The epidemiology of rabies in Zimbabwe. 2. Rabies in jackals (*Canis adustus* and *Canis mesomelas*)

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ABSTRACT

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The epidemiology of rabies in *Canis adustus* (the side-striped jackal) and *Canis mesomelas* (the black-backed jackal) in Zimbabwe is described using data collected from 1950–1996. Cases in the two species made up 25,2% of all confirmed cases, second only to domestic dogs. Since the species of jackal cases was not recorded on rabies submission forms, the country was divided into areas according to species dominance and jackal cases were assigned to either *C. adustus* or *C. mesomelas* dominant zones or a sympatric zone where the relative status of the species is not known. Jackal rabies in both species is maintained in the commercial farming sector. Jackal rabies in the *C. adustus* zone occurs as dense epidemics, which begin at a single focus and spread centrifugally. The foci were initiated by rabid dogs, but once initiated the epidemic is maintained by *C. adustus* independently of other species. The extent of outbreaks in the *C. adustus* zone was limited by geographical (landuse type and jackal species interface) boundaries. Jackal rabies in *C. adustus* zones showed two seasonal peaks with the main peak occurring during late summer and the second peak during winter. In the *C. mesomelas* zone jackal rabies was more sparse but it occurred during most years. *C. mesomelas* is also able to maintain rabies independently of other species, although the epidemiology of the disease in this species is unclear. Transmission of rabies cycles between the two jackal species zones does not appear to occur as epidemics terminate when crossing the *C. adustus* and *C. mesomelas* interface boundaries.

Keywords: *Canis adustus*, *Canis mesomelas*, epidemiology, jackal, rabies, Zimbabwe

INTRODUCTION

Jackals, which account for 25,2% of all confirmed rabies cases in Zimbabwe, constitute the second most important vector of rabies after domestic dogs

(Bingham, Foggin, Wandeler & Hill 1999). Although the number of human rabies cases caused by jackals is relatively small, with only four (2,3% of 174) laboratory-confirmed cases in Zimbabwe having been caused by them in the period 1950–1996, the potential of jackal rabies as a zoonotic threat is important: of all rabid jackals submitted for laboratory confirmation during this period, 26% (254/971) had bitten people (Central Veterinary Laboratory, Harare, unpublished data).

Two species of jackal occur in Zimbabwe (Skinner & Smithers 1990): *Canis adustus* (the side-striped jackal) and *Canis mesomelas* (the black-backed jackal). *C. mesomelas* lives in mated pairs or small family units with sedentary home ranges, or as single itinerant individuals (Ferguson, Nel & de Wet 1983). Home ranges of breeding pairs are mutually

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exclusive and vary considerably in size. In two study areas in South Africa adult 95% home range sizes were on average 10,6 and 27,7 km² (Ferguson *et al.* 1983). Breeding takes place during the winter months (Skinner and Smithers 1990) and dispersal from the natal home range occurs during winter in the first or second year of life. Dispersing jackals can move considerable distances during this dispersion, in one case over 126 km (Ferguson *et al.* 1983). Some young adults remain with their parents to help raise subsequent litters (Moehlman 1979). Little is known of the ecology of *C. adustus*, other than that it also breeds during the winter months (Bingham, unpublished data).

Two biotypes of rabies, distinguishable antigenically and genotypically, occur in terrestrial animals in southern Africa (King, Meredith & Thomson 1994; Von Teichman, Thomson, Meredith & Nel 1995). The biotype found in herpestid species, particularly the yellow mongoose (*Cynictis penicillata*) and the slen-

der mongoose (*Galerella sanguinea*, Foggin 1988) is thought to be an ancient virus indigenous to southern Africa, which shows considerable antigenic and genetic diversity. That found in canid species (domestic dogs *Canis familiaris*, jackals and bat-eared foxes *Otocyon megalotis*) shows little diversity and is thought to have been introduced in recent times, a claim supported by historical data (Swanepoel, Barnard, Meredith, Bishop, Brückner, Foggin & Hübschle 1993).

The objectives of the study described in this paper were to elucidate the epidemiological trends of jackal rabies in Zimbabwe.

