ho outside of the rutting season
**   = data of the male Ho during the rutting season

The linear regressions of the average body temperatures during the course of the day are shown in Figures 64 and 65 according to the seasons.
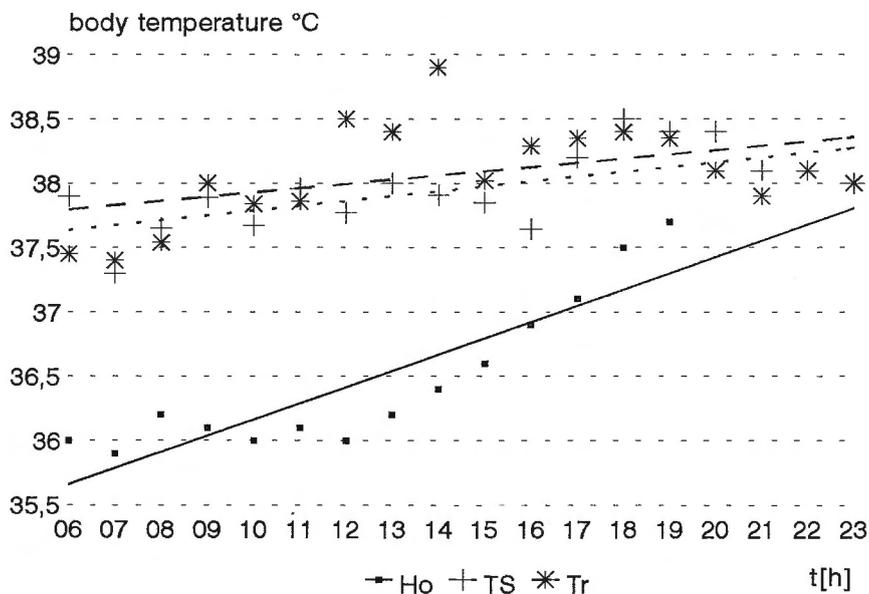
Fig. 64: Mean daily curve of the body temperature of the animals examined in winter

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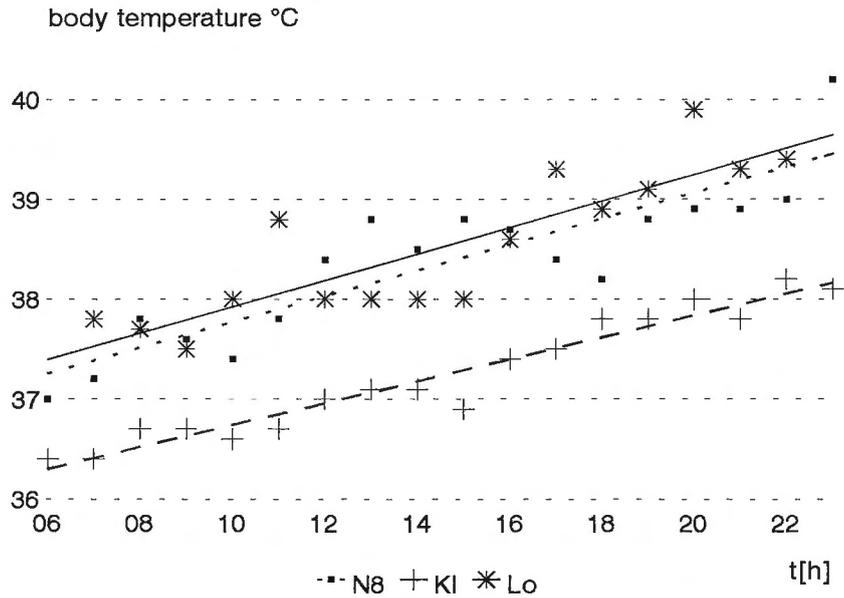
body temperature °C

Fig. 65: Mean daily curve of the body temperature of the animals
examined in summer except for the dehydration data

The regressions of the average body temperature in winter go lower
than in summer. The adult male Ho, however, significantly deviates
from this basic pattern because he was temporaryly in rut. During the
rut, a rise of the body temperature can be observed. A comparison of
the body temperature within and outside of the rut is shown in Fig.
66.
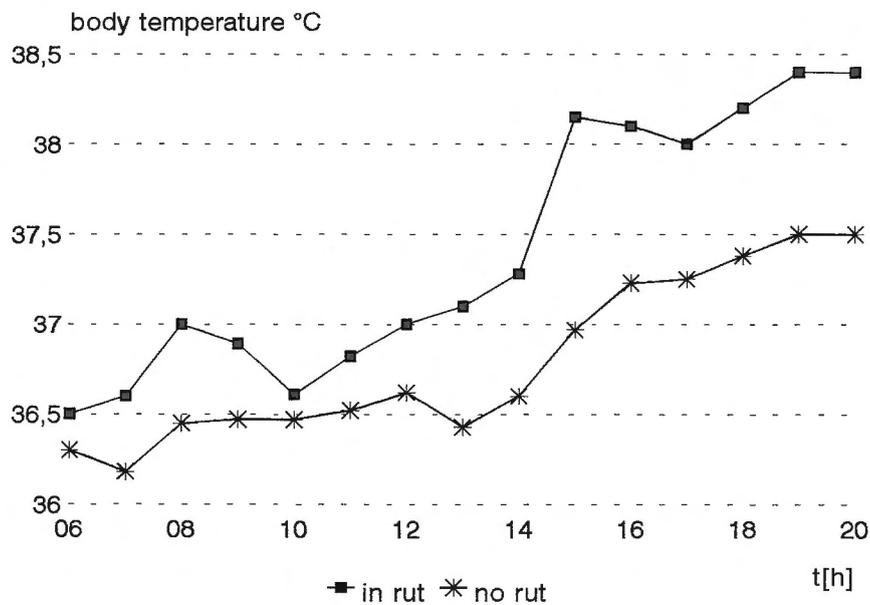
body temperature °C

Fig. 66: Measurement data of the body temperature of the male Ho
within and outside of the rut

While for the male Ho there was a significant difference of the body temperature within and outside of the rut, no difference could be found for winter and early summer.

A gradual increase of the daily variations in temperature could be seen with all animals in summer during the dehydration experiment. Fig. 67 shows the temperature curve of three females with the daily maximum of the air temperature shortly before and during the dehydration phase.
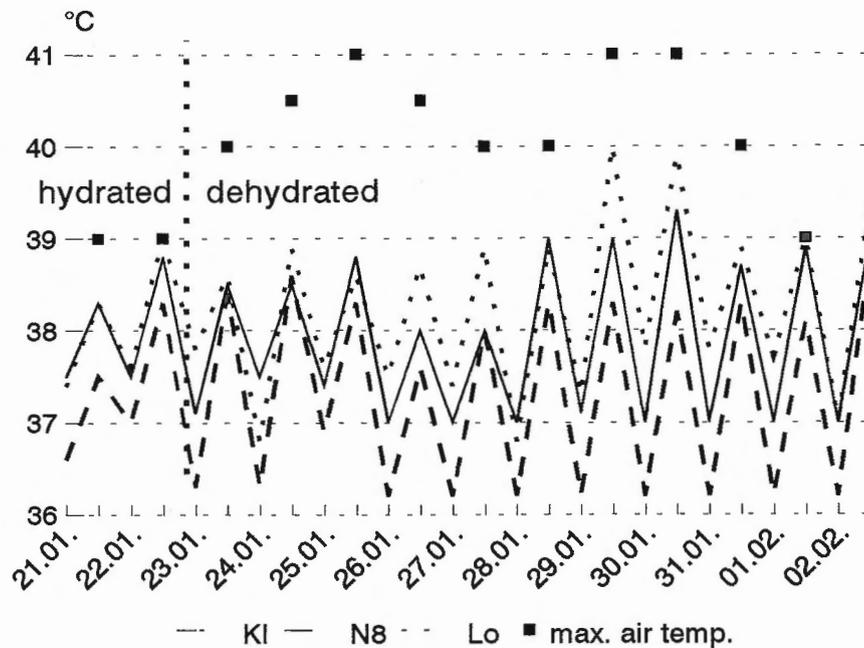
Fig. 67: Temperature curve of the three dromedaries during the dehydration experiment

Before the experiment the animals had drunk every day. The variations in temperature measured then were between 0.8 and 1°C. With increasing water shortage the variations became stronger and after eight days of forced abstination reached the maximum values of 2.7°C. All animals showed a morning drop in body temperature in relation to the average temperatures without dehydration. At the same time a clear rise in temperature in the evening can be observed with the females K1 and N8.

For the females K1 and N8 the daily variations in body temperature before and after the dehydration experiment are shown depending on the maximum air temperature and on the water intake (Fig. 68 & 69). The amount of data for the female K1 is much bigger due to the life of the

transmitter. Apart from that, the female N8 had a fever for three weeks, which in addition limited the usable amount of data. Both figures show a clear dependency of the variations in temperature on the state of hydration and on the air temperature.
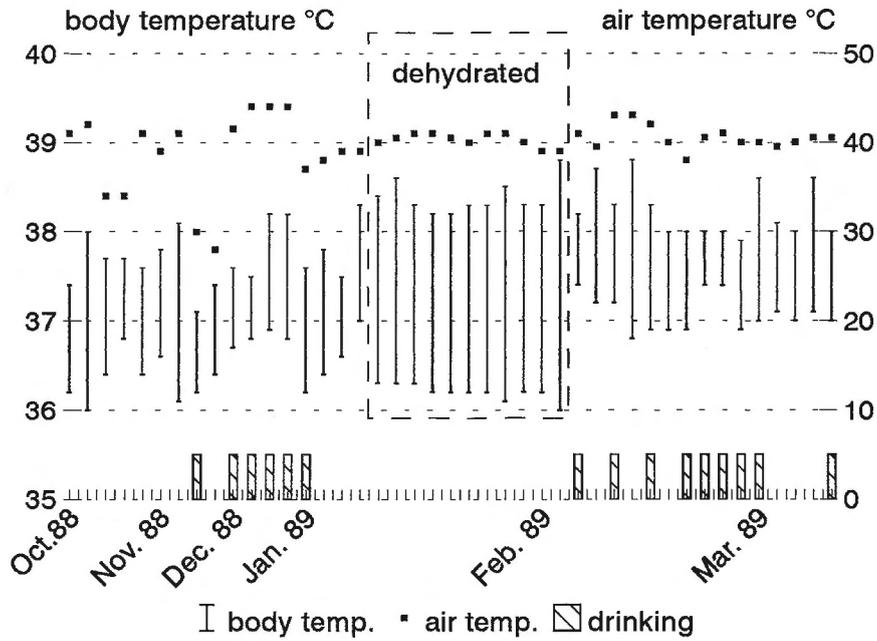
Fig. 68: Daily variations in temperature of the female K1 depending on the water intake and the maximum air temperature
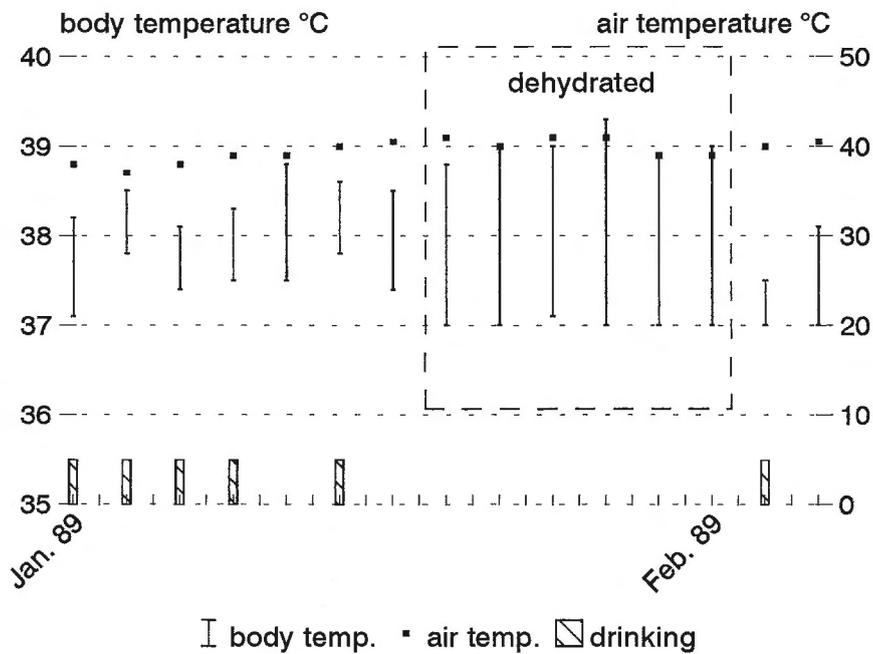
Fig. 69: Daily variations in temperature of the female N8 depending on the water intake and the maximum air temperature

The following Figures 70 to 72 show the respective linear regressions of the average body temperature of the females under normal conditions and at the time of dehydration.
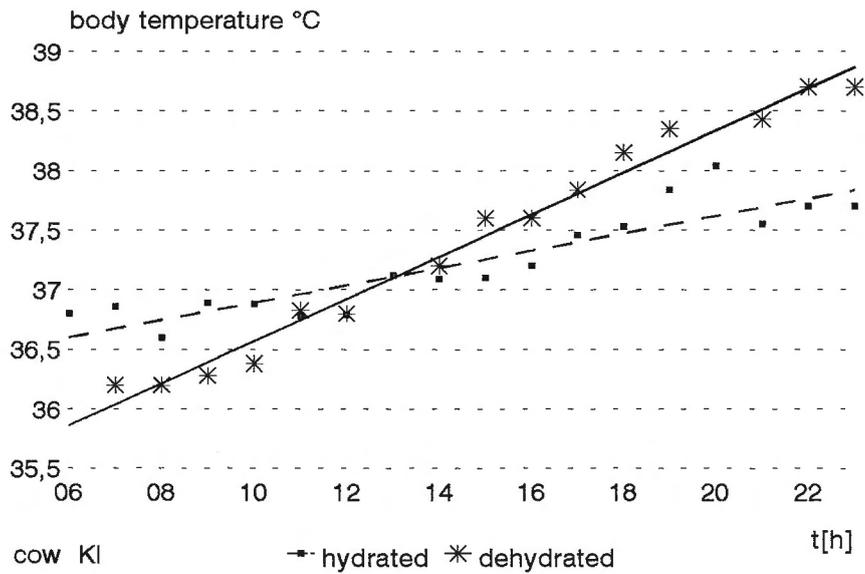
Fig. 70: Linear regression of the average body temperature in the course of the day with the female K1
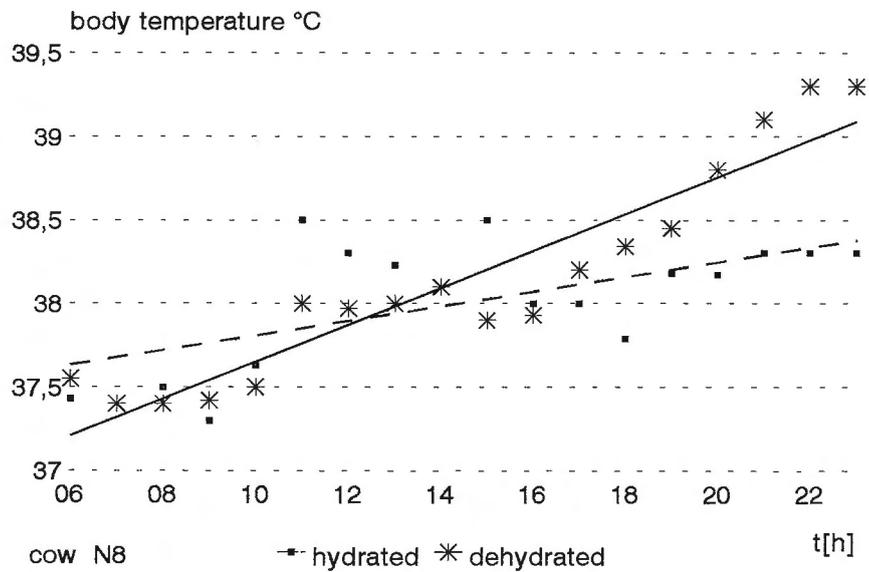
Fig. 71: Linear regression of the average body temperature in the course of the day with the female N8

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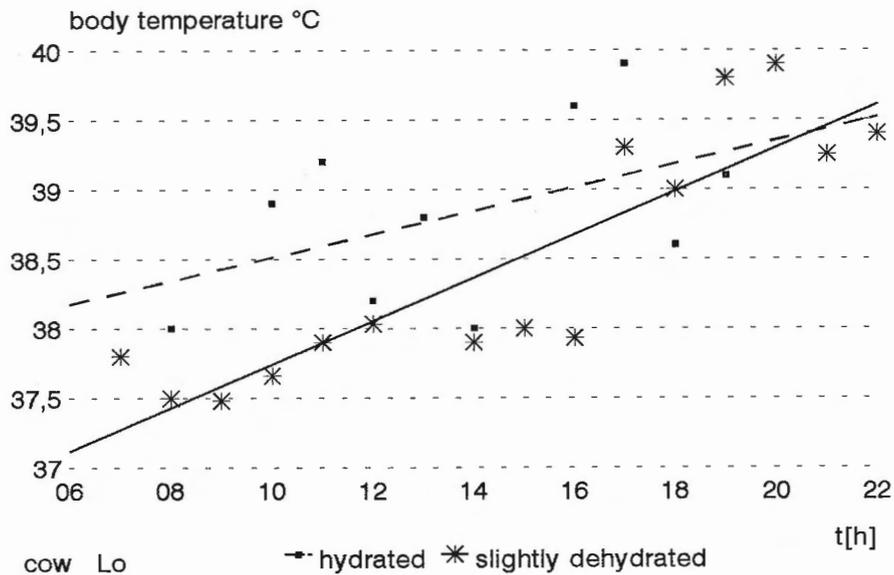
Fig. 72: Linear regression of the average body temperature in the course of the day with the female Lo

The female Lo was obviously not as much dehydrated as the other experimental animals. She had walked around the barriers of the trough on January 26, 1989. In addition, there are only relatively few data outside of the dehydration phase, since the transmitter was implanted two weeks before the dehydration experiment and failed immediately afterwards.

The course of the average temperature curves of the females studied in summer during the dehydration experiment is shown in Fig. 73 in relation to the air temperature and activity. All animals have their minimum temperature in the morning between 6 and 8h; the air temperature is clearly below the respective body temperatures. In the morning activity phase, the temperature of all animals goes up slightly, while the air temperature rises sharply. During the hottest time of the day, between 12 and 16h, the body temperature remains relatively low with regard to the air temperature and is 2-3⁰ below that. The animals now rest in the shade and ruminate. In the afternoon activity phase the body temperature rises even though the air temperature drops and reaches its maximum value between 20 and 22h. At night, during the longest resting phase, the body temperature again falls to the lowest morning value.
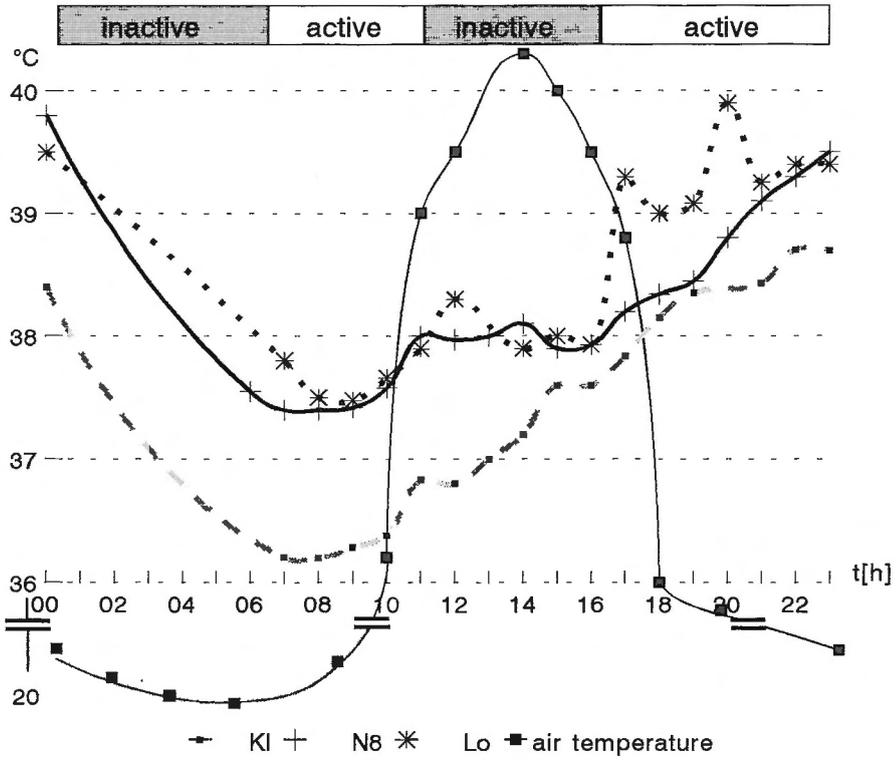
Fig. 73: Body temperature curve during the dehydration experiment in relation to air temperature and activity

Due to the daily variations in body temperature and the individual differences in temperature of the dromedaries a mild rise in temperature due to illness is hard to discern with selective measurements.
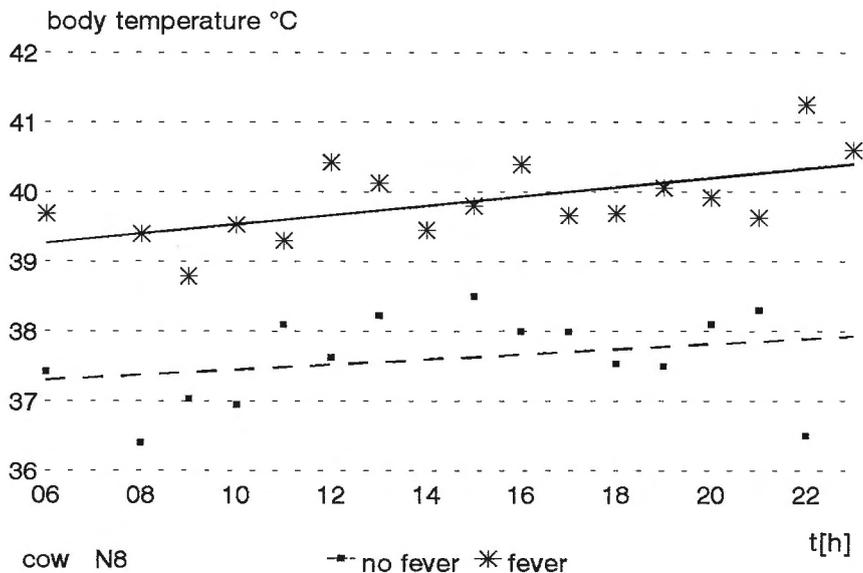
Fig. 74: Body temperature of the female N8 with and without fever

In the middle of February the female N8 had injured her leg and the wound was severely inflamed after a few days. From February 15 to March 3, 1989, she showed obvious signs of weakness. She lay often, limped when walking and could hardly follow the group when they changed places. In this time the daily temperature curve increased by app. $2°C$; the animal obviously had a fever. On March 4, 1989, the female was outwardly well again and the body temperature was "normal", too (Fig. A13.7).

Measurements of the temperature before and during drinking showed a noticeable lowering of the body temperature. The jumps in temperature (n=15) were between 1.5 and $3°C$ with water temperatures between 24 and $29°C$.

12.3   Discussion

The temperature studies in hand are to be considered a pilot study that showed interesting aspects despite the small amount of data.

The body temperature of the dromedaries is variable and there are individual differences. The maximum daily differences in temperature depend on the air temperature and the state of hydration. In general they are less in winter than in summer. However, when the animals go to the trough in summer regularly, the daily variations in temperature are in the range of the winter readings. Parallels could be demonstrated compared with measurements of the body temperature of tame dromedaries (SCHMIDT-NIELSEN et al. 1957).

The higher temperature of the male Ho during the rutting season can be put down to the changed hormonal situation that causes an increased activity and at the same time a reduced food intake. In the rut the male is always restless, herds his females and chases away rivals. Outside of the rut he leads a rather quiet life with long resting phases that are only interrupted by feeding. SCHMIDT-NIELSEN (1957) already points out the different body temperature curve of males during the rut, but does not give more detailed information.

The studied animals showed clear differences to SCHMIDT-NIELSEN's results during the dehydration experiment. The maximum daily

variations in temperature here were only 2.7°C, while the temperatures of SCHMIDT-NIELSEN's experimental animals were at a maximum of 6.2°C. It has to be considered on principle that the experiments of SCHMIDT-NIELSEN could take place under defined domestic and feeding conditions. By contrast, the experimental animals had the chance to lay down in the shade, to change their activity pattern, to select their food, and all of these possibilities were actually practiced.

While the troughs were closed off, a general shift of activities to the cooler hours of the day could be observed; the animals went to the shady trees earlier than before and stayed inactive for longer. A clear difference in behavior was conspicuous with one group where some members could walk around the barriers and drink, whereas others were not able to do so. The non-drinkers already went into the shade between 8 and 9h in the morning and rested there, while the "drinkers" were active in the sun for up to 1½ hours longer and ate.

Four days after the troughs had been closed off, another group went into the sand areas where the succulent *Calandrinia balonensis* was available in large amounts and was now used almost exclusively. Before that, these animals had lived near the trough in the bushland for several weeks.

The experimental animals were obviously less dehydrated due to the free-range situation. A dehydration like in SCHMIDT-NIELSEN's experiments, which was achieved by keeping the animals in a shade-free paddock and exclusively feeding them dry hay, is not possible in Australia under natural conditions.

The results in hand showed considerable differences compared with those of SCHMIDT-NIELSEN concerning the time of day when the animals had their maximum body temperature. He describes an experimental animal that had its maximum temperature around 19h (SCHMIDT-NIELSEN et al. 1957); in other cases (SCHMIDT-NIELSEN 1959, SCHMIDT-NIELSEN et al. 1967) the highest body temperature of the dromedaries was measured shortly after the highest air temperature was reached, without precise indication of the time of day. Both could not be confirmed for the experimental animals. During the hottest time (12:00-16:00h) the dromedaries had a relatively low body temperature that went up until

late in the evening (21:00-23:00h). This trend was also to be seen with tame control animals on the camel farm in Alice Springs, who mostly had their highest temperature in the late evening hours (Fig. A13.9).

The relatively low values of the body temperature during the hottest time of day can be put down to the fact that the dromedaries could afford to keep their temperature low by sweating. Even when the troughs were closed off they still got enough water via the food. The further increase of the body temperature in the late afternoon until in the evening went hand in hand with the general increase in activity. The animals used the now lower ambient temperature to give off the heat energy that is produced inside the body by metabolism processes. The steeper the gradient is between body and air temperature the higher is the passive heat release to the outside.

SCHMIDT-NIELSEN (1957) describes the lowering of the body temperature after drinking. He noticed a drop in the rectal temperature of 2°C within 45′ at a water temperature of 10°C. The measurements in hand showed comparable values but at far higher water temperatures. The lowering of 3°C within 1h at a water temperature of 26°C is probably a maximum value.

When evaluating all results, the position where the temperature is taken must be taken into account. The measurements were done inside the peritoneum, therefore the transmitters could shift because of the intestinal peristaltic. Near the liver and in areas of intensive microbial metabolism activity higher temperature than in a peripheral position can be expected. SCHMIDT-NIELSEN's results are based on measurements of the rectal temperature which is always below the core temperature (SCHMIDT-NIELSEN 1957). To determine this core temperature the used method is probably more suitable.

SCHMIDT-NIELSEN could describe the physiological performance of the dromedaries under extreme conditions while the experiments in hand give information on how the animals regulate their heat balance under natural conditions in times without a water shortage. Regarding this topic there is still an enormous need for research. Suggestions are given in the general final discussion.

13.   FINAL DISCUSSION

The dromedary has found an optimal habitat in the arid areas of Australia. Compared with the conditions of domestic or free-ranging dromedaries in the Near East and North Africa, central Australia offers the animals excellent living conditions with regard to the climate and the condition of the soil, but above all because of the varied and rich food supply.

In the endless, almost deserted areas the dromedary has neither competitors for food nor natural enemies. Because of the island position of the new habitat there have not been any dangerous diseases for the dromedaries from the start; the uncompromising import regulations and the additional strict epidemic control in the country will not let this factor become likely in the future.

In contrast to all the other animals imported into Australia the dromedary had all chances to establish itself as a harmonizing part of the ecosystem. Originally coming from regions with extremely limited resources, the dromedary treats them with care even in times of plentiful supply. Among the large mammals dromedaries are adapted the best to arid areas; their foraging behavior corresponds to that of wild animals, and they never damage their habitat by overgrazing when they can roam around freely. This is particularly true for the Australian dromedaries, but was already pointed out by GAUTHIER-PILTERS (1980). Because of their relative independence from water they can use grazing places that lie very far apart or far away from water. Unlike cattle, horses and sheep, dromedaries do not destroy the surrounding of the troughs, neither by eating up the vegetation nor by trampling down the ground, and they only stay at watering places for a short time.

Since dromedaries are very mobile and not territorial and consequently have no investment in a particular area, they can do extensive migrations at any time and can therefore constantly use new resources. The extremely wide food spectrum and the ability to use plants intensively that are avoided by other animals, provide the dromedaries with good chances of survival even in periods of drought. Their adjusted activity pattern allows the dromedaries to adapt themselves

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fast to the respective environmental conditions while conserving energy. Because of their flexibility, also regarding habitat and range utilization, they are able to optimally use their new habitat in Australia.

The serious change in climate which began 20.000 years ago, has transformed the previously green center of Australia into deserts and semi-deserts. With the progressing drying up, all giant forms of the herbivorous marsupial which had developed in the Pleistocene gradually became extinct. At the same time the colonization of the fifth continent by man began who probably contributed to the vanishing of the giant marsupials (ARCHER et al. 1985). In this very short time regarding the evolution, no large leaf-eater that is adapted to dryness could develop, and the dromedary is about to occupy this free niche extensively. This introduced animal obviously lives in harmony with the found ecosystem and so far there have not been any indications for a possible change of this state. It is very unlikely that there will be an overpopulation of the Australian dromedaries, since the reproduction rate is relatively low despite the best living conditions. Ecologically catastrophic effects which e.g. occurred with the introduction of rabbits (*Oryctolagus cuniculus*) and which lead to the extermination of a number of animals and plant species, are not to be expected by the dromedaries.

