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A systematic and population genetic approach to the rabies problem in the yellow mongoose (*Cynictis penicillata*)

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ABSTRACT

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This paper reviews recent studies on the biology, systematics and population genetics of yellow mongoose populations in terms of possible implications for the epidemiology of rabies. Based on parallel studies, the existence of three distinct subspecies of yellow mongoose may have a direct bearing on rabies epidemiology; at least subspecific affiliation should be considered as a factor to be controlled for in rabies studies of the species. A direct correlation was found to exist between population genetics, social structure (and vagility) and aspects of the epidemiology of rabies in the yellow mongoose. The high frequency of enzyme polymorphisms restricted to single populations can be understood in terms of the well developed social structure and low vagility of yellow mongooses, which in turn explains the phenomenon of rabies outbreaks being restricted to highly localized foci which may flare up over a period of several years. Further research is required to establish whether predictable population genetic differences exist between high and low rabies-prone populations.

INTRODUCTION

The yellow mongoose (*Cynictis penicillata*) is a diurnal, burrow-dwelling, social carnivore which is widely distributed in open habitats throughout the southwest Arid Biome of Southern Africa (Davis 1962; Skinner & Smithers 1990). Recent evidence suggests the existence of three discrete subspecies (Taylor & Meester, in press; Fig. 1). The species has been considered to be the chief wildlife vector of rabies in South Africa (Snyman 1940; Zumpt & De Bruyn 1967; Zumpt 1976). The area of greatest rabies incidence in the sandveld of the central and northwestern Orange Free State and western Transvaal corresponds with the highest estimated population densities of *C. penicillata* (at least one animal per ten morgan or less, Snyman 1940; Zumpt 1976; Fig. 1). Past practices of eradication of yellow mongooses (and other species such as *Suricata suricatta* and *Xerus inaurus*) to control rabies are both inefficient (as survivors have been shown to increase litter sizes and expand their populations exponentially) and ecologically damaging as yellow mongoose are important predators in the control of insect populations (Zumpt 1968; 1976).

Previous workers on rabies have emphasized the link between life history attributes of vectors and rabies epidemiology. According to Snyman (1940), it is only through "intensive study of the life-history and migratory habits of the vectors ... that knowledge concerning epizootology of the disease would be gained". Snyman (1940) attributed the high incidence of rabies in *C. penicillata*, not to inherent susceptibility

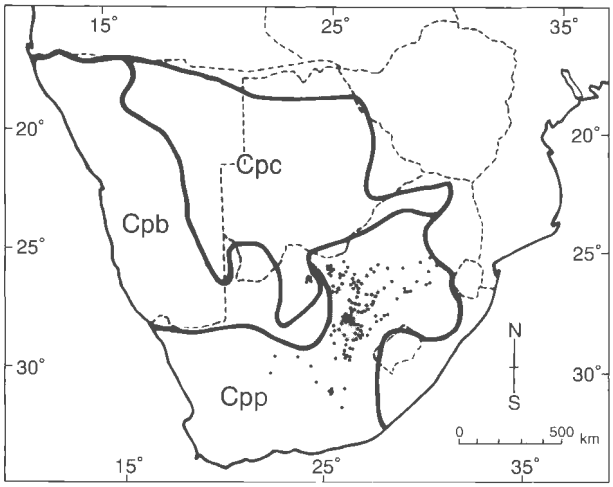

FIG. 1 Map of southern Africa showing distribution of three subspecies of yellow mongooses in relation to the area of maximum population density (shaded area) and the location of individual farms which were proven to have infections of rabies between 1928 and 1939 (from Snyman 1940). Cpp = *Cynictis penicillata penicillata*; Cpb = *C. p. bradfieldi*; Cpc = *C. p. coombsii*

of the species to rabies, but rather to its abundance and communal, burrow-dwelling lifestyle. Zumpt (1976) considered that in parts of its range where the ground squirrel is absent, the yellow mongoose has different "living habits" and is therefore a lesser danger as far as dissemination of rabies is concerned. Zumpt (1968) found that yellow mongooses of 1–2 year's age were much more prone to rabies than other age classes. As the seasonal peak in rabies corresponds exactly with the peak in pregnancy rate (October), Zumpt (1976) proposed that the eviction of subadults from the burrow at the time the young are born forces subadults to establish new territories at a time when food is scarce. These and other stresses could trigger rabies in the species. However, recent evidence (Rasa, personal communication) shows that the young are not evicted in their second year but are retained in the natal colony for several years as "helpers".