MATERIALS AND METHODS

The sources of data and data analysing techniques have been described elsewhere (Bingham *et al.* 1999). The jackals from which specimens were taken for rabies diagnosis were not always identified

Sample key

1. Jackal cull, Banket, 100% (*n* = 11) *C. adustus*
2. Jackal cull, Harare west, 62% (5/8) *C. adustus*
3. Rabies submissions, Harare and surrounding areas: 91% (124/136) *C. adustus*
4. Jackal trapping operation, Selous, 80% (12/15) *C. adustus*
5. Jackal cull, Wedza, 100% (*n* = 5) *C. adustus*
6. Rabies submissions, Kwekwe district, 81% (65/80) *C. mesomelas* (Foggin 1988)
7. Estimate based on sightings, Mvuma, 80% *C. mesomelas* (G. Sharp, personal communication)
8. Jackal cull, Mwenezi, 85% (44/52) *C. mesomelas*
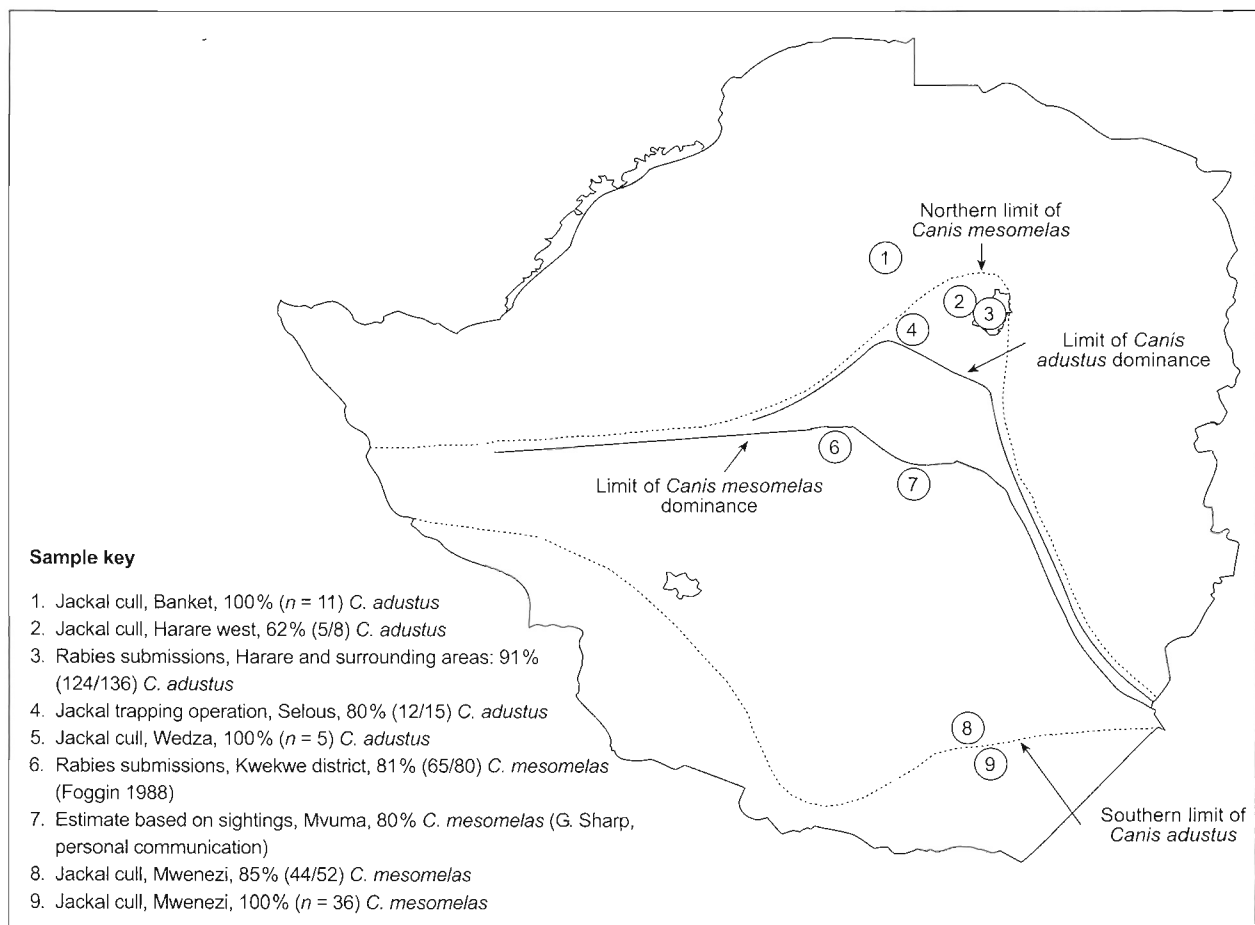9. Jackal cull, Mwenezi, 100% (*n* = 36) *C. mesomelas*