The dromedary which today is of no importance for the Australian economy could in the future be of use as a source for protein. First projects toward this trend are already in the planning stage (CISC 1993). Experiments showed that some wild ungulates provide cheaper meat than domestic animals (AKIMUSCHKIN 1972). Furthermore, the dromedary that predominantly feeds on leaves could contribute to the increase of productivity in areas of cattle breeding; in Kenya for example dromedaries are kept in some regions to reduce the bush so that more grass for the cattle can be obtained (EVANS et al. 1979). Because of its modest requirements and its foraging behavior the dromedary would be excellently suitable for these purposes in the Australian arid areas, too.

With the study in hand it was possible to provide a multitude of results, still a number of questions has remained unanswered. They should be the subject of further research.

Parallel studies of defined plant contents at the time of the maximum use of certain food plants are still to come in the field of nutrition ecology. This study mainly takes into consideration the already existing standard analysis results, and the underlying plant material was not always from the region or the season in question. The specific contents of primary and secondary plant substances can be different depending on the season and the region. The conspicuous resistance of the dromedaries to substances that are poisonous for other animals species becomes particularly important in this context and should be examined quantitatively more closely. Parallel to this, qualitative and quantitative determinations of the salt intakes from food as well as from the drinking water or from the occasional use of saline soils are of interest. A continuous measurement of the water content of the consumed food and the determination of the actually taken in amount of water when drinking should round off the detailed studies regarding nutrition physiology.

Long-term studies concerning the quantitatively recordable measurement of the impact dromedaries have on the vegetation or concerning a possible increase in productivity in cattle farming areas, as they have already been established for other regions (EVANS et al. 1979), are not only of economical interest. In the research paddock the dromedaries e.g. mostly ate forbs covering the ground and above all the strongly abundant *Sclerolaena* species which are ignored by cattle and of course compete with the grasses. In addition, due to the dromedaries' browsing, the bush vegetation is kept relatively short and its spreading out is largely restricted. The present results already show first signs but should be examined under defined conditions more closely. The following simple experimental arrangement could give conclusive answers: four similarly structured paddocks are created within one vegetation type: the first one is for dromedaries, the second one for cattle and in the third one dromedaries and cattle would be kept; the fourth paddock would be a control area with neither dromedaries nor cattle. The density of the populations in the paddock would have to be varied depending on environmental conditions. The

respective resulting changes in the vegetation would have to be evaluated by regular recordings.

The extensive migrating activities of the dromedaries in Australia are at the moment checked via satellite-telemetric measurements (CISC 1993). So far the transmitters have only been put on dromedary females; a comparison of the migration pattern of males in relation to the females, however, is considered useful since different migration patterns are to be expected (DÖRGES 1995).

Another future approach lies in the long-term study of the body temperature of the dromedaries in relation to relevant factors. The pilot study could show in part that the temperature curve of wild-living dromedaries obviously deviates from that of domestic dromedaries which have been examined so far. These changes can probably be put down first of all to the different conditions. But the position where the temperature is taken is also important in this context. A correlation of the continuously measured core temperature to the temperature in the periphery taking into account the behavior and all effective external factors would certainly provide important findings about the thermoregulation of wild-living dromedaries. At the same time the temperature transmitters could transmit additional physiological parameters like heart and respiratory rates, and oxygen content of the blood which are continuously recorded by automatic measuring stations. The longer life of new transmitters could for the first time make possible seasonal comparisons of the body temperature of the same individuals. Additional necessary physiological measurements regarding this topic, such as the dependency of the body temperature on the hormone balance, could even be clarified by blood or urine tests. By now, the population in the research paddock has become used to the catching devices around the troughs. These could be used to close off single animals for a short time to draw blood, since an immobilization in this situation would not make sense.

All above described research approaches would be possible with the population in the research paddock that is already used to people. This potential should be used for the future so that the adaptation of this highly specialized animal species in its new environment can be studied fundamentally.

14.   ECOLOGICAL ABSTRACT

The studies were carried out continuously in the border areas of the Gibson and Simpson deserts and in the Amadeus basin in central Australia from July 1986 until October 1989.

The main study area, a 213km^2 research paddock, was located on the cattle farm Newhaven, 360km north-west of Alice Springs, at the edge of the Gibson desert. On a small scale it contains the most important landscape types and vegetation units which are typical for central Australia. Water was available for the dromedaries at two cattle troughs.

Regarding the climate, the area is marked by dry and mild winters with occasional mild nighttime frosts, and hot and relatively humid summers. The precipitation is around ϕ 275mm per year, the potential evaporation rate around 3.000mm.

A total 18 dromedaries were successfully immobilized, four more were caught; all animals were fitted with collars and ear tags, 14 of which with radio transmitters.
The study is mainly based on the continuous observation of at the end of the project 79 individually known dromedaries.

The food spectrum was analyzed by direct observation, examinations of stomach contents and feces were done in addition. Dromedaries are mainly leaf- and forb-eaters with an utterly wide food spectrum. In the research paddock 236 (80%) of the 292 classified plant species were eaten by the dromedaries. 26 additional food plants were identified in other areas. Even though grasses were preferred from time to time, the quantitative proportion in the annual average was only 3%.
The dromedaries are generally very flexible with their food selection, but they also show preferences independent from the supply. Immediately after rainfalls perennial grasses were preferred until the forb plants had grown big enough. Now and then there was a mass development of forbs which were then used almost exclusively by the dromedaries. In winter Fabaceae (*Swainsona-*, *Indigofera-*species) and Compositae (*Helipterum-*, *Calocephalus-*species), in summer

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Nyctaginaceae (*Boerhavia*-species), Portulacaceae (*Portulaca-*, *Calandrinia*-species) and Zygophyllaceae (*Tribulus-*, *Zygophyllum*-species) dominated.

The evergreen shrub and tree vegetation was used all-year-round but with varying intensity depending on the available ground vegetation, but above all in dry periods. *Acacia-*, *Atalaya-*, *Eremophila-*, *Rhagodia-* and *Eucalyptus*-species were preferred then. At the flowering time or after the development of fruits the respective species were eaten almost exclusively.

With the exception of periods of drought, the dromedaries in central Australia have sufficient food plants with high moisture content (partly succulents) at their disposal all-year-round, so that they can be largely independent from surface water. However, if water is available, it is used. Drinking water was available for a short time in rainwater puddles and all year round in cattle troughs. The drinking frequency was dependent on the water content of the food as well as on the air temperatures. In summer the animals drank every day to every other day, in winter irregularly or not at all.

Despite the high salt concentration in the drinking water (up to 10,000 ppm) the dromedaries could regularly be observed eating saline soil and crystalline salt from the salt lakes.

Preferences in habitat were clearly marked seasonally. The open bushland was preferred all year round. In winter the salt lakes and salt marshes with the adjoining dune areas were frequently used. In the summer months, the animals preferred depressions with large trees and sand areas with *Calandrinia-* and *Crotalaria*-populations.

The annual home ranges were estimated to several thousand to 10,000km^2. They depend on the respective ecological situation. There are indications for regular extensive migrations or seasonal utilization of the same ranges.

In the research paddock, clear seasonal differences in the range utilization could be determined. In the summer months the groups used small home ranges of sometimes less than 20km^2 each for weeks. From these grazing areas they regularly went several kilometers to the

troughs and returned to the same range without a stay. The different groups had home ranges which were far apart and contained different vegetation units. During the winter months the groups showed a clear restlessness: particularly the groups with males roamed through the area in irregular patterns and initiated extensive migration activities as soon as they encountered groups of females with a male. This way the entire available area was used by all groups in irregular patterns while the individual groups again kept a clear distance to each other. These migrations were restricted in the research paddock by the fence. Observations outside the research paddock and at the edge of the Simpson desert confirm this general pattern.

The estimated lifespan of wild-living dromedaries is about 30 years. Females are reproductive up to this age. The sexual maturity of cows generally begins when they are three to five years old, i.e. a female can successfully raise 9-10 calves.

Births take place during the entire year but with a clear maximum during the months June to November. The normal birth intervals are about 24 months, but only 12-15 months if the previous calf has died. With an average lifespan of 30 years the growth rate is 10.5%.

With natural population densities which are around 0.05-0.15/km^2 according to the author's calculations in different areas in central Australia, an impact on the vegetation was not to be discerned. This also applies to the comparatively high density of 0.3 in the research paddock. With an experimental density of 2.0, particularly in an extreme drought, there was damage to the point of destruction to some preferred shrubs and trees.

Telemetric studies of the body temperature were done with seven animals. In winter the average daily variations in temperature were around 1.0^{0}C, in summer around 1.5^{0}C and under dehydrated conditions in summer around 2.3^{0}C. During the dehydration experiments the groups changed their grazing area and preferably used regions with a rich supply of succulents (*Calandrinia*-species). Furthermore the dehydrated animals changed their rhythm of activity: in the morning they went into the shade two hours earlier than the animals that were not dehydrated.
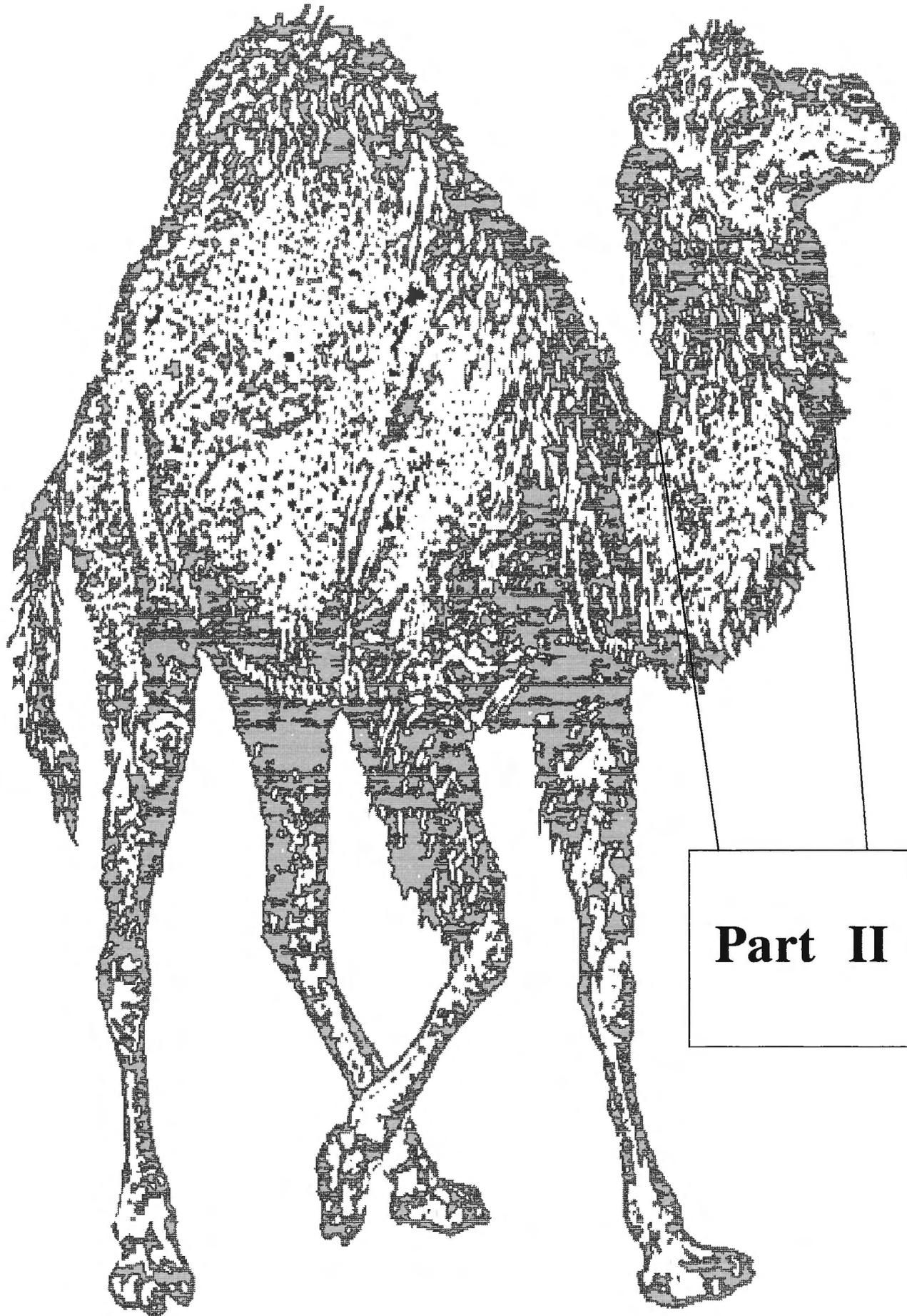
Part II

1.   INTRODUCTION

Field studies on large mammals have been the center of the etho-
ecological interest for about 30 years. Apart from the investigation of
primates and carnivores, research particularly focussed on a vast number
of ungulates in various habitats (overview in LEUTHOLD 1977). The
essential result of these investigations is the fact that the different
forms of the social organization can be interpreted as adapted to the
conditions of the environment (JARMAN 1974, KLINGEL 1975, WICKLER 1970).
Based on this approach, the social system of an inhabitant of extreme
desert habitats, like the dromedary, is of particular interest. The
results do not only provide an additional element of basic biological
research by making the social system known, but at the same time they
can contribute to an extended understanding of the studies which try to
look at the evolution of social behavior in relation to relevant
ecological factors.

In the suborder of the tylopodes (Tylopoda) only the genus Llama with
its two wild species guanaco (*Lama guanicoë*) and vicuna (*Lama vicugna*)
has been investigated in the field (FRANKLIN 1974, 1980, 1983). No
comparable studies about large camels existed until the beginning of
this investigation. The two-humped camel or Bactrian camel (*Camelus
ferus*) is only to be found as a wild animal in undeveloped desert areas
of Mongolia and China. Despite the political opening of China these
areas are difficult to get to for strangers, and long-term field studies
have not been possible up to now because of logistical bottlenecks. A
few isolated observations were collected and complemented by
speculations about the family life (ZHIRNOV & ILYINSKY 1986).

The dromedary (*Camelus dromedarius*) is only known in its domesticated
form; the wild form already became extinct in prehistoric times
(GAUTHIER-PILTERS & DAGG 1981). Field studies concerning the social
organization therefore have to be carried out on dromedaries that have
turned feral to find out in which way their family life is adjusted to
desert conditions, which are generally characterized by scarce resources
which are unpredictable with regard to temporal and spatial
distribution. When this project was begun, almost nothing was known
about the behavior of the Australian dromedaries. There were only the
publications of McKNIGHT (1969, 1976) with the emphasis on distribution
and size of population, and of NEWMAN (1975, 1979) who had primarily
worked on the food spectrum on the basis of stomach analyses of shot

animals. Some behavior patterns of domesticated dromedaries in Australia have been described by BARKER (1964).

First results concerning the social organization could be obtained in 1984 during a three month preliminary investigation (KLINGEL 1985). This was only in isolated cases based on individually known animals but the basic pattern of the social organization in winter became evident. Above all the pilot study made it possible to investigate the feasibility of a long-term study on feral dromedaries in suitable areas of central Australia. Observations regarding the behavior in the zoo as well as that of domestic and free-ranging dromedaries in North Africa have been described by PILTERS, later GAUTHIER-PILTERS (1954, 1956, 1959, 1960, 1974, 1975, 1981). One field study concerning the social and maternal behavior of domestic dromedaries in Kenia (SCHULTE 1988), (SCHULTE & KLINGEL 1991) exists. Since all previous observations were only done on domestic animals who are influenced by humans and who come from herds with an unnatural composition, an application of the results to free-ranging dromedaries is not or only partly possible.

The project in hand made it possible for the first time to carry out long-term studies in free-ranging populations on a larger number of individually known animals and at the same time doing comparative observations in other areas. The studies focussed on the investigation of the social behavior under natural conditions and the clarification of the social organization. Characteristic associations of individuals of different gender- and age-classes, their stability, and seasonal changes within the social associations could be documented. The respective mechanisms which lead to changes were analyzed and determined. A huge number of observations regarding the social behavior could be documented with the free-ranging population which is basically not possible with tame dromedaries due to domestic conditions.

From the sum of all observations an attempt was made to define the adaptive value of the social organization of the dromedary to the characteristics of the habitat. The ecological conditions during the entire study time and other ecological aspects of the investigated population are described in HEUCKE (1995). At the same time the main features of the social organization, like morphological and physiological features as well, are determined genetically (WILSON 1975) and can thus be considered a phylogenetic heritage. Therefore it can only be speculated which ecological conditions lead to the development of this form of social organization and whether the family life of the

recent dromedaries in the area in which they are to be found today could correspond to that of the extinct wild population.

2.   ADDITIONAL METHODS

2.1   Individual identification

Dromedaries can be recognized by external features and by individual foot prints. The individual identification in the region of Newhaven was granted with all animals after the end of the setting-in period. Each individual was given a name the abbreviation of which is stated in the text, e.g. Bd = Bierdeckel (beer mat), Hb = Hellbraune (light brown cow), H2 = Halsband 2 (collar no.2). A complete list of individuals with name, abbreviation, sex, age, duration of observation and particular marks is listed in the Appendix (Table AT0). In the social context the evaluation of foot prints gained particularly importance with the accidental findings of dead newborn calves.

2.2.   Determination of the age

With 16 immobilized animals the age could be determined more accurately. From the development of the teeth the determination of the age was done according to the method of RABAGLIATI (1924), which provides reliable results up to an age of 7 years. The age of adult animals with a complete set of teeth was determined with the degree of wear of the teeth. The age of the animals born during the study period in the research paddock is mostly known exactly to the day, otherwise to the week. With older calves and subadults, the age could be estimated by comparison of size. The age of the adult animals was estimated.

2.3.   Analysis of the group structure

At each sighting the total number of dromedaries and the respective group structure were recorded, distinguished according to gender and age-classes. The age-classes were defined as follows:

adult	> 5 years
subadult	1.5-5 years
calves	1.5 years or until weaning

The age-classes of the individually known animals in the research paddock could be determined exactly. When unknown animals were sighted their age was estimated.

2.4.   Observation methods

Because of the regular approaches, sometimes several times a day, the dromedaries became used to the presence of the observers. The animals increasingly allowed shorter observation distances, after six months eventually a distance of 20-30m which became even less during the course of the studies.

On checking tours in the research paddock the animals fitted with a transmitter together with their groups could be recorded daily, occasionally several times a day. Groups without transmitters could only be sighted irregularly, but their location could often be determined by the evaluation of tracks.

At each sighting the group structure, group size, general and individual activity patterns, social interactions, specific behavior, and the distance of individual animals to each other were recorded. During the activity phase the nearest neighbor of certain key animals was recorded at times. To check individual partner preferences the nearest neighbors during the resting phases were evaluated. The investigation for partner preferences was done adjusted temporally, i.e. because of group changes of the key animals the partners possible at times were checked for.

At migration activities the order of the individuals was noted down. In addition, the position (coordinates, vegetation type, openness of the terrain, condition of the ground) and weather conditions (air temperature, relative humidity, degree of cloudiness, wind velocity) were recorded.

In monthly intervals continuous observations were done with several groups over a period of 24-48h to determine individual time-budgets according to the interval method of ALTMANN (1974), and/or continuously, using a rest-light amplifier (NOCTRON II^R) at night. Besides the rhythm of activity, the main emphasis was put on social interactions, leadership of the group, communication, nursing times, and specific behavior patterns. The respective duration of the nursing could only be determined by measuring the time the calf remained at the udder. Therefore the measured nursing time does not quite correspond to the actual daily drinking time. During the activity phase the distances of the individuals to each other were estimated, during the resting periods the respective "nearest neighbors" of the animals were noted down. All behavior patterns were taken down, photographed, and documented on video, S-8, and 16mm-film.

3.   RESULTS

3.1   Social organization

The social organization of the dromedary is characterized by group-forming and non-territoriality. Cows live in cow-groups which are joined by a bull during the breeding season. Cows are only single in specific situations. Bulls live in bull groups, but adult bulls can live solitarily for longer periods of time.
Basic pattern and dynamics of the social organization are shown in Fig. 75:

(1) Bull groups occur throughout the year and consist of a changing number of adult and/or subadult bulls
(2) Outside the main reproduction time, in summer, the cows live in cow groups without an adult bull. These groups consist of adult cows with their young, other adult cows, and male and female subadults.
(3, 4) At the beginning of the breeding season in winter (April to May) almost all adult bulls are in rut. The cow groups are taken over by a bull who then herds them for three to five months.
(5) After taking over a group, the herding bull chases away all subadult bulls who then join bachelor groups. However, he tolerates the young cows who remain in their mothers' group.
(6) Before parturition the pregnant cow leaves the group and gives birth in a remote area. She then lives alone with her calf for up to three weeks.
(7) Mothers with young calves join together, forming the basis of a new cow group (core group).
(8) Toward the end of winter the herding bull loses interest in the cows and leaves them voluntarily. He then lives solitarily or joins other bachelors.
(9) Weaker adult and above all young bulls who did not have a chance to take over a cow group during the main breeding season come into rut a second time in summer or in fall. They then also herd cow groups but are driven away by the dominant bulls at the beginning of the winter at the latest.

Altogether 1.114 different dromedary groups were sighted and analyzed. 323 of these were bull groups, 517 cow groups with one or more adult bulls, 253 cow groups without a bull, and 21 mothers with newborn calves.

summer | summer

Fig. 75: Social organization of the dromedary

135

1. bull group
2. cow group
3. bull joins cow group
4. bull herds cow group
5. dominant bull expels subad. males, these join bachelor groups
6. pregnant cow segregates before parturition
7. cows with young calves form new core group
8. bull leaves cow group voluntarily
9. younger or weaker bulls herd cow group temporarily

= ♂

= ♀

Size of symbols corresponds to respective age class

3.1.1 Bulls

The number of members of all analyzed bull groups was between one and 25. The medium group size was 5 ±3, with an average of two adult and three subadult bulls. A classification of the group structure is shown in Fig. A14.10 in the Appendix.
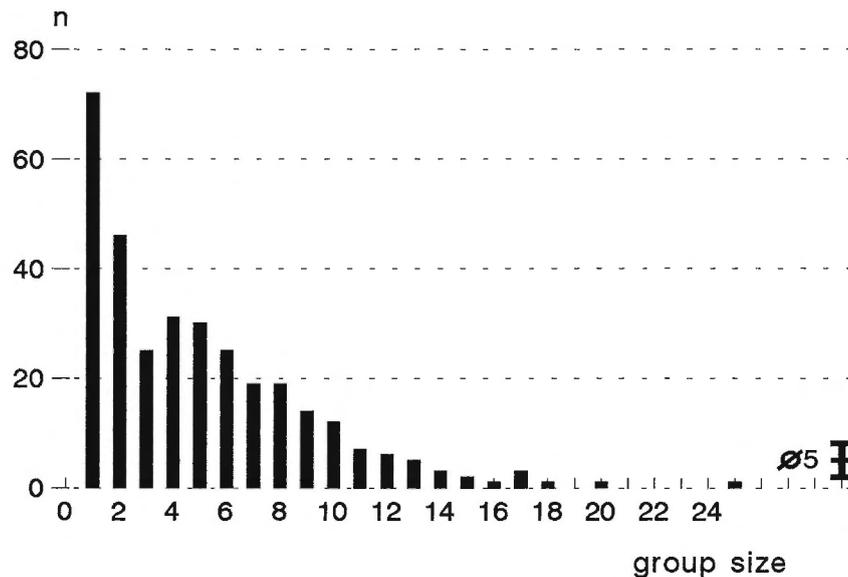
Fig. 76: Group size of all sighted bull groups and solitary bulls
(n=323)

The solitary bulls are nearly exclusively older animals who join other bachelors mostly only for a short time. Bull groups are generally very instable. The members of one group occasionally even changed several times a day. Larger bull groups often split up into two or more smaller groups, whose composition kept on changing. When bull groups encountered each other, an exchange of the members regularly took place. Even bulls who had grown up together and who had been chased away from the cow group by the new group-holder as subadults at the same time and then had joined a bachelor group together, had no discernibly stronger relationship with each other than with other conspecifics of the same age. Bull groups thus are random temporary associations whose stability is determined by the frequency of encounters with other dromedaries and therefore depends on the population density. The longest period of time one bull group had the same members because of a lack of contact to conspecifics was 21 days. On average bull groups remain unchanged over 4-5 days.

Fig. 77 shows the pattern of social relations of adult bulls with five examples. With adult bulls the continuous change between living solitarily and temporarily belonging to a bull group becomes particularly obvious. The only stable phase in belonging to a group can be observed during the rut, when the bull herds a cow group. However, in exceptions the bull can remain inactive in a cow group for a longer period of time, which was particularly obvious with the bull Bd. Outside of the rut he remained steady with the cow group without showing the typical behavior of a group-holder. At this time it had been proved that the group did not have any contacts to other dromedaries; it can be assumed that Bd remained with the cow group for such an unusually long time for this reason. A few months later it became clear that he really was a fully grown up strong bull when he took over another cow group. When fighting for the cows, Bd was injured severely by the adult bull aA so that he then died three days later. Generally adult bulls tend to have only short-term associations with other dromedaries without individual preferences.

The social life of seven subadult bulls is shown in Fig. 78. Per age class each three of them had grown up in the same cow group, only Ch lived in a group with other young females as the only young male. Following the nursing phase some young bulls remained in the original group until this was taken over by an adult bull. In the case of the young bull Gu this phase of a stable life in a cow group with calves was particularly long since his mother died (of old age) in January 1988. Gu remained in the cow group until he was 22 months old and was then chased away by the new group-holder like the other young bulls. Subsequent to the initial stable phase the membership to a group of all subadult bulls is extremely changeable.
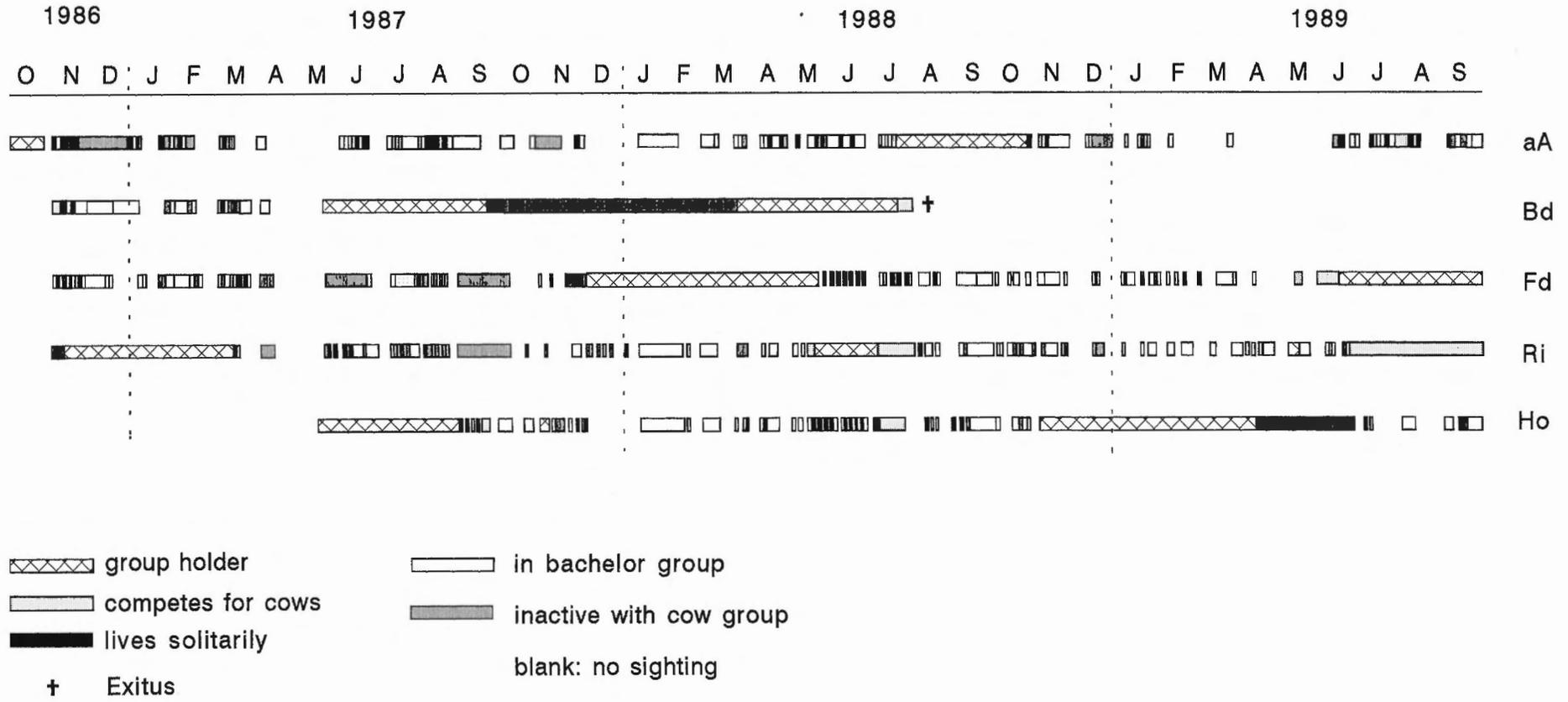
Fig. 77: social life of 5 adult bulls

1986	1987	1988	1989
O N D	J F M A M J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S

KS
TS
RS

12 months old

Te
Sn
Gu

2 months old

Ch

in cow group with calves   nursing phase

in cow group without calves   in bachelor group

*   newborn   blank: no sighting
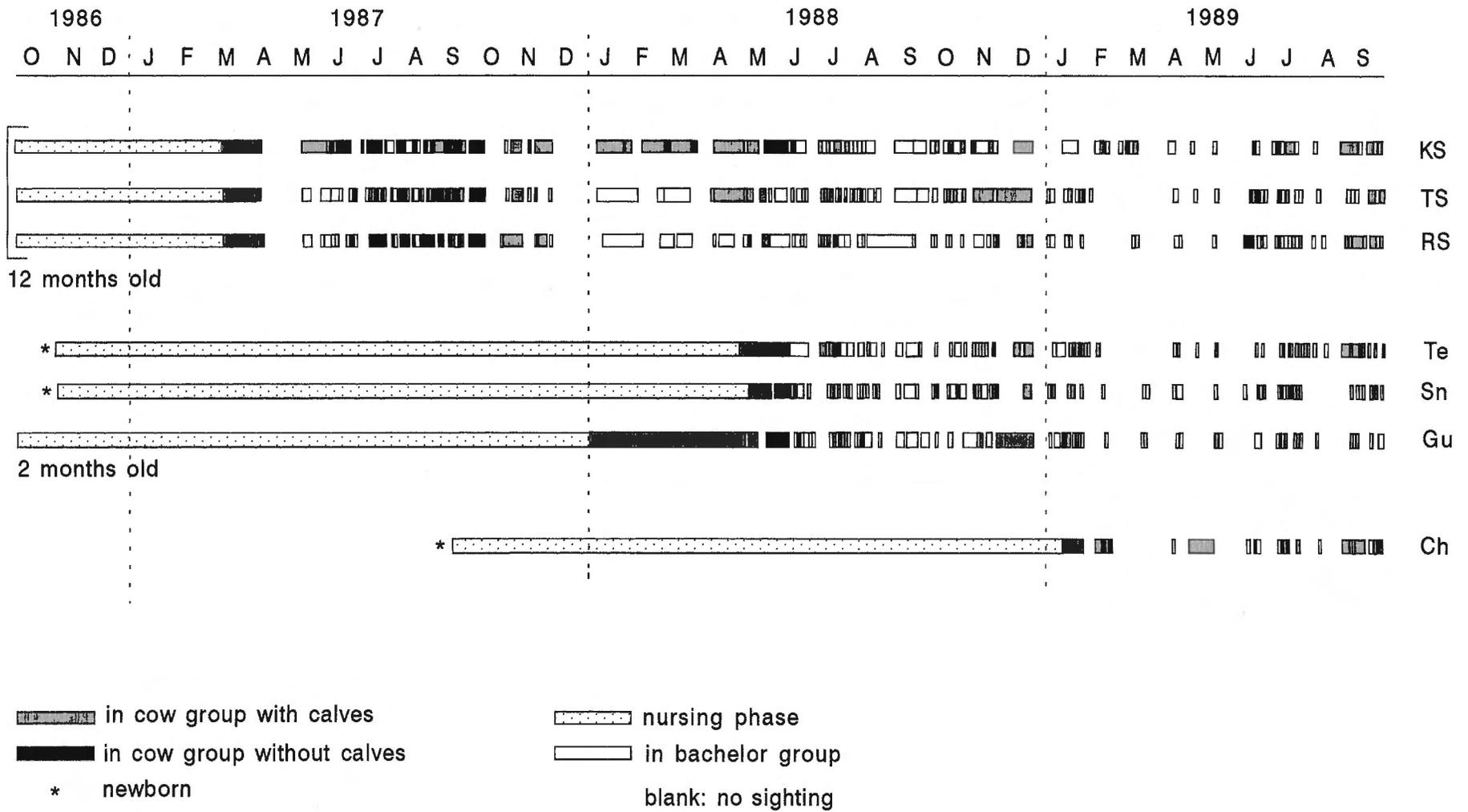
Fig. 78: social life of 7 subadult males

3.1.2 Cows

A total of 770 cow groups was analyzed. The 21 sightings of various mothers with calves are not taken into consideration here. For the evaluation with regard to group size and structure a distinction was drawn between cow groups with and without an adult bull.