Genetic structure of population is known to be largely determined by species' mating systems (Wright 1965). Recent studies of population genetics of fossorial mammals such as prairie dogs (Chesser 1983) and pocket gophers (Patton & Yang 1977; Patton 1985; Hafner, Hafner, Patton & Smith 1987) have demonstrated a correlation between genetic parameters of populations [such as Wright's (1965) F statistics] and aspects of life history such as social organization, vagility, and habitat heterogeneity).

If correlations exist both between factors in the life history of yellow mongooses and rabies epidemiology, and between life history and population genetic parameters, as suggested above, then it follows that population genetic parameters should be correlated with aspects of rabies epidemiology in the yellow mongoose. This paper reviews evidence for such a hypothesis, based on recent studies on the systematics and population genetics of the yellow mongoose (Taylor 1990; Taylor, Meester & Rautenbach 1990a; Taylor, Campbell, Van Dyk, Watson, Pallett & Erasmus 1990b; Taylor & Meester, in press). If a causal link can be found between population genetic factors and aspects of rabies epidemiology and incidence, rabies prone populations could be recognized by having different genetic profiles from rabies-free populations. Population genetics could therefore be used as a technique for independently assessing the risk of rabies in different areas, or for exploring biogical factors underlying rabies epidemiology.

The aims of this paper are:

- to present an annotated bibliography, as well as a brief overview of the biology of the yellow mongoose;
- to review the subspecies taxonomy of the species in terms of possible implications to rabies epidemiology; and
- to review recent studies of population genetics in the species, in order to test the hypothesis that life history, population genetic and epidemiological parameters are correlated in the yellow mongoose.

MATERIALS AND METHODS

This paper reviews earlier studies, from an epidemiological rather than a systematic perspective. Details on morphometric and colorimetric techniques used to quantify morphological patterns of geographical variation in the species can be found in Taylor (1990); Taylor *et al.* (1990a) and Taylor & Meester (1993). Chromosomal and enzyme electrophoretic (population genetic) methods are described in detail in Taylor (1990) and Taylor *et al.* (1990b). Captions to Fig. 2, 4 and 5 also give brief details of methods used.

RESULTS AND DISCUSSION

Biology

Table 1 gives a breakdown of much of the research conducted on the yellow mongoose. A full review of this species is given in Taylor & Meester (1993).

While yellow mongooses are predominantly insectivorous, preferring termites (Isoptera), beetles (Coleoptera) and locusts (Orthoptera), they are highly opportunistic feeders, and rodents, fruits and other insects may feature highly in their diet where available (Table 2). Diet appears to vary considerably both locally and seasonally (Table 2; Avenant & Nel 1992). As yellow mongooses are important insect and

TABLE 1 Bibliography of studies of the biology of the yellow mongoose, *Cynictis penicillata*

Subject	No. of studies	References[a]
Distribution	8	1–8
Taxonomy	2	9, 10
Fossils	2	11,12
Genetics	3	10, 13, 14
Feeding	10	1, 3, 4, 15–21
Reproduction	7	1, 3, 5, 19, 20, 22–24
Behaviour	3	20, 23, 25
Rabies	5	15, 16, 22, 23, 26
Functional anatomy	3	27–29

