Namib Desert Chacma Baboon (Papio Ursinus) use of food and water resources during a food shortage

by

William J. Hamilton III

Institute of Ecology University of California Davis, CA 95616

ABSTRACT

The three chacma baboon, Papio ursinus, troops resident in the bed of the Kuiseb River shifted from an abundant diet of grasshoppers late in 1972 to fig fruits and acacia seeds. As open waterholes along the Kuiseb River dried, intertroop, intratroop, and interspecific competition with gemsbok, Oryx gazella, for acacia seeds intensified. The baboons shifted to excavating acacia seeds and fig fragments from the riverbed sands and adopted new plant foods including some plant species toxic to other animals including humans. New tood plants and food plant parts required long processing and excavation times or were of a relatively low quality. Young individuals apparently learned to incorporate new foods by observing individuals who were probably eating those plants for the first time in several years.

CONTENTS

1	Intr	ntroduction					
2	Methods						
3	Results						
	3.1	Water sources and usage					
		3.1.1	Daily cycle at waterholes	398			
		3.1.2	Competition at waterholes	398			
		3.1.3	Baboon movements associated				
			with waterholes	399			
		3.1.4	Seeps	399			
	3.2	Food plants					
		3.2.1	Water content of plants	399			
		3.2.2	Toxic plants	400			
		3.2.3	Low quality plant foods	402			
		3.2.4	Acacia seed and fig fragment				
			collection	402			
	3.3	Destruction of plants by baboons					
	3.4	Animal foods					
4	Discussion						
	4.1	4.1 Bases of dietary differences between					
		troops	S	406			
	4.2 Social transmission of information						
	about plant foods						
5	Cor	iclusion	s	406			
6	Ack	Acknowledgments4					
7	Ref	References					

1 INTRODUCTION

Between October, 1972, and May, 1973, colleagues and I observed three chacma baboon troops residing in the Kuiseb River canyon, Namib Desert, South West Africa/Namibia. Intermittent additional observations continued during 1979. Localized and limited water resources and their relationship to plant foods are considered here. Other aspects of the foraging behaviour of these troops are considered elsewhere (Hamilton et al., 1978a; Hamilton and Busse, 1978).

Baboon troops may adjust their use of home ranges to accommodate seasonal shifts in the position of water supplies (Altmann and Altmann, 1970). In the relatively arid highlands in eastern South Africa, Stoltz and Saayman (1970) found that chacma baboon troops came daily to water and were dependent upon the location of waterholes to the extent that the distribution of water sources limited the seasonal distribution of troops. The Kuiseb River canyon baboon troops are also strongly dependent upon localized water sources. They do not persistently occupy the narrow canyon portion of the Kuiseb canyon where there is a constant water source but insufficient food. Downriver below Homeb the absence of suitable sleeping cliffs appears to limit the distribution of

troops (Hamilton and Tilson, 1982). Observations of water dependence noted here contrast with Hall's (1962) report that Cape Peninsula chacma baboons do not regularly drink free water. Baboons there consume bulbs, leafy vegetation and other items with relatively high water content. This diet combined with the cool, mediterranean Cape climate, presumably permits them to maintain an adequate water balance. Hamilton and Tilson (1982) suggest that in the downstream portion of the study area solitary males may live for prolonged intervals without access to free water, possibly because they are able to obtain fruits with a high water content.

Elsewhere baboons are confined to areas providing daily access to water and are thus limited to home ranges incorporating riparian forests, lake and marsh edges, and artificial water distribution points. The subject population inhabits the linear Kuiseb River riparian forest and woodland where it crosses the central Namib Desert. The area is rainless for extensive intervals. Baboons obtain water throughout the annual cycle from limited pools or from the river when it flows.

2 METHODS

Observations were made from 40 stone and bark hides located opposite water holes, fig trees, sleeping cliffs and other points of special baboon activity (see Hamilton et al., 1977). When activity foci changed new hides were constructed when baboons were absent.

Water content of food was determined by placing samples in sealed plastic bags. Samples were field weighed, oven dried to constant weight at 90°C, then reweighed.