Cow groups without a bull consisted of 1-27 members. The medium group size was 9 ±5 with an average of five cows, two subadults, and two calves. The group structure of all sighted cow groups without a bull is shown in Figures A14.7-9 in the Appendix.
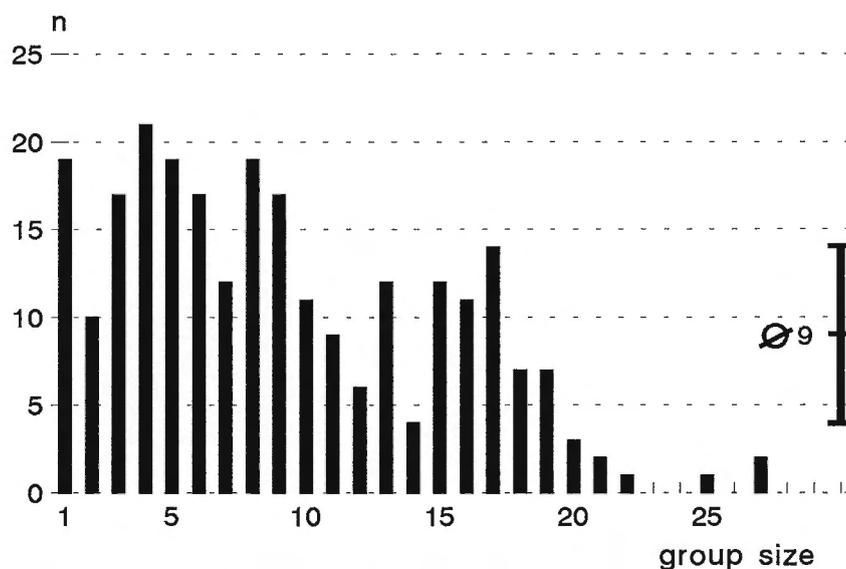
Fig. 79: Group size of all cow groups without a bull and frequency of sightings of solitary cows (n=253)

Cow groups with a herding bull consisted of two to 45 members, the average group size was 14 ±7 with one bull, 7 cows, 4 subadults, and two calves. The group structure of all analyzed cow groups with a bull is shown in Figures A14.1-6 in the Appendix.

Normally only one bull herds the cows. Cow groups with 2 to 7 adult bulls (Fig. A14.4-6) occur in transitional phases of up to 8 weeks during which the bulls compete for the cows.
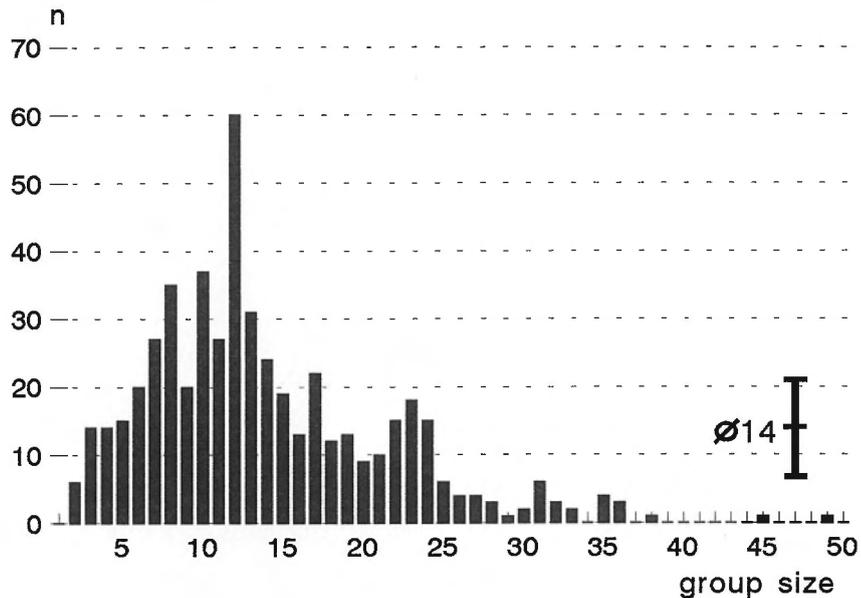
Fig. 80: Group size of all sighted cow groups with a bull (n=517)

Dromedary groups are dynamic concerning the duration of membership of individual members. Neither bulls nor cows have obvious individual relationships among each other or with each other. The only durable bond exists between the cow and her calf as long as it is nursed. While bull groups are purely random short-term associations, the cow groups show mechanisms that strengthen the bond between the individuals and thus lead to the stability of the groups.

Only during the rut the bull who herds the cow group has an extremely stabilizing effect. The bull prevents any closer contact of his group members with other dromedaries. Only cows can join at any time. Therefore, in this time the group structure remains largely constant and is only changed when pregnant cows leave shortly before the birth of a calf (see below). In contrast to the group stability forced upon the cows by the bull there is the voluntary bond between cows. Cows with calves of one age-class develop particularly strong bonds. They form the core of a cow group and stay together even without a herding bull until the calves are weaned. The time lactating cows lived together could be determined exactly with three core groups and was 15, 16, and 18 months. The core groups can be joined by other dromedaries for a shorter or longer period of time.

Cows showed individual instable phases regarding the membership to a group which are primarily due to reproduction biology.

1. Parturition: Before the birth of a calf, dromedary cows isolate themselves from their group if this is herded by an adult bull (n=42). The highly pregnant cow then segregates, in one case as far as 15km, and gives birth in a remote area of the home range with good cover. However, if no adult bull is with the group at the time of birth, the cow does not segregate (n=3). Mother and calf are nevertheless being isolated since the group moves on. Cow and calf live by themselves for up to three weeks after the birth but then the cow actively looks for other mothers with young calves. In the meantime mother and calf can join any group for a short time. Changes do not take place any more when she has found one or more mothers with calves. From this joining together the core group develops which remains stable for 15 to 18 months, corresponding to the nursing phase of the young animals.

2. Weaning: In summer, outside of the rut, the weaning phase of the young animals leads to frequent changes of groups by the mothers. A calf is actively being weaned by its mother by keeping it from nursing. Normally the calves are persistent and try to force further nursing by constantly pressing their mothers. Obviously because of that the mothers regularly left the core group, roamed around and were to be found in various groups. If the calves followed their mothers, this happened again. If the weaning phase is in winter these changes do not take place because of the activity of the herding bull (Fig. 75).

3. Prenatal restlessness: In addition to weaning, a prenatal restlessness can trigger off further fluctuations. In 7 cases cows segregated noticeably (3-8 weeks) before the date of birth from their groups and were then either alone or with other groups, preferably in those with young calves. They avoided groups with bulls in rut, though.

Cow groups without a herding bull are open for all conspecifics. Their stability therefore depends on the frequency of encounters with other groups. During the summer, i.e. outside of the rut, considerable changes in size and composition of the groups are typical. However, core groups consisting of mothers with calves remain stable.

Some adult cows that did not have calves for a longer period of time also lived together relatively stable (n=6). They did not change the group actively for >2 years since the above described instable phases

were not relevant here. However, the group was subject to strong changes because of immigrations and migrations particularly of subadult bulls.

The social life of five adult cows who could be observed over the entire period of studies, illustrates the stability and dynamics of the social relationships and their causal factors (Fig. 81). More examples of the lives of adult cows are in the Appendix, yet without taking into consideration their membership to a group (Fig. A.15).

The cows N16 and K1 are having their calves at the beginning of November 1986. They join together in the middle of November and form the core of a cow group together with two more mothers for 18 months. Only from May 1988 on their fate is different. The cow N16 remains in the group which had been taken over by a bull in April. Her male calf is being chased away by the new group holder in May so that weaning is superfluous. N16 only leaves the group when she has the next calf and shortly after that stays steadily in the next core group whose group-holder still changes several times. The cow K1, however, is in a group without an adult bull from the middle of May 1988 on. K1 changes groups often which at first is due to the weaning of her calf. From August on she lives in a small group consisting of one bull and another cow. In early October 1988 K1 has a calf that does not survive due to infanticide. In November 1988 the bull is being replaced and K1 is taken over into the group of the stronger bull. In the middle of June 1989 another change of bulls takes place, the composition of the group remains unaltered.

At the beginning of the investigations the cows RT and T2 already had one-year-old calves. Between November 1986 and January 1987 they temporarily show some group changes together, the causes of which could not be clarified. Only during the weaning of their calves did both cows change the group several times independent from each other but later join again. Both cows showed a prenatal restlessness which is correlated with a clear changing phase. The calf of the cow T2 does not survive, but she nevertheless joins the core group and remains there steadily without a calf until she has her next calf in October 1988. In comparison, RT remains steadily in the core group until the weaning of her calf. Before the birth of her next calf another changing phase due to prenatal restlessness occurs.
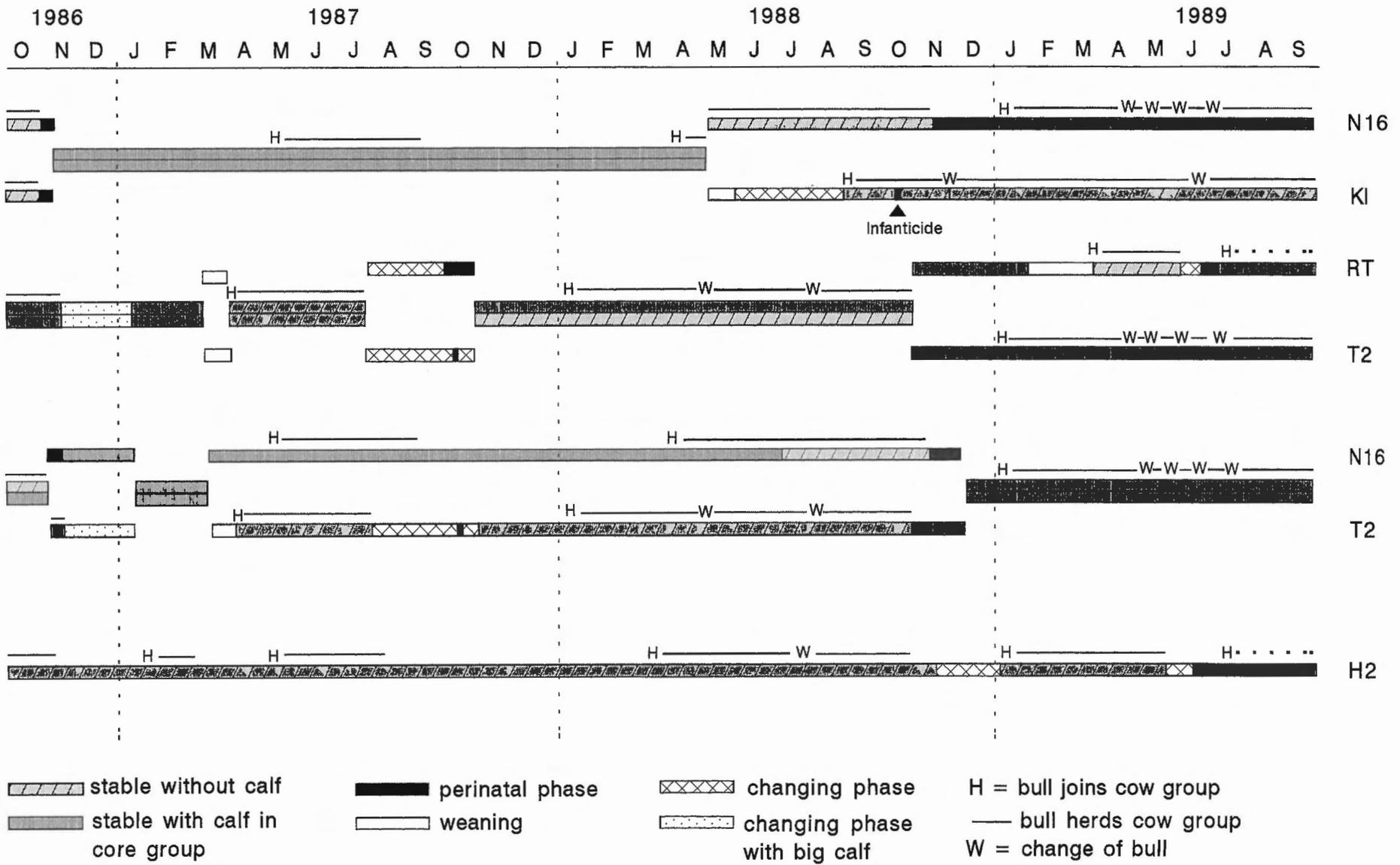
Fig. 81: social life of 5 adult cows

The common phases of life of the cows N16 and T2 are shown additionally to demonstrate an unusual case: for the longest part of the study period they live in different groups and only after the birth of their second calves in November 1988 join up in a coherent long-lasting core group. The observed joining together of the cows with calves from the previous year (T2) with the core group with young calves (N16) in Jan./Feb. 1987 is uncommon and does not occur again in any of the following observations. It has to be taken into account that at this point in time all animals were in the 18km^2 horse paddock where they met much more often than in the research paddock.

The cow H2 has been without a calf since the beginning of the studies. She does not change the group actively over a period of 25 months. Only in summer 1988/89 a short changing phase occurs for unknown reasons. After that she remains steadily in one group. Following another changing phase which is now due to prenatal restlessness, she has a calf in June 1989 and joins a core group. The cow RT with her calf later becomes a member of this group, too.

Fig. 82 shows the social life of 8 subadult cows. The end of the nursing phase of 7 animals and thus their mothers were known. At the beginning of the studies N8 was already app. two years old and her mother could therefore not be ascertained. With four female calves the end of the nursing phase was in summer, a time where the cows mainly live in groups without a bull. Here the mothers segregated and their daughters tried to follow them with varying success.
This leads to the changing phase of the cows Mo, Pa, B and Ko. As soon as the young animals managed to get into a group with conspecifics of the same age they remained there. The following changes in the group structure were not initiated actively by the subadult cows but were due to the separation of group members by a rutting bull. In the other three cases (Ka, Tö, In) the daughters remained stable in the group, which their mothers eventually left. In two cases this only happened at the birth of the next calf, but in one case clearly before that (Ka).

Fig. 82: social life of the subadult cows

In the research paddock a total of 472 changes in the structure of cow groups was observed and the causes were recorded. Short-term (<2 days) immigrations or migrations were not taken into consideration (Fig. 83):

In 12.9% of all observed cases adult bulls caused the change in the structure of cow groups. Particularly during the rut the bulls are constantly looking for cows or cow groups and temporarily join them. In most cases (94.5%) they are being chased away by the group-holder and as a result attempt to join another group.
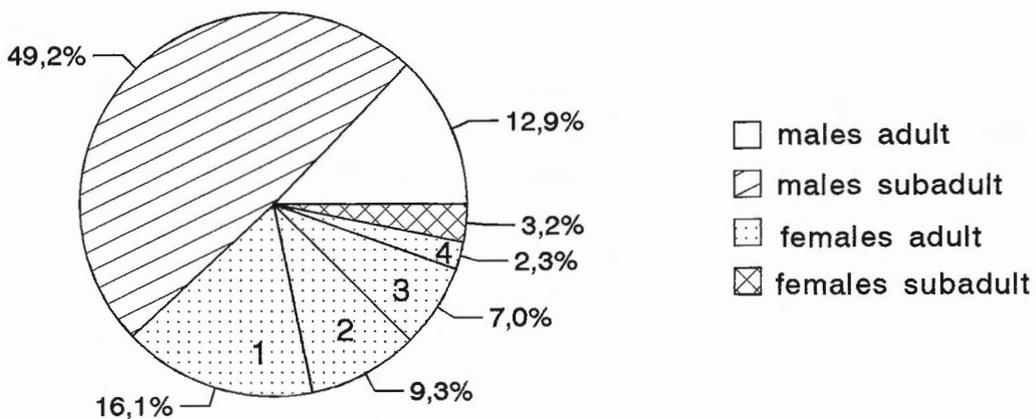
Fig. 83: Cause of changes in the structure of cow groups (n=472)

Subadult bulls tend to change groups frequently and cause the most fluctuations with 49.2%. After being chased away from their original group they attempted to join other groups, preferably those with younger dromedaries. They were being chased away from these, too, and eventually joined bachelor groups.

Adult cows contributed to a change in the group structure at 34%. The factors which set off changes are mainly found in the above described individual instable phases (1). In some cases the causes could not be discerned. The changes were caused at 9.3% by the segregation of the cow before the birth of her calf (2).

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Single cows with small calves show tendencies toward frequent group changes (3). This unstable behavior occurs when a cow with her calf is looking for other mothers with young calves. She then temporarily joins others. Furthermore, relatively frequent changes in groups of each two cows with calves of the same age were observed, who repeatedly joined other cows without calves, but then segregated again (4).

Subadult cows only caused a change in the structure of other groups at 3.2%. 13 of the 15 observed cases were to be noted with subadult cows whose weaning phase was in summer.

3.2   Behavior

3.2.1 Bulls

The most distinctive behavior of the adult bulls is determined by the rut. The rut lasts six months on average and with the majority of bulls occurs between April and September. In the research paddock 15 adult bulls were observed. Fig. 84 shows the summarized seasonal distribution of rutting behavior.
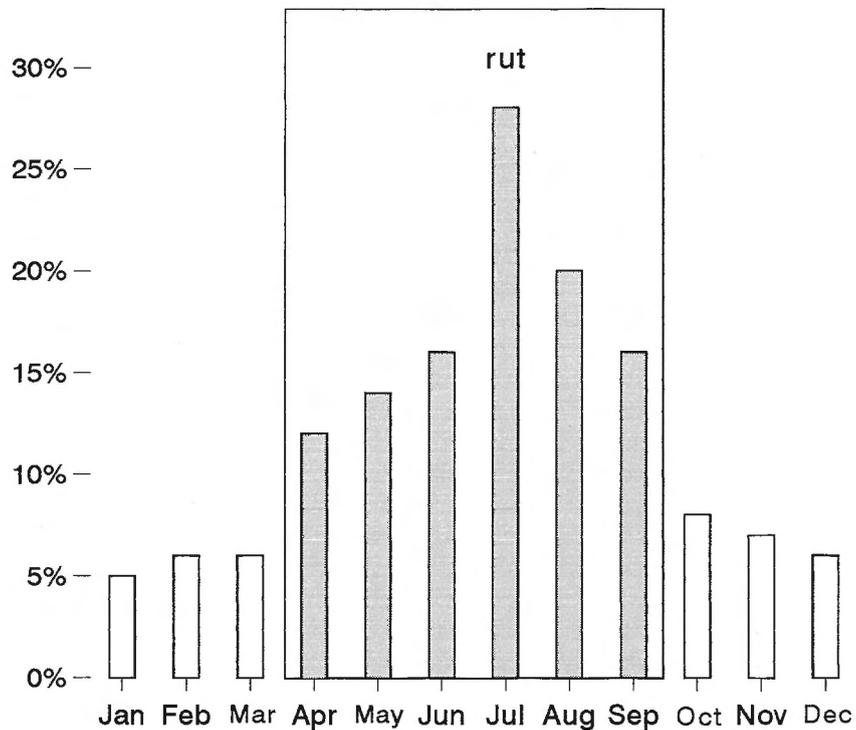
Fig. 84: Percentage of rutting behavior of 15 adult bulls, total of
observations of adult bulls = 10.789

Externally the rut can more or less be seen by the secretion of the occipital glands, often by a swelling of the testicles, but always by the typical behavior. Rutting behavior is only shown when cows are present. Usually it occurs at the age of 4-5 years, in individual cases it can already take place from the age of three up.
The rutting periods of the adult bulls last between a few weeks to up to 7 months and occur in irregular intervals of 3-17 months (Fig. 85). The duration of the rut depends on internal and external factors. The constitution and the hormonal condition of the bull are apparently decisive but also his self-assertion toward competitors. At the

beginning of the main breeding season in winter more or less all adult bulls are in rut. The strongest ones then take over a cow group and defend it against rivals. The remaining bulls try to compete for the cows but in 94.5% (n=191) of all cases are being chased away by the group-holder and either migrate or stay at the periphery of the group. Depending on his constitution the group-holder herds the cows for 3-5 months, but he can be replaced by a competitor before that.

Some bulls that do not have a chance to take over a cow group during the main breeding season come into a second rut in spring or in summer. For lack of competitors they then succeed in herding a cow group. In some cases these bulls even succeed in reproduction (n=5). Mostly the bulls stayed in bachelor groups or solitarily in summer, even though there were contacts or even short-term associations with cows.

3.2.1.1   Individual rutting phases

Dromedary bulls have individual reproduction phases that are synchronized only in part. Case studies of the rutting phases of 9 adult bulls in the research paddock are shown in Fig. 85. The first five animals are shown in detail in Fig. 77 concerning their social life.

1. The bull aA has been in rut since the beginning of the studies in August until the middle of October 1986 and herds a cow group which he leaves voluntarily. In the entire year 1987 the bull does not show any interest in the cows; he lives in bachelor groups or by himself, in summer now and then inactively with cows. Only in winter 1988 he comes into rut again and herds a cow group from the end of July until the end of October which he leaves voluntarily. In 1989 he occasionally competes for the cows but cannot assert himself.

2. The bull Fd is in rut for a short time in winter 1987, but takes over a cow group for the first time presumably in summer 1987/88 which he has to hand over to a stronger competitor (Ri) at the beginning of the main breeding season. After having been out of rut for 10 months, Fd again takes over a cow group in winter 1989 and defends it until the end of the investigations.
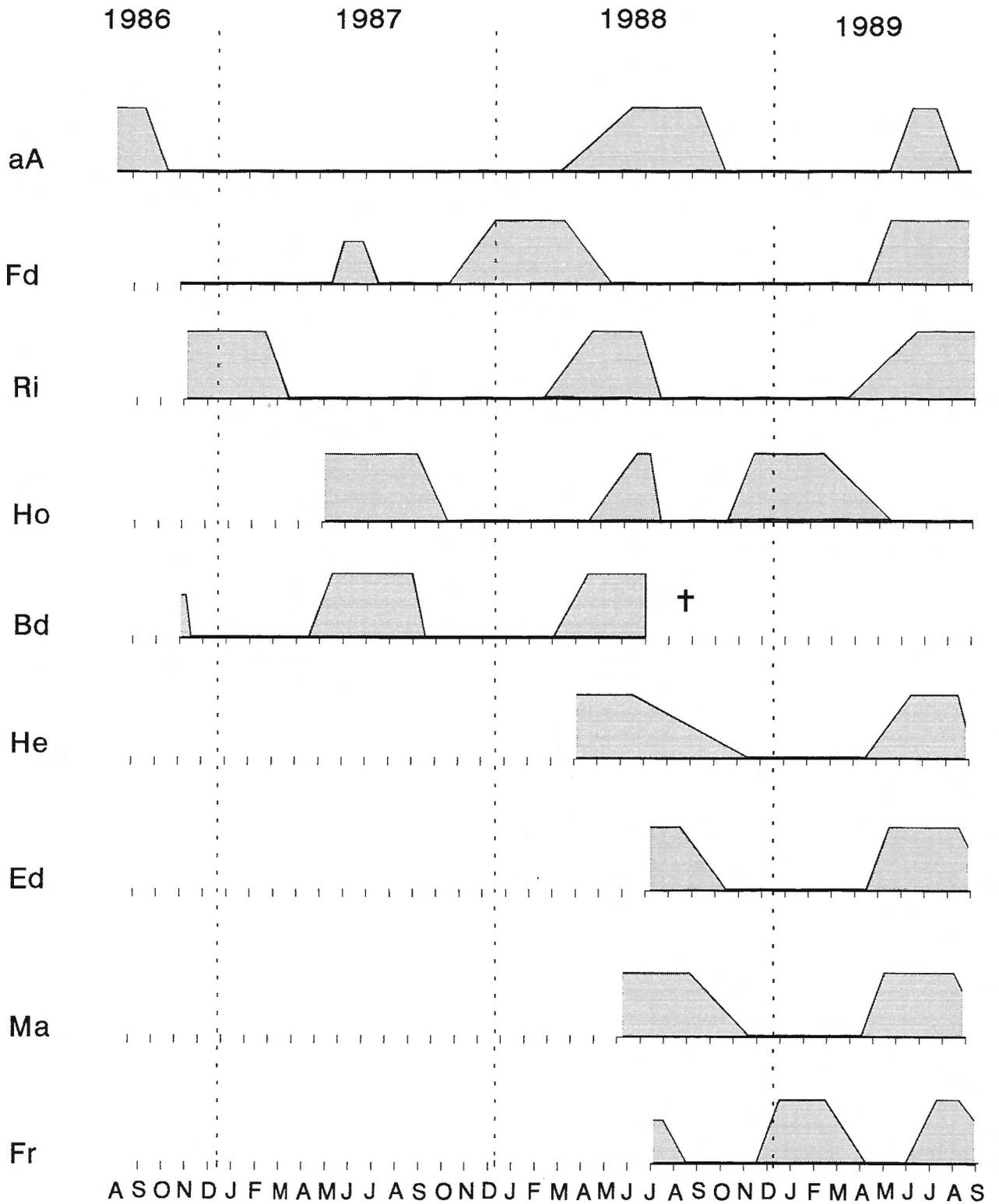
Fig. 85: Rutting phases of 9 adult bulls. The height corresponds to
the intensity of the rutting behavior

3. The bull Ri is in rut in summer 1986/87 and herds a cow group from November until March which he leaves voluntarily. After having been out of season for 12 months, Ri can prevail over the bull Fd in May 1988 and takes over his cows for two months but then has to hand them over to the bull aA. In the next winter Ri competes for cows but he does not succeed to prevail over the group-holder Fd.

4. At the main breeding season in winter 1987 the bull Ho herds a cow group for four months. In the following winter of 1988 Ho competes for cows but cannot take over a group. He comes into rut for a second time in fall, herds cows for five months, then stays inactively with the group and eventually leaves it voluntarily. It is unusual that this took place during the main breeding season, but the bull was injured, though.

5. The bull Bd is in a subsiding rutting stage in November 1986 when he immigrates into the research paddock. In Winter 1987 he becomes group-holder from May until September, afterwards stays inactively with this group and is being chased away in April 1988 by the bull He. Immediately after that Bd takes over another cow group which had been without a bull until then, and he defends it until July. Bd dies in July 1988 because of an injury from a fight.

6. The bull He immigrates in April 1988 and is the owner of a cow group until November. By the end of this phase he shows a noticeably diminished rutting behavior and hands over his cow group to the bull Ho without much resistance. After having been out of rut for 5 months, he becomes group-holder again in the next winter.

7. The bull Ed immigrates in July 1988, at first lives in bull groups but is clearly interested in cows. In August he first takes over two cows whom he surprises during the births of their calves; the calves cannot follow and die. This group is joined by more cows with calves. Ed herds them until the end of October, subsequently stays inactively with them and eventually leaves them voluntarily in January. After having been out of season for six months, Ed again takes over a cow group from the bull Fr in the next winter.