[a] 1 Smithers 1971; 2 Pringle 1977; 3 Rowe-Rowe 1978; 4 Stuart 1981; 5 Rautenbach 1982; 6 Lynch 1983; 7 Lynch 1989; 8 Taylor & Meester 1989; 9 Lundholm 1955; 10 Taylor 1990; 11 Hendey 1974; 12 Savage 1978; 13 Fredga 1972; 14 Taylor *et al.* 1990; 15 Snyman 1940; 16 Zumpt 1968; 17 Herzig-Strachil 1977; 18 Du Toit 1980; 19 Lynch 1980; 20 Earle 1981; 21 Avenant & Nel 1992; 22 Zumpt 1969; 23 Zumpt 1976; 24 Rasa, Wenhold, Howard, Marias & Pallett 1992; 25 Wenhold 1991; 26 Zumpt & de Bruyn 1967; 27 Pocock 1916; 28 Radinski 1975; 29 Apps, Viljoen & Taylor 1989

rodent predators, wholescale eradication of the species in rabies-infected areas could be ecologically harmful. Snyman (1940) found that numbers of insects increased locally after eradication programmes. The yellow mongoose is still regarded as vermin by many farmers who blame them for killing newborn lambs. There is no evidence for this assertion. Large snakes, water monitor lizards, and raptors such as black eagles are the most important natural predators of yellow mongooses.

Yellow mongooses occupy burrows which they often cohabit with suricates (*Suricata suricatta*) and ground squirrels (*Xerus inaurus*). Estimates of group size vary considerably though the range is from one to about 13 (Table 2, and references therein). Although yellow mongooses forage singly (and not co-operatively as in other social mongooses such as *S. suricatta, Mungos mungo* and *Helogale parvula*), they den communally, and have attained a certain level of division of labour, e.g. retention of juveniles in the colony as "helpers" (Earle 1981; Wenhold 1991; Rasa, personal communication). The social system is probably intermediate between those of the solitary and the other social species of Viverridae (Wenhold 1991). In the past there has been much disagreement about the degree of sociality in the yellow mongoose, with various authors referring to the species as solitary, social and "semi-social".

TABLE 2 Summary of variation in some life history features of *Cynictis penicillata*. Numerical superscripts indicate the same references as those listed below Table 1

Region	Diet (top 3 items)	Group size	Litter size	Reproductive season	No. of litters
OFS	Isoptera, Orthoptera, Coleoptera[19]	4,1[19]	1,8[19]	Aug–Nov[19]	1?[19]
Cape Province:	Coleoptera, Orthoptera, Isoptera[4]	–	–	–	–
Postberg	Isoptera, Rodentia, Coleoptera[21]	–	–	–	–
Beaufort West	Orthoptera, Coleoptera, Isoptera[21]	–	–	–	–
Mt Zebra NP	Coleoptera, Orthoptera, Isoptera[18]	–	–	–	–
KGNP	–	4,5[24]	1,8[24]	Aug–Feb[24]	2[24]
Karoo	–	2[24]	2[24]	Aug–Oct[24]	1[24]
Transvaal:	Rodentia, Orthoptera, Isoptera[16]	–	–	–	–
	Orthoptera, Coleoptera, Lepidoptera[5]	–	–	–	–
Vaaldam, SALNR	Isoptera, Orthoptera, Mammalia[17]	–	–	–	–
Vaaldam	Isoptera, "other insects", fruit[20]	8[20]	–	–	–
		3,9[23]	–	–	–
	–	–	3,5[22]	July–Dec[22]	1[22]
Vaaldam	–	13[24]	2,0[24]	Aug–Dec[24]	2[24]
Natal	Orthopthera, Coleoptera, Plant[3]	–	2,3[3]	–	–
Botswana	Coleoptera, Isoptera, Orthoptera[1]	1 or 2[1] (up to 8)	3,2[1]	July–March[1]	–
Namibia	–	3[24]	2[24]	Aug–Feb[24]	2[24]

[a] KGNP = Kalahari Gemsbok National Park

[b] SALNR = SA Lombard Nature Reserve

Table 2 also reflects the degree of variation in independent estimates of litter size, duration of reproductive season and the number of litters/female/season. There seems to be a distinction between northern and southern populations, the reproductive season seems to be shorter in the Karoo, Transvaal and Orange Free State (August–December), with only one litter/year normally, while populations from the Kalahari Gemsbok National Park, Etosha National Park and Windhoek extend the reproductive season from July/August–February/March, and typically have two litters/season (See references in Tables 1, 2).

