

Aardwolf mating system: Overt cuckoldry in an apparently monogamous mammal

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It is generally believed that in any monogamous species, according to evolutionary theory, males should attempt to maximize their reproductive success by being promiscuous, when such opportunities arise. Similarly, it is an even more fundamental principle that monogamous males vigorously guard oestrous females in order to avoid being cuckolded. This competition for mating opportunities is particularly evident in birds, as seen in numerous records of attempted and forced extra-pair copulations, particularly in waterfowl. Nevertheless, records of true cuckoldry — raising of another unrelated male's offspring as a result of promiscuous matings — include only a few examples of birds, and none of mammals (except man). The aardwolf is an apparently monogamous mammal that practices regular promiscuous matings, as a result of which some males would appear to be cuckolding their neighbours. The conflicting interests and the reproductive consequences for males and females are considered in terms of this mating system.

Daar word algemeen aanvaar dat die mannetjies van enige monogame spesie, volgens die evolusieteorie, sal probeer om hul welslae met voortplanting soveel moontlik deur promiskue paring te verbeter wanneer die geleentheid hom voordoet. 'n Ander, selfs meer fundamentele standpunt is dat 'n monogame mannetjie sy bronstige wyfie noulet-tend oppas om te voorkom dat sy met ander paar. Dié mededinging om paringsgeleentheid is by voëls — veral watervoëls — besonder opmerklik, soos waargeneem kan word in gepoogde en gedwonge buite-paarse kopulasie. Verslae oor werklike paringsbedrog, d.w.s. waar een mannetjie 'n ander een se kleintjies grootmaak nadat buite-paarse kopulasie plaasgevind het, verwys slegs na enkele voorbeelde onder voëls, maar nie na 'n enkele een onder soogdiere (behalwe die mens) nie. Die maanhaarjakkals is 'n oënskynlik monogame soogdier wat dikwels buite-paars paar, sodat sommige mannetjies ander se kleintjies grootmaak. Die botsende belange en die voortplantingsgevolge vir mannetjies en wyfies word in hul samehang met dié paringstelsel bespreek.

'Cuckoldry is a form of sperm competition peculiar to organisms exhibiting extensive male parental care and can be defined as a male's involuntary rearing of another male's offspring as a result of the latter male (the "cuckolder") having inseminated the mate of the former male (the "cuckold").¹ Among the aardwolf, *Proteles cristatus*, a mated pair occupies a well-defined territory throughout the year but, during a two-month mating season in winter, extra-pair copulation regularly occurs (40% of observations, $n = 10$). These copulations presumably result in some males cuckolding their neighbours. Despite this potential cuckoldry, all males guard their cubs while they are confined to the den. Although cuckoldry has been recorded in apparently monoga-

mous birds² this is the first record of it occurring in a non-human mammal.

Trivers³ has predicted that in monogamous species in which males provide parental care, 'a mixed strategy will be the optimal male course — to help a single female raise young, while not passing up opportunities to mate with other females whom he will not aid.' With regard to the males' reproductive success, such behaviour is clearly adaptive and has been observed in Bank Swallows, *Riparia riparia*,⁴ and two species of flycatcher (*Ficedula* spp.).⁵ From the females's point of view, however, such behaviour may be maladaptive to the secondary female if she already has a mate, because her mate may defect from his paternal duties if he realises he is being cuckolded.^{4,6} It has been argued, therefore, that in order to prevent the possible defection by her mate, a paired female should avoid having extra-pair copulations with opportunistic males.⁶ In this paper a mechanism is suggested whereby this deadlock can be avoided and where both partners can increase their fitness through being promiscuous.

Aardwolf social behaviour was intensively studied for three years (from 1981 to 1984) on Benfontein, an 11 000-ha game farm in the northern Cape Province of South Africa. During this period 12 adults were observed for over 1 000 h and followed over 800 km. Aardwolves were followed in a four-wheel-drive vehicle at a distance of 15–30 m. At night, visual contact was maintained by using the headlight of the vehicle and a spotlight, and all observations were recorded on a pocket dictaphone. The aardwolves were undisturbed by the lights or by the sound of the human voice. Observations on aardwolves are continuing, but on a less quantified basis.