8. The bull Ma immigrates in June 1988 and is very interested in cows. In August he finds two cows that he herds until the beginning of November but then leaves voluntarily. In winter, after having been out of season for six months, Ma can take over a cow group directly at the beginning of the breeding season which he defends until the end of the studies.

9. The bull Fr is the youngest of all bulls shown here. His age is estimated at 5-6 years in 1988. He is in rut when he immigrates into the research paddock in winter 1988 but has no chance to take over a cow group. In summer Fr finds a cow group without a bull and herds it until April 1989 when he has to hand it over to the bull Ed. After being out of rut for only a short time, Fr competes for cows again in the main breeding season of 1989 but cannot prevail over the older bulls.

3.2.1.2   Rutting behavior

During the rut bulls show a characteristic behavior. The "gurgling" whose acoustic component has been described as "blo-blo-blo"-call by GAUTHIER-PILTERS (1956) also occurs in other functional contexts when the animals are agitated. A distinct increase occurs during the rut. The entire course of the behavior is as follows: The bull first bows his neck and head, and in this bowed position begins to utter a muffled guttural growling, then with a jerk moves his head back while the head remains pointed upwards, mostly in an ankle of about 45° to the longitudinal body axis. The initially low growling becomes a piercing gurgling sound as the head is moved upwards. In an upright position of the head the sound can be repeated several times. If the animal is very agitated, a sac of the soft palate, the Dula (arab.), is being extruded (Fig. 86) and blown up, and large amounts of saliva foam can be produced.

With the low frequency of the gurgling sound the bulls can be heard over large distances, clearly more than 2km during a calm. Dromedary bulls react to the purely acoustic signal with attention, checking of the surroundings and specific heading for the supposed rival. By playing sound records this behavior could be triggered off. The acoustic component of the gurgling thus has a key function. Depending on the situation it is being supplemented and enforced by respective optical signals.
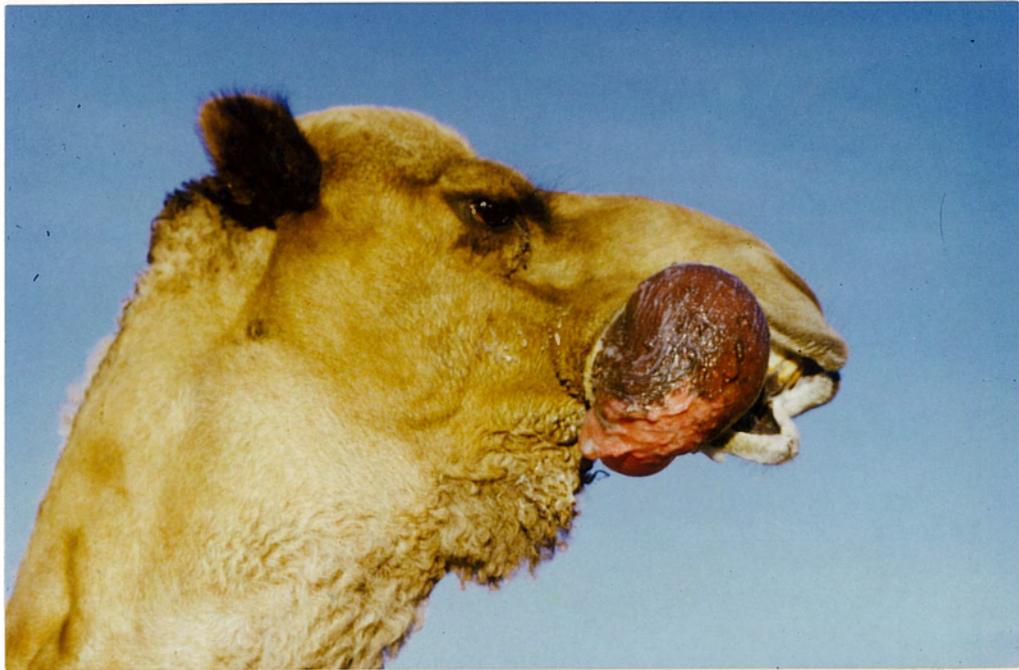
Fig. 86: Extruding of a sac of the soft palate when gurgling; bull =
        Ri

Toward conspecifics of the same sex bulls show a lot of agonistic
behavior patterns the elements of which are mainly ritualized. Only in
very rare cases a fight arises.

The avoidance of contact by dominance display is an essential
instrument before confrontations: Group-holders try to intimidate
approaching competitors already over larger distances by optical and
acoustic signals and so keep them away from the cow group. In open
country this is done when the approaching rival is app. 1km away.
First the above described gurgling is shown, which already persuades
weak or less strongly motivated opponents to retreat. In addition the
herding bull demonstrates with some optical signals: he paces up and
down in front of the cows, extrudes his dula in a "demonstrative" head
position and produces large amounts of foam. Then he stands in front
of his group and threatens toward the rival (Fig. 87). To support this
he shows the tail-lashing ritual (Figures 89 & 90) even from larger
distances.
At a further approach the herding bull trots toward the rival with
short steps in a displaying manner. While doing this he holds his neck

and head stretched out low, with each steps bangs upper and lower jaw together so that it can be heard from a distance and produces foam (Fig. 88).

Fig. 87: Group-holder (He) displays his dominance by threatening posture toward the rival

Fig. 88: Group-holder (Bd) trots towards rival. Note the skinniness

As soon as the rivals stand face to face both gurgle with tossed heads and eventually stand parallel to each other. They continue to gurgle, straddle their hind legs and begin with the tail-lashing ritual (Fig. 89).

Fig. 89: Broadside displaying of competing bulls (Bd & Ho) with beginning tail-lashing ritual

Both front legs are stretched out, and neck and head are erected. Depending on the excitation the hind legs are more or less straddled. The tail is being lashed up and down rhythmically, when lashed down far below the abdomen. The bull urinates while doing this and distributes the urine on his hindquarters when lashing up its tail (Fig. 90). Occasionally they defecate. In addition to the tail lashing ritual the bull repeatedly wipes the back of his head across his withers and distributes the secretion of the occipital glands. By doing this he impregnates himself with his own scents which have a very pungent smell for humans. With the jerky head movements large amounts of the white saliva foam are spread across his own body and the surrounding area.

The tail-lashing ritual is supported by gurgling, blowing up of the Dula and further foam production at the mouth (Fig. 91). In addition the bulls grind their teeth. The sounds which are produced by this are

typical for increased excitation and also occur at the copulation foreplay and during the copulation.
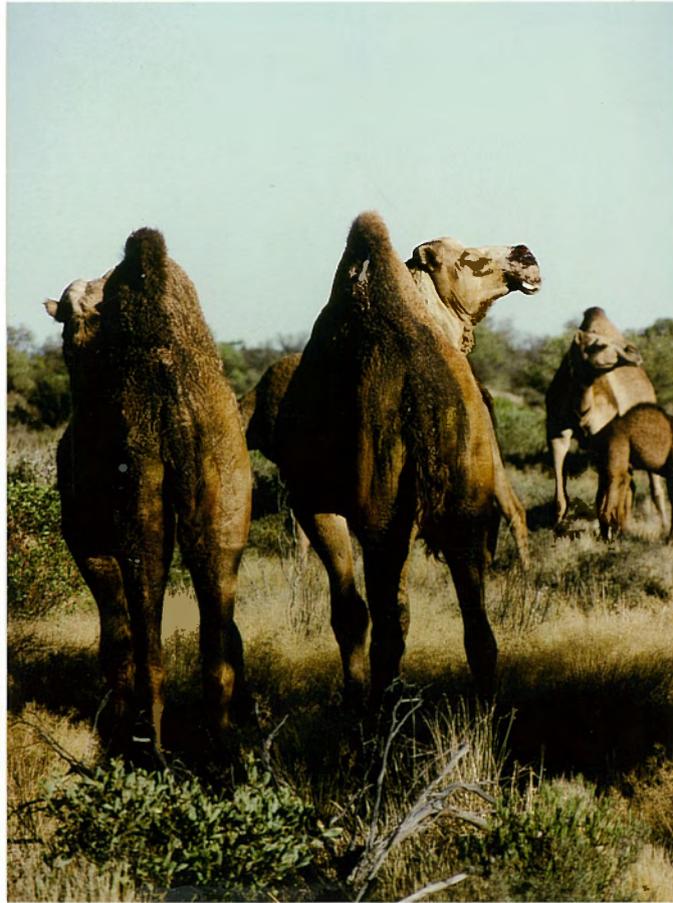
Fig. 90: Hindquarters of bulls perfumed with feces and urine (Fd & Ri)

The next increase in the confrontation is the parallel walk which has been termed "promenade à deux" by KLINGEL (pers. comm.), in which the group-holder tries to lead the rival away from his cows and to drive him away. Both bulls often walk in step next to each other (Fig. 92) and display their dominance by a threatening posture, blowing up the Dula, producing foam, and ritualized urinating with tail-lashing. During the promenade they jostle against each other with their shoulders, try to push each other away and occasionally snap at each other. The promenades are interrupted for a short time by head and mouth wiping which can be done by both bulls at the same time or one after the other (Fig. 94). For that purpose they slightly bend their front legs, bow the neck, turn the head, and use smaller shrubs, tufts of grass, or the ground to do sweeping wiping movements with the backs of their heads. The secretion of the occipital glands is being

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distributed and in addition foam is being wiped off by wiping the mouth at the same time. Promenades can drag on for several kilometers and the animals do not even get out of the way of larger shrubs. These are then often marked with urine. The bulls place their hindquarters directly in the shrubs, urinate and distribute the urine by carrying out sideways sweeping movements with their hindquarters. When using smaller shrubs they stand over them and urinate on them.

During the promenade the superior bull can show a strange display (Fig. 95). He all of a sudden throws himself to the ground, rolls while moving his legs vehemently, throws his head back and spreads saliva foam and the secretion of the occipital glands on the ground, or on shrubs or tufts of grass. The rival is standing by almost unheeding. When the partners are equally strong, though, the rolling is sometimes done at the same time (n=5) or after one another (n=8). No reactions of conspecifics to the markings which are produced by wiping and rolling were observed.

Fig. 91: Increased excitation of competing bulls (Bd & aA). The hind
legs are clearly spread farther apart than at the beginning of
the tail-lashing ritual (ref. Fig. 89)

Fig. 92: Promenade à deux of the bulls Bd & Ho

Fig. 93: Stronger excitation increases the foam production; here at
the promenade à deux (Bd & Ho)

Fig. 94: Wiping during the promenade, Bd is wiping, Ho is walking

Fig. 95: Rolling as a demonstration of superiority, bull = Bd

The duration of the promenades obviously depends on the relative strength and the endurance of the involved bulls. Periods lasting between a few hours and up to two days are absolutely normal. However, in extreme cases they lasted - with interruptions - up to eight weeks.

Usually these promenades cause one of the involved bulls to give up and leave. But if all ritualized sequences of behavior do not lead to a decision, a fight can erupt.

Serious fights are extremely rare. During the whole study period only three were observed. The previous development could be documented in two cases. In the third case the fight between two herding bulls was initiated on the part of the observers. In exceptional situations a fight can thus even erupt between two group-holders. Usually herding bulls avoid closer contact to each other. The other two observed fights developed from long lasting promenades of equally strong partners, and the elements of which became increasingly aggressive. In one case the fight was initiated by an aggressive chase (Fig. 96 & 97). As soon as the bulls stopped they repeatedly pressed against the side of the body of the rival, snapped at his mouth or nose, and began the neck wrestling (Fig. 98).

Fig. 96: Aggressive chase before the fight, Ri chases aA

Fig. 97: Biting intention during the aggressive chase, Ri

Fig. 98: Initiating phase for the neck wrestling, Ri & Fd

During the neck wrestling the rivals first stand facing each other, later they stand diagonal to each other. The bulls constantly attempt to push down the rival's neck, bite each other in the nape of the

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neck, and the throat, lean over the front of the rival's body from above and at the same time snap at his front legs. This leads to an aggressive wrangling, accompanied by loud bellowing (Fig. 99), while both attempt again and again to bite the opponent's front legs but also his belly or genital organ (Fig. 100).

Fig. 99: Aggressive wrangling at the neck wrestling, aA & He

Fig. 100: Biting intention at the fight, aA & He

All movements are directed at making the opponent fall and standing over him. If this is achieved, the stronger bull pushes on his rival's neck with his own neck and thorax (Fig. 101).

Fig. 101: Final element of the fight; termed "strangling phase" by
GAUTHIER-PILTERS (1954), He strangles aA

Fig. 102: Mutual blocking; the bull with the stretched out hind legs
(He) tries to remove his leg from the clutch of the rival (aA)

Apart from the already known types of fights, neck wrestling, pushing, and biting (GAUTHIER-PILTERS & DAGG 1981), a new variation, the blocking, could be observed and documented by photographs and film (Fig. 102). The opponent, who for this purpose lets himself fall down, clutches the front foot of the rival with his tucked under front leg so that both immobilize each other for some time. In the observed case, the involved bulls were not able to get free for 20 minutes. Even in this position the bulls still snap at each other aggressively and can hurt each other seriously (Fig. 103).

Photo Fig. 103: Aggressive biting during the mutual blocking, He & aA

During the breeding season the herding bull usually prevails over his rivals. Rarely do fights lead to his replacement, occasionally to a splitting up of the cow group. The frequent biting wounds are relatively harmless and heal up after several weeks (Fig. 104). Fights can have lethal consequences, though: During a fight an opponent (Bd) was bitten in the Dula; it was pulled out far and torn off in part at the base of the muscle. The bull died three days later as a result of a sepsis (Fig. 105). During the violent biting fights it can happen that an opponent gets hold of the lower jar of the other one so that the jar breaks off in the area of the diastema. The front part of the lower jar then hangs down and the animal is eventually not able any more to eat sufficiently. Altogether three bulls with broken lower jars were observed.

GAUTHIER-PILTERS (1954) describes that the neck wrestling of the dromedary bulls is generally directed at strangling the opponent or breaking his spine. In the research paddock lethal effects of this variation of fight were not observed. One death of a bull by strangling in a camel farm in Alice Springs was reported, though (SMAIL pers. comm.).

Fig. 104: Harmless bite in the area of the nose of the bull Ri
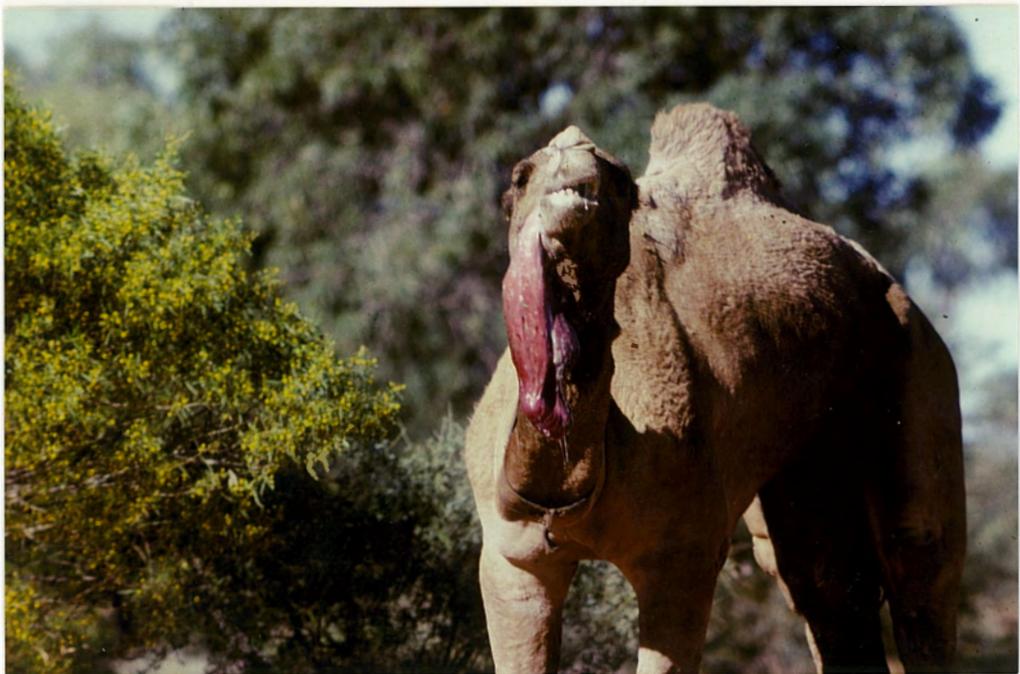
Fig. 105: Torn out soft palate of bull Bd, lethal injury

At the approach of subadult bulls who are inferior to the group-holder from the start, he displays his dominance much less. He mostly attacks without advance warning. For this purpose he gallops toward the other bull with his head held forward, upper and lower lip turned out, and his neck stretched out, held almost horizontally (Fig. 106).

Fig. 106: Bd chases away inferior rivals

The inferior bull instantly turns to run away and the group-holder then pursues him at a full gallop, often for several hundred meters (up to 600m). When bachelor groups approached, the strongest of the group was always attacked specifically, the others fled simultaneously. As soon as the supposed rivals are chased away, the group-holder returns to his cows in a demonstrative posture, with highly erected head, gurgling loudly, and producing foam (Fig. 107). After his arrival, the bull stands in front of the cows and displays his dominance in the above described manner with gurgling and tail-lashing in the direction of the driven away bull or bulls.

Weaned young bulls are being chased away by the group-holder this way a few days after he has taken over the cow group but without a dominance display in front of the cows. Young bulls that are weaned while the bull owns the group are tolerated and herded, too. The group-holder does not tolerate play fighting between male calves or subadult bulls right next to himself. He threatens the young bulls

shortly by uttering growling sounds in a low frequency with his body stretched out. If the young bulls ignore this, he separates the playmates immediately and by biting them aggressively without any advance warning. Some young bulls got gaping wounds as a result of this, particularly in the area of the thigh.

Fig. 107: Bull Ed returns to the cow group displaying his dominance after successfully driving away a rival

Toward cows friendly as well as aggressive rutting behavior is shown. Taking up contact: If cows are present, bulls first demonstrate impressing display behavior. The elements are clearly different from displaying toward bulls. Above all the demonstrative tail-lashing is not shown with cows. When a bull approaches a single cow or a group, he gurgles, extrudes his dula, and walks toward them with highly erected head. In front of the cows he lifts his head diagonally upwards, shows the bushy throat beard (Fig. 108) and repeatedly wipes the back of his head across his withers while gurgling at the same time. First contacts are naso-nasal, afterwards the bull walks around the cow, sniffs at her rear end and possibly shows flehmen. The cow usually stands calmly but sometimes shows appeasement by lifting her tail in a crescent shape (Fig. 111). The bull continues to gurgle, follows the cow and begins to herd her or the group actively.

Fig. 108: Bull He takes up contact with the cow group

Herding: If a bull takes over a cow group at the beginning of the rutting period, he first joins them without demonstrating his dominance. After a few days he begins chasing away associated bachelors and herding the group actively. In one case it was conspicuous that the group-holder tolerated a subadult bull in his group and even specifically herded him back at encounters with other groups, while cows that happened to come from the group of the other bull were chased away. While in all other groups no hierarchy could be found, the bull as a holder of a cow group is unrestrictedly dominant. He demonstrates his position by display and if necessary agonistic behavior toward the cows. Without disturbance from the outside, he is mostly lying a little apart, where he can constantly watch all members. At migrations he is the last to leave (Fig. 109). In dense vegetated areas the bull is anxious to hold the group together as closely as possible. Depending on the condition of the terrain, he follows each cow that walks away from the group for more than 50-200m with his head ostentatiously highly erected. Normally the cow turns around immediately and returns to the other animals. If she does not respond immediately, the bull chases her back aggressively while biting her rear end or her legs. When herding, the bull constantly patrols safeguarding around the cows. This behavior occurs increasingly when other dromedaries are nearby. At encounters, above

all with other cow groups with a bull, the bull stands gurgling in
front of his cows and tries to intimidate the other bull and to
persuade him to go away. This way any closer contacts between cow
groups with a bull are already effectively avoided from the start. If
this is not successful, the bull drives away his cows in utmost
agitation, in extreme cases as far as 10km.

Fig. 109: Walking dromedary group; the bull walks at the end

If the group was close to the fence when it encountered other
bachelors, the bull used the fence as a barrier. He drove the cows to
the fence, paced up and down in front of them, displaying his
dominance by gurgling and tail-lashing. In several cases the bull kept
the cows like this in one corner of the fence for several hours.

Urine testing and flehmen: The bull first tests the cow's receptivity
via olfactorial signals. He repeatedly sniffs at her rear end,
particularly in the genital region, and then shows flehmen. If a cow
urinates, the bull first sniffs and shows flehmen at the cow,
afterwards at the urine spot. When showing flehmen he inhales deeply,
throws his head up with the neck strongly bent, slightly bends the
head back and remains in this epitomized position (Fig. 110) for some
time, up to one minute. He opens his mouth, turns the upper lip up and
lets the lower lip hang down loosely. In addition he dilates his
nostrils and slightly puts his ears back.

The flehmen is also shown by dromedary cows, subadults, and calves, but much less frequently and intensively.

Fig. 110: bull Ho shows flehmen

Mating behavior: If a cow is in estrus, the bull is almost exclusively interested in her. He is always nearby, gurgles, grinds his teeth, pursues her and sniffs at her, shows flehmen and repeatedly puts his neck and head on her withers or on the rear base of the hump.

The permanent following increases to a pre-copulative chase in which the bull drives the cow at a gallop (Fig. 111). Doing this he occasionally snaps at her until the cow all of a sudden sits down in a sternal sitting position. The bull stands behind her panting and grinding his teeth, gurgles, extrudes his dula and produces large amounts of saliva foam. Afterwards he climbs over the sitting cow, remains standing for a short time and observes the surrounding area. Then he bends his hind legs and mounts her in the manner typical for tylopodes (Fig. 112).

31 copulations were observed, the duration was between 3 and 8 min., 4 min. on average. Distinctly shorter copulations (1-2 min.) were observed in three cases. They developed from conflict situations without any prior signs of receptivity of both partners. These cases were obviously "dominance copulations" (see below).

Fig. 111: Chase before the copulation, bull Fd chases KH

Fig. 112: Copulation, Fd & As

3.2.1.3   Activity

Herding bulls spend much time doing group tasks like checking of the surroundings, fighting against rivals, holding together the group, leading his cows away from other groups, avoiding contact to other bulls, but little time eating and resting. After one to two months they are noticeably emaciated (Fig. 88). Toward the end of the breeding season, they slowly lose interest in their cows, obviously dependent on their condition. They let themselves be chased away without much resistance, even by an otherwise weaker bull. Mostly they leave their group voluntarily, even if they have still defended it vigorously a few days earlier.

By contrast, bachelors - whether in rut or not - spend almost their entire activity phase feeding and they are thus in good shape.
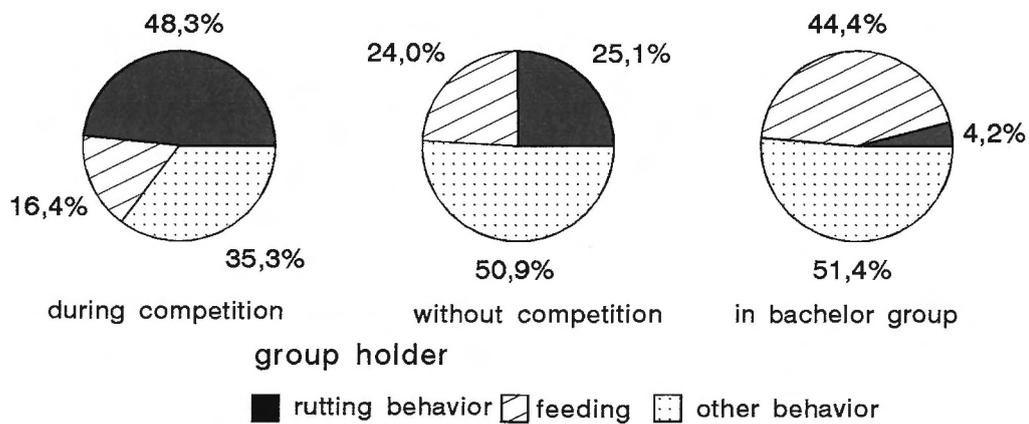
Fig. 113: Summarized activity pattern of 9 adult bulls; the individual results are shown in Figures A16.1-2, detailed classifications are shown in Table AT5 in the Appendix.

The day activities of 9 adult bulls that herded cows during the rut summarized from comparable periods of time are highly significantly different compared with those of times in which the bulls lived in bachelor groups and were not in rut (Fig. 113). In addition, the rutting phases were subdivided depending on whether the bulls were in competitive situations, i.e. if other bulls were nearby, or not.

A clearly situation-dependent shift of the activities becomes evident. Even in situations in which the group-holders have no competition, they eat significantly less than in times outside of the rut. In individual cases the time the group-holder spends feeding decreases to far below 10%, while the cows spend about 50% of their time feeding (Fig. 114).

<div style="text-align:center">

Feeding   Feeding

5%   47%

other behavior   other behavior

95%   53%

bull   09./10.07.88   cows

</div>

Fig. 114: Food intake of a group-holder over 24 hours compared with his cows in a competitive situation

Despite individual differences, the tendencies are the same with all bulls. The results were tested for statistical significance according to the Wilcoxon-Test (DIEHL-KOHR 1987) (Table AT6 in the Appendix). The result was, that feeding and rutting behavior are always significantly different in all three situations, while walking, standing, lying, and all other activities, here summarized under "Other", are not always significantly different.

Outside of the rut the day activity of the adult bulls is mainly limited to feeding and resting. This inactive phase with regard to reproduction, which for most bulls is in summer, is marked by a general calm and lethargy. Even if cows are present, the bulls behave neutrally toward each other and toward the cows, too. Migrations are limited to walking to the trough and to occasional changes of the home ranges (HEUCKE 1995). Since the day activity is mainly determined by the food intake, the bulls now noticeably gain weight.

3.2.1.4   Dominance hierarchy

Within the bachelor groups an individualized dominance hierarchy cannot be seen. The adult bulls are clearly superior to the subadults which points to an anonymous class hierarchy depending on size or age-class. Normally all members of one bull group eat together, often even from one shrub, without any aggressions toward each other. Even during the resting phases they are lying together without a certain order of resting in the shade of a tree. On the way to the trough and when changing places the bulls do not keep a defined march formation.

Outside of the rut the adult bulls behave neutrally toward each other or they go out of each other's way. However, in interactions the subadult bulls show a submissive behavior toward adult bulls. Interactions between adult and subadult bulls only occur rarely in bachelor groups, e.g. at play fighting of young bulls, which take place too close to a resting adult bull. Mostly the demonstrative posture or gurgling of the adult bull is enough to persuade the young bulls to terminate the game. Seldom the adult interferes whereupon the young bulls immediately signal appeasement with their tail lifted up crescent-shaped (Fig. 120). Serious aggressions between adult bulls outside of the rut could not be observed. Only between younger bulls wrangling occurred when they searched for preferred food plants in times of drought. The adult bulls were never disputed their right to this limited food source by the subadults. When chewing on bones, again only subadult bulls would occasionally engage in slight, more playful quarrelling in contrast to the cows (see below).

The bull groups are very variable with regard to size and composition. There are constantly changes by immigrating and migrating (see Chapter 3.1.1). This alone is a reason against the development of an individualized dominance hierarchy. The dominance of the adult bulls during the rut is correlated with their respective constitution and so is reversible. Reversals of the dominance could be noted several times (n=12); repeated reversals occurred, too (n=5).

The frequency of mutual sightings of the peaceful cohabitation in bull groups in contrast to those in competitive situations is shown exemplary for five bulls in Figure 115. It has to be taken into

account here that all bulls were not in rut at the same time. Some of the bulls in rut were in bull groups, others were herding a cow group.
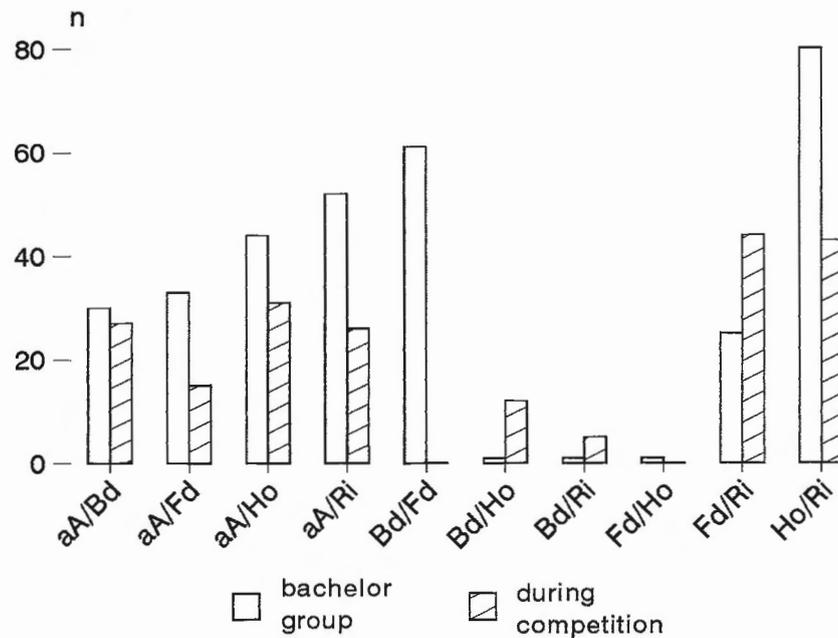
Fig. 115: Frequency of the peaceful cohabitation of five bulls in bachelor groups in contrast to occurring competition during the rut.

The decisions resulting from the disputes only have short-term aftereffects. Often there were repeated disputes even in the same reproduction period, but they always occurred from one to the next breeding season.

In the meantime the bulls lived together without any aggression with the same bulls they vehemently fought against or tried to chase away during the rutting time. This also speaks against the presence of an individualized dominance hierarchy.

Without the presence of cows the social behavior of bulls in bachelor groups during the rutting season is the same as outside of the rut.