Systematics

The value of basic taxonomic work in illuminating epidemiological investigations is underlined by biological studies of the multimammate mouse, a reservoir host of a number of diseases affecting man, including bubonic plague, Lassa fever and Banzi and Witwatersrand viruses. The species complex was found to consist of two chromosomally-distinct, cryptic species, *Mastomys natalensis* and *M. coucha*; the distribution of the latter was found to be closely correlated with the incidence of human plague cases, and it was found that only *M. coucha* was susceptible to the virus and played a role in the maintenance of the zoonosis (Green, Keogh, Gordon, Pinto & Hartwig 1980; Isaacson, Taylor & Arntzen 1983). A similar example concerns the resolution of a species complex of *Anopheles* mosquitoes, which varies with respect to malaria transmission (Paterson 1963). Apart from the *Mastomys* complex, "chromosomal species" have been described in at least three further medically important rodent species, *Aethomys chrysophilus*, *Tatera leucogaster* and *Saccostomus campestris* (Gordon & Rautenbach 1980). The implications of these results for plague epidemiology have yet to be explored.

Williams-Blangero, Van de Berg, Blangero, Konigsberg & Dyke (1990) demonstrated the existence of clear genetic differences between the five recognized subspecies of baboons, and pointed out the dangers inherent in failing to control for sub-population heterogeneity when conducting biomedical studies on baboons. This conclusion can be extended to apply to epidemiological studies involving valid subspecies, as is the case in the yellow mongoose.

A recent study demonstrated the existence of three discrete subspecies of *C. penicillata* which can be differentiated on morphometric and colorimetric grounds (Taylor 1990; Taylor & Meester 1993; Fig. 1): *C. p. penicillata* from South Africa excluding the northern Cape and northern Transvaal; *C. p. bradfieldi* from northern Cape, southern Botswana, and most of Namibia; and *C. p. coombsii* from northeastern Namibia, most of Botswana, and the Transvaal north of the Soutpansberg. *C. p. penicillata* is larger in size and redder and more saturated in colouration than other subspecies, and possesses a white tail tip; *C. p. coombsii* is smallest in size with a yellowish, faded but grizzled colouration, and no white tail tip and *C. p. bradfieldi* is intermediate between the other two subspecies in size and colour (Fig. 2).

Subspecies are separated by zones of differentiation which correspond either with geographical barriers such as the lower Orange River Valley and the Soutpansberg Mountains, or with the ecotone marked by the westward limits of Kalahari sands (Fig. 3). It has been hypothesized that past climatic regimes resulted in fragmentation and isolation of subspecies and accumulation of genetic differences (Taylor & Meester, in press). In view of this indirect evidence for genetic differentiation between subspecies, future studies on the epidemiology of rabies should control for such sub-group heterogeneity. Furthermore, since subspecies have attained a measure of evolutionary divergence, it is possible that differences have occurred in the genetic contribution of an individual's response to pathogens such as the rabies virus. Genetic differences between subspecies may explain, at least in part, why rabies incidence is so much higher in *C. p. penicillata* than in the other two northern subspecies. However, variation in rabies incidence also occurs within the range of *C. p. penicillata*. Subtle but constant morphological differences were found between Cape and Orange Free State/Transvaal populations of yellow mongooses (Taylor & Meester 1993b) and these may indicate genetic differences underlying greater rabies susceptibility in the latter group. However, increased population densities seems to be a critical factor as shown in Fig. 1.

Population genetics

Genetic structure of populations

While morphometric and colorimetric characters were useful at the level of distinguishing subspecies of yellow mongooses, genetic and chromosomal differences were found at the level of individuals and populations but not subspecies (Taylor 1990; Taylor *et al.* 1990b).