Feeding and territoriality

The aardwolf is a solitary forager and feeds almost exclusively on *Trinervitermes* termites, licking them off the soil surface as they forage at night.^{7,8} The aardwolf social unit consists of an adult pair, which occupies a territory with only their most recent offspring (one to four cubs are born each year). Pair bonds are relatively stable, lasting from two to five years. The duration of all the pair bonds active during the study period, and the reasons for their termination, are illustrated in Table 1. Two unpaired males (Achilles and William Tell), left by the death or desertion of their mates, each abandoned his territory in favour of pairing with a breeding female in an adjacent territory. Feeding requirements appear to be an important factor in determining territory size;^{8–11} ten territories (five over two years) all had approximately 3 000 *Trinervitermes* mounds.⁸ Yet, breeding requirements appear to be a more important territorial consideration, as each of these males left a territory with a high mound density in order to pair with a successfully breeding female in a territory with a lower mound density.⁸

The main form of territorial maintenance is by scent-marking: pasting on grass stalks with a secretion from the anal gland. Residents also aggressively defend their territories by chasing intruders and, if necessary, fighting them. A mated pair share exactly the same territory, and both undertake territorial maintenance. The scent-marking activity is concentrated along territorial boundaries.⁸ A territorial boundary was defined by

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Events that led to the termination of pair bonds: (1) Eurydice died and was replaced by Nausicaa. (2) Nausicaa died and was replaced by Calypso. Apollo remained in his natal territory when his father, William Tell, abandoned his territory to replace Achilles. (3) Nausicaa's only cub died, after which she deserted Achilles to replace Eurydice. Achilles abandoned his territory and displaced Cyclops as Seven Winds' mate. (4) Cyclops was displaced by Achilles. (5) Achilles died and was replaced by William Tell. (6) William Tell, Cyclops, Galatea, Robin Hood, Telemachus, Muses and Errol Flynn all died — possibly from eating poisoned locusts. (7) Cyclops established a new territory (with Galatea) on the eastern border of his previous territory. (8) Telemachus remained in his natal territory when his putative father, Robin Hood, partially deserted to live in a territory further east (outside the study area). Robin Hood often returned to his old territory, particularly during the 1984 mating season, and then behaved as if he were the resident male.

Table 1. Duration of pair bonds in six aardwolf territories between July 1981 and July 1986.

Territory	1981	1982	1983	1984	1985	1986
WT	William Tell & Eurydice	(1)	William Tell & Nausicaa		(2)	Apollo & Calypso
X	Achilles & Nausicaa	(3)	Territory abandoned then assimilated by neighbouring territories			
A	Cyclops & Seven Winds	(4)	Achilles & Seven Winds		(5)	William Tell & Seven Winds (6)
C	No territory	(7)	Cyclops & Galatea			(6)
RH		Robin Hood & Maid Marion	(8)	Telemachus & Maid Marion		(6)
EF			Errol Flynn*, Muses* and Zebra			(6)

*Since there were two males in this territory they were clearly not monogamous. However, this is regarded as an exceptional situation.

joining the hectare cells in which the adult residents deposited more than one pasting per hectare during the non-mating season (August–May). The boundaries are fairly stable during this period: aardwolves seldom venture beyond their territories, and rarely paste while outside. Females tend to conform to this pattern throughout the year, whereas the males exhibit a sudden change in behaviour from the start of the mating season (Fig. 1).

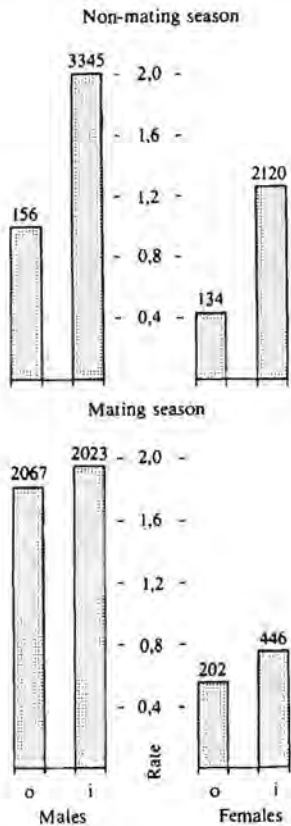


Fig. 1. Rates (pastings per 100 m travelled) at which male and female aardwolves pasted inside (i) and outside (o) their territories during the mating and non-mating seasons of 1982/3 and 1983/4. Total numbers of pastings are indicated.