3.2.2   Cows

Reproduction characteristics: Dromedary cows are poly-estrous, the cycle is described with 3-4 receptive days which alternate with 10-20 days of the an-estrus (NOVOA 1970). Information concerning puberty and pregnancy vary depending on geographical and ecological conditions. The sexual maturity generally starts off at an age of three to four years (WILLIAMSON & PAYNE 1978) which also applies for the investigated population. With three cows the time of the first fertile estrus could be determined with 3 to 3.5 years. Some cases, however, point to a sexual maturity in young cows that starts off clearly earlier:

1. Copulation between the 23-months-old cow Bi and the adult bull Ri - a fight of the adult bulls preceded the copulation.

2. Repeatedly obvious traces of copulation (Fig. 119) on the 22- and 23-months-old cows Ko and Pa.

3. Clear signs of pregnancy or false pregnancy of the 2.3-year-old cow In. She showed the typical curves of the belly, but above all a distinct udder development.

It is striking that all observations of young cows that were mature at an early age only concern animals born in the same year. The cows were born between June and September 1987 and they were weaned in January 1989. Their youth development took place in times of particularly good food conditions. In all mentioned examples no reproductive success could be proved because the field studies were terminated. However, ABDUNAZAROV (1970) points out that the puberty in young cows in Turkmenistan can already start at an age of 8-12 months. According to own observations the pregnancy lasts 370 ±5 days (n=16). Bibliographical references vary, but are generally stated with 13 months or 370-390 days (SCHWARTZ et al. 1992). They reach from 336 days in Israel (BODENHEIMER 1954) over 389.9 ±2.1 (MEHTA et al. 1962) to 405 days (RAM et al. 1977) in India. Dromedary cows in domestic systems have their first calf at an age of 5-6 years (SPENCER 1973). The age determinations carried out on three cows during the immobilization (HEUCKE 1995) indicate that primigravidae in the research paddock were younger with 4 to 4.5 years. In addition a tendency was observed in which the loss rate among newborns of primigravidae was clearly higher compared with that of more experienced cows. Of seven assumed firstborns only two calves survived. The calculated loss rate of the calves of primigravidae is

thus at 71.5% compared with 16.2% of more experienced cows which is clearly less. Births take place in central Australia throughout the whole year, but with an obvious increase of 93% in the six months June to November (Fig. 116):
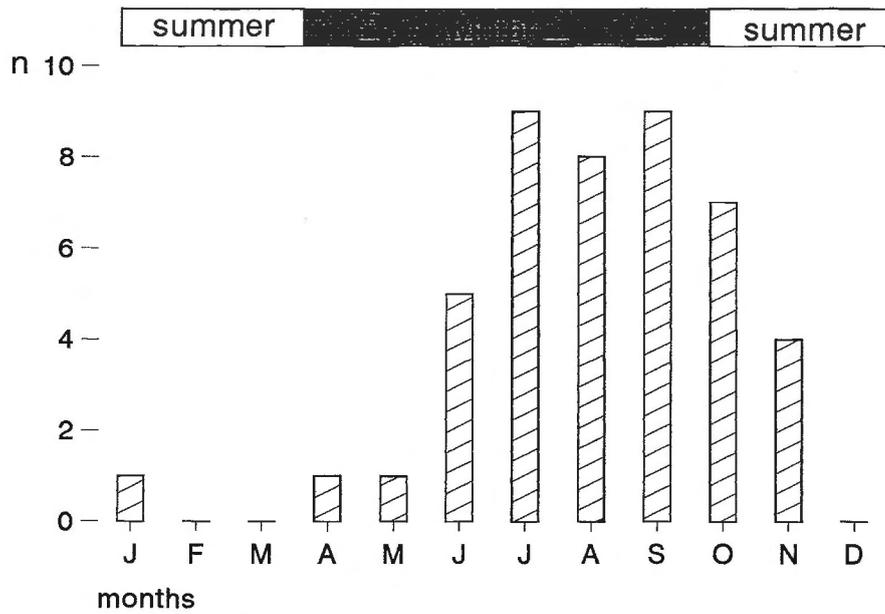
Fig. 116: Distribution of births (n=45)

If the previous calf survived, the birth intervals were between 19 to 24 months. A distinct shortening occurred if the previous calf died (Fig. 117).
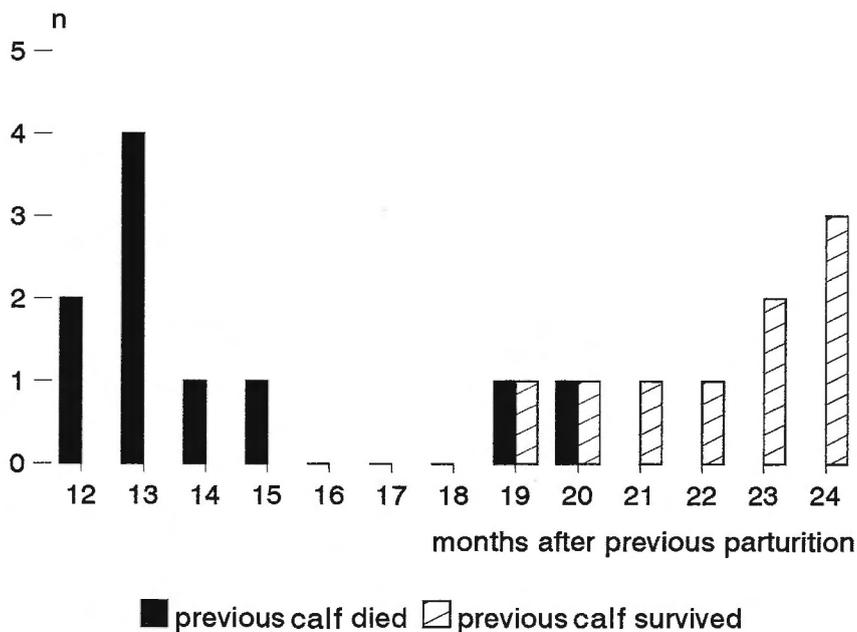
Fig. 117: Observed birth intervals (n=19)

3.2.2.1 Behavior in the functional context of reproduction

Estrus

The behavior of cows in estrus differs strikingly from the normal behavior. They are restless, walk about nervously, and often utter undirected deep grumbling sounds. Some actively seek the contact with a bull or walk in front of him with the tail lifted. Others often stand with tensely spread apart hind legs in a demonstrative signal position and repeatedly pass small amounts of urine. In nearly all observed cases significantly less time was spend feeding during the estrus (Fig. 118). The activity of 15 cows at the time of the estrus was tested compared with a relevant period of time in the an-estrus. For some cows several phases of estrus could be recorded, so that the random samples amount to 23. The individual data are shown in Fig. A17.1-5 in the Appendix. All random samples were tested for statistical significance with the Wilcoxon-Test (DIEHL/KOHR 1987) (Tab. AT7 in the Appendix).

estrus   non-estrus

☐ Feeding ◩ Walking ⬛ Standing ⊠ Lying
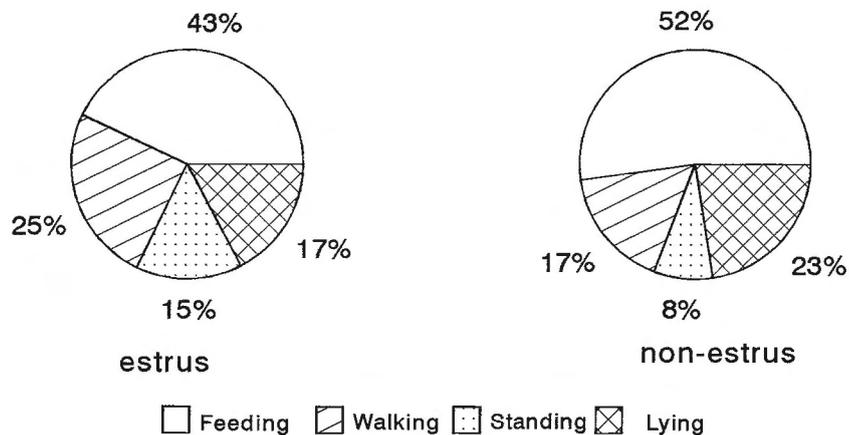
Fig. 118: Activity of cows in the estrus and an-estrus: The differences in feeding are highly significant, walking and standing are significantly different.

Normally several copulations take place during the estrus which could be seen by the typical traces of copulation if no direct observation was done. These traces are caused by the friction of the bull's sternal calocity on the rear base of the cow's hump so that the hair is rubbed off and bald spots develop (Fig. 119). According to the observations, traces of copulation do not develop with playful mounting. During the copulation the cow bellows loudly and persistently. In addition she bites and snaps rather playfully at head, throat, shoulder, and neck of the bull during the mating.

Generally the cow in estrus is constantly accompanied by the bull who presses and follows her. He is almost exclusively interested in the cow. Copulations are therefore very well predictable from the typical behavior patterns (ref. Chapter 3.2.1.2). But they can as well occur spontaneously without prior signs. In several cases it was observed that for instance both partners all of a sudden jumped up unexpectedly during the midday resting phase, then did a short chase and afterwards copulated (n=5). Before the resting phase nothing conspicuous was to be seen, still the copulations were no "dominance copulations". Copulations after the fertilization have to be interpreted as such. They occur spontaneously particularly in conflict situations and with clearly shorter duration (1-2 min.; n=3). With two cows copulations even took place when they had already been pregnant for three and five months, respectively.

Fig. 119: Typical traces of copulation in the area of the rear hump of the cow Lo

Copulations are a social attraction within the group. Above all subadult bulls, but all the other group members, too, come running, throng around the copulating couple and watch. In some cases the bull interrupted the mating to chase away young bulls that disturbed too much. After the copulation the cow is usually surrounded by the other group members who sniff at her extensively.

Pregnancy

Differences in the behavior of pregnant cows compared with that of cows who were not pregnant only become conspicuous toward the end of the pregnancy due to the imminent birth. The signal-like lifting of the tail which has been described by different authors only for pregnant cows (e.g. GAUTHIER-PILTERS & DAGG 1981, SCHWARTZ et al. 1992) is done by all cows and even by subadult bulls (Fig. 120). Subadult and adult cows show it as soon as a bull has taken over a new group and also in other conflict situations. The lifted tail bent forward crescent-shaped is therefore not to be understood as an indication for pregnancy but unmistakably as an appeasing gesture (n=713).

Fig. 120: Gesture of appeasement: Crescent-shaped lifted tail of subadult bull TS immediately after the immobilization dart had hit

Some cows showed this behavior even outside of conflict situations as soon as the bull approached, even toward subadult bulls that were group-holders for some time in summer (Fig. 121); a correlation to pregnancy cannot be found here. Only shortly before parturition the signal was shown occasionally or permanently by highly pregnant cows even if the bull was not present. However, subadult bulls exclusively

showed the crescent-shaped lifting of the tail in serious conflict situations and thus much less. The behavior was not observed with adult bulls.

Fig. 121: Appeasement of the cow H4 - right - when the subadult group-
holder TS approached, here largely hidden by H4

The gesture of appeasement of adult cows gets a strong optical signalling effect by the simultaneous "strut". The cow cranes her neck and walks in front of the bull extremely stiff-leggedly in a stretched posture. The strut was only observed in pregnant cows, particularly between the 6. and 12. week of pregnancy. After that the behavior did not occur any more (n=15).

Toward the end of the pregnancy, shortly before the birth, the cow becomes increasingly restless, she eats less than the other cows and stands or walks more often with crescent-shaped lifted tail, even if no adult bull is nearby. Highly pregnant cows repeatedly nudge against their ventral sides with their noses and regularly look in the direction of their belly. They are generally more restless and more often change their lying position during the resting phases.

As an example for the restlessness prior to parturition, Fig. 122 shows the individually classified behavior elements of the group N11 during the morning activity phase. The cows As and Pf are highly pregnant, As's calf was born on September 14, 1987, Pf's calf was born on September 19, 1987.
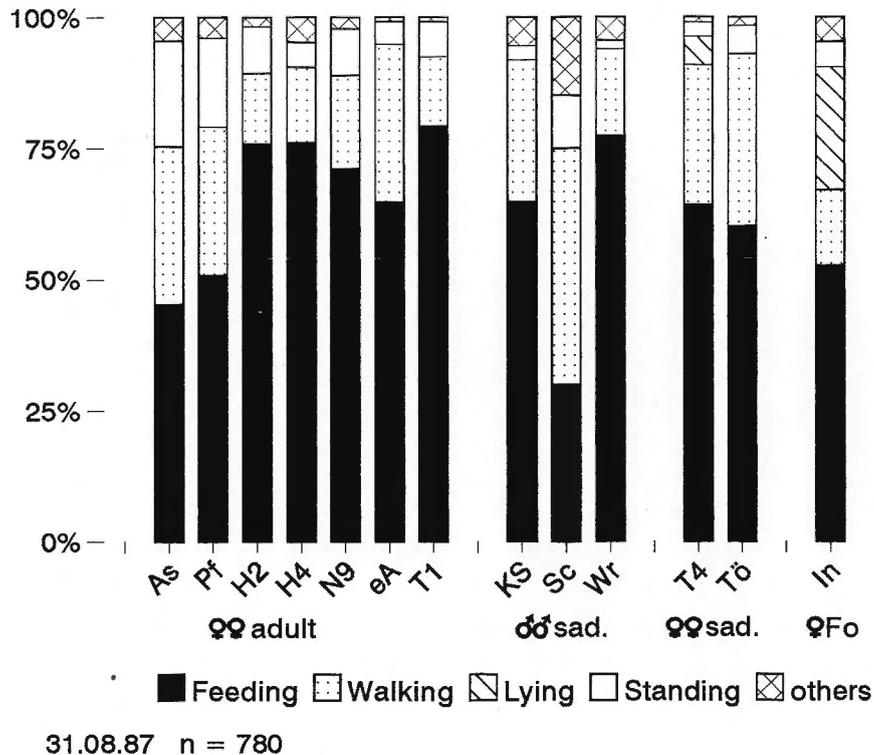
Fig. 122: Individual activity patterns of the members of the group N11 on August 31, 1987, between 07:00 and 12:00 h (interval = 5 min.). Shown according to gender- and age-classes, the cows As and Pf are highly pregnant

Segregation

If the cow group is herded by a bull, the highly pregnant cow generally segregates from the group 8-24 hours before parturition. Even though the bull attempts to hold all group members together, the segregation is successful except for a few exceptional cases (Chapter 3.2.4).

In difficult terrain the cow can segregate by actively staying behind or specifically leaving to the side. However, in open terrain the bull notices these segregation attempts earlier (Fig. 123). In two such cases the cows first tried to leave the group as described above, but were each time discovered by the bull and herded back. Only when they went away in the direction the group walked and always remained in the bull's field of vision, they had the chance to change their direction with sufficient distance to the bull and to specifically leave which both cows did.

Fig. 123: Segregation attempt which first failed of the highly
pregnant cow Wd who was discovered by the group-holding bull
and immediately signalled appeasement

The cow then goes into habitats that provide better shelter, mostly sand dunes or sand plains with dense vegetation, and usually walks several kilometers away from the group, in one case more than 15km away.

Of the 45 births that took place during the study period, the birth place of 28 calves was known. Fig. 124 shows the distribution of these birth places in the different habitat types whose characteristics are described in detail in HEUCKE (1995). A clear habitat preference stands out for the births of the calves. 82% of all cows went into

sand areas or sand dunes with dense vegetation for this purpose. Repeated use of the same area for the birth of the next calf was not observed.

Symbol	Legend	Symbol	Legend
⌷	saltlake/saltmarsh	◇	open plain
⊠	open bushland	☐	sandplain/dunes open
⊞	dense bushland	▦	sandplain/dunes with dense vegetation
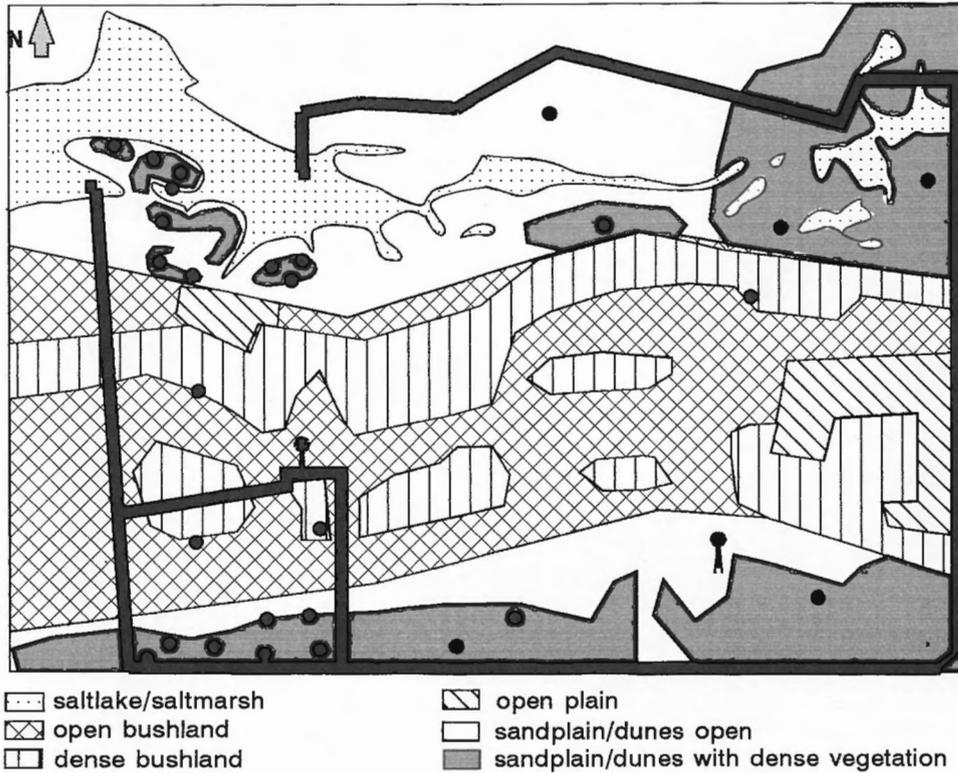
Fig. 124: Habitat preference for the birth (n=28)

Birth

In a total of 6 births the entire process was observed completely, in addition immediate prenatal behavior could be documented with two cows and immediate postnatal behavior with three more cows.

The duration of the observed birth processes from the appearance of the front legs until the parturition of the calf showed considerable individual differences and was between 16 and 53 minutes. In one more case a bull disturbed which extended the birth to 70 minutes. Excluding this exceptional situation, the mean duration of birth is 31 minutes.

Already 1-4 h before the expulsion phase the cow becomes extremely restless, she walks about restlessly with crescent-shaped lifted tail, lays down repeatedly, rolls, and vocalizes strongly. All cows still uttered the loud and penetrating calls repeatedly during the expulsion phase. Contrary to other descriptions (GAUTHIER-PILTERS 1959, SCHULTE 1988) the observed births did not proceed completely silently.

Fig. 125: Begin of the birth with the cow N16, the calf's front legs
          have just become visible

An excerpt of the protocol of September 14, 1987, describes the
general basic pattern for immediate prenatal behavior with subsequent
parturition with the cow As as an example. Even though As lived in a
group without a bull at that time and did not segregate, her behavior
corresponds to that of the other cows before and at the births of
their calves, only the duration fluctuated as expected.

14:25: As stands in the shade in the middle of the group members, tail
       is lifted crescent-shaped, she bellows loudly and penetratingly
       several times

14:26: As walks about restlessly in a circle, lifts her tail
       repeatedly, walking looks very unusual - hind legs are spread
       further apart than normally

14:28: As goes about 20m away from the group, constantly holds her
       tail lifted up, other group members do not react

14:30: As feeds on *Acacia victoriae* for a short time, stands at the
       shrub and appears tense, walks ten more meters in the shade,
       now stands by herself

14:33: As still stands in the shade, wags her tail, standing appears
       tense

14:35: As walks, urinates, defecates, walks away 30 more meters from
       the other group members, repeatedly bellows loudly and
       penetratingly, and lifts her tail crescent-shaped

14:37: As sits down with legs tucked under, lays on her right side, rolls, kicks her hind legs, front legs are straightened, remains lying on her side calmly

14:39: As sits up, repeatedly bellows and then lays her head on the ground, remains sitting calmly like this

14:42: As stands up, lifts tail and walks around with her legs extremely apart - other group members walk away

14:44: As stands with crescent-shaped lifted tail

14:46: As walks about restlessly with crescent-shaped lifted tail, calls out once

14:47: As sits down, lays on her left side, rolls and kicks several times - the calf's front legs become visible

14:49: As lays flat on her right side, rolls several times, repeatedly kicks with her hind legs

14:51: As sits

14:52: As lays on her left side - the calf's head becomes visible

14:53: As lays on her right side, rolls and kicks with her legs, sits briefly, and slowly and carefully stands up, repeatedly bellows doing this - the calf's head and front legs are expelled

14:54: As walks a few steps

14:55: As alternately stands and walks

14:57: As bellows and keeps going in a circle, the calf is expelled halfway

14:58: As sits down very carefully, first sitting partially on her side, then lays down completely on her left side and rolls slightly

14:59: As lifts her head, looks toward her belly and subsequently rolls on her left side

15:00: As lies completely flat on her left side and kicks her legs

15:01: As lies completely motionless on her left side

15:02: As lifts her head and bellows several times

15:03: As sits up and looks back at the almost completely expelled calf, then stands up all of a sudden, the umbilical cord tears while doing so

15:04: Calf is expelled, As turns around to the calf, stands in front of it, lowers her head and sniffs at its front end

Mother-infant behavior

Immediately following the birth repeated naso-nasal and naso-anal contacts with the calf take place which are accompanied by low grumbling sounds from the mother. After that all cows showed mainly resting behavioral elements and laid down next to the calf mostly after 5-10 minutes. The afterbirth appeared 14-24 min. later and was delivered standing. For this the cow interrupted her resting phase

shortly. Neither the afterbirth nor the rests of the embryonic
membranes were eaten by the mother.

Newborns free themselves from the embryonic sac by kicking vigorously,
the mother does not help. Often up to 24h after the birth rests of
dried embryonic membrane are clearly visible particularly in the neck
area of the calf.

Dromedary calves obviously have considerable difficulties with the
motoric coordination within their first hours of life. After
undirected kicking movements lying on the side which first of all help
to get free from the embryonic membrane, directed movements, like for
example lifting the head, only occurred after 6 min. at the earliest,
usually only after 10-12 min. First attempts to sit down were observed
after 12 min., successful sitting after 23 min. at the earliest. First
attempts to stand up were done after 26 min. However, none of the
observed calves succeeded in standing steady on their legs within the
first hour of life.

Fig. 126: Attempt to stand up of the calf Ch at the age of two hours
          as the mother cow As approaches

While the mother mainly sits and rests for up to 90 min. after the parturition, the calf repeatedly tries to stand up. After about 2h the mother resumes the food intake, but she does not go farther away from the calf than 20-30m, repeatedly calls and constantly keeps up visual contact. In regular intervals she returns to the calf that makes more attempts to stand up as soon as she approaches (Fig. 126).

Five of the six observed parturitions took place in the afternoon in winter. The observation of the postnatal behavior was therefore impeded by falling darkness and had to be broken off early. It was common to all observations, though, that the calves had not stood up after 2-3h. Only once the behavior of the mother and the calf could be documented continually for up to 4h after the birth at good lighting conditions. Here the calf was observed standing for a longer time with first attempts to walk only after 3½h. The first nursing could still not be observed but first attempts at nursing. The calf first searched for the source of milk at the front end of its mother, further searching movements were directed toward the hind legs and the navel, the time until the first nursing was >4h.

In the first two days of life the movements of the calves are very unsteady and little controlled. They mainly rest and sleep, only stand up shortly for nursing, walk about a few steps and then mostly lie again. The mother always stays nearby when looking for food and does not go farther away than 50m while doing so. Generally the calves gradually become more mobile as of the third day of life. The home range of mothers with young calves is very limited because of the relative immobility of the calf and was clearly below 1km^2 during the first days of life, mostly between 0.01 and 0.05km^2. Only in one case mother and calf already walked more than 1km on the first day to go to a habitat which provided better shelter, in which they then stayed in comparable small home ranges. An example for the gradual increase of the home range depending on the age of the calf is shown in Fig. 127:
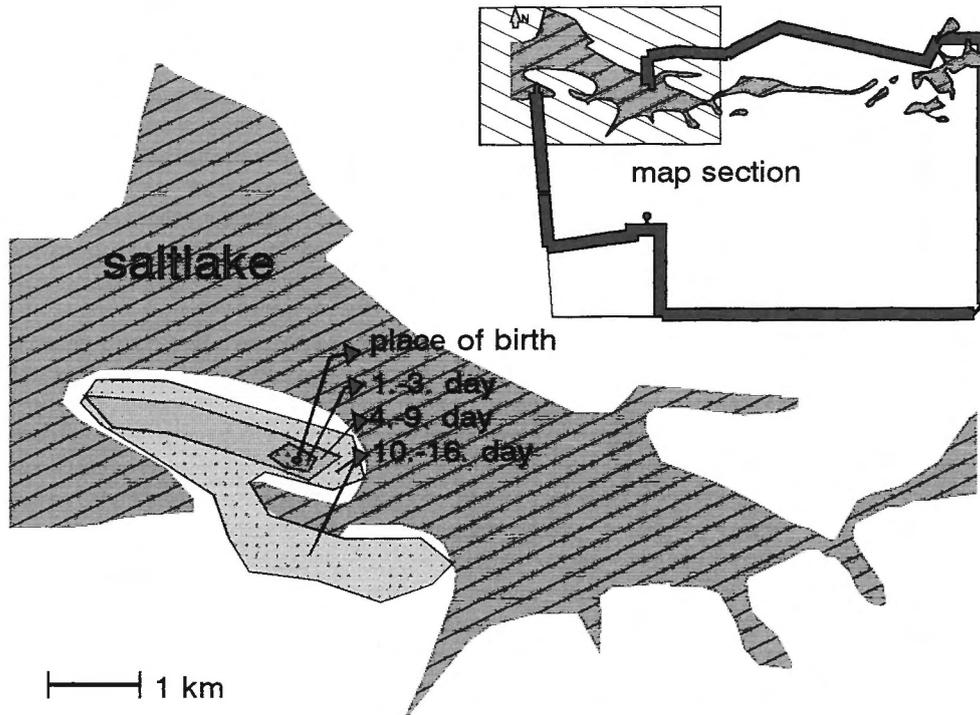
Fig. 127: Home ranges of mother and calf depending on the age of the
calf with the Cow T4 and her calf Si as an example

Mother and child first live on their own. The duration was extremely
different, between two and 42 days, 14 days on average (Fig. 128).
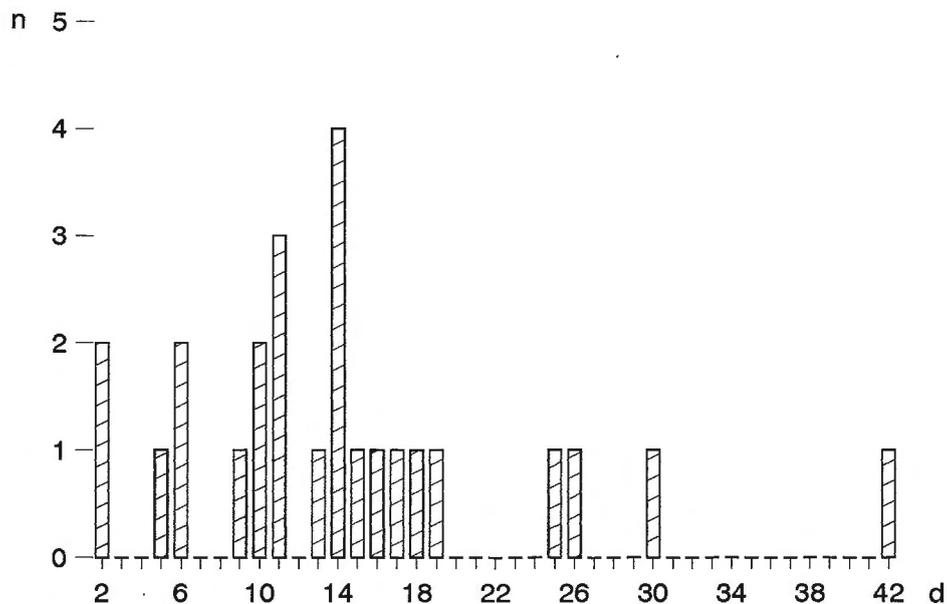
Fig. 128: Duration of time in days (d) cow and calf lived by
themselves after the birth, n=25

The intervals between the birth of the calves and the permanent joining with another cow with calf are the basis for Fig. 128. In the meantime short-term associations with various other dromedaries could take place which usually did not last more than one day. The cows that had calves almost at the same time, would make contact relatively fast (d<10). It is also likely that cows who give birth at the same time in the same area join together immediately (d=0). One observation points to this: two cows isolated themselves from their group at the same time and together went into a dune area for the births of their calves. The births took place within only 2h. Both cows were subsequently abducted by a bull and the calves did not survive (Chapter 3.2.4). With the cows that lived alone with their calves for more than 20 days, it is conspicuous that the birth took place in the summer months, accordingly in a time in which only a few births took place at all (Fig. 116).

Within the first week of life of the calf an active avoidance of contact to conspecifics was observed on the part of the mother, except for other mothers with young calves. One cow practiced the avoidance of contact very clearly: She lived in a remote sand dune area with her calf and regularly stood on the top of the dune where she observed the surrounding area while the calf mainly rested in the valley of the dune. When a group - which happened to be her original group - after four days came up to her as close as app. 200m, the cow instantly turned in the direction of the calf and specifically went away with it. As soon as the group had left the area, the cow returned to her previous home range with her calf where she then stayed.

If the calf was found by other dromedaries within the first three days of life, a very lively welcoming ceremony took place which the mother mostly tolerated standing closely to her calf, but in some cases interrupted. In nine cases a welcoming ceremony like that could be observed which basically proceeded according to the following pattern:

- Mother has discovered conspecifics and stands closely to the calf, calf is lying.

- Conspecifics approach quickly, some of them, particularly subadults, run and jump. As soon as they are app. 5m away from the calf, they stop, go and stand in a semicircle, growl from time to time and watch interestedly.

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- After some time mostly an older cow dares to take the first step, walks slowly toward the calf, lowers her head and greets it naso-nasally. Afterwards all other group members go to the calf one after the other and greet it naso-nasally. Usually the mother stands by growling softly and lowers her head repeatedly toward the calf.