Baboon foraging success was reconstructed late in the study from earlier measurements of baboon foraging success at food plants. The number of items ingested per minute was noted for focal individuals. Similar food items were collected from areas where baboons were observed foraging. These samples were then weighed and dried. It was thus possible to determine, probably to within less than 10%, the rate of dry weight food intake for selected food items. Data are adequate for comparisons only for adult females.

Distances in the Kuiseb River were measured from the road entry into the Kuiseb River at Homeb, approximately 19 km upriver from the Namib Research Institute at Gobabeb. Distance markers were painted on stones at 0,5 km intervals upriver. Thus a designation 31,0 indicates 31,0 km upriver from Homeb. Troops were given letter designations; L (lower) troop, the downriver troop, M, the middle troop and U, the troop furthest upriver.

3 RESULTS

3.1 Water sources and usage

Five sources of water were available to these baboons: open water in pools, seasonal flows of water in the river, excavations to water in riverbed sands, seeps along the canyon walls and the water content of plant and animal foods.

At the beginning of the study in October, 1972, pools were present throughout the home range of all troops. During the course of the study pools in the L troop home range went dry, with pools furthest downstream disappearing first. Baboons from this troop excavated waterholes or improved excavations made by other mammals and used them for a period of five months. During an interval of five days before the seasonal flood arrived all free water was gone within the L troop home range.

3.1.1 Daily cycle at waterholes

Both the L and M troops often slept on cliffs in the immediate vicinity of waterholes (Hamilton, 1982). On these occasions the early morning progression was always directly to water some time during the first hour following descent from sleeping cliffs. On other occasions the route of progression might bring the troop to the waterhole at any time, but especially late in the day. Hall (1963) reported that in upcountry South West Africa baboons came to water on nine of 10 observation days between 14h00 and 17h00 and on the other occasion they visited water at midmorning. This pattern probably agrees with the timing of maximum water need by the troops Hall observed. The Kuiseb River troops, however, are not so fortunate as to have the free water available to them at midday, and in order to effectively utilize their home range they were away from water at midday and sometimes throughout the day. During October, 1972, when grasshoppers were abundant throughout the L troop range (see section 3.4) this troop limited daily movements to less than a kilometer on either side of a waterhole (km 10.7) near a sleeping cliff. With the decline of grasshoppers and the replacement of this dietary item by seeds and fruit, more extensive travels became necessary and the L troop ranged further from this water source.

3.1.2 Competition at waterholes

In November and December, 1972, large numbers of gemsbok (*Oryx gazella*) moved into the Kuiseb to calve. At that time the open waterholes were rapidly drying up, particularly in the lower stretches of the canyon inhabited by the L troop. The gemsbok exca-

vated waterholes as described elsewhere (Hamilton et al., 1977). Excavated waterholes are subject to collapse and go through a long term cycle of physical characteristics and animal clientele. They may fill with sand or the water table may drop below a level where further excavation by any species does not reach water. At the pool most actively used by the L troop, at km 10,7, an excavation dug by gemsbok to replace a nearby hole that had collapsed, also caved in and then blew shut on November 17, 1972. The collapsed hole remained as an open bowl and gemsbok worked at the hole daily for the next eight days but succeeded only in reaching wet sand. This eliminated the last suitable drinking site at that location at that time. There were still two other holes dug by jackals, Canis mesomelas, in use by birds in the immediate vicinity, but both of them had been sunk horizontally and downward through a layer of sand to a gravel layer which made excavation by gemsbok, mountain zebra (Equus zebra hartmanna), and baboons futile.

Gemsbok excavations and excavations dug by baboons were preferred by gemsbok to shrinking open pools, which developed green algal blooms and were heavily populated by insects and dying fish. Occasionally baboons improved collapsed gemsbok excavations so that they become usable again by gemsbok. For example, after one waterhole (km 10,7) collapsed and blew shut on December 5, 1972, gemsbok dug at this hole daily but were unsuccessful in reaching water. Following the reopening of this hole by baboons six days later gemsbok began to visit it almost at once and were able to push their muzzles deep enough into the newly excavated shaft to drink. In the following days gemsbok maintained this waterhole, excavating large volumes of sand. Use of water excavations was a matter of bullying for access, with gemsbok always winning. At this waterhole a single male gemsbok remained an hour at midday. When he approached, the baboons dispersed. Other baboons stood within 2 or 3 m of the gemsbok, who occasionally lowered his head and made a brisk step towards them, resulting in uncontested retreat by the baboons.