FIG. 1   The distribution of relative abundance of *C. adustus* and *C. mesomelas* based on culling and trapping operations, rabies submissions and sightings. The region between the limits of *C. mesomelas* and *C. adustus* dominance demarcates the area where neither species is dominant or where the relative status of the two is not known. The limits of the respective species distributions are based on Skinner & Smithers (1990)

according to their species, and were therefore designated to species according to the area from which the specimen originated. The limits of the species distributions are described by Skinner & Smithers (1990). To further classify areas according to species status, reliably identified jackals were obtained from several culling or trapping operations and from cases submitted for rabies examinations from the Harare area. In addition, miscellaneous records and personal communications were used. Fig. 1 shows the results of this survey. This method established the zones where one or other species is dominant, and a zone, referred hereafter as the sympatric zone, where both species live in roughly equal proportions or where the relative status of the two is not known.

Prevalence data on all laboratory-confirmed rabies cases which occurred from 1950–1996 inclusive were used in the analysis. Jackal case totals from the first 2 months of 1997 were used for displaying monthly prevalence only.

Canine teeth were available from 267 *C. adustus* or jackals from the *C. adustus* zone. Since jackals give birth to their young in a very limited period in September and early October (Bingham, unpublished data), it was possible to classify the ages of the animals into four discrete age groups according to the tooth developmental stage. The ageing technique involved examination of the canine teeth visually and radiographically. Permanent canine teeth which had closed pulp cavity (PC) foramina were radiographed and the diameter of the tooth and its PC at the point where the PC was widest were measured with vernier calipers. The tooth specimens were divided into age groups as follows: Juveniles having deciduous teeth and estimated to be up to 6 months of age; subadults having permanent teeth with open pulp cavity (PC) foramina and estimated to be 4–9 months old; young adults having PC diameters constituting 55% or more of the tooth diameter and estimated to be 7–16 months old; and mature adults having PC values under 55% estimated to be over 12 months old (Bingham, unpublished data).

To study the jackal case frequency pattern at a local level, cases within quarter degree squares in the area and time period of each epidemic were counted by month. In the main epidemic areas a quarter degree square is approximately 26,5 km x 27,6 km (731 km²). To get an overall picture of the pattern of the epidemic, the cases for all quarter degree squares were added together by month, taking the first month as that in which the first jackal case occurred. This procedure was carried out by a computer programme which, when counting the cases for each quarter degree square by month, removed all leading months with nil cases and aligned all quarter degree square counts by the month with the first case.

To study the species responsible for maintenance of *C. adustus* outbreaks and the temporal pattern of

rabies at a local level, three 50 x 50 km blocks were defined around the towns of Chinhoyi, Mvurwi and Marondera (for region names see Fig. 1 of Bingham *et al.* 1999). All three blocks were well within the limits of commercial farmland and had experienced waves of successive jackal rabies outbreaks. Within these blocks dog and jackal cases were counted for each year. A similar analysis was carried out for 100 x 100 km blocks around Bulawayo, Kwekwe and Triangle, all within the *C. mesomelas* zone.

To study the role of other species in the initiation of jackal outbreaks, the index jackal case from each outbreak was identified and cases in carnivore species which occurred within a period of 12 months and a radius of 100 km of the index case were identified using a database search programme. To study the relationships between individual jackal cases and cases in other species, similar search programmes were compiled, using appropriate time and distance values.