- After welcoming the calf, adult cows usually walk away from it but subadult bulls and cows run and jump and initiate mostly turbulent running games. In high spirits they repeatedly return to the calf, but are then kept away by the mother. Adult bulls that are not in rut behave neutrally toward the calf, only sniff at it briefly and then move on. However, when a bull greets the calf the mother is particularly watchful.

After welcoming the calf the other dromedaries move on, and mother and calf stay behind. They remain by themselves until they join together with other mothers with calves, or until they are taken over in a group with a bull. When mother and calf actively join a group for the first time, similar welcoming ceremonies take place. This only happens at a later time. The calf is then much more mobile and already takes part in the running games initiated by the subadults and other calves. Mostly it seeks contact with its mother and bellows loudly when looking for her. Aggressive elements by conspecifics were often observed during the first encounters with the calf. Particularly subadult bulls kicked the calf, bit its hind legs during the running games and repeatedly showed biting intentions, which can probably be interpreted as playful aggression.

Nursing:
All cows always only nurse their own calves. Before nursing the cow sniffs at the calf, particularly in the anal region, and only after the olfactorial check she allows the nursing. She then stands still with her hind legs slightly apart, occasionally ruminating. The calves for their part also try to nurse at other mothers (n=15), though. In all observed cases the nursing intentions of strange calves had an immediate rejection by the respective cow as a result. Only in an exceptional situation one calf succeeded in nursing at a strange mother, when she was under drugs during the immobilization.

The calves in principle try to use any opportunity that comes up to nurse. Synchronous nursing occurred frequently, for instance when the group remained standing for a longer period of time which happened regularly before as well as after resting phases. But also in conflict situations, e.g. as the trough was blocked off for some time and the dromedaries several times stood undecidedly in front of the gate, all calves regularly used the situation for nursing. Social stimulation with regard to nursing is obviously also effective within a group. It was often observed that as soon as a calf started nursing, the others were encouraged to do so, too.

Nursing can be initiated by the mother as well as by the calf, mostly it was initiated by the calf that often wandered about calling loudly for its mother. The nursing was broken off by the mother in about 40% of the cases, in 60% of the observations the calves could end the nursing voluntarily (n = 1.191). The breaking off by the mother was rather due to situation dependent causes, individual differences could not be determined here. With older calves the breaking off of the nursing by the mother occurred more often, though.

Fig. 129: Nursing dromedary calf Bo with mother T1

Of the 35 observed young animals the actual duration of the nursing phase could be determined with 9 animals. It covers a period of 18 months on average (547 ± 69d), gender specific differences were not ascertained. One calf was nursed up to the age of 21 months, with

another one (An) the nursing phase was terminated early by external factors after 381 days, when adult bulls separated the calf from its mother. At this time it was 12.5 months old, so that the separation did not have negative consequences. This and two other observations indicate that the calves are already able to feed independently to a sufficient extent under one year of age. According to that they are not dependent on their mothers' milk supply any more. Table 15 provides an overview of the respective nursing phases:

Table 15: Nursing phase of the young animals in the research paddock

Individual	Nursing phase	Duration (d)
male foals		
Gu	28.08.86 - 02.01.88	493
Te	01.11.86 - 14.06.88	592
Sn	03.11.86 - 27.05.88	572
Ch	14.09.87 - 02.02.89	507
female foals		
Ka	01.11.86 - 27.05.88	574
In	16.07.87 - 21.06.89	708
Bi	29.08.87 - 19.01.89	510
Pa	19.09.87 - 08.01.89	478
Ko	22.09.87 - 25.01.89	492
An	01.08.88 - 16.08.89	381

The length of the nursing phase is determined by social but also by ecological factors. Even though it is hard to prove ecological causes because of the small amount of data, it is conspicuous that the nursing phase of four calves who were born in 1987 with ϕ 497d is clearly below that of the calves of the previous year (ϕ 558d). The childhood development of the calves of 1987 took place in periods of time with a lot of precipitation with a predominant food surplus, while the childhood development of the calves of the previous year included a period of drought and thus belonged to phases with mainly limited food resources. The unusually long nursing phase of one calf (In) that was born in 1987 is due to individual characteristics of its mother (T1). Even though she had the opportunity to leave the group for weaning her calf, she did not do so. With her next calf T1 was particularly solicitous, too.

The nursing intervals are individually different and also depend on external factors, as described above. During the day nursing took place every 2-3 hours on average, at night it was less, though. Seasonal differences stand out with the nursing intervals at night. In winter the intervals are clearly longer, independent from the age of the calf (Fig. 130).

The duration of the individual nursing events was between 0.5 and 6.8 min., 3.2 min. on average. No significant differences concerning the daily total nursing time (GSD) could be ascertained with regard to the age of the young animals. Young calves (< 3 months) had a GSD between 36 and 41 min. with ϕ 38.2 min., while the GSD with >one-year-old calves was between 14 and 20 min., i.e. at ϕ 15.9 min. While the GSD is highly significantly different among the age-classes, the differences regarding the nursing intervals are less. Fig. 130.1-4 shows interval and respective duration of the individual nursing events of calves of different age-classes with some examples.

Young calves nursed an average of eight times in 24 hours (8.2 ± 1.5), older calves seven times on average (7.3 ± 1.8). Generally there was the tendency that nursing events at night were longer with ϕ 4.3 (± 1.2) min. than the ones during the day with ϕ 2.8 (± 0.4) min. While the number of individual nursing events can very well be different depending on the season, the daily GSD is uniformly dependent on the age-class. Individual differences in the GSD are minor compared with this.

duration of suckling (min)

summer   time

■ Ka (GSD = 37,2 min) ⊠ Sn (GSD = 39,7 min) ☐ Te (GSD = 40,8 min)

duration of suckling (min)

winter   time

■ Bi (GSD = 36,3 min) ⊠ In (GSD = 38,1 min)
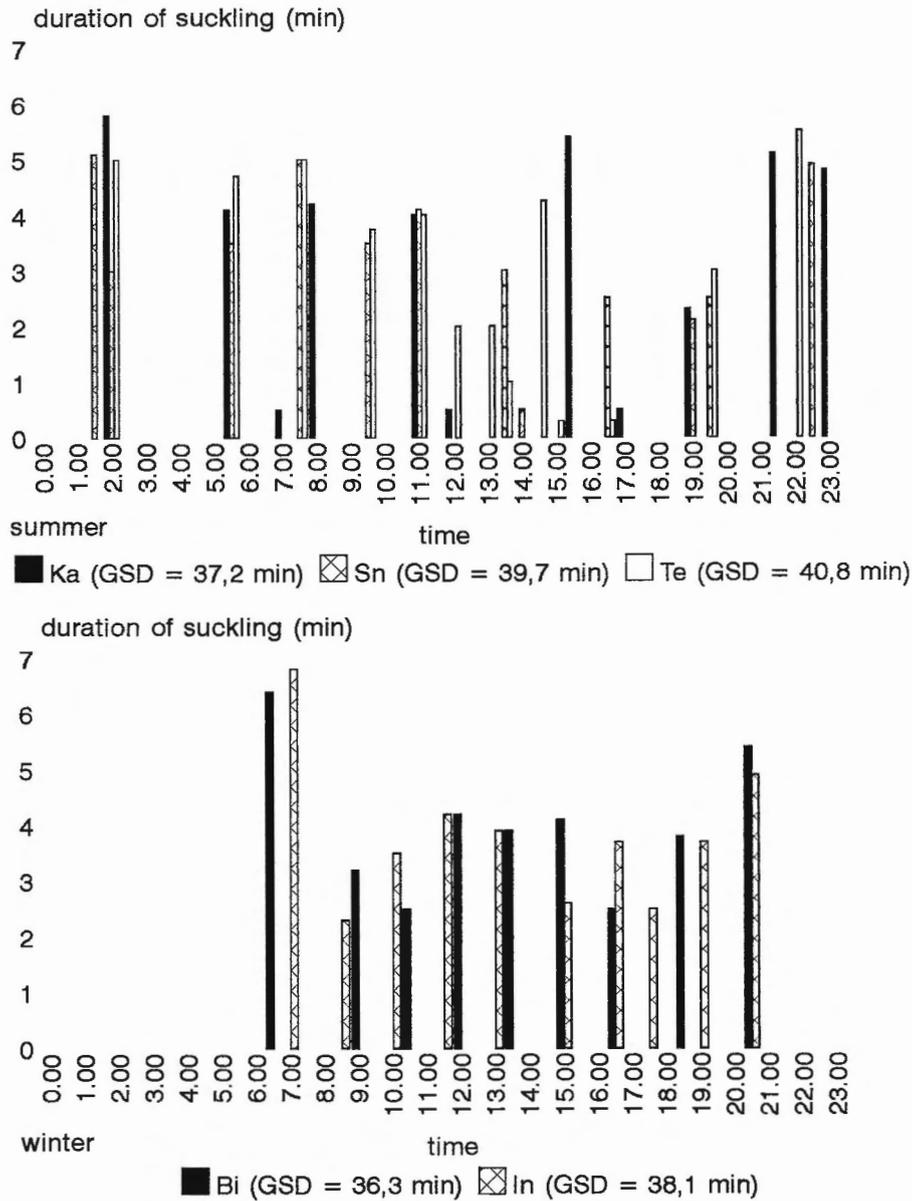
Fig. 130.1-2: Examples for the nursing behavior of < 3-months-old calves from summer and winter

Apart from the age-dependent changes of the GSD the examples also show the synchronous nursing, for instance in the morning immediately after getting up, or in the evening before the resting phase. It is conspicuous that the nursing even with very young calves did not occur during the night. Only in rare cases, when the dromedaries' sleep was disturbed, this could be observed (2%). The longer early morning nursing in winter can be explained as a compensation for the missing nursing events at night.
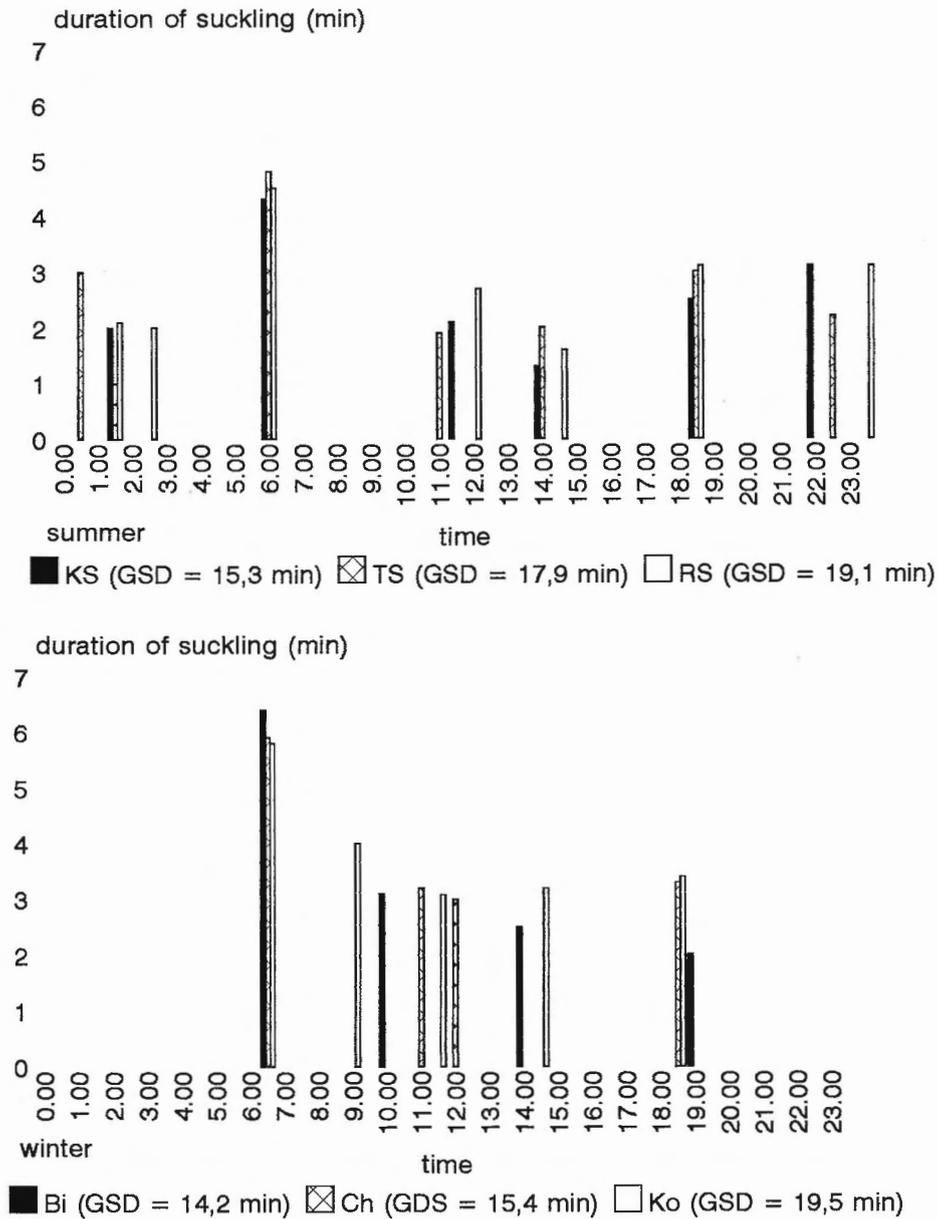
Fig. 130.3-4: Examples for the nursing behavior of > 1-year-old calves
from summer and winter

Until the weaning phase the calves are being nursed regularly. The
weaning of the calf is done by the mother step by step refusing at the
nursing intention of the calf. It can last for several weeks. Often
the mother leaves the cow group in the course of the weaning, as long
as she has not yet been herded by a bull. Bull calves in the weaning
phase are mostly chased away by an adult bull after the cow group has
been taken over, and they are thus separated from their mother.

The close "nearest neighbor"-relations are striking in the mother-infant behavior. During the nursing phase the calves were the nearest neighbors of the mothers at 90% (Fig. A18.1 in the Appendix). Differences with regard to the time of day as well as age dependent differences were observed: at night the young calves (age < 1 year) always lay next to the mother; in summer they were mostly nursed two to three times a night and laid next to their mother after each nursing. But also during the winter observations the young calves lay next to their mother even though they did not nurse. Older calves, on the other hand, did not always lie next to their mother. During the day the young calves often lay together in a group while the mothers were busy feeding. At the midday rest they mainly lay next to their mother again.

3.2.2.2   Social behavior

Agonistic behavior elements are only to be observed rarely in dromedary cows in contrast to the bulls. They confine themselves to defending the calf and to monopolizing rare, valuable food resources which could only be observed with bones, though. This source of mineral matters which is obviously needed particularly by adult cows, regularly was the reason for quarrels. A cow had hardly found a bone and chewed on it, when all the other cows would come and stand in a semicircle around the chewing animal and would try to get hold of the desired object, as soon as the bone was dropped. The resulting scramble was accompanied by loud bellowing and in some cases increased to biting.

Only when defending the calf, cows also became aggressive toward adult bulls. Normally they showed a submissive behavior toward herding bulls. Toward all the other group members the cows are tolerant. They feed from one shrub together, jointly rest under a tree, nibble at each other, and generally do not show aggressions. Often it was observed with cows of one core group that a mother stayed close to the resting calves while the others moved about a little farther in search for food. The cows remaining close to the calves could take turns several times.

Even though the cow groups are relatively stable, single adult cows do not have a closer individualized relationship to each other, and only in a few cases partner preferences could be determined.

1. Partner preferences

During the activity phase the nearest neighbor of certain key animals was noted down at times. The analysis of these data did not show significantly positive results. The nearest neighbors during the activity phase are thus - as expected - purely accidental.

To check individual partner preferences, the nearest neighbors during the resting phases were then evaluated. A total of 7.840 dromedary couples resting next to each other were recorded. The investigation for partner preferences was done according to periods of time, i.e. the respective temporarily possible partners due to group changes of the key animals were checked for.

On principle predictable statements to nearest neighbors only exist between mother and child until the weaning of the calf (see above). Fig. 131 shows the nearest neighbors of calves in a core group, more examples are to be found in the Appendix under Fig. A18.5-6.

female calf Ka   male calf Te   male calf Sn
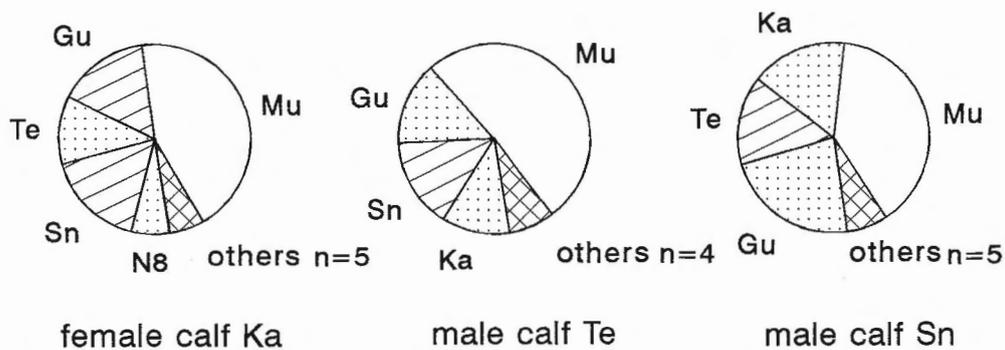
Fig. 131: Distribution of the nearest neighbors of calves of one core group during the resting phases during the day; Mu = mother

Aside from the preference to the mother, the calves of one core group have a clear tendency to each other; in Fig. 131 the calves Ka, Te, Sn, and Gu. In an exceptional situation, in which cows with calves of the previous year joined this core group for four months (see. Chapter 3.1.2), it could in addition be observed that the young calves were lying together significantly more often with other young calves than with all the other group members, including the older calves. As soon as the calves are weaned, however, the situation changes. The weaning of the young bulls is accompanied by a change to bachelor groups, the composition of which again constantly changes; therefore the following

pictures of the same animals after weaning do not show any preferences (Fig. A18.5-6).

In a few cases partner preferences could also be observed between subadult and adult animals. Particularly young cows specifically walk toward a certain partner at the beginning of the resting phase and lay next to it. The partners can be subadult cows that have already lived in the core group, or they can be other adult cows.

Here some examples:

1. Preference among young cows of different ages

Ka lived in a core group with four calves as the only female calf. N8 had joined the core group as an app. 2-year-old cow in November 1986 and had lived in that group until the end of the rearing phase of the calves in May 1988. The average group size was 17; during Ka's nursing phase N8 was a partner more often than the other group members, but not as often as the other calves of the same age. After the breaking off of the core group N8 was visited specifically by the now > 2-year-old Ka at a comparable group size, which suggests a clear partner preference (Fig. A18.5 in the Appendix).

2. Preference among young cows of the same age

Female calves that have grown up together can have preferences to each other even after weaning. Examples for this are the nearest-neighbor evaluations of the young cows Bi and Ko (Fig. A18.6 in the Appendix). For 10 months Bi lived in a core group with ϕ 13 members in the horse paddock with only one other female calf Pa; in the research paddock there was another core group with ϕ 17 members and the calves Ch, In, Mo, and Ko that were the same age as Bi and Pa. Only in July 1988 the joining together of both core group from horse and research paddock was possible. After weaning, Bi as well as Ko show a preference to the young cow whom they had lived together with in the core group the longest; Bi to Pa and Ko to In. The comparison to the male calves shows clear gender specific differences in the partner preference following the nursing phase (Fig. A18.5-6).

3. Preference between young cow and adult cow

The evaluations of the cows T4, Tö, and Hl each in relation to the proportional mutual sightings (Fig. A18.4 in the Appendix) give indications for partner preferences of subadult to adult cows. The situation becomes particularly conspicuous with the cow T4 whose age could be determined more accurately by the development of the teeth while she was immobilized. While the cow still showed a strong

affinity to the adult cow N9 at an age of about 4 years the following distributions do not show clear preferences except for a preference to her calf (Fig. 132).
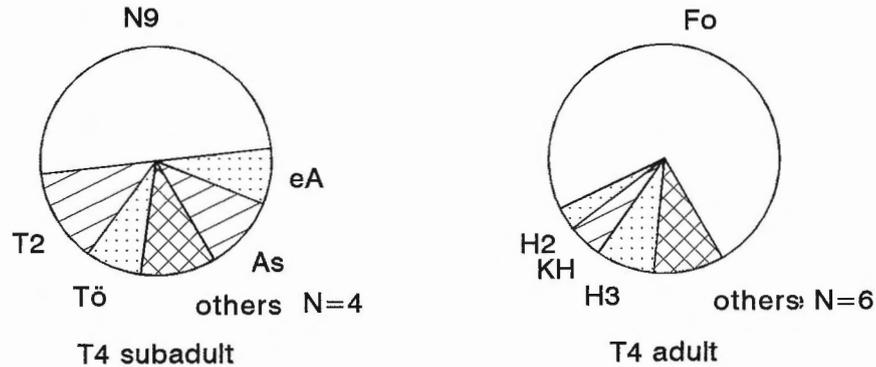
Fig. 132: Partner preferences depending on the age with the example of the cow T4

Some additional observations point to a close relationship between these cows: 1. at the immobilization attempt of the cow N9 the subadult cow T4 immediately came to her after the dart had hit, stayed close to her following this and even tried to pull out the dart with her teeth. 2. At copulations of the cow N9 (n=3) T4 jumped around the couple during the entire duration of the mating particularly intensively, in one case it was only her; afterwards she constantly followed N9 and sniffed at her intensively.

These tendencies become understandable when the fact is taken into consideration that subadult cows usually live in the same group until the birth of their first calves. The number and the composition of the members of these groups does not change as much as that of the bull groups.

While with almost all subadult cows partner preferences could be observed, these only exist rarely between adult cows. The cases in which they are suggested are probably due to the particular situation in the research paddock where all animals met each other relatively often compared with the natural situation. The observations during the long resting phases during midday in summer furthermore show that other factors can be relevant for the place selection of an individual: due to the changing position of the sun it became necessary for some animals to change their resting place. They either pushed among the other dromedaries that were still lying in the shade

- without individual preferences - or they chose new shady places at the periphery. Most of the adult cows clearly did not show any partner preferences. Even the five adult cows that had immigrated together in June 1989 and first lived isolatedly, did not show a higher affinity to each other than to all the other group members after they had joined another group.

While subadult cows live in the same group for up to five years, adult cows change the group every two years on average, each time at the birth of a calf. During the rearing phase until the weaning the young animal is the nearest neighbor of the cow at 90%. Preferences that develop after that are usually only short-lived, since the cow has her next calf after an average of six months and then changes to a new group. Partner preferences can occur between adult cows, too, particularly if both did not have a calf for a longer period of time and therefore stayed in a group longer. Examples for this are the relationships of the adult cows eA to H4, and H2 to H4 (Fig. A18.2 in the Appendix). Another example are the cows K1 and Wd who lived in one core group from November 1986 until May 1988. After the weaning of their calves they stayed together in various groups, at times only the two of them roamed around (Fig. A15 and A18.1 in the Appendix). An additional observation supports the special relationship of the two cows: When K1 was immobilized, only the cow Wd looked after her. She went to her, sniffed at her, and nibbled at the immobilization dart. Such interactions were observed in other immobilizations either of the calf of the respective cow and/or of animals that obviously had a preference to the immobilized animal.

Fig. 133 shows the nearest neighbors of two adult cows chosen as examples. Pf shows the typical pattern, but H2 shows preferences; more examples are to be found in the Appendix in Fig. A18.1-3.
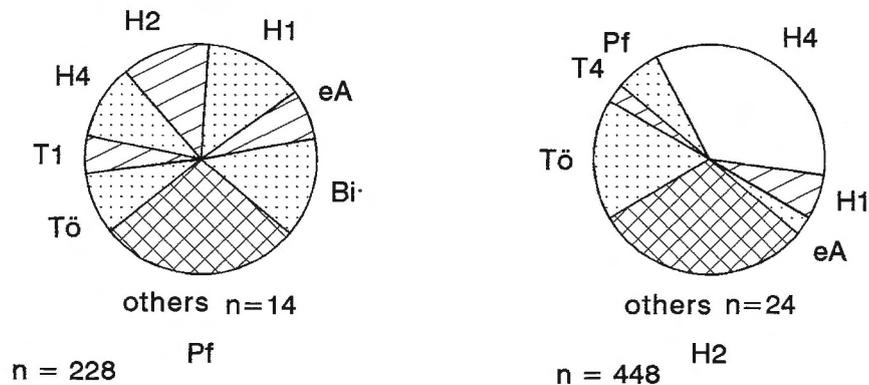
Fig. 133: Nearest neighbors of two adult cows (Pf & H2).

With several immobilizations observations could be made which probably point to help and in addition show partner preferences between adult cows in extreme situations. The cow KW had to be given four immobilization darts because the drugs did not work (HEUCKE 1995). Due to the longest response time of the drugs this example is suited best to demonstrate the contexts. It has to be said, however, that comparable behavior patterns were also recorded with other immobilizations.

The cows Hb and We have already lived together > 1 year with the cow KW in a core group. Here are the essential excerpts of the protocol of January 30, 1988:

12:45: Group N17, Σ 22, in the grid square G6, all are lying, weather: overcast skies, T=30°C.

13:00: Rain drops, animals stand up and move toward south.

13:05: First immobilization attempt with cow KW, everyone starts running!

13:15: KW sways for the first time, stands, other group members stand around her, distinct grumbling, various naso-nasal contacts.

13:23: N17 moves on, K1 is leading, KW sways, lower lip hangs down.

13:30: Rain! N17 members run, KW in last position.

13:43: KW stands, son Wi suckles, (misunderstanding?).

13:45: KW stands with legs apart, Wi sniffs at her face, cow Hb remains constantly close to her.

14:15: KW stands, lower lip hangs, bellows loudly.

14:16: Hb and Wi with KW, Hb sniffs at KW naso-nasally, son suckles.

14:35: KW specifically goes to We, several naso-nasal contacts.

14:37: Second immobilization attempt, needle breaks off!

14:40: KW constantly stays with We, actively seeks contact, turns to her udder in infantile posture! Hb permanently stays close.

14:50: Third immobilization attempt, KW hardly jumps up at all, stands with We and Hb, son Wi comes and sniffs at immobilization dart; Hb bites the dart, KW bellows.

15:08: N17 members lay down one after the other, Hb stands with KW who leans on her.

15:20: KW stands with legs apart, bellows, Ha suckles at KW (not her son!).

15:27: KW lays down, stands up immediately.

15:50: KW specifically goes to the bull Bd, lays her head under his belly (infantile behavior?, appeasement?), KW constantly sways after Bd and leans on him.

16:20: Fourth immobilization attempt! KW now actively goes to Hb.

16:28: KW stays with Hb, leans on her.

16:30: Hb constantly stays close to KW, nibbles at the immobilization
 dart!

17:03: Hb has pulled out one immobilization dart, drops it, KW
 bellows...

With regard to the cooperation in the society opposing observations
could be made, too. Here an example: In January 1988 the cow Tr had an
inflamed eye for three days which at times impeded her to such an
extent that she repeatedly ran against shrubs or trees and eventually
wandered around uncoordinatedly. She called out loudly several times
but the other group members did not respond. Only the cows Hb and We
who had lived together with Tr in a core group repeatedly looked back
at her but then moved on with the other group members. When the cow Tr
was immobilized in April 1988, a similar behavior occurred as
described for the cow KW. Again it was the cows Hb and We who were now
constantly close to her.

Unlike the cows there are no partner preferences discernible with
adult and subadult bulls. Even young bulls that have grown up in a
core group after weaning do not show a significantly higher affinity
to the former partners than to other conspecifics.

2. Dominance hierarchy and leadership

There is no dominance hierarchy between adult cows. Subdominant
behavior was only shown toward adult bulls by cows as well as by male
calves and subadult bulls. However, experienced older cows have a
certain leading function. They are able to trigger off movements of
the group and mostly lead in migrations. When changing places the
individual group members often walk one behind the other, no
individualized march formation is kept. Mostly an adult cow is leading
and the bull usually walks at the end (Fig. 134).

cow ad. 89% · bull juv. 5% · bull ad. 4% · cow juv. 2%

first animal

cow ad. 10% · bull juv. 6% · bull ad. 84%

last animal
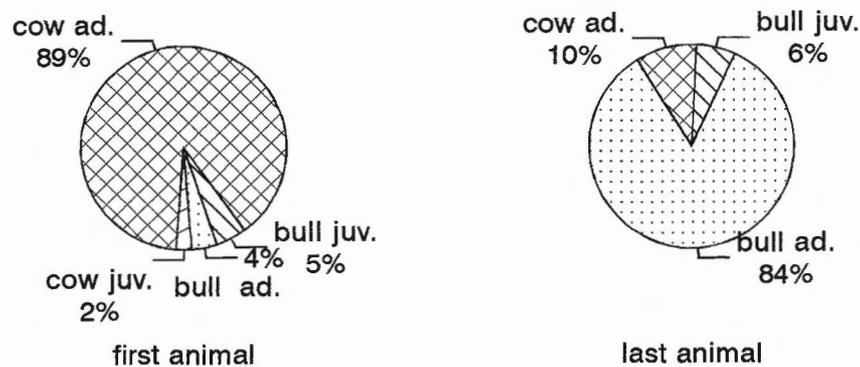
Fig. 134: Analysis of the march formation of all individually recorded movements of cow groups with bull (n=2.118), summarized according to gender- and age-classes

Directly in front of the trough the order changed, though: mostly the adult bulls drank first. However, during the daily wandering about the bull stays at the end, only in exceptional situations, e.g. when other adult males are nearby, the bull occasionally walks at the head. Individual classifications of the march formation showed that certain individuals lead the group much more often than others, like the cow eA with > 80% or the cow K1 with > 70%. Both lived in different groups for the most part of the observations. It is conspicuous that older cows were mostly group leaders, whereas very old cows were not. For instance one oldest cow of the group (T3) was never the first. She could regularly be found among the stragglers and at migrations was always the last during her last three months of life which was then even tolerated by the group-holder.