3.1.3 Baboon movements associated with waterholes

Water was freely available in the upriver portion of the L troop home range but they nevertheless made a persistent effort to maintain a water supply in the more favourable foraging area in the downstream portion of their home range. The deteriorating water situation forced them to the upper reaches of their home range where they regularly interacted with the M troop (Hamilton et al., 1975, 1976), limiting downstream movement and food use there by that troop. Since food resources were more limited in the remaining portions of the M troop home range they were forced to use the upriver portions of their home range more extensively, with particularly negative consequences for the U troop, which they dominated. The shortage of food for all troops was followed by adoption of marginal plant foods, noted below (sections 3.2.2, 3.2.3, 3.2.4).

3.1.4 Seeps

Several seeps along the canyon walls occasionally were visited by individual baboons. Flow rates from these seeps were trivial compared with river bottom excavations. They were, nevertheless, important to low ranking individuals, their chief clientele, since these individuals were sometimes unable to gain access to excavations during troop visits to them, and they chose to leave with the troop when it departed.

3.2 Food plants

Some novel food plants were sporadically consumed by baboons during the time of food and water shortage. The main plant food diet before water and food shortages developed were acacia seeds, fig fruits, Euclea fruits and green grass, which together comprised on the average 83% of the feeding time for all troops (Hamilton et al., 1978a). Stress or starvation foods all consumed in limited quantities - may, nevertheless, have been critical supplements to the diet.

3.2.1 Water content of plants

Water content of some baboon plant foods is noted in Table 1. Some vegetative and fruit parts have a high water content and, since they were adopted by baboons as dietary items later in the study when water supplies were marginal, it seemed possible that they were adopted mainly for their water content. Additional evidence noted below, however, suggests that these are simply scarcity foods, adopted to meet food shortages.

Moist foods did permit occasional prolonged absences from the waterholes. In January, 1973, the L troop made three excursions from their base near its only remaining water source to eat ripe figs 5.1 km downriver. These excursions lasted four, four and five days. Consumption of fig fruits with a 87% water content presumably made these prolonged excursions possible. When these fig safaris ended, the troop left the fruiting tree to return to their water as a cohesive group. But during the course of the return journey individuals began to move at their own pace, and by the time the first individual arrived at the water the trailing element of the troop lagged over 2 km behind. On one such trip, the first eight individuals to reach the waterhole were all adult or subadult males. The last in-

TABLE I: Water content of some Kuiseb River chacma baboon food plants.

Species	Part	Water Content h (percent)	Range	Number of Samples
Euphorbia uvasmontana	Pith	90.6	75	Ť
Nicotiana glauca	Pith	90.5	86.5 - 93.0	6
Datura innoxia	Root core	88.6	88,2-89,0	2
	Pith	87.3	-	1
Ficus sycomorus	Ripe l'ruit	87.2	83.5 - 92.9	6
Ficus cordata	Ripe fruit	85.6	70.5 93.0	6
Datura innoxia	Root	81.8	81.8	.0
Ficus sycomorus	Green fruit	77.7	77.7	1
Salvudora persica	Terminal flush	75.0	-	0
	Stripped leaves	72.5	72 1 72.9	2
Ficus cordata	Green fruit	68.5	64.0 - 73.0	2
Cyperus marginatus	Green shoots	64.4	63.1 - 65.7	3
	Green buds	63.2	63.0 - 63.4	2
Acacia eriolobu	Green seeds	61.3	59.4 - 62.5	3
Cyperus marginatus	Corms	52.0	51.8 - 52.2	2
Ficus sycomorus	Fruit, dried (fog)	12.9	12.4 - 13.5	6
	Fruit, dried (late day)	10.6	9.8 - 11.7	6
Acacia albida	Seeds, ground pods	3.4	2.2 - 4.5	2
	Seeds, tree pods	2.3	2.3	1
	Seeds, loose, ground	1.5	1.4 - 1.6	2

dividuals, two mothers carrying infants, arrived more than two hours later. These observations emphasize the marginal conditions prevailing at that time and the greater impact of these conditions upon females and other lower ranking individuals.