Thirteen of 28 protein and enzyme loci analyzed were found to be polymorphic in one or more of the eight populations sampled (Taylor *et al.* 1990; Fig. 4; Table 3). No genetic differences were found between populations representing *C. p. bradfieldi* and *C. p. penicillata* (Fig. 5). Polymorphic alleles tended to be restricted to individual populations, indicating extreme genetic heterogeneity. Wright's (1965) F_{ST} of 0,585 appears exceptionally high for a medium-sized, widely distributed, potentially mobile mammal such as the yellow mongoose (i.e. 58,5% of the total

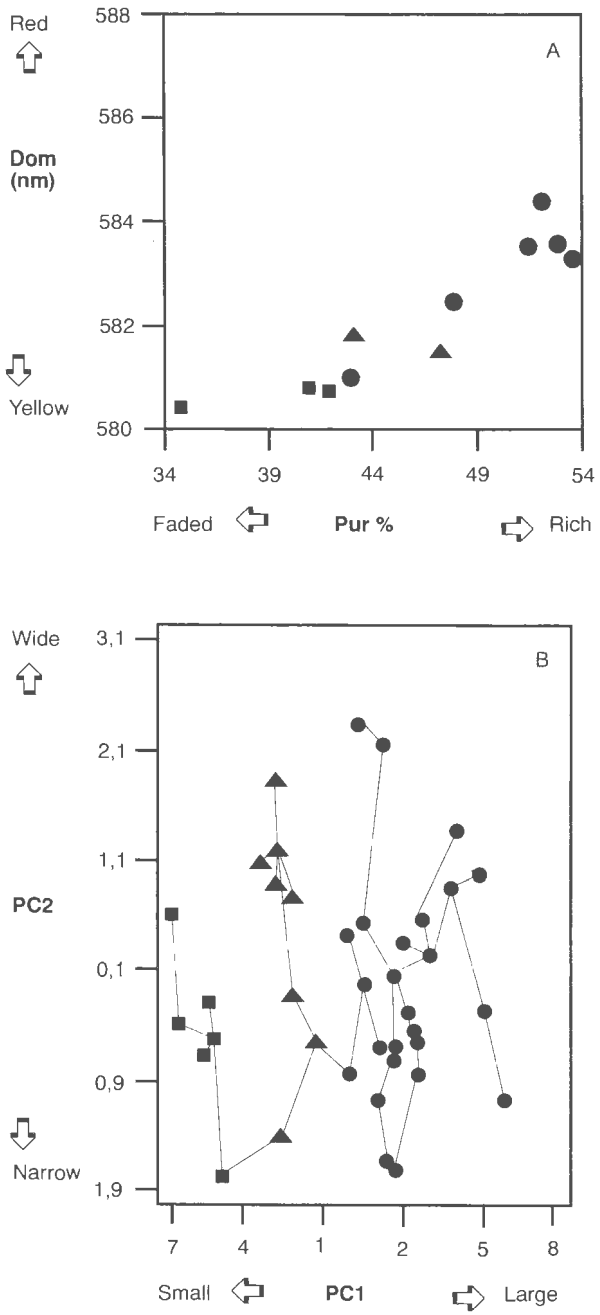

FIG. 2 Plots showing patterns of colorimetric (a) and cranometric (b) variation between subspecies of yellow mongooses (closed circles = *Cynictis penicillata penicillata*; triangles = *C. p. bradfieldi*; squares = *C. p. coombsii)*:

(a) bivariate plot of two colorimetric variables, dominant wavelength (DOM; nanometers) and excitatory purity (PUR; % saturation). Continuous colour variables were obtained using a tristimulus colorimeter and chromaticity charts according to standard methods detailed in Taylor *et al.* 1990a. DOM refers to the "redness" of a colour while PUR refers to the degree of saturation (faded or rich)

(b) bivariate plot of first two principal components from a principal component analysis of 14 cranial measurements in 39 pooled localities representing 287 "adult" yellow mongoose skulls. A minimum spanning tree, has been superimposed to indicate phenotypic resemblance between adjacent points. Details of methods given in Taylor & Meester, in press