3.2.3 Behavior of calves and subadults

There are significant differences in the general activity pattern of calves and all other age-classes. The calves, particularly young calves, are lying clearly more often during the main activity phase.
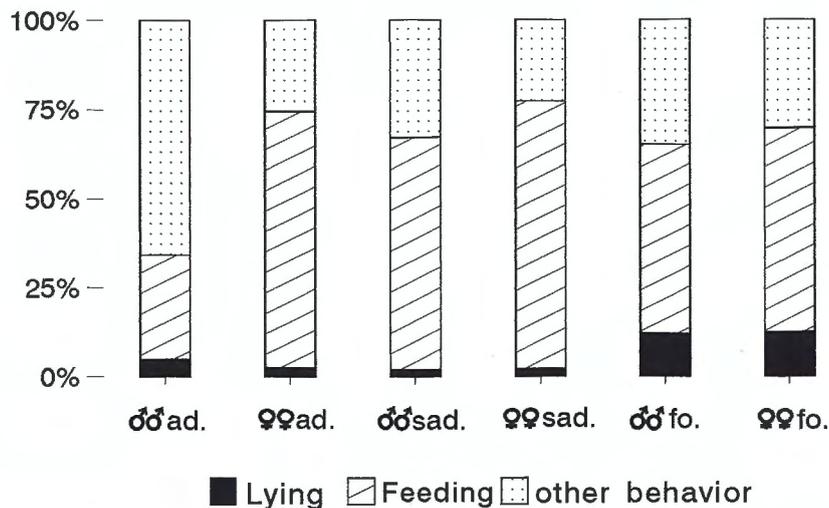
Fig. 135: Activity pattern of different gender- and age-classes at the main activity phase in winter (8-11h); (n=15.546)

Fig. 135 shows the summarized activity pattern during the winter months between 08:00 and 11:00 h in the morning, the time of day in which the dromedaries are mainly busy feeding, classified according to gender- and age-classes.

This summarized presentation already makes clear that calves, regardless of their gender, generally are lying and resting more often during the main activity phase than the other dromedaries. On the other hand the percentage of feeding is less than in the other age-classes, which is attributed to the additional milk supply. The adult bulls are an exception who are mainly in rut during the winter and therefore only spend little time feeding. The gender specific differences of the other activities are explained by playing. Male calves and subadult bulls spend significantly more time playing than female calves or subadult cows (Fig. 137). An additional evaluation of the general activities of calves shows a gradual shift in relation to the age. Despite individual differences, the trend is the same with all observed calves (Fig. 136).

45,3%

23,0%

39,4%

17,0%

37,7%

37,6%

1. month (n=266)

2.-5. month (n=822)

22,8%

21,4%

43,4%

44,8%

33,8%

33,8%

6.-12. month (n=1356)

12. month until weaning (n=3536)

■ Lying ⊘ Feeding ⊡ other behavior
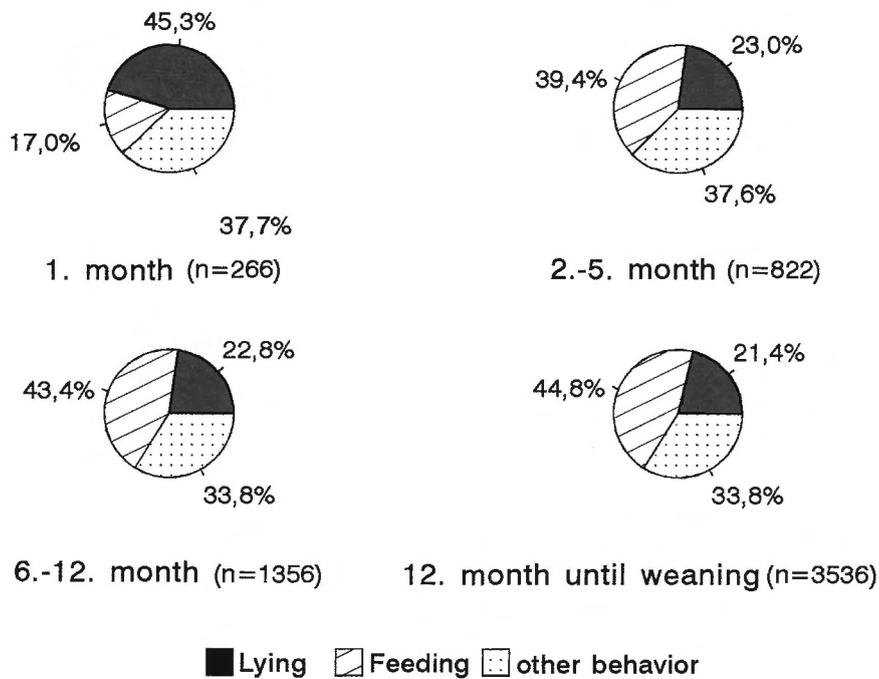
Fig. 136: Pattern of the summarized day activity of calves in relation to the age with the example of the female calf In

In the first month of life lying and resting dominates. Calves generally begin looking for food by themselves at an age of 2-3 weeks. They first nibble at any plant part but show specific feeding only

from the above indicated age. Therefore the average proportion of feeding of 17% in the first month of life in the demonstrated example can be explained. With increasing age the percentage of lying decreases, at the same time the percentage of feeding increases.

Playing:

Playing behavior is almost exclusively shown by calves and subadults. Only in rare cases which were limited to exceptional situations, playing was observed with adults, too (n=16). Dromedaries show different running game variations. According to the observations play fighting is mostly limited to male calves and subadult bulls. Active mounting in the course of mating games was shown by calves and subadults of both genders (n=36).

Playing behavior was recorded 1.598 times altogether. The distribution depending on the time of day is adjusted to the respective seasonal activity pattern and is shown in Figures 137 and 138.

In winter a distinct maximum is to be seen between 10:00 and 12:00 h. The young dromedaries have then already spent 3-4 hours mainly feeding, and they still play relatively often during the short resting phase at midday. In summer, however, they mainly play during the cooler times of day.

n = 806
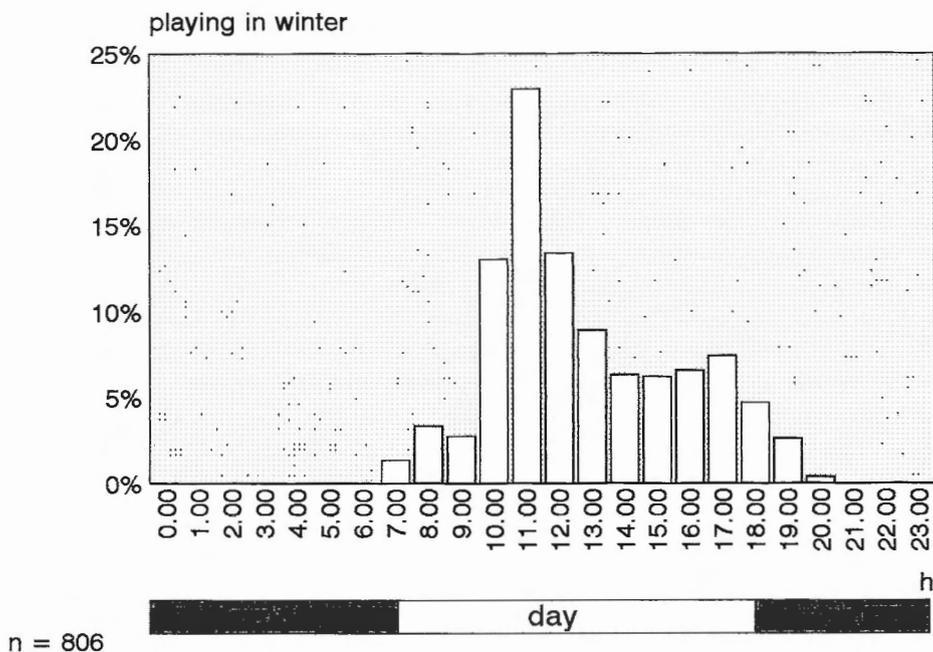
Fig. 137: Distribution of the playing behavior in winter depending on the time of day
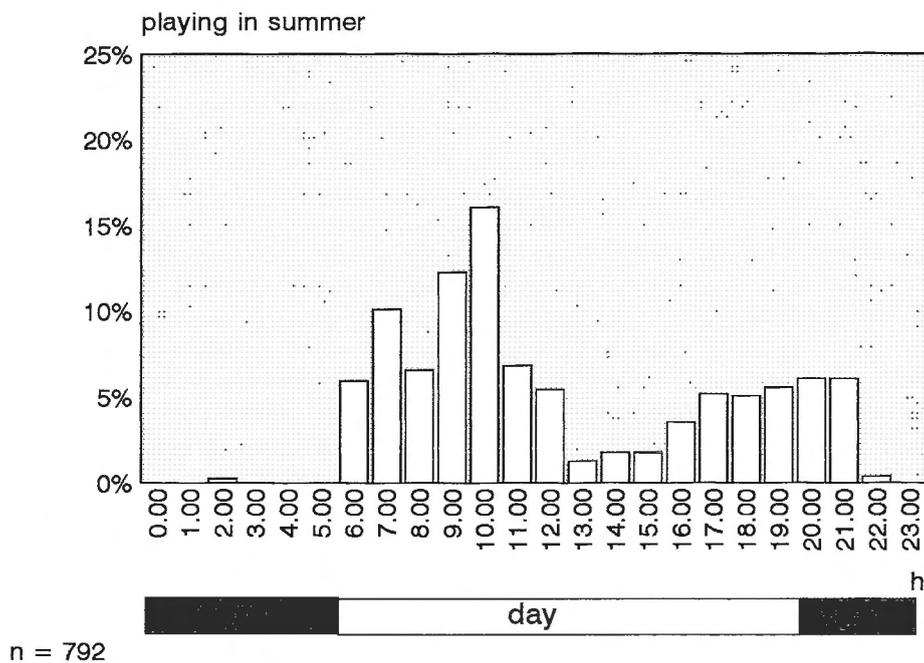
Fig. 138: Distribution of the playing behavior in summer depending on
the time of day

Fig. 139 shows the proportional classification of playing for the
different gender- and age-classes. Calves have the largest share of
all recordings with > 77%. Clear gender specific differences can be
determined within the respective age-classes (Fig. 140):
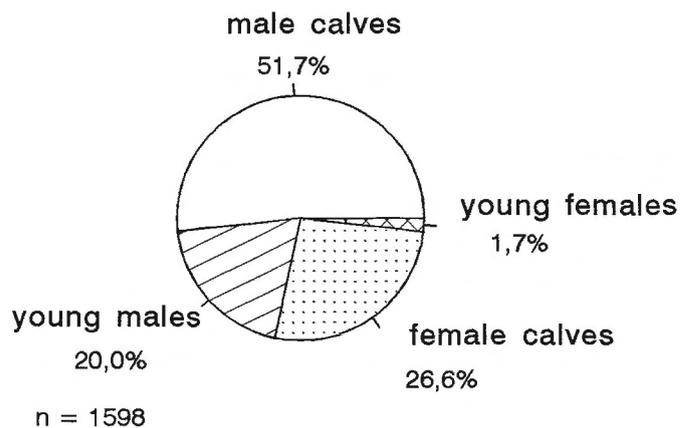
Fig. 139: Proportional playing behavior classified according to
gender- and age-classes

males
66%

females
34%

males
92%

females
8%

age class calves

age class subadults
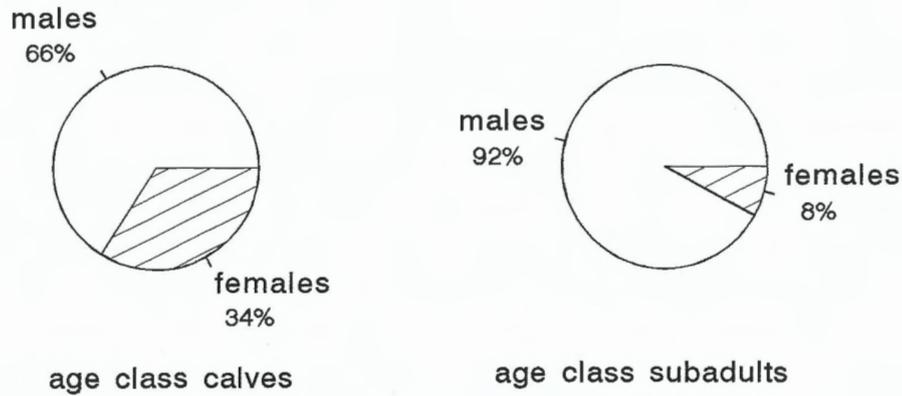
Fig. 140: Proportional gender-specific playing behavior within the
age-classes

In both age-classes cows are playing substantially less than bulls.
While they are still participating at 34% as calves, their share as
subadults drops to < 10%. The reason for this is the play fighting in
which the female young animals only participate extremely seldom. Male
calves begin with play fighting from an age of three weeks up. The
essential elements of the fighting behavior are already distinct at
this age (Fig. 142-143). Play fighting behavior occurs up to the age
of about five years (Fig. 141). The young bulls test and perfect the
different fighting variations which they employ seriously in later
competitions for cows. Play fighting was not observed any more with
adult bulls.

Fig. 141: Play fighting of subadult bulls (RS & KS) at the age of four
years

Fig. 142: Play fighting of male calves(Sn & Te) at the age of three
         weeks; here beginning neck wrestling

Fig. 143: Play fighting of male calves (Sn & Te) at the age of three
         weeks; here biting each other's front legs to force the
         opponent to the ground

3.2.4 Reproductive strategies

Dromedary bulls apply three different reproductive strategies:

1. Possession of a cow group:
The prevailing strategy is monopolizing of cows by adult strong bulls. The possession of a group is limited and mainly occurs in winter. For the bull the strategy means a considerable investment under high energetic effort and at the same time the risk to be injured or even killed after gaining the resource and/or when defending it. At the main breeding season in winter only the strongest bulls are able to practice the possession of a cow group. In summer weaker bulls also succeed in doing this because of the decreasing competition by the otherwise stronger bulls. While the probability that cows come in estrus is relatively high in winter, it is noticeably lower in summer (Fig. 116). The possession of a group is mainly attempted or practised by all adult bulls and is therefore to be interpreted as the general reproductive strategy of the bulls.

2. "Sneaker"-strategy:
Younger bulls who are clearly inferior to the group-holders do not take on a dispute let alone a fight. They stay nearby or at the periphery of the group and try to "sneak" their chance for reproduction without prior investment. Is the group-holder involved in an intensive promenade or in a fight with a rival, the "sneakers" take advantage of the situation. They start driving the cows and attempt to copulate. Some of them succeeded in the subsequent copulation. "Sneaker"-behavior was exclusively observed with younger bulls. The success of the strategy among other things depends on the competition by the other bulls, above all on the strength of the group-holder. Strong herding bulls do not tolerate bachelors at all in the vicinity of their group.

3. Infanticide:
With bulls in rut a clear aggression toward newborn calves could be observed, above all the abduction of the mother after the birth. The still relatively immobile calf cannot follow and subsequently dies.
In one case the entire course of the behavior could be observed continuously and documented by video-recordings. After a successful segregation from her group the cow Tr was surprised by a strange bull

and was chased away from her calf by force immediately after the parturition. Here the excerpt of the protocol of August 7, 1988:

12:00: Together with the cow Lo the cow Tr segregates from her group which is herded by the bull He. For the parturition of their calves both cows walk app. 3km away from their original group into an area which provides a lot of shelter in the north-west of the research paddock in the sand areas with dense vegetation.

14:00: Bachelor group consisting of two adult and five subadult bulls is resting ruminating in the next dune valley, about 2 km away from the cows Lo & Tr.

16:00: Begin of the birth with the cow Lo, Tr stands app. 50m away, but walks away as soon as she notices the observers.

16:47: End of the parturition with the cow Lo, after first naso-nasal and naso-anal contacts the mother lays next to her calf, both rest.

17:40: Begin of the parturition with the cow Tr, location is about 500m away from Lo with calf. Tr changes between lying-rolling position and walking, front legs of the calf become just visible.

17:50: Calf is partially expelled, Tr is standing. Bachelors from 14:00 h all of a sudden come running from south-west (against the wind). The adult bull Ed is leading, both adult bulls show distinct development of foam at the mouth.

17:53: Bulls stand in a semicircle app. 20m away from the cow, both adult bulls are gurgling. Only Ed walks toward Tr, sniffs at her rear end, sniffs at the partially expelled calf and shows flehmen, afterwards he gurgles. Tr stands motionless. Other bulls are interested but first keep a distance of 20-30m.

18:00: Tr sits down to finish the parturition, Ed stands next to her and mounts as soon as the cow is sitting. Tr bellows loudly and perseveringly, Ed carries out violent copulation movements on the cow and the partially expelled calf, the calf is being crushed and kicked strongly. Other bachelors come closer, particularly the adult bull Ma. Ed interrupts the "copulation" and chases away all bachelors.

18:05-18:45: 8 copulations take place altogether which are regularly interrupted by chasing the bachelors away. All copulations are triggered off by the cow sitting down to finish the birth. In the meantime Tr repeatedly stands up, bellows vehemently, and walks about in a circle, the bull Ed repeatedly sniffs at the cow's rear end with the partially expelled calf.

18:50 Calf is expelled, it kicks and has survived the procedure contrary to all expectations. Tr stands up, only sniffs at the calf briefly and is being lead away immediately by the bull. Bull Ed ignores the calf, gurgles strongly and drives the cow aggressively forward. - Falling darkness makes further observation impossible -.

On August 8, 1988, at daybreak both calves are found separately at their respective birth places alive and externally unhurt. The mothers

are app. 2km away, both herded by the bull Ed. Since a return of the
mothers at that point in time cannot be ruled out completely the
observers wait until 14:00h. After being fed the calves are then
released app. 30m away from the mothers and in sufficient distance to
the observers. Both young animals try to get attention by calling out
loudly, only the bull Ed is interested, comes to them briefly and
sniffs at them intensively. But both mothers only look up shortly and
do not show any intention to approach their calves. Obviously the only
short time between birth and abduction was not enough to bring about a
bonding between mother and child.

Infanticide can be practised by bachelors as well as by the group-
holder. Group-holders were responsible for the death of the newborns
in at least two cases. In one case, because of an exceptional
situation, a cow (H4) was not able to segregate from the group in time
before the parturition, since the bull (Ho) kept together all group
members in the horse paddock in one corner of the fence. Later the
group was found roaming around extremely restlessly and agitatedly,
particularly H4 was chased aggressively by the group holder. The calf
was only found on the next day in the afternoon. With the evaluation
of traces it could be reconstructed without any doubt that the calf
had lived at least for a short time and the bull had been immediately
nearby. The bull had chased the cow back to his group right after
parturition so that the calf was isolated and then died.

Another case: the cow K1 was not able to segregate since she only
lived together with the bull and another cow. Whenever she tried to
segregate, the bull followed her and eventually the other cow, too.
The calf was found two days after its birth; evaluations of traces
showed that it had lived and that the group-holder (Ma) had been right
next to the calf.

Another observation points to direct aggression of bulls in rut toward
newborns: after successful segregation and the birth of her calf the
cow T1 was discovered the next morning by her original group. The
group-holder (Ho) was extremely agitated and demonstrated clear
aggression toward the newborn. He kicked it and repeatedly showed
violent biting intentions. Even though the bull was definitely

stronger the mother tried to fend off the attacks on the calf - at this point the observers intervened and chased the bull away (since the calf survived, it is excluded from the infanticide-category in Fig. 145).

Fig. 144: Direct aggression of the bull Ho in rut toward the newborn female calf In; the bull specifically kicks the calf, at the right border of the picture the head of the mother Tl who tries to defend her calf against the aggression of the bull

Shortly after that an encounter of mother and calf with the adult bull Fd, who was at that time not in rut, went totally different. The bull briefly sniffed at the calf, greeted the mother and then moved on (the observations were done in 1987 in the horse paddock where all animals met more often than in the future research paddock because of the higher density). After five days being by themselves, mother and child were taken over anew in the original group of the group-holder Ho. Even at this point in time the bull still showed aggressive behavior toward the calf who now was much more mobile and could get out of the bull's way.

Another observation demonstrates the tolerance of bulls who are not in rut toward newborns: the cow N16 had her calf on November 20, 1988.

Shortly before parturition she only moved app. 500m away from her original group which was accompanied by the bull He. In November the bull was still with the cow group after holding the group for 8 months, but he only showed clearly diminished rutting behavior, if at all (Fig. 85). Exactly one hour after the birth the group went to the calf that was welcomed by all group members one after the other. The bull came last, approached the calf slowly, first sniffed at its anal region, greeted it naso-nasally and afterwards strolled on. The next day He was replaced as the group-holder by the bull Ho almost without resistance. According to that He was clearly not in rut any more at this time.

survived
n=31 71%

died of
infanticide
n=5 (12%)

died probably of
infanticide
n=2 (5%)

died of
unknown reason
n=5 (12%)
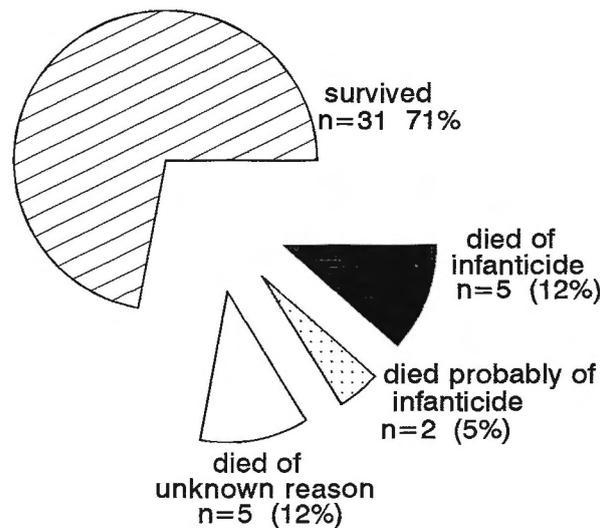
Fig. 145: Causes of calf mortality in the research paddock

Infanticide is an essential factor in the mortality rate. Of a total of 45 recorded births the fate of the calves could be documented in 43 cases: two cows could not be found after the birth of their calves until the project was finished. 12% of all calves definitely died by infanticide. In 5% infanticide may be supposed as the cause of death. In these cases the mothers were sighted after the birth accompanied by an adult bull in rut, but the calves were not to be found. The proportion of young animals who died by infanticide could thus even raise to 17%. In the other 12% of calves who died the cause of death could not be determined.

The reproductive success of the infanticidal strategy could be documented in three cases:

Two cases refer to the above described situation in which the bull Ed chased the cows Lo & Tr away from their calves in August 1988 and stayed together with them until January 1989. Even though matings were not directly observed here it can be assumed that they took place. Both cows were consistently herded by the bull and defended against rivals, besides they both showed traces of copulation several times. In September 1989, i.e. 13 months after the infanticide, the calves fathered with sufficient likelihood by Ed were born.

In the third case the infanticidal bull Ma had copulated several times with the cow Kl three weeks after the death of the calf. She was highly pregnant by the end of the project.

4.   DISCUSSION

Among the large mammals dromedaries are adapted the best to desert conditions (SCHMIDT-NIELSEN 1964). Apart from the morphological and physiological adaptations it is to be expected that the social system is also adjusted to the conditions of the habitat. The dromedary became extinct as a wild animal in prehistoric times (GAUTHIER-PILTERS & DAGG 1981). Consequently there can only be speculations about the family life of the wild populations, assuming that the basic pattern of the social organization is determined genetically (WILSON 1975). For instance comparative investigations on horses (*Equus przewalskii* f. caballus) whose feral populations everywhere show an identical family life regardless of the habitat (KLINGEL 1982) point to the genetic determination of the social organization. In addition, the horses who have turned feral have the same social system as their relatives the plains zebra (*Equus quagga*) and the mountain zebra (*Equus zebra*) whose wild populations could be investigated (KLINGEL 1964, 1967, 1972, 1975; JOUBERT 1972; PENZHORN 1984).

The social organization of the dromedary is characterized by non-territoriality and group formation with an extreme flexibility. Non-territorial systems are very adaptive for desert animals. Their habitat is in general characterized by scarce resources which are unpredictable with regard to temporal and spatial distribution, briefly: determined by "unpredictable conditions". A territorial investment in the sense of a monopolization does not occur, and ecologically dependent migrations are therefore possible at any time without a loss of investment. The mobile reproduction unit, as the social system adapted ideally to arid conditions, has been realized with the dromedaries. Long-term individualized associations which - like with the plains zebra - have the same members over several years (KLINGEL 1967) are not to be found here, though. Compared with most of the other social systems of ungulates the cow groups are very stable with core groups which last up to two years. In the same period of time the bulls change several times dependent on hormonal factors.
The basic mechanism of the new group formation is the mutual attraction of cows with young calves. The duration of the subsequent association is determined by the lactation phase and is independent from the presence of a herding bull. Family relationships which e.g.

mark matri-linear groups with elephants (*Loxodonta africana*; MOSS 1983, 1988) or deer (*Cervus elaphus*; CLUTTON-BROCK et al. 1982), are therefore not relevant for the group formation of the dromedary. Associations on an individual basis with partners that are not related are rare with ungulates anyway, and the dromedary is one of the few exceptions apart from the above mentioned equids.

The voluntary association of the cows proves to be very useful: Cows with calves of the same age have basically the same "interests"; the mobility of the calves and their activity pattern only adjust very slowly to that of the adolescents or adults. Young calves for instance lie clearly more often and longer, which limits the group's range of action. Furthermore lactating cows have a higher need for nutrients, mineral matters, and water than their other conspecifics and e.g. show the highest drinking frequency (HEUCKE 1995). Home ranges close to the trough in summer are typical for cow groups with calves. And their range utilization and migration pattern shows clearly more energy- and water-conserving elements in relation to that of the other dromedaries (HEUCKE 1995). At the same time the young animals grow up together with conspecifics of the same age who have a comparable motivation for playing and thus for perfecting of behavior patterns needed later. Because of the described functional contexts it can be explained why cows with young calves did not remain steadily in the groups with cows who already had app. 1-year-old young calves. The needs, the maternal investment, and also the activity pattern of the cow shift step by step dependent on the growing of the calf; the cycle is only concluded with the weaning. The social relationships are thus exclusively build via the common rearing of the young and lose their importance with the weaning of the calves. The advantage of the association is obvious: Individuals with the same interests optimize their living conditions and that of their offspring by this. Aside from the general advantages of living in groups which are basically in the functional context of predation avoidance or risk minimization by dispersion or confusion effect (overview in VOLAND 1993), the dromedaries show an additional social adaptation by forming "functional associations". In those the individual mothers behave cooperatively, e.g. by one mother staying close to the calves while the others move on a little further for feeding, which could be documented by a number of observations.

Mechanisms which favor the formation of core groups are to be seen on the part of the cows in a very distinct preference for certain habitats which are visited for the birth of the calves. Sand plains or dunes with dense vegetation, enough food, soft ground, and sufficient cover were clearly preferred. GAUTHIER-PILTERS (1974) on the other hand quotes statements of nomads according to which dromedary cows in the Sahara at the birth of a calf return to the place of their first births, which can be as far away as 1.000km. The repeated visiting of the same area for the birth of the next calf was not observed with any cow in the research paddock. Keeping such established birth places is hardly imaginable for such a mobile animal species whose habitat is characterized by unpredictable conditions, unless cyclical migrations took place for which there has not been any evidence so far. The habitat preference for the birth clearly enhances the probability that cows with young calves meet and join together in core groups.

The social system which provides the best adjustment for ungulates in arid habitats with unpredictable conditions seems to be the stable family group (KLINGEL 1985), but it is not practiced by the dromedary. It is not verifiable to what extent the specific reproduction biological features are causally responsible for this. One decisive factor lies in the long relative immobility of the calves during the first days of life which is unusual for ungulates. The home range of a stable family group would at times be extremely limited by a birth, which means quite a disadvantage in desert habitats. In addition, a stable family group would in an extreme case even be spread across a minimal home range for several months because of the very poorly developed synchronization of the cows, which contradicts a good adaptation to desert habitats.

The polygynous reproduction system gives the individual bull only limited chances for a reproductive success. To enhance the individual fitness it could be expected that the bulls monopolize their cows - and thus their once "won" reproduction resource - as long as possible and defend them actively.
But obviously the dromedary bulls are not able to herd the cows for more than six months because of the irregular rutting cycles. Even though the possession of a cow group means the result of quite an investment for the bull, he mostly gives it up voluntarily toward the

end of the rutting period. The constitutional limits presumably force
the often clearly emaciated bull after a certain time to leave the cow
group, but he could as well stay inactively with the cows. Even the
bulls who were still in very good shape and not emaciated at all left
their groups voluntarily. The reason for that are probably hormonal
changes which have been sufficiently studied on domestic dromedaries.
YAGIL & ETZION (1980) ascertained a distinctly higher testosterone
level with corresponding changes in the behavior at the rutting
season. AGARWAL et al. (1986) investigated the concentrations of the
thyroxine (T4) and the tri-iodiothyronine (T3) in bulls. Both
parameters were significantly higher outside of the rut, the ratio of
T4:T3 was almost doubled at the rut, though. The authors conclude that
this ratio is the decisive factor for the beginning of the rut. AZOUZ
et al. (1992) proved an extremely high prolactin-level in the blood
outside of the rut which dropped significantly with the beginning of
the rut. At the same time the concentration of the pituitary hormones
FSH (spermiogenesis) and LH (testosterone production) increased
noticeably. The testosterone and cortisol levels were also
significantly higher during the rut than outside of the rut. The
authors assume that the overproduction of the prolactin outside of the
rut is responsible for the loss of the libido and the limited
fertility of the bulls, as it has an impeding effect on the release of
the hormones FSH and LH. While the hormonal adjustments are well
studied with domestic dromedaries there have not been analyses like
that so far for free-ranging dromedaries.

The observed behavior is still very well useful for adult bulls as a
strategy for the maximization of the reproductive success. They invest
the most at the main breeding seasons and gather strength in between
them. Because of the distinct seasonality in the reproductive cycle
the probability that cows come in estrus is the highest with 93% in
the six months from June to November. Afterwards reproduction is
possible in isolated cases but the possession of a group with all its
disadvantages can at this time not be rated a successful strategy.
Obviously the expense of the possession of a group is much higher for
adult bulls in summer than the reproductive advantage and thus it is
not "worthwhile" for the bull to continue holding the cow group. The
observed age dependent seasonal distribution of the group-holders can
be assessed accordingly: young, inexperienced bulls herd the cow group
in summer, too, but the strongest bulls practice the possession of a

group exclusively during the main reproduction time in winter. EL-NAGGAR & RATH (1987) describe a comparable pattern for domestic dromedary bulls among whom the sexual activity of the clearly younger and weaker "summer-rutters" begins with the abating rut of the stronger "winter-rutters". The most permanent possession of a group of up to one year which was only observed with one bull is considered an exception but still shows alternatives. He even stayed with the cow group outside of the main reproduction period but without demonstrating the typical rutting behavior. Apart from that, contacts to other dromedaries were very rare during this time. Which causal factors had an effect here remains unclear: most herding bulls were solitary after leaving their cow group, a social attraction by other bulls is thus obviously not relevant. This bull had no competition, but other bulls without competition left their groups voluntarily, too.

Nevertheless the question remains whether bulls who do not give up the possession of a group voluntarily could have an advantage by doing so. The results up to now give reasons against it, and aside from the described exception the bulls behaved clearly seasonal, with obvious rutting phases and obvious non-rutting phases with a correlated leaving of the cows. A behavior like that would be imaginable in populations in which the reproduction chance is evenly distributed over the year. Dromedary cows who are kept in direct proximity to the equator show a distinct aseasonality in the distribution of births (SCHWARTZ et al. 1992). Under these conditions it would be adaptive for a bull to monopolize the cows as permanently as possible which at the same means for him to be in rut all year long and thus to be able to reproduce. But the limited rut of the bulls kept there shows that the chance for an individual fitness maximization by a long-term possession of a group is governed by physiological limits for the dromedary bull.

The socio-biological infanticide of the dromedary is particularly important; moreover it is the first proof of a successful reproductive strategy of bulls in ungulates. Rutting bulls show a distinct aggression toward newborn calves, but above all they abduct the mother after the birth - the calf cannot follow and dies. The death of the calf leads to a fertile post-partum estrus of the mother which increases the individual chance for reproduction of the bull.

In the socio-biological terminology, apart from the direct killing of young animals, Infanticide is any behaviour that makes a direct and significant contribution to the immediate death of an embryo or born member of the perpetrator's own species (MOCK 1984). Socio-biological infanticide is favored in associations which are characterized by relatively stable harem systems controlled by one or more males, and in which the males compete for access to the females. Infanticide occurs as soon as new males take over the harem (HRDY & HAUSFATER 1984). For these the clearly earlier estrus of the respective mother resulting from the death of an infant means a reproductive advantage. Infanticide favored by the sexual selection mainly occurs among the mammals in primates (STRUHSAKER & LELAND 1986), carnivores (PACKER & PUSEY 1984), and rodents (LABOV et al. 1985).

VOLAND (1993) summarized the prerequisites for adaptive socio-biological infanticide as follows:

- "Infanticidal males should only kill strange offspring but not their own children"
- "Infanticidal males should inseminate the mothers of their victims after killing the children"
- "Infanticide should lead to a shorter birth interval"

In all observed and categorized cases the infanticidal bull was not the father of the calf. Due to the social system of the dromedaries the possibility that a bull takes over the same cow group in the next rutting period is very little anyhow because of the low density in the area in which they are to be found. Even in the research paddock with a comparatively high density (HEUCKE 1995) and the additional "unnatural" situation, that all animals met again and again, this did not happen. The groups fluctuate dependent on reproductive and also on social factors. In addition, different extensive migration patterns of bulls in relation to the cows are assumed which could not be proved up to now. However, it cannot be completely excluded but is unlikely that the same individuals under natural conditions come together again in the following year. The risk of killing the own offspring is therefore minimized and the statistical probability nearly excludes that bulls kill related calves.

The bulls monopolize the cow after the loss of the calf for at least two months which corresponds to app. three phases of estrus. The insemination - and thus the own reproduction - is therefore very

likely. In three cases the reproductive success of the strategy could be ascertained beyond doubt.

The loss of the calf leads to a fertile post-partum estrus with the cow and thus a clear shortening of the birth intervals. The birth intervals were 22.2 months on average if the previous calf survived, but only 14.4 months if the previous calf died (HEUCKE 1995).

The criteria for socio-biological infanticide are thus fulfilled. All observed infanticide cases happened within the first days of life of the calf. Later occasional aggressions of bulls against calves were noticed, but the calves were then much more mobile and could get out of the way. So the infanticide is positively correlated with the immobility of the calves.

The segregation of the cow before parturition can be considered a useful strategy to avoide infanticide, since the herding bull is not the father of the unborn calf fathered the year before. Therefore he is not interested in this calf but only in the cow, the reproduction resource. Cows in groups without a bull did not segregate. They had their calves surrounded by the group and it can be excluded that all these births were so-called "sudden births" (FRASER 1968). At the birth of their next calves the same cows segregated from their group, when this was herded by a bull. The segregation behavior probably occurs due to the permanent restlessness which is triggered off by the group-holder. In the main rut in which most of the births take place he is always eager to keep his cows as closely together as possible in a small area. For the slightest reason, e.g. if bachelors are nearby, his nervousness increases. Significantly more intensive herding is the result which can increase to the aggressive chasing away of the cow group. If the cow does not segregate before parturition, mother and child are subsequently still passively isolated since the other group members move on. But in most cases the births take place at times in which a bull herds a cow group, who can then become a threat to the calf. Cows that are already isolated cannot fight against rutting bulls that happen to come along. But there is only a slight probability that a single animal is being found in its hiding place by other conspecifics. A higher frequency of infanticide dependent on the population density is thus obvious.

Even though there is only one observation about it, it probably depends on the group size whether the cow can segregate. If there are only two cows, as in the observed case, they are more easily kept

together and controlled better by the bull. From this point of view the general tendency of cows from relatively small groups which join together to larger associations in summer can be evaluated anew. Apart from other factors, the preventive infanticide avoidance or the risk minimization can be decisive for the formation of larger cow groups.

Infanticide is the exception with ungulates, it has so far only been assumed with horses:

DUNCAN (1982) points to infanticide under domestic conditions. According to the horse breeders at the annual exchange of the stallions young male foals were specifically killed by adult stallions who had been with a mare group for the first time. The attacks took place immediately or up to a few weeks after the stallion had "taken over" the mares. A stallion who had already killed six foals at these exchanges was then kept for >2 years with the same mares and afterwards did not kill foals any more.

BERGER (1983) investigated the reproductive success of a feral horse population in Nevada. Mares whose family stallion did not change had a clearly higher reproductive success than the ones whose stallion changed. The author infers to feticide due to induced abortions which were caused by forced copulations of the new stallions.

In a long-term study about the wild horses in the Camargue neither infanticide nor induced abortions occurred (DUNCAN 1992). Furthermore there is no indication for infanticide or feticide with other equids with the same social organization (KLINGEL 1966, 1967; JOUBERT 1974; PENZHORN 1984).

A TV-documentation about feral horses of the Namib shows that conditions can arise that favor infanticide (SYCHOLT 1985). After a period of drought the phenomenon repeatedly occurred with this horse population living in the extreme desert habitat that mares were isolated from their family group for a longer period of time at the births of their foals and thus were exposed to the aggression of strange stallions. In one case a sexually strongly aroused bachelor showed direct aggression against a newborn foal who could not walk due to weak joints. The stallion repeatedly kicked the foal even though the mother tried to defend it; afterwards he copulated with the mother. Later the stallion lead away the mare, the foal was left behind and died. In the second case the death of the foal happened because the mother was aggressively chased away immediately after the birth. In this case it was the group holder who had taken over the

mare in his group only shortly before. Both variations show clear parallels to the infanticide of the dromedary: isolated cows are discovered by strange bulls and are driven away from their calves. The still immobile young animals cannot follow and die. Or the group-holder practices the same behavior if the cow does not succeed to isolate in time before the birth. With regard to the adaptive value of the behavior there are differences, though: Horses under normal conditions have a foal each year, regardless whether the previous foal survives or dies. Still the foal fathered by the infanticidal horse stallion has an advantage, since the nursing phase of the killed foal does not take place and thus the energetic investments of the mother are only of benefit to the new embryo. Dromedaries on the other hand only have a calf every two years and only if the previous calf dies the cow comes in estrus shortly afterwards. The infanticidal bull gains within a minimum of time a cow in heat. This cow would have been fertile only after seven months at the earliest if the calf had survived. The shortening of the birth intervals is the advantage for the infanticidal bull.

The parallel behavior pattern of horse and dromedary male is conspicuous, too, who directly after the birth mounted and attempted to copulate with the female; the dromedary bull even tried it several times during the expulsion phase. Since these copulations certainly cannot lead to a conception, the behavior can rather be explained as a dominance-copulation. With the dromedary bull a "misunderstanding" could be suggested too, as the cause for the copulations was the cow sitting down for finishing the parturition.

Since the segregation behavior of the cow before parturition is very adaptive from the socio-biological point of view, the question remains whether an earlier joining with the group would be more advantageous. The relatively long time the cow remains alone with her calf can mean additional dangers for mother and calf. In habitats with natural predation pressure they would undoubtedly be better protected within a group. Still the isolation-behavior with active avoidance of contact to conspecifics, excluding other mothers with calves, is practiced. With the exception of man the dromedaries in central Australia do not have any natural enemies. The dingo (*Canis lupus* f. dingo) could be considered the only predator of newborns. But only in exceptional circumstances, if the mother is not with the calf, the dingo has the

chance to kill a calf. Obviously the observed isolation behavior helps to avoid aggressions by other dromedaries; particularly rutting bulls but also high-spirited subadults often showed aggressive behavior toward the still uncoordinatedly moving calves.

Furthermore the time of the birth is important und thus the probability to meet other mothers with young calves. During the main breeding season the cows congregated faster in core groups than in summer.

There are opposing reports about the site fidelity of the bulls. BASKIN (1976) describes territorial behavior of rutting bulls around watering places in the Turkmenia desert. They marked the ground with the secretion of their occipital glands; YAGIL (1985) also describes dromedary bulls in rut as being territorial. GAUTHIER-PILTERS & DAGG (1981) on the other hand point to the fact that territorial behavior was not observed with free-ranging dromedaries in the Sahara. The results of the study in hand clearly speak against a territoriality. Dromedaries do not monopolize areas which they mark by scents. Feces and urine are distributed randomly; feces are usually not sniffed at, urine only of cows, particularly at the time of the estrus. According to EL-NAGGAR & RATH (1987) the pungent smelling urine sprayed by competing bulls during the tail-lashing ritual apart from a high concentration of testosterone possibly contains pheromones with which they "perfume" themselves. The wiping of rutting bulls which only occurred with increased excitation of competing bulls in the course of the "promenades", and the specific urinating on shrubs has no territorial function according to the observations. Even older male calves and subadult bulls showed the specific urinating on shrubs during playing. Territoriality and scent markings are not necessarily correlated with each other (SCHENKEL 1966). Although the wiped off secretions on plant parts were clearly noticeable visually as well as olfactorially to the observers for several days; reactions of other dromedaries to the markings were not to be seen. Neither the competitor nor the other group members went specifically to the marked spots to sniff at them. Even other dromedaries who happened to be directly nearby passed without noticing them. A possible explanation would be that the markings are behavioral relicts which originally were in the functional context of the territory-marking, but do not have a discernible function with the recent dromedaries.

WEMMER & MURTAUGH (1980) emphasize the olfactorial component of the secretions with the closely related Bactrian camel bull (*Camelus ferus f. bactrianus*), but do not give information about a reaction of conspecifics. Under domestic conditions, two Bactrian camel bulls marked the border fence of their adjoining enclosures regularly with the secretions of their occipital glands. GAUTHIER-PILTERS (1954) describes the wiping off of the secretion on objects and shrubs by dromedary bulls in rut even without the presence of competitors. The also non-territorial eland bulls (*Tragelaphus oryx*), who wipe the hair of their heads in the mud or in their own urine and mark objects with it, show a comparable behavior (WALTHER 1988). CHARNOT (1964) assumes a stimulating effect of the secretion of the occipital gland on the cows. Presenting of the secretion triggered off aggressions in an otherwise tame dromedary cow. She snapped at it bellowing (GAUTHIER-PILTERS 1954). This and another observation with tame dromedary cows in Kenia (KLINGEL pers. comm.) point to the conclusion of a social function of the secretion of the occipital gland.

YAGIL & ETZION (1980) stress that the androgen concentration of the secretion of the occipital gland is identical with the one in the blood. In the social context, a function of the olfactorial marking is therefore very well imaginable, though specific marking of other dromedaries was not observed. Rutting bulls often put their necks and heads on the withers or the rear base of the humps of the cows, particularly in the mating foreplay. A transmission of the secretion that often runs down the neck of the bull is therefore possible. Furthermore the bull repeatedly brushes against or touches all group members while herding. Maybe the "group smell" created by this can explain the above described incomprehensible behavior of a bull at the encounter of his group with that of another bull: he specifically herded a subadult bull back who had migrated to the other cows, but chased away an adult cow coming from the strange group. However, isolated cows who did not have longer contact to other rutting bulls were allowed to join the group. Here it can only be assumed that they did not have scent markings any more. The frequent rubbing of the nape of the neck of rutting bulls and thus the marking of the own body with individual scents could have a key function at the recognition and assessment of the respective physiological condition. The secretion of the occipital gland according to the observations clearly has no

territorial but another social function. The evaluation of this topic should be the object of further detailed investigations, though.

Without doubt the wiping and the specific urinating on shrubs during the "promenades" in the presence of the rival also has a strong visual signalling effect. The rolling is unusual in this context which is also described for New World camels but here is interpreted as a displacement activity at an inhibited aggressiveness (GAUTHIER-PILTERS 1960). Dromedary bulls of the same strength demonstrated the rolling during the "promenades" either simultaneously or one after the other. If only one bull showed the behavior then it was exclusively the eventually stronger one. So the rolling during the promenades gains the function of a superiority gesture. It seems to be unusual that the bull lays down to demonstrate his superiority and thus presents himself although very active to aggressive to the rival but still physically clearly smaller. But the rival is usually standing by nearly unheeding when the opponent is rolling, and does not show any intention to use the supposed favorable situation for an attack. Obviously this behavior also underlies strict rules and is part of the competitive disputes carried out mainly ritualized anyway.

Only in rare cases serious fights arise. With domestic dromedaries fights are said to take place at the rutting season only between leading bulls (GAUTHIER-PILTERS 1960). In the research paddock this was only achieved after prior intervention by the observers. Herding bulls usually avoid any closer contacts to other dromedaries and keep a clear distance to each other. Via the contact avoidance strategy of the herding bulls competitive situations between group-holders are thus quite unlikely from the start. Rutting bachelors on the other hand often try to provoke the group-holder. Obviously only a few of them are ready or able to fight seriously for the possession of the cows.

GAUTHIER-PILTERS (1959) describes that all fight movements are directed to make the opponent fall and to strangle him with his own body weight. It can even happen that both bulls strangle each other (GAUTHIER-PILTERS 1960). In the research paddock lethal effects of this variation of fight were not observed, but the death of one bull by strangling in a camel farm in Alice Springs was reported (SMAIL pers. comm.). The observed injuries with lethal consequence make clear that it is biologically useful for the individual bull to possibly avoid serious fights with the help of a number of rituals.

Outside of the rut the social behavior of the dromedaries is marked by an extraordinary "composure". The activity of the members of a group is mainly synchronized. They eat together, walk about while doing it and have obvious common resting phases. In summer the animals often rested lying closely together in the shade of a tree. At the same time they reduce the influence of the radiation heat of the ground, besides the other dromedary is then noticeably cooler than the ambient air temperature (SCHMIDT-NIELSEN 1964). Even during the night rest in winter, particularly in cold nights, it could regularly be observed that the animals were lying together with bodily contact which reduced the heat loss of the individual. During the midday resting phase in winter and at the night rest in summer, too, the distances of the individuals to each other were clearly bigger. The observed behavior can thus be evaluated as an adaptation to the respective environmental conditions.

Dromedaries have the ability to recognize other dromedaries individually (SCHULTE 1988). Despite this, individual partner preferences were only to be observed seldom. In contrast to the studies with domestic dromedaries (SCHULTE 1988), adult cows who had lived in a social unit for a long time showed such preferences under normal conditions only faintly. SCHULTE's results are also different from the study in hand with regard to the night resting places which can be put down to the domestic conditions of his animals. The domestic dromedaries had shown a distinct site attachment with the selection of their sleeping place in the enclosure, combined with a relatively stable "nearest neighbor"-relation. On the other hand, free-ranging dromedaries spend each night at another place and the nearest neighbors are random with the exception of the mother-calf-couples and a few more exceptions of subadult cows. Only the bull lays significantly more often apart, which can hardly be put down to an individual avoidance but rather fulfills the function of the "better overview". It could as well be that the chosen method is not enough to determine closer individual bonds. Maybe the nearest neighbor is even irrelevant; this approach is supported by the observed behavior during the midday resting phases in summer. However, the exceptional situations at the immobilization provide better indications for possible individual bonds which go beyond the mother-calf-relationship. The cow who was hit by the immobilization dart specifically sought certain individuals during the response time of

the drugs, or others exclusively "cared for" the immobilized animal. Some tried to pull out the immobilization dart with their teeth which one cow even managed to do. This behavior is certainly complex, and apart from simpler and quite probable possibilities for an explanation, like the attraction of the "new", maybe also point to help. Concerning the cooperation in the society, contrary observations could be made at the same time. The behavior of the other dromedaries during the immobilization and the described situation with an obviously helpless animal indicate this. Despite these unusual observations the subject of individual partner preferences with adult cows has not yet been settled sufficiently. Subadult cows on the other hand showed clear individual preferences. Furthermore the social attraction of individuals of the same age-class could be observed regularly with young animals which does not correspond to an individual partner preference, though. GAUTHIER-PILTERS (1981) also describes that young animals often stay together and form small sub-groups within the herd.

The analyzed individual sequences in the migration order do not give obvious indications for certain "leading animals" in a group. Normally the bull walks at the end of the group and an adult cow is leading. In some groups several adult cows were equally often in the leading position. They could even take turns within a short time. In other groups, however, one particular cow was often the first. These were exclusively experienced, older individuals who generally proved to be particularly watchful and cautious. The frequent occurrence of older cows at the front of the herd has also been described by GAUTHIER-PILTERS (1974). Some cows frequently set off first at disturbances and the other group members followed. But from this connection it cannot be concluded that they had the function of an "active leader" but rather that of a "passive leader". Still it can be expected that adult older individuals know good grazing lands or other attractive places in the home range due to more experience and it is thus useful for the other group members to follow this animal. The final position of the bull obviously has the function of the "better control". This behavior can also be considered useful at the flight from predators, by the strongest animal bringing up the rear. It could not be observed that the bull defended the cows due to the special situation in Australia where natural enemies of the dromedaries are missing.

With regard to the dominance order there were no indications for individualized relations but for an anonymous class hierarchy in which the adult bulls are dominant. Outside of the functional context of the reproduction, competitive situations are rare, though. In the observation period food resources, water, and salts in the form of salt earths were available in sufficient amounts, compared with the Sahara even in overflow (HEUCKE 1995). However, SCHULTE (1988), who could observe very competitive situations via the salt supply of domestic dromedaries in Kenia, also states that an individualized dominance order was not to be seen. Only in the extremely dry winter of 1987 it could be supposed that some individuals were able to "control" preferred food resources. The adult bulls often broke branches from shrubs or trees and by this reached the few remaining particularly green leaves. As soon as the other dromedaries heard the cracking of the twigs they came running. It was typical that the cows who ate from these twigs together with the bull at the same time signalled appeasement by a crescent-shaped lifted tail. Submissive behavior like that did not occur with subsequent food intakes under conditions which had improved in the meantime. At the same time only two cows independently from each other had "invented" a new variation of getting food in this extremely dry season. They jumped up specifically to reach the green leaves of preferred tree species, mostly *Acacia aneura* or *Atalaya hemiglauca*, which they otherwise cannot reach. An imitation of this behavior which was certainly conspicuous for the other group members was not observed.

The crescent-shaped lifted tail, (termed verbally as "curl" in the English literature), was interpreted as an indication for pregnancy by some authors (GAUTHIER-PILTERS & DAGG 1981; SCHWARTZ ET AL. 1992). MUSA & MERKT (1987) already point out that this is not the case. The signal is indeed shown by pregnant cows, but in the study in hand it could definitely be settled that it is an appeasement gesture. Some ungulates lift their tail or roll it up in alarming situations, like giraffes (*Giraffa camelopardalis*) or elephants (LEUTHOLD 1977). Juvenile gerenuks (*Litocranius walleri*) also show "tail-curling" as a signal of submissive behavior (LEUTHOLD 1971), which RÄDER (1982) could also ascertain with adult females.

Social systems gain a particular importance concerning their adaptive value by the comparison to other animal species that live under similar ecological conditions. The comparison of the social organization of the closest relatives of the investigated species is also useful:

The closest relative of the dromedary, the Bactrian camel or two-humped camel, has up to now not been investigated with regard to its family life. The wild population is estimated at only 500-800 animals (ZHIRNOV & LUSHCHEKINA 1992). But the few existing observations indicate certain parallels to the dromedary: ZHIRNOV & ILYINSKY (1986) describe seasonally varying group sizes with ϕ 3.7 animals in August and ϕ 12.8 animals in December; BANNIKOV (1975) reports about herds of up to 200 animals in winter. The group seems to be composed of a few cows with their calves who are temporarily joined by one to two bulls, one of which is the "dominant bull" (ZHIRNOV & ILYINSKY, 1986). While nothing has been known about the reproduction characteristics of the wild population so far, those of the domestic Bactrian camels correspond mainly to those of the dromedaries (KHANNA & KHAN 1988).

According to the studies of FRANKLIN the South American tylopodes have completely different forms of cohabitation. Their social organization is characterized by feeding territoriality of stable family groups (FRANKLIN 1974, 1980, 1983). The vicuna lives in stable family groups consisting of one bull and several cows, the group size depends on the quality of the feeding territory. Young animals of both genders are chased away by the family bull before the birth of the new calves and they join nomadic bachelor groups or mixed groups. Adult animals are not allowed to leave the group and strange adult or young females are denied to join; the family groups of the vicunas are closed social units. The guanaco on the other hand shows a higher flexibility. In the social associations, family groups prevail which are territorial in some areas but which migrate in others. Bachelor groups or single bulls are there as well as associations of adult females with their young who do not admit adult males; besides that there are mixed groups, too. The family groups of the guanacos are open for new members, at the same time adult animals can also leave the group; in contrast to the vicunas' closed social units they are semi-open associations.

Bachelor or non-territorial semi-open "family groups" consisting of one adult bull and several cows, as well as associations of adult cows with young animals can also be found among dromedaries regarding the group structure. However, in the mechanism of the group formation, the dynamics of the social system, and above all with regard to the territoriality there are distinct differences. Feeding territoriality of family groups is obviously useful with the South American tylopodes due to sufficient food resources all year round. In the habitat of the dromedaries, however, the food resources are neither temporally nor spatially evenly distributed and thus not to be monopolized. Above all the particular immobility of the dromedary calves contradicts the adaptivity of stable family groups, particularly under extreme conditions. Vicuna and guanaco calves on the other hand show an extreme vitality. They already stand 15 min. after the birth and, like other ungulates, are able within a short time to follow the nomadic family group (FRANKLIN 1983). Some observations on zoo animals already point to the essential differences: "Newborn Old World camels are still a little helpless on their legs the first days after the birth. New World camels on the other hand already walk completely steadily one hour after the birth and it is not rare that they begin running and making leaps two days later" (PUSCHMANN 1975).

Non-territorial individualized associations are the exception with ungulates: they only occur with the three equids *Equus quagga*, *E. zebra*, and *E. przewalskii* (overview in KLINGEL 1975). In contrast to the dromedaries they live in stable family groups for years. Similar structures occur with the dromedary at the rutting season, when one bull herds a cow group. Substantial differences concern the stability, the mechanism of the formation of new groups, and also the social relations. With the mentioned equids a clear individualized hierarchy is developed, the highest-ranking cow is at the same time the leading animal (KLINGEL 1972). Besides, the social bonds within the group are much more distinct with these equids than with the dromedary.
In contrast the social system of the equids, who mainly live in deserts and semi-deserts, like the Grevy-zebra (*Equus grevyi*), the african wild ass (*Equus africanus*) and the asiatic wild ass (*Equus hemionus*), is marked by mating territoriality (summary in KLINGEL 1987).

The other ungulates living under comparable ecological conditions do not show parallels to the dromedary in their social organization either, since they live in anonymous herds. In place of this social type the likewise non-territorial eland antelopes live gregariously in bunches of 5-50, sometimes in herds of several hundreds of animals. Often there are mixed associations, but also pure male and female groups. Old bulls are occasionally solitary (WALTHER 1988). As inhabitants of semi-deserts and deserts, the East African (*Oryx beisa*, WALTHER 1978) and the South African oryx (*Oryx gazella*) live gregariously, but mostly only in herds of 2-20, sometimes in herds of 100-200 animals. There are male, female, and mixed associations, often with a well distinct hierarchy and ad-hoc monopolization at the mating. Single old bulls are possibly territorial (WALTHER 1988).

Slight parallels to the dromedaries are shown in the social structure of the giraffes who according to the investigations of PRATT & ANDERSON (1985) temporarily form stable mother-calf groups consisting of a few females with young animals of about the same age. These associations are clearly more instable compared with the core groups of the dromedaries.

Two factors basically have an effect on the social system of ungulates: the food supply with regard to its variety and amount as well as its temporal and spatial distribution, and the openness of the habitat with the consequences for the cohesion of the group as well as for predation avoidance and flight (KLINGEL 1975). Compared with the ungulates of open habitats whose social system is marked by mating territoriality, the mobile reproductive unit of the dromedaries is better adapted to extreme conditions. In comparison to ungulate species that practice the anonymous development of herds, the individualized association is to be considered a higher developed social system.

The following reflections are certainly in the range of speculation but it can be assumed with a certain likelihood that the ecological conditions under which this social system has developed were marked by extremes. The ancestors of the wild dromedaries were common in the arid areas of Arabia, of the Middle East, and toward the middle of the Pleistocene even in North Africa (GAUTHIER-PILTERS & DAGG, 1981). The

latter is verified by fossil findings of *Camelus dromedarius* from Morocco (CHARNOT 1953) and Algeria (MIKESELL 1955). As a wild animal, the dromedary due to its morphological and physiological adaptations was probably able to settle in extreme habitats where many other ungulates could not exist, which also indicates a clear reduction of the inter-specific competition. Presumably the predation pressure was comparatively low in the area in which they were to be found at that time. That would at least explain why the dromedaries could prevail without such enemy avoidance strategies, known from ungulates of the hider type, despite the extreme immobility of the young calves. The social system adjusted to the specific reproductive characteristics and to extreme habitats increases the survival of the individuals via diverse mechanisms. Even if it is not verifiable any more it is still imaginable that the wild population had a corresponding family life.

According to the results the social organization of the dromedary is unique. The social system is excellently adapted to the unpredictable conditions of the habitat and has to be interpreted as the best possible compromise of reproduction biological forces and social adaptation to desert conditions.

5.   ABSTRACT

Within the framework of this study long-term observations regarding the social organization and behavior of individually known free-ranging dromedaries were possible for the first time.

The social system of the dromedary is characterized by group formation: Cows live together in cow groups, which are temporarily herded by a bull. Bulls live in bachelor groups, older bulls tend to live solitarily. All social units are non-territorial.

Cow groups are based on core groups formed by the joining together of cows with calves of the same age. The core groups are joined by other adult cows without calves, young cows and young bulls for varying periods. The core group is stable for 1.5-2 years, corresponding to the nursing phase of the calves. The stability of core groups is independent from the presence of a herding bull.

The reproductive cycle of the dromedaries in central Australia is marked by an extreme seasonality. Bulls have individual, only partly synchronized rutting phases, which last from a few weeks to eight months and occur in irregular intervals of 3-18 months.

At the beginning of the winter nearly all adult bulls are in rut and compete for access to the cows. The strongest ones take over a cow group and subsequently herd it for 3-5 months. The duration of the possession of a cow group depends on the hormonal situation and the condition of the bull as well as on the competition by other adult bulls.

After taking over a cow group the herding bull chases away all attached older and subadult bulls who then join bachelors groups. The young cows are tolerated and remain in their mothers' group even if the mothers segregate before the parturition of the next calf.

93% of the parturitions occured between June and November. The herding bull is usually not the father of the calves who are expected during his time as the group-holder. Cows segregate from their group noticeably before parturition, go into sand plains or sand dunes with dense vegetation that provide good shelter and give birth in seclusion. The significant habitat preference of the cow for the birth of her calf favors the formation of new core groups.

Dromedary calves can neither be assigned to the follower nor to the hider type. Compared with other ungulates of the follower type they show an extreme immobility within their first days of life. The home range of mothers with young calves is therefore particularly limited. Mother and calf live alone for up to three weeks and subsequently join other mothers with young calves. From this association the next core group develops which again remains stable for 1.5-2 years.

Bulls in rut show a distinct aggression toward newborn calves, above all they abduct the mother, the still immobile calf cannot follow and dies. The loss of the calf leads to a fertile post-partum estrus of the mother which increases the individual chance for reproduction of the accountable bull.

The discovery of the socio-biological infanticide with the dromedary is of particular importance. Moreover it is the first evidence for a successful reproductive strategy of bulls in ungulates. Only bulls in rut practice the infanticide, non-rutting bulls behave neutrally toward newborn calves. The infanticide is positively correlated with the immobility of the calves. The segregation of the cow prior to partition is a clear counter-strategy to the infanticide by the group-holder.

Group-holding bulls obviously gradually lose interest in their cows toward the end of the reproduction period dependent on hormonal factors. They allow then to be chased away without much resistance by an otherwise weaker bull, but mostly they leave their group voluntarily.

Outside of the main breeding season the cow group is often joined by a weaker or younger bull who then herds it. In a few cases these bulls had the chance to reproduce. But mostly the cows remained without a bull in summer even though there were contacts and short-term associations.

The social organization of the dromedary is unique and does not show any parallels to systems of other ungulates known so far. The adaptive value of the social system regarding the ecological conditions of the habitat and possibilities of its development in the course of the evolution are discussed.

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