3.2.2 Toxic plants

The cactiform euphorbia, Euphorbia avas-montana, occurs sporadically on the rocky sides and rim of the Kuiseb canyon. It was more abundant in the home range of the M and U troops than in the L troop's home range and was only eaten by members of those troops during the course of this study. The spiny arms of this plant, 7—10 cm in diameter, were pulled from the top by hand until they broke. The bifid spines were then bitten off before the freed chunk was processed further. This involved peeling back the leathery green skin and masticating the fibrous core (Plate 1).

I carefully cut free a small portion of this material and lightly chewed a 1cm cube. This produced a strong burning sensation and subsequent illness. Watt and Breyer-Brandwijk (1962) appropriately characterized the effects of this plant upon humans as stupifying.

Euphorbia was an occasional dietary item for the M troop. Euphorbia plants wihin their home range showed no sign of previous damage by baboons. The damage to these plants by the M and U troops in 1973

was still evident in 1978. There was no indication that additional use of these plants had occurred during the intervening years. In East Africa another cactiform cuphorbia, Euphorbia candelabrum, is consumed in some areas by olive baboons, Papio anubis (Hediger, 1951; Lock, 1962). Lock (1962) reports that baboons are the only vertebrate consumer of this plant.

Dalura innoxia and Datura stramonium are annual plants, highly toxic to some animals (Watt and Breyer-Brandwijk, 1962). They grow along the sandy banks of the Kuiseb River following floods. Only the cores of stems and root tops were eaten by baboons. I observed only L troop members eating these plants in 1973. The nature of damage to these plants is typical and conspicuous and the rejected parts remain in place for several days. I regularly walked the entire length of the home range of the other troops without finding uprooted Datura plants, so it is unlikely that these plants were taken by members of either the M or U troops during the period of intensive observations. Plants were either pulled from the ground and eaten or chewed in situ. Only a small piece was taken from each plant (Plate 2) and only a small number of plants in a stand were attacked. The amount of material eaten was determined by taking damaged plants and carving off adjacent sections of the same size and in the same position and weighing them. Seven such determinations gave values of 0.11, 0.12, 0.32, 0.67, 1.87, 1.90 and 1.95 grams of fresh plant tissue. Since some baboons ate parts of several plants, two to three grams is an ap-

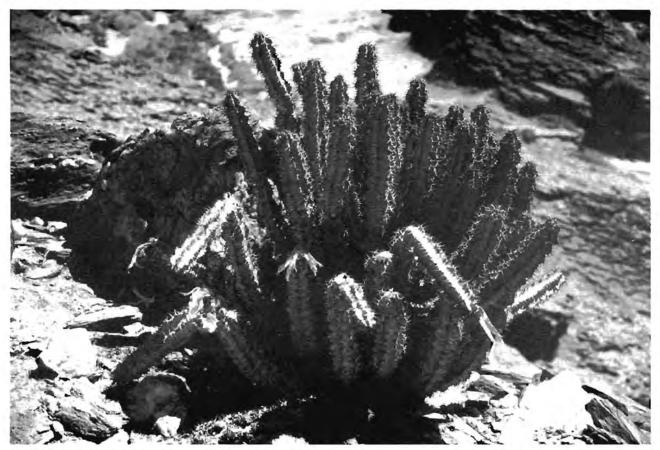


PLATE I: Euphorbia avas-montana, damaged by baboons toraging.



PLAT 2: Typical baboon damage to Datura plants. The plants are uprooted and the basal stems partially eaten. Foilage is ignored.

proximation of the maximum mass taken per baboon per day. This contrasts with the usual intake of another unpalatable plant, *Salvadora persica*, which adult males often eat in portions exceeding 40 grams in less than five minutes.