Observations on jackal rabies were reported on a 125 km² ranch (location 9 in Fig. 1) in the Mwenezi district where surveillance is poor. Only *C. mesomelas* had been reported in this area. Over a period of 3 years starting in early 1991 the residents of the ranch reported all suspicious behaviour in jackals and other animals. Where available, carcasses were retained for rabies confirmation.

RESULTS

General trends

From 1950–1996, jackals constituted 25,2% of all confirmed cases of rabies in Zimbabwe and they were the most frequently diagnosed species category during the years 1966–1967, 1971–1973, 1981 and 1993–1995.

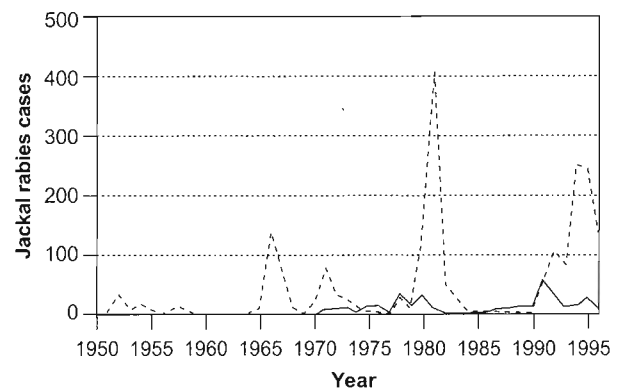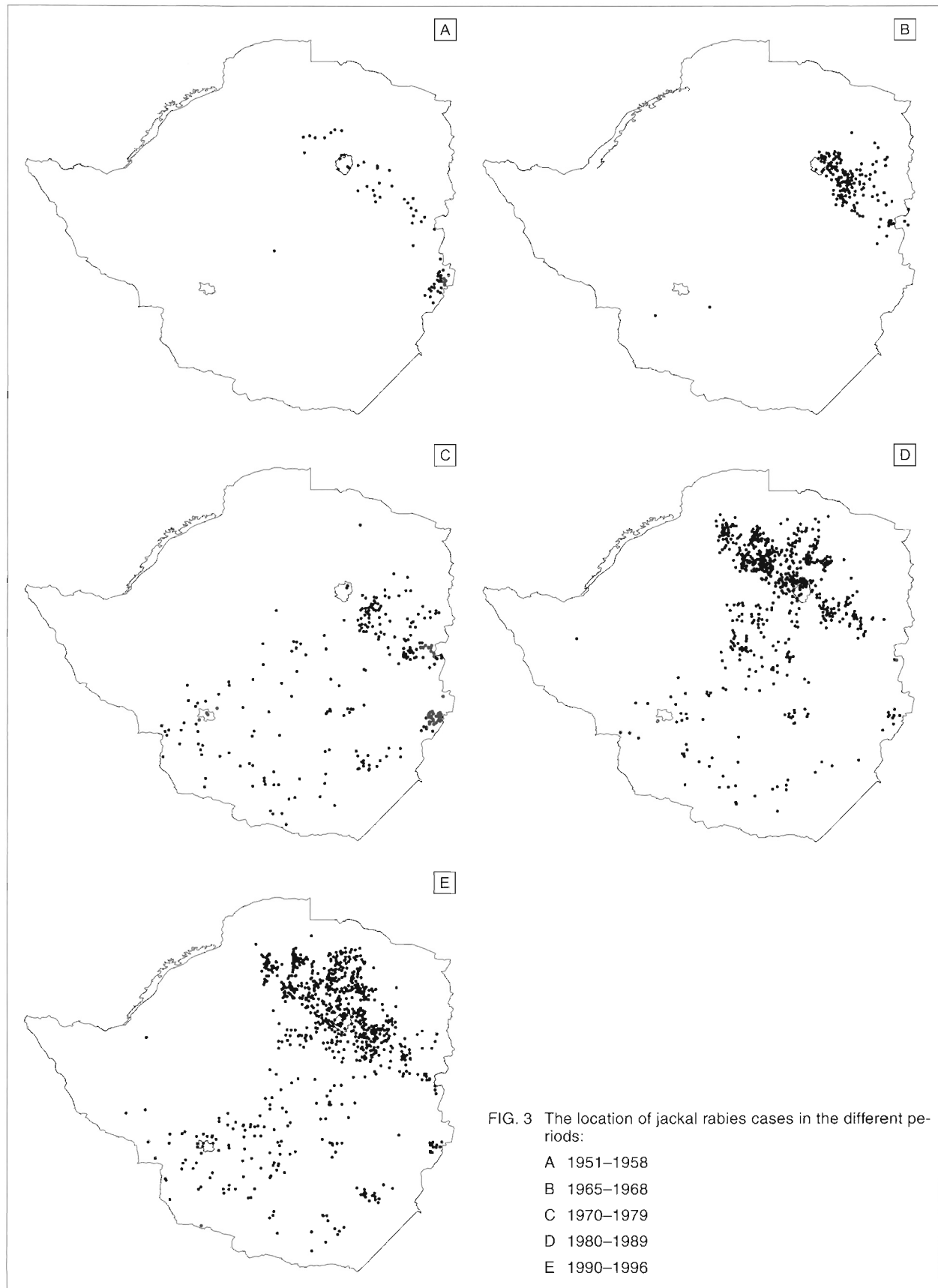The annual prevalence of rabies in *C. adustus* and *C. mesomelas* zones is given in Fig. 2. Jackal rabies