Mating season — scouting period

The start of the mating season is indicated when the adult males begin to make frequent 'scouting' excursions into neighbouring territories, although initially they do not paste while outside their own territories. As the season progresses, however, a few of the more aggressive males start pasting and by the time the females come into oestrus (about a month later), they may be pasting more intensively outside their territories than inside. The development of this pattern is illustrated for the male Achilles during the 1983 mating season (Fig. 2).

In order to establish a relative measure to indicate the frequency with which males were pasting outside their territories, a pasting index (PI) was calculated for each individual (Table 2).

PI = DO × PR

where DO = percentage distance travelled outside the territory, and PR = rate at which the animal pasted while outside his territory (pastings per 100 m travelled).

This measure is used for the following reasons: (i) By using DO, the data become independent of sample size, therefore each individual is given an equal chance of being observed — inside or outside his territory. (ii) PR is the actual rate at which the individual pasted while outside his territory, and combined with DO represents the relative density of pastes to which aardwolves in neighbouring territories would be exposed.

The pasting index clearly shows that during the mating season Achilles pasted more often outside his territory than did any of the other males. His territory was bordered by those of William Tell, Cyclops and Robin Hood/Telemachus. It is worth noting that in 1983 and 1984 it was in the latter two territories (C and RH), and not WT, that he spent most of his time when outside his own territory (see Fig. 2). William Tell, that had the the second highest PI value, correspondingly spent little time in territory A, but mostly visited territories RH and EF. This extra-territorial pasting behaviour is not considered to be a means of extending the intruding male's territory, because he does not replace the resident male. Rather, it is suggested that the extensive pasting by the intruding male is an advertisement of his quality both to the resident male (by intimidating him), and to the female (by advertising his prowess as a male).

If one assumes that all adult males attempt to pursue a mixed reproductive strategy (MRS), then, at the start of the mating

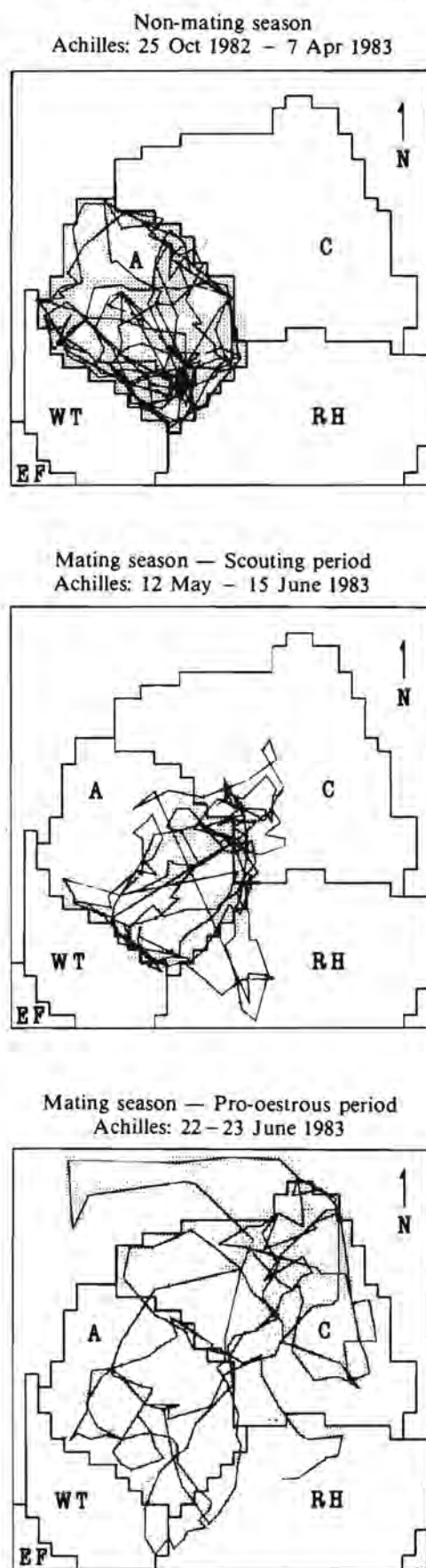


Fig. 2. Maps illustrating the paths followed and the scent-marking activities of the male, Achilles, during the non-mating season, and the two periods of the mating season in 1982/3. Shaded areas represent those hectare cells in which he deposited one or more pastings. Territories are illustrated in bold outline and labelled with the initials of the resident male (see Table 2). Overlaps of territory boundaries are not illustrated, but territory A is drawn in full.