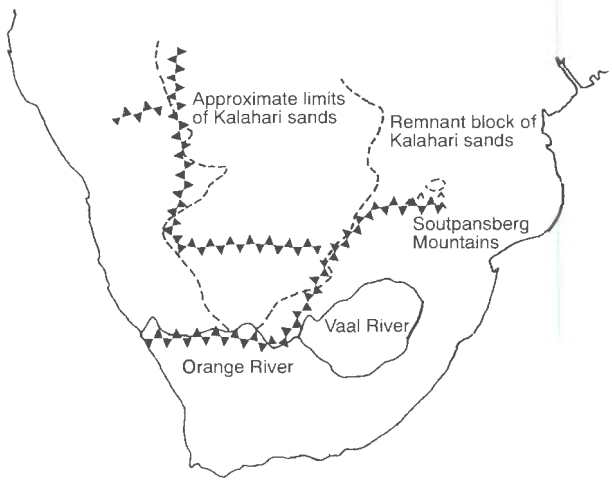

FIG. 3 Map showing relationship between location of morphometric stepped clines in *Cynictis penicillata* and biogeographical features such as the Orange River, Soutpansberg Mountains and the present limits of Kalahari sands (from Taylor & Meester, in press)

genetic variation occurred between rather than within populations). This value is higher than values recorded for populations of humans (0,148), house mice (0,12) Scandinavian moose (0,096), coyotes (0,080), prairies dogs (0,103), vlei rats, *Otomys irroratus* (0,375) and deer mice (0,075), although not as high as values recorded for pocket gophers, *Thomomys umbrinus* (0,752) and Karoo bush rats, *Otomys unisulcatus* (0,665; Taylor *et al.* 1990b; Taylor *et al.* 1992; and references therein).

The extraordinarily high F_{ST} value for *C. penicillata* can be explained by restricted vagility, possibly due to social structuring or habitat heterogeneity. Recent behavioural studies of the yellow mongoose (Rasa, personal communication) revealed that:

- the species is spatially and socially stable over periods of years (i.e. vagility is low);
- the dominant male (whose tenure may encompass several years) conducts the majority of matings;
- young remain with their parents as helpers over several years; and
- matings occur between neighbouring colonies.

These factors promote genetic homogeneity in a restricted area, but genetic heterogeneity between wider geographic areas. Another factor that may explain the postulated low vagility in yellow mongooses is the necessity for suitable soils for burrowing. Although

burrows are often excavated by the ground squirrel (*Xerus inaurus*), Snyman (1940) noted that several islands occur throughout the distribution of *C. penicillata* where the species is absent or very scarce, e.g. the hard lime soils of the eastern slopes of the Gaap Plateau of the Northern Cape.

Genetic structure of *C. penicillata* populations can therefore be explained by life history results obtained by independent studies. Low vagility in the yellow mongoose also explains the epidemiology of rabies in the species whereby rabies outbreaks caused by *C. penicillata* tend to be confined to restricted foci; an outbreak in the Bloemfontein district took 12 years to spread across five adjacent farms. In other cases successive outbreaks could often be traced to the same area on the same farm, up to 11 years later (Snyman 1940). Thus a strong correlation is obtained in the yellow mongoose between population genetic parameters, life history attributes and epidemiological aspects.

Genetic heterozygosity

A relationship has been established between low genetic heterozygosity and increased susceptibility to disease (O'Brien & Evermann 1988). Populations of yellow mongooses showing extremely low heterozygosities and possible inbreeding effects may therefore respond differently to the rabies virus than highly variable populations. A relationship may exist between heterozygosity and the ability of individuals to acts as reservoirs to the rabies virus over long periods.

Expected average heterozygosity (h) for yellow mongooses varied from 0–0,065 with a mean of 0,034 (Table 3) which is very similar to the mammalian mean of 0,039 calculated for 128 species of mammals (Wooten & Smith 1985), and higher than for other carnivores such as the raccoon (0,028; Dew & Kennedy 1980) and coyote (0,009; Hamilton & Kennedy 1986). Since many populations sampled consisted of only a few individuals, variation in heterozygosity of yellow mongoose populations needs to be tested more rigorously with samples of at least 20 individuals/locality. The relatively high heterozygosity for *C. penicillata* is consistent with a low F_{IS} (inbreeding coefficient of Wright 1965) of 0,039 (Taylor *et al.* 1990b).