FIG. 2 The number of jackal rabies cases per year from the *C. adustus* (dotted line) and *C. mesomelas* (solid lines) zones

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FIG. 3 The location of jackal rabies cases in the different periods:

A   1951–1958
B   1965–1968
C   1970–1979
D   1980–1989
E   1990–1996

in the *C. adustus* zone was characterized by large, unstable epidemics separated by periods in which the disease was unreported and probably extinct, except in limited areas. The prevalence of jackal rabies in the *C. mesomelas* zone has been less variable and at a lower reported frequency since the early 1970s.

The geographical locality of the cases for different periods is shown in Fig. 3. The first jackal cases were reported in 1951 near the eastern border. During the next 7 years jackal rabies was confined to the Chipinge area and from Mutare to the area northwest of Harare (Fig. 3A). No jackal rabies occurred from 1959–1964. From 1965–1968 an intense but geographically limited outbreak occurred in Mashonaland East (Fig. 3B), which was followed by an outbreak in the same region in the 1970s (Fig. 3C). Since the early 1970s, jackal rabies has increased in the middle and southwestern regions of the country (Fig. 3C), which had previously reported a negligible number of cases. From 1979–1984 and from after 1990 several outbreaks occurred in the Mashonaland area (Fig. 3D and 3E), some of which were simultaneous.

Jackal rabies in the *C. adustus* zone

Seasonality

Cases from the *C. adustus* zone had a bi-modal pattern with high prevalence in January to March and July/August (Fig. 4). The lowest number of cases were reported in October.

The seasonal changes in rabies prevalence were plotted for the *C. adustus* zone cases during the three major epidemic periods (Fig. 5). Although the lowest prevalences were found during October and November in all three periods, there was a marked difference in the peak prevalence. During the 1965–1975 period there were two peaks of equal level in March/April and in July. During the 1978–1985 period the highest points were in February and July and these were also of approximately equal level. In contrast, the 1990–1996 period had a pronounced peak in February/March, but none during mid-year. Fig. 6 displays the reported jackal cases from the *C. adustus* zone in each month from 1990. A consistent peak in reported prevalence occurred during the initial months of the year.