The lethal dosage of Datura stramonium is reported to be 224 grams for a horse, 193—386 grams for a cow, and 96-256 grams for goats and sheep (Watt and Breyer-Brandwijk 1962). Ingestion of stems and leaves may lead to poisoning of stock, including domestic ostriches, cattle, horses and sheep. All parts of the plant are reported to be poisonous, including stems, roots, fruits, leaves and flowers. However, there is no specific information concerning the toxicity of stem and root pith compared with the root and stem walls, and baboons may have selected parts of low toxicity. D. stramonium has a long history of deliberate usage by humans as a stimulant to inspire temporary lunacy, sometimes with tragic results. Meunscher (1951) states that all parts of D. stramonium are poisonous and identifies human symptoms as "headache, nausea, vertigo, extreme thirst, dry burning sensation in the skin, dilated pupils, loss of sight and voluntary motion; in extreme cases mania, convulsions and death" (Meunscher 1951, p. 214). After the negative experience following the lead of baboons in eating Euphorbia pith I opted against personal evaluation of this material.

When D. stramonium was eaten by baboons during the 1973 drought I assumed it was because of its relatively high water content (Table 1), a conclusion apparently supported by the observation that the other two troops had a surfeit of free water while the L troop was water limited. However, I later observed the use of this plant, again by the L troop, in May, 1973, after the river flooded. Fresh grass (Poa sp.), Zygophyllum simplex and other palatable, high water content forbs were available in abundance at that time and were being consumed in the immediate areas where D. stramonium was being utilized. During 1972—1973 the L troop members were the only consumers of D. stramonium but in the 1976 to 1979 interval R.L. Tilson (personal communication) observed use of this plant in the manner described here by the M troop.

Gemsbok completely bypassed *D. stramonium* plants even when they were starving and when they were grazing on unpalatable *Tamarix usneoides, Ricinus communis* and *Salvadora persica* vegetation.

These observations seem to suggest that baboons have a greater tolerance for some poisonous plants than do humans and some herbivorous ungulates. Limited use of these plants may be as a food supplement during duress or as a narcotic.

3.2.3 Low quality plant foods

Consumption of basal corms of *Cyperus marginatus*, a plant which occurs within the space of all three

troops, was exclusively used by the M troop in 1972—1973 after other staples were strongly depleted. Their use of this plant can probably be related to the differing resource conditions for each troop that developed during the study period. For example, the L troop continued to forage on more easily processed acacia seeds, and the fact that they made no attempt to utilize the substantial Cyperus patches within their home range may be related to the continued availability of this alternative food. R.L. Tilson (personal communication) saw no Cyperus consumption by any of these baboons in the interval between 1976 and 1979. This Cyperus species resembles a bunch grass. The fibrous leaves were ignored by mountain zebra, gemsbok, steenbok (Rhaphicerus campestris), klipspringer (Oreotragous oreotragus) and, usually, by baboons. The part of the plant utilized by baboons is the bulblike storage bodies at the base of leaves. Extensive processing is necessary to secure them. Sand and gravel at the base of plants are removed by hand. Then baboons attempt to free a part of the clump, including leaves, corms and roots by tugging on the leaves. When the plant is uprooted it is meticulously separated, one leaf stem at a time. Basal corms are covered with short, stiff, spiny leaflets which are removed until the corm is exposed and eaten.

Extraction of *Cyperus* plants is a process favouring adult males, who can more effectively pull clumps free. They also usurp females who have initiated excavations or have freed parts of clumps. Since *Cyperus* occurs in a small number of large patches in the M troop home range, supplanted females abandoning their positions to males may immediately resume excavation activities at other clumps. In doing so, however, they relinquish the excavations they have developed and must start again at undeveloped sites. Juveniles are usually ineffective in their excavation and tugging efforts, and their main use of *Cyperus* involves further sorting and processing of clumps or parts of clumps already uprooted and abandoned by adults.