season, all males should scout around neighbouring territories (as they do) to become firmly acquainted with the neighbour's individual scent, and to gauge his commitment to defend his female.¹³ As the mating season progresses, some males will start pasting in their neighbour's territories, and will revisit the same areas (den and middens) to gauge the resident's response to their (the intruders') pastings, repasting over them.⁸

As a result of their neighbour's response to their pasting, and their behaviour in direct confrontations, the more aggressive individuals (e.g. Achilles) may increase their rate of pasting in their neighbour's territory until one of them backs down. Because of the cost of pasting, only the 'fitter' individuals will be able to afford such a strategy.¹² Conversely, the less fit aardwolves (e.g. Cyclops) soon cease to paste in the territories of their more aggressive neighbours.

Mating season — pro-oestrous/oestrous period

About a month after the start of the mating season some of the females start coming into oestrus. Most of them mate within the course of the following month. About a week before the female permits copulation (pro-oestrous period), numerous males may start visiting her territory and their pasting behaviour reaches a peak. During pro-oestrus three females (one in 1983 and two in 1984) were also observed pasting quite extensively outside their territories (Table 2). All three females were visiting previous territorial boundaries: one territory had been deserted and the other two had been drastically reduced since the previous mating season. I also noticed that during pro-oestrus these females pasted more extensively than normally, along their territory boundaries and just outside them. This was most noticeable in the case of Maid Marion (territory RH) when she visited Achilles' territory. It would appear therefore, that during pro-oestrus, females, particularly those paired with less aggressive males, paste outside their territories in order to encourage extra-pair males to visit them.

During pro-oestrus, males frequently 'flirt' with the female (run towards her, then veer off and prance past with the tail held high in the air, clearly exposing the anal gland) and chase or fight other males that they encounter. By the time the female comes into oestrus (which may last up to three days) most of these intruders have ceased to visit her — leaving only the resident male and, in some cases, an aggressive neighbour (with a high *PI* value). The 'courting' of an extra-pair female and the scent-marking of her territory are remarkably similar in concept to the female-chasing of Bank Swallows.⁴ Among swallows, up to four or five males regularly chase extra-pair females during their fertile period. This sometimes results in copulations occurring when the paired male fails to guard his mate successfully.

Aardwolf copulation lasts from 1 to 4.5 hours. Although the penis remains inserted for the entire period, there is no copulatory tie as is typically found in the canids.¹⁴ The first ejaculation occurs after one or two hours and then at approximately hourly intervals. During this time the more aggressive intruder may interrupt the mating pair and even displace the resident male. (In 1982 Achilles displaced Robin Hood while he was mating with Maid Marion. She then followed Achilles, but I lost sight of them in the long grass. In 1986 Apollo displaced a neighbouring male during copulation, then mated with the neighbour's female the following night.) Of ten copulations witnessed, six involved the resident pair and the other four (two with ejaculation) involved intruding males. In all instances the female was a willing partner. An interesting feature of the mating behaviour is that, except when disturbed by another male, copulation is always ended by the female's entering a den and forcing the male to dismount. Possibly to counteract this, and thus prolong copulation and the number of ejaculations, the more aggressive males (e.g. Achilles and William Tell) lead the female away from the den before mounting her.

Table 2. Pasting indices (PI) and the percentage distances that adult aardwolves travelled outside their territories before and during the 1983 and 1984 mating and non-mating seasons.

Name	Territory	Non-mating season			Mating season			Total distance travelled (km)
		Distance outside (%)	PI	Total pastings	Distance outside (%)	PI	Total pastings	
Males		8,2	8,8	3501	52,3	95,0	4090	426,5
Achilles	A	9,6	18,0	1365	60,9	131,7	2326	194,6
William Tell	WT	3,3	7,6	1039	31,6	77,7	987	75,4
Cyclops	C	0,6	0,6	207	66,7	58,7	110	23,5
Errol Flynn	EF	0,8	2,1	237	21,8	41,3	184	30,7
Muses	EF	21,6	2,6	127	21,5	25,3	236	36,0
Robin Hood	RH	11,3	9,7	401	67,4	60,7	218	50,2
Telemachus*	RH	5,8	0,0	125	66,7	3,7	29	16,1
Females		15,6	6,7	2254	38,1	21,3	648	337,9
Seven Winds	A	20,0	2,0	616	10,7	—	109	161,0
Nausicaa	WT	21,6	26,6	531	19,7	24,3	195	54,7
Galatea	C	10,6	1,5	219	—	—	15	25,3
Zebra	EF	4,4	2,4	483	74,1	54,1	148	43,7
Maid Marion	RH	8,9	19,3	405	66,5	27,9	181	53,2