Although the species as a whole does not display reduced heterozygosity or inbreeding, the limited vagility (high F_{ST}) of *C. penicillata* implies that there is a potential for much reduced heterozygosity where certain isolated or peripheral populations may have been subject to one or more severe bottlenecks. This may apply to an isolated population occurring north of the Soutpansberg in the northern Transvaal on a relic block of Kalahari sandveld. During Pleistocene interpluvials, Kalahari sands were much more extensive than present, and as the sands retreated during subsequent pluvials, relic blocks were left behind. These relic blocks of Kalahari sandveld are known to be associated with speciation and subspeciation of certain amphibians (Broadley 1978; Jacobsen 1987). Yellow mongooses from northern Transvaal closely resemble Botswana Kalahari individuals in size and colour but are distinct from geographically

TABLE 3 Distribution of alleles, percent polymorphism, mean heterozygosity (h) and standard error (SE) of h, for 12 polymorphic protein and enzyme loci analyzed using starch gel electrophoresis in eight populations of yellow mongooses. (Population numbers as in Fig. 4)

Proteins/enzymes	Localities								
	1	2	3	4	5	6	7	8	
Aspartate aminotransferase-1		b	b	a, b	b	b	b	a, b	b
Aspartate aminotransferase-2		b	b	b	b	b	b	b	a
Alcohol dehydrogenase		b	a, b, c	b	b	b	b	b	b
Catalase	c	a, b	c	b. c	c	c	c	c	
Esterase-2		–	–	–	–	–	a, b	–	–
Esterase-3		–	–	–	–	–	a, b	–	–
Glucose dehydrogenase	b	b	b	b	b	b	a, b	b	
Glycerol-3-phosphate dehydrogenase	a, b	b	b	b	a, b	b	b		
Postalbumin-1		–	–	–	–	–	a, b, c	–	–
Phosphogluconate dehydrogenase	c	c	c	a, b, c	c	c	c	c	
Phosphoglucomutase		b	b	a	b	b	b	b	b
Transferrin		–	–	–	–	–	a, b	–	–
Mean percent polymorphism	4,5	9,1	4.5	9,1	0,00	18.5	9,1	0.0	
Mean heterozygosity (h)	0,024	0,052	0,030	0,052	0,000	0,065	0,053	0,00	
SE		0,024	0,037	0,030	0,036	0,000	0,032	0,037	0,000

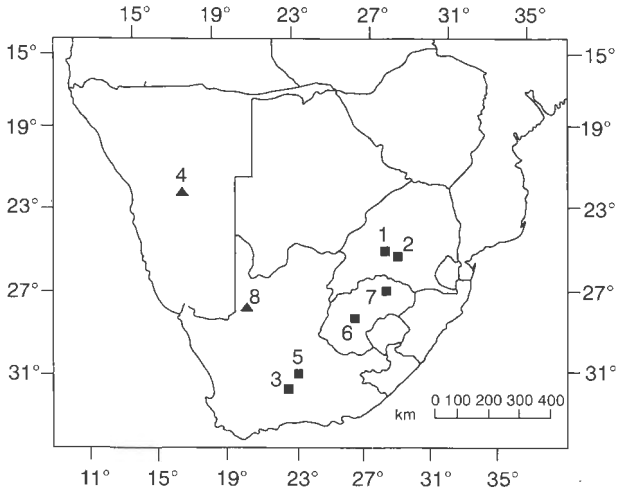

FIG. 4 Map showing localities from which specimens of yellow mongooses were obtained for electrophoretic analysis. ▲ represent *Cynictis penicillata bradfieldi*; ■ represent *C. p. penicillata* (from Taylor *et al.* 1990b)