At the same time that water excavations were being heavily used abundant *Salvadora* leaves yielded 3.2 times the dry weight production per unit effort of tree *Acacia* seed and fig fruit collection. *Salvadora* vegetation was not consumed prior to extreme resource depletion, and was an exclusively adult male activity. These data show that, in addition to foods with lower yields per unit time such as fig and acacia seed excavation, some low quality and abundantly available foods also may be added to the diet.

3.2.4 Acacia seed and fig fragment collection

Following exhaustion of pod seeds of acacias and the fruits of *Ficus sycomorus* and *F. cordata*, individual



PLATE 3: Chacma baboons excavate sand for dehydrated fig fruit fragments left from previous fruiting episodes. Two females and a juvenile work in the sun. Two adult males excavate in cooler, filtered shade, preferred excavation sites.

seeds of the acacias and dried fragments of the figs were systematically excavated by members of all three troop in the dry riverbed sand beneath these trees (Plate 3). Fig fruits so obtained were fragments from earlier processing when more favourable conditions prevailed or were dessicated fruits which fell to the ground and had been covered by dry wind blown sand. As at Cyperus clumps, males were at an advantage and regularly supplanted females at excavations.

Comparison of foraging success rates were made by observing the collection rates both from tree borne fruits and pods and from excavations. Then samples were collected and dry weights compared. Success in excavation could be determined by observed movements from hand to mouth. Mean fragment size was determined by making excavations in the same areas where baboons had worked. The collection rate of seeds from trees for Acacia erioloba, A. albida and Ficus cordata are averaged here because the identity of excavated seeds and figs could not be determined by observation. The rate of collection of figs and acacia seeds from trees for L and M troop females was 2.76 times greater than for fruits and seeds obtained from excavations, equilibrated to dry weight. For Cyperus

corms the comparable value is 3.27, again compared with tree borne acacia seeds and fig fruits. Probably the energy yield difference between tree fruits and seeds and excavated items is greater than these values because, for fig fragments, baboons deliberately drop many relatively unripe fruits after picking and inspecting them, while nothing that was excavated was rejected.

3.3 Destruction of plants by baboons

Kuiseb baboons were highly destructive to some plants selected for food. Cyperus clumps were thoroughly uprooted and virtually eliminated in many places by the M troop. Along many stretches of the dry river bed the main stems of all Nicotiana glauca plants were eaten through and none of these plants flowered in 1973 (Plate 4). Three adult males from L Troop climbed into a small fruiting fig (F. cordata) tree or sat on adjacent boulders plucking fruits. As conveniently reached fruits were consumed these males pulled over major



PLATE 4: Typical extreme damage to a Nicotiana glauca plant by baboons. Green leaves have sprouted, then the plant has died of drought.

branches until they broke so that higher fruits were brought within easy reach. Over half of the woody branches and trunks of this tree were destroyed in less than two hours (Plate 5). This tree did not recover vegetatively noticeably in the next six years, and probably did not fruit again during that interval. In October, 1985, it had barely regained the dimension of the tree damaged by male baboons during a single day 12 years earlier. It appears that within — group competition is, at least for conditions reported here, a more powerful determinant of foraging behaviour than any gain which might result from resource conservation.

3.4 Animal foods

The capture of larger prey, birds and mammals, by these troops and by Botswana chacma baboons is reported elsewhere (Hamilton et al.,, 1978a; Hamilton and Busse, 1978). This is a sporadic and opportunistic activity. Baboons elsewhere occasionally take young antelope, but there are no observations of baboons attacking the young of the resident Kuiseb canyon steenbok or klipspringers. Both live and dead fish are regu-

larly collected by baboons from pools. Details of this activity are reported elsewhere.

Baboons shift from a vegetarian diet to animal matter when it becomes available (Hamilton and Busse, 1978). Some time prior to the inception of this study there was an outbreak of grasshoppers (Schistocerca gregaria) throughout the riverbottom. In October, 1972, they had already been present at high densities for several months (M.K. Seely, personal communication) and were so abundant that they were devouring all new growth on Acacia albida and A. erioloba trees. Each large tree harboured numerous grasshoppers. These flying insects would flush before an intruder, and during each flush a few would fall to the ground. In the heat of the day they would take flight again immediately, but in the early hours of the day they remained on the ground and were easily captured by baboons. The high density of chitinous grasshopper exoskeletons in the faecal remains of baboons and the substantial accumulations of such faeces at the sleeping cliffs of all three troops demonstrated their prolonged dependence upon this resource. Only the L. troop was being observed in October and November, 1972. Members of that troop consumed only a few Ficus sycomorus fruits and acacia seeds when grasshoppers were plentiful.