* In 1984 Telemachus remained in his natal territory as a subadult (see Table 1).
PI is the rate of pasting outside territory × % distance travelled outside.

Paternal care

The nature of its diet (termites) precludes the aardwolf from carrying food back to the den as brown hyaenas, *Hyaena brunnea*,¹⁵ and striped hyaenas, *H. hyaena*, do,¹⁶ nor can it regurgitate food for the cubs as the canids typically do.^{17,18} The only way in which the male can help in raising its young is to defend them at the den. While the cubs are under three months old and confined to the area around the den, the male may guard them for almost the entire period that the lactating female is foraging. As *Trinervitermes* termites are very small and widely dispersed food items, the female aardwolf needs to forage for at least six hours a night.⁸ In midsummer, this leaves only two to three hours of foraging before dawn for the dedicated male.

The guarding behaviour (time at the den) of males was difficult to quantify (Table 3), because aardwolves frequently change their dens (particularly if disturbed). Nevertheless, it was most pronounced in Achilles and William Tell. Not only did these males spend extended periods at the den, but they aggressively chased any black-backed jackals, *Canis mesomelas*, which approached within 70 m. By contrast, Muses and Errol Flynn appeared to be afraid of jackals, and on three occasions during the 1982 breeding season jackals were observed, unchallenged, within 10 m of their den. Since cubs never emerged from this den, I presumed they were eventually killed by jackals. Skinner and van Aarde,¹⁹ who studied aardwolves in the Transvaal, have also seen males guarding their dens.

Implications of cuckoldry

It has been argued by Gladstone⁶ that females of monogamous species, in which there is extensive male parental care,* should avoid extra-pair copulations in order to assure paternity to her mate and, hence, his care of her offspring.^{4,6} This apparently happens in some colonial-nesting egrets where the females call loudly to attract the attention of their mates when extra-pair males attempt to 'rape' them.⁶ (The premise that the evolution of monogamy requires a significant degree of paternal care^{3,6,20} has been seriously challenged in recent years.²¹⁻²³) The following argument nevertheless holds true for the many monogamous species in which paternal care is well developed.

Gladstone's⁶ argument is based on the assumption that a monogamous male is likely to defect if he suspects that he is being cuckolded. Evidence supporting this premise has been found

in the dunnock, or Hedge Sparrow, *Prunella modularis*.²⁴ This species has a highly variable mating system, ranging from polygamy (one male to to females), through monogamy to polygyny (one female to two males). Davies²⁴ has shown that where two males share a territory with a female, the beta male will not feed the chicks unless he has mated with her; and with two males helping her, they raised significantly more chicks than a monogamous pair. Thus, polygynous females actively attempted to escape the mate-guarding attentions of the alpha male in order to mate with the beta male. Presumably, if the male of a monogamous pair were to defect, the female would raise even fewer chicks. This has been found in the secondary or widowed females of Pied Flycatchers, *Ficedula hypoleuca*,²⁵ Song Sparrows, *Melospiza melodia*,²⁶ and two species of tits (*Parus* spp.).²⁷

Variations in the degree of paternal care exhibited by the hoary marmot *Marmota caligata* suggest that defection may also be possible in mammals.²⁸ Males living with one female, but in isolation from other males, interacted significantly more with their young than those males living in groups. Thus the isolated males, with guaranteed paternity, showed greater paternal care than did males with cubs of uncertain paternity. Although my data were

Table 3. Relative degrees of paternal care exhibited by males (in rank order), and the probable number of females successfully mated during the 1983 and 1984 mating seasons.