Rabies infection rate of the different age classes

Rabies submissions from young adult jackals (those estimated to be 7–15 months of age) from the *C. adustus* zone appeared to be less likely to be diagnosed positive for rabies than other age groups (Table 1). The number of samples received from the *C. mesomelas* zone was too small to carry out a similar analysis.
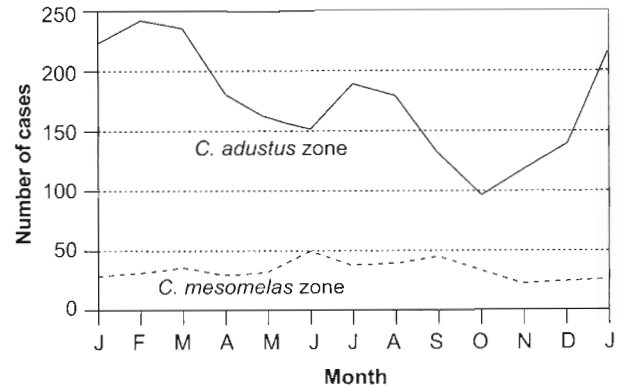

FIG. 4   The seasonal occurrence of rabies in *C. adustus* and *C. mesomelas* zones from 1950–1996 inclusive
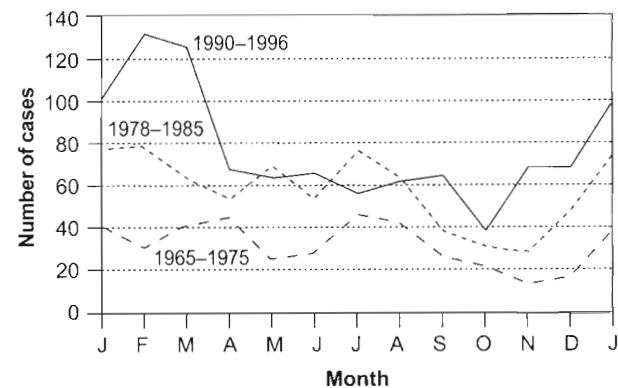

FIG. 5   The seasonal occurrence of rabies in the *C. adustus* zone separated into the three main epidemic periods: 1965–1975, 1978–1985 and 1990–1996
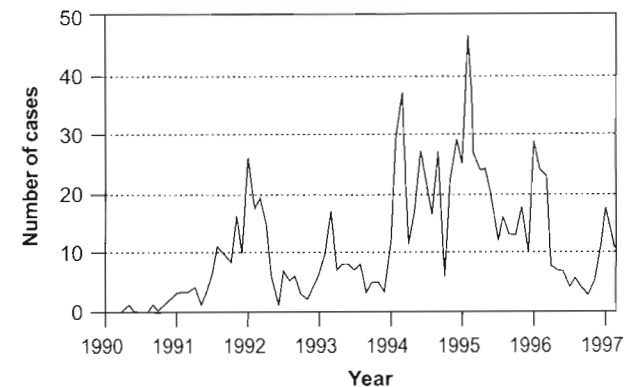

FIG. 6   Jackal rabies cases reported by month in the *C. adustus* zone from 1990 to February 1997

Geographical trends

From 1950–1996 88,5% of 2 050 jackal cases from the *C. adustus* zone were reported from the commercial farming sector, 4,9% from the communal sector, 6,3% from urban areas and 0,2% from protected

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TABLE 1 Rabies positivity of the different age classes of 267 *C. adustus* specimens and jackals specimens from the *C. adustus* zone. Juveniles are those animals with deciduous teeth, sub-adults have open canine tooth pulp cavity foramina, young adults have canine pulp cavities of over 55 %, while mature adults have pulp cavity percentages below this value

Age class	Approximate age	Total	Positive	Percent positive
Juvenile	Below 6 months	15	13	86,7
Sub-adult	4–9 months	50	42	84,0
Young adult	7–16 months	53	23	43,4
Mature adult	Over 12 months	149	119	79,9

TABLE 2 The numbers of carnivore species diagnosed rabid 12 months before and within radii of 50 km and 100 km from the index cases of 13 jackal rabies outbreaks in the *C. adustus* zone

Outbreak	Dogs		Jackals		Other carnivores	
	50 km	100 km	50 km	100 km	50 km	100 km
Chipinge 1952	12	18		0		0
Marondera 1965	3	12		1		1 (cat)
Marondera 1971		4	1	7		1 (mongoose)
Chipinge 1