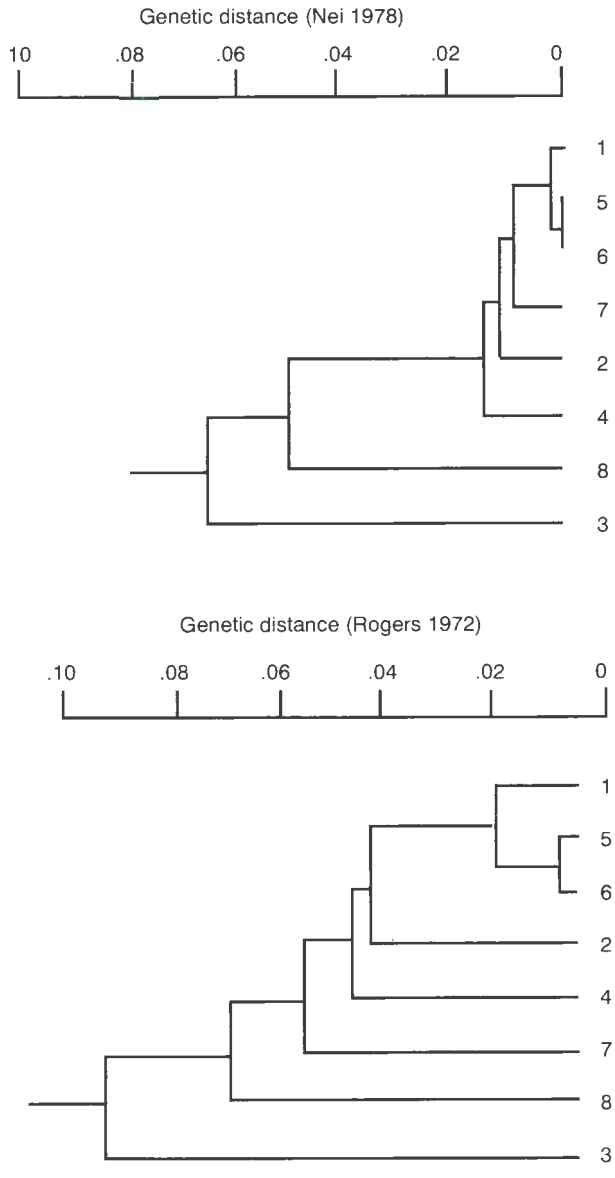

FIG. 5 Phenograms of Nei's (1978; above) and Rogers' (1972; below) genetic distances between eight populations of yellow mongooses. Numbers refer to localities indicated in Fig. 4. Localities 4 and 8 represent *Cynictis penicillata*; other localities represent *C. p. penicillata* (from Taylor *et al.* 1990b)

closer populations from the southern Transvaal. Two field trips to sample specimens from this northern Transvaal isolate proved fruitless; no specimens were even seen and local landowners were not aware of the animal, suggesting that the population size has been greatly reduced or that the population has become extinct.

Other populations that may have experienced bottlenecks, and therefore possible inbreeding effects including altered susceptibility to rabies, are those from marginal habitats where population densities are extremely reduced. Yellow mongooses were found to be relatively uncommon at Riemvasmaak in the northwestern Cape (Erasmus, personal communication) and in the Karoo National Park (Taylor, personal observation). Single individuals from each of these two populations were sampled for electrophoretic analysis; unique alleles at different loci were found to be "fixed" in each population (Table 3), accounting for the genetic separation of these two populations from other populations from better-populated parts of the species' range (Fig. 5).

Chromosomal polymorphism: presence of microchromosomes

The basic karyotype ($2n = 36$; NF = 72) of the yellow mongoose was found to be constant for five populations studied in the Cape Province, Orange Free State, Transvaal and Namibia. (Taylor 1990), representing two subspecies, *C. p. bradfieldi* and *C. p. penicillata*. The karyotype is also identical to that published by Fredga (1972) for *C. p. coombsi*.

Single extranumerary microchromosomes were found in four of the five populations examined (Taylor 1990). The presence of microchromosomes (or B-chromosomes) has been reported in a number of species including, among carnivores, the silver fox (Kuokkanen, Lohi & Makinen 1985) and the raccoon dog (Makinen, Kuokkanen & Valtonen 1986).

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