Name	Paternal care (rank order)	Probable number of successful matings per year	Potentially cuckolded
Achilles	1	3	—
William Tell	2	1	—
Telemachus	3	—	(1984)*
Errol Flynn	5	1	(1983, 1984)†
Muses	5	1	(1983, 1984)†
Cyclops	5	1	1983, 1984
Robin Hood	7	1	1983

* Because Telemachus was looking after half-siblings one would expect him, through kin-selection, to show a relatively high degree of alloparental care.²⁰
† Errol Flynn and Muses were possibly sharing paternity and thus cuckolding each other.

not quantified, this same pattern appeared to occur in the present study, with Achilles and William Tell showing the most paternal care.

A feature introduced above, but not considered by Gladstone,⁶ is that of the mixed paternity of offspring. Provided the cuckolded male has copulated with his resident female, he still has some chance of paternity. Therefore, he should not defect unless: 1) he has an alternative female with which he can breed exclusively, 2) by devoting energy into raising the young he is likely to affect his future reproductive output negatively.²⁹ Apart from the example of the dunnocks mentioned above,²⁴ caring for broods of mixed parentage has been observed in Pied and Collared Flycatchers.⁵ This has also been observed in the aardwolf, as Muses and Errol Flynn (who shared a territory) both mated with their female, Zebra, and both guarded the cubs (see Table 1).

It appears, therefore, that an apparently monogamous female can preclude the threat of her resident mate defecting when she is promiscuous, if she mates with him as well as with the aggressive neighbour, thereby granting both males some chance of paternity. The advantages of this system to the female are that: 1) her offspring will gain the higher quality genes of the intruder;⁶ 2) she may produce 'sexy sons' — with the cuckolding tendencies of their father;³¹ 3) if she is fertilized by both males, she will increase the genetic variability of her offspring.³²

As oestrus may last for up to three days, the female clearly has the opportunity to mate with more than one male, and I have seen this happen with three females during single oestrous periods. Her method of terminating a mating attempt, by entering a den and forcing the male to dismount, also gives the female the ability to limit the number of times a particular male ejaculates. This introduces the subject of sperm competition, and of which male is likely to sire the most cubs.^{33,34} There are no data on this subject for the aardwolf, but the fact that mixed paternity has been recorded for some mammals in the laboratory³⁴ and in the wild³⁵ suggests that this is also possible in the aardwolf. There is some circumstantial evidence to support the hypothesis. In 1982 the female, Seven Winds, was possibly mated by both Cyclops and Achilles and later produced a litter of four cubs. When these cubs first emerged from the den, two of them were distinctly larger and darker than the other two, and may possibly have been sired by a different father. I am at present collecting blood from adults and cubs for paternity tests in an attempt to answer this question.

On the basis of the above argument the question that now presents itself is why cuckoldry is not more common in other 'monogamous' animals? Forced extra-pair copulations are a feature of many waterfowl, and has been recorded in 39 species.³⁶ McKinney *et al.*³⁶ have suggested that in at least four species this behaviour constitutes an MRS of the type postulated by Trivers.³ Although they believe that the females may derive some benefit from forced copulation inseminations (e.g. through increased genetic diversity of offspring),³² they point out that the trauma involved in these assaults is often so great (bodily damage or even death) that females actively avoid them and may expend a great deal of energy doing so. This avoidance of forced copulations by the female should naturally prevent cuckoldry from occurring on a regular basis.⁶ Nevertheless, extra-pair copulations have also been recorded in over 60 other apparently monogamous birds,³⁷ and closer investigation of the mating system of these species may reveal that cuckoldry is indeed a relatively common phenomenon.

Among monogamous mammals, however, particularly canids, extensive research has failed to produce any evidence of a mating system similar to the aardwolf's. I suggest that the reason lies in the differing social structures of these animals. For example, in some species of foxes (*Vulpes* spp.)¹⁷ and jackals (*Canis* spp.),¹⁸ the residents of each territory are composed of an adult

pair and their most recent offspring. In addition, when food supplies are not limiting, a number of sub-adults often remain in their parents' territory, undertaking territorial maintenance but not breeding. It is these extra defenders that probably prevent intruders from gaining access to the female. In the aardwolf, however, all sub-adults leave their natal territory,⁸ and thus an aggressive intruder has only the resident male to subdue. He does this by thoroughly scent-marking his less aggressive neighbour's territory, thereby intimidating him and simultaneously advertising his prowess to the female. Ultimately he might even fight with the resident, if necessary, when the female comes into oestrus. The overtiness of this extra-territorial behaviour suggests that cuckoldry is an established feature of aardwolf biology, thus making it the only non-human mammal in which this is believed to occur.