PLATE 5: A Fictus cordata tree heavily damaged by baboons in the course of fruit gathering. Over 60 per cent of the total trunk diameter was broken and killed by baboons. One fruit crop was removed by adult male baboons during part of one day.

4 DISCUSSION

4.1 Bases of dietary differences between troops

Kawamura (1959) suggested that, for Japanese macaques, Macaca fuscata, dietary differences between troops were based upon socially transmitted information, a conclusion apparently supported by observations that these monkeys are idiosyncratically innovative in response to novel foods supplied by humans (reviewed by Frisch, 1968). Differences between the baboon troops noted here in choice of foods can not convincingly be attributed to differences between troops in their knowledge about the utility of fauna and flora. While the home ranges of these troops overlapped there were large exclusive portions of home ranges. It was, therefore, possible for each troop to differentially diminish particular resources within their respective home ranges. Switching between alternative foods may be based upon the same information for each troop which is, nevertheless, differentially expressed depending upon the availability of options. Kawamura (1959) gave no information about the current situation for the plants he considered. Hence the important conclusion that between - group differences in diet are based upon the availability of different information remains speculative. In an analysis of object manipulation behaviour by these same Kuiseb troops we (Hamilton et al., 1978b) also concluded that intertroop differences in manipulative behaviour could be attributable to differences in the availability of objects to manipulate and in the advantages to be gained from doing so.

4.2 Social transmission of information about plant foods

Cyperus consumption by the M troop provided strong circumstantial evidence that social transmission of foraging strategies took place within that troop. During the initial interval of Cyperus corm processing and consumption two, three and four year old individuals regularly sniffed the muzzles of adults who were eating. Muzzle sniffing is an investigatory behaviour, apparently used to identify foods new to the sniffing animal. In Botswana I have experimentally provided novel fruits, grains and seeds to chacma baboon troops. When individuals test these foods other baboons approach and sniff their muzzles. Hall (1962) observed a captivity reared four-year-old male chacma baboon incorporate native plants into his diet when he was released into a Cape Reserve baboon troop. This male observed other baboons feeding and muzzle sniffed them when he was incorporating new plant foods into his diet.

These observations suggest that muzzle sniffing is a behaviour correlated with the adoption of novel foods. If this conclusion is correct, *Cyperus* consumption had not taken place by the M troop during the previous independent lifetime of the muzzle sniffers, i.e., for more than four and less than five years. One of the probable advantages of group life to baboons is the availability of information about food items such as *Cyperus* which are shortage staples requiring extensive processing. The concept of pooled information has been identified as one possible advantage of mixspecies bird flocks (Krebs, 1973; Giraldeau, 1984), and is probably also applicable to social primate species. The value of social transmission of information should be greatest for long lived omnivores living in regions with a relatively variable environment.

5 CONCLUSIONS

Baboons in the Kuiseb Canyon shifted to alternative foods as search time for formerly preferred foods increased. Newly incorporated plant food items included one species, Cyperus marginatus, which required extensive processing and one species, Salvadora persica which was an abundant but low quality food. Toxic foods were also selectively incorporated into the diet without obvious adverse effect. Low quality, high processing time and relatively toxic plants are incorporated into the diet only when higher quality and more rapidly secured plants are unavailable. Evidence noted here shows that some plants may not be eaten for several years. Euphorbia, was eaten in 1973, but was not used again during the next five years and was probably not used during several years before 1973. Cyperus processing probably did not take place by any M troop member for more than four years before 1973. These observations suggest the importance of group memory of food plants used under adverse conditions.

6 ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the support of Nature Conservation, Administration, South-West Africa/Namibia for the conduct of this and other Namib Desert studies. I am especially indebted to the late B.J.G. de la Bat for pleasant and stimulating discussions about baboons and their behaviour.

During the conduct of this investigation Mary K. Seely, Director, DERU, extended logistic support and general encouragement, for which I am grateful.

Observations reported here were made by Ruth E. Buskirk, William H. Buskirk, Marian E. Hamilton, Ronald L. Tilson and Mary K. Seely. Tilson and Erna Rae Burger offered particularly useful comments on an earlier draft of this paper.

This study was supported by the Institute of Ecology, University of California, Davis and the National Science Foundation (USA).

REFERENCES

ALTMANN, S.A. and ALTMANN, J.

1970: Baboon Ecology: African Field Research. U. Chicago Press, Chicago.

FRISCH, J.E.

1968: Individual behaviour and intertroop variability in Japanese macaques. In: Primates. P.C. Jay, ed., Holt, Reinhart and Winston, New York.

GIRALDEAU, L.A.

1984: Group foraging: The skill pool effect and frequencydependent learning. Am. Nat., 124: 72-79.

HALL, K.R.L.

1962: Numerical data, maintenance activities and locomotion of the wild chaema baboon, Papio ursinus. Proc. Zool. Soc. Lond., 139: 181-220.

HALL, K.R.L.

1963: Variations in the ecology of the chacma baboon. Symp. Zool. Soc. Lond., 139: 288-327.

HAMILTON, W.J. III, BUSKIRK, R.E. and BUSKIRK, W.H. 1975: Chacma baboon tactics during intergroup encounters. J. Mammal., 56: 857-870.

HAMILTON, W.J. III, BUSKIRK, R.E. and BUSKIRK, W.H. 1976: Defence of space and resources by chacma (Papio ursinus) baboon troops in an African desert and swamp. Ecology, 57: 1264-1272.

HAMILTON, W.J. III, BUSKIRK, R.E. and BUSKIRK, W.H. 1977: Intersexual dominance and differential mortality of Gemsbok Orvx gazella at Namib Desert waterholes. Madoqua, 10: 5-19.

HAMILTON, W.J. III, BUSKIRK, R.E. and BUSKIRK, W.H. 1978a: Omnivory and utilization of food resources by chacma baboons, Papio ursinus. Am. Nat., 112: 911-924.

HAMILTON, W.J. III, BUSKIRK, R.E. and BUSKIRK, W.H.

1978b: Environmental Determinants of Object Manipulation by Chacma Baboons (Papio ursinus) in Two Southern African Environments. J. Human Evol., 7: 205-216.

HAMILTON, W.J. III and BUSSE, C.

1978: Primate carnivory and its significance to human diets. Bioscience, 28: 761-766.

HAMILTON, W.J. III and TILSON, R.L.

1982: Solitary male chacma baboons in a desert canyon. Am. J. Primat., 2: 149-158.

HAMILTON, W.J. III and TILSON, R.L.

1985: Fishing baboons at desert waterholes. Am. J. Primat. 8: 255-257.

HEDIGER, H.

1951: Observations sur la psychologie animale dans les parcs nationaux du Congo belge. Explor. Parcs. Natn. Congo Miss. J. Lebrun, 1.

KAWAMURA, S.

1959: The process of sub-culture propagation among Japanese macaques. Primates, 2: 43-60.

KREBS, J.R.

1973: Social learning and the significance of mixed-species flocks of chickadees. Can. J. Zool., 51: 1275-1288.

LOCK, J.M.

1962: Baboons feeding on Euphorbia candelabrum. E. Afr. Wildlife, 10: 73-76.

MEUNSCHER, W.C.

1951: Poisonous plants of the United States. New York, Mac-Millan.

STOLTZ, L.P. and SAAYMAN, G.A.

1970: Ecology and behaviour of baboons in the Northern Transvaal. Ann. Transvaal Mus., 26: 99-143.

WATT, J.M. and BREYER-BRANDWIJK, M.G.

1962: The medicinal and poisonous plants of southern and eastern Africa. Livingstone, Edinburg.