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Transition from a hunter-gatherer to a settled life-style among the !Kung San (Bushmen): Effect on glucose tolerance and insulin secretion

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In earlier metabolic studies among the hunter-gatherer !Kung San of the north-western Kalahari (in 1970 and 1974), relatively impaired oral glucose tolerance and low insulin secretion were found. A genetically similar San community that has followed a settled life-style for the past 15 years was the subject of the present investigation. A group of 24 adult males underwent 2-hour oral glucose tolerance tests, with measurement of plasma glucose, serum insulin and C-peptide concentrations. Glucose tolerance had improved significantly and serum insulin levels were even lower when compared with the results of the previous studies. Methodological differences do not appear adequately to explain these changes, which we attribute largely to enhanced insulin sensitivity, probably related to the much higher carbohydrate intake of the settled San community.

Tydens vroeëre metaboliese studies is gevind dat die !Kung San van die Noordwes-Kalahari, wat jagter-versameelaars is, se glukoseverdraging by mondtodiening taamlik aangetas en hul insulienafskieding betreklik laag is. 'n Geneties vergelykbare San-gemeenskap, wat reeds die afgelope 15 jaar 'n gevestigde lewenspatroon gehad het, is tydens die jongste ondersoek bestudeer. 'n Groep van 24 volwasse mans se glukoseverdraging is 2 uur na mondtodiening getoets, waarby die konsentrasie van plasmaglukose, seruminsulien en C-peptiede bestudeer is. In vergelyking met die resultate van vroeëre ondersoeke was die glukoseverdraging aansienlik beter en die seruminsulienvlak selfs nog laer. Die verskille kan oënskynlik nie bevredigend deur metodologiese verskille verklaar word nie en word hoofsaaklik aan groter insuliengevoeligheid toegeskryf, wat waarskynlik met die gevestigde San-gemeenskap se aansienlik hoër inname van koolhidrate verband hou.

There is considerable interest in the changes in carbohydrate tolerance that may accompany changes in life-style. In some populations that have become increasingly affluent over a relative-

ly short period, a high prevalence of diabetes has emerged.^{1–3} A unique situation exists in Southern Africa with respect to the !Kung San, who have undergone a transition from hunter-gatherer to settled life-style over the past decade and a half.⁴

In 1970, 50-g oral glucose tolerance tests were carried out on 15 adult !Kung San (8 men and 7 women) living a typical hunter-gatherer existence in the Dobe region of north-western Botswana. The pattern that emerged was one of relative glucose intolerance accompanied by low insulin secretion.⁵ In 1974 Jenkins *et al.*⁶ reported similar findings amongst 6 adult San of the same population group. We now report on a study of a comparable group of !Kung who have followed a settled way of life in Chum!kwe, north-eastern Namibia, for at least 15 years. They are culturally and genetically similar to those who lived in the Dobe and /ai/ai areas of Botswana, the subject of the earlier studies (see map, Fig. 1). Metabolic findings in the present study are compared with those of the two previous investigations, since there are few (if any) !Kung existing as hunter-gatherers at the present time.

Subjects and methods

Subjects

The !Kung San (Bushmen) today number about 6 000 with approximately one-third living in Botswana and the remainder in Namibia and southern Angola. The subjects all belong to the Žu/ōasi (Žu = people; /ōa = real; si = plural suffix) subgroup of the !Kung San; all were born and remained within a radius of about 100 km of Chum!kwe, Namibia (Fig. 1).

Twenty-four males were studied, 17 were members of the Defence Force stationed at a camp in the region. They were aged between 18 and 40 years (the Žu/ōasi do not know their dates of birth). Each man had a minimum food intake of tea and biscuits in the early morning, a dish of maize porridge with sugar and milk at 10h00, tinned meat with spaghetti or potatoes at 13h00 and sweetened drinks or beer in the evening. This diet is adequate in terms of calorie and protein intake, but because most of the men had families living just outside the camp it is possible that some of the food was shared with their relatives, whom they visited every day. As soldiers, the Žu/ōasi receive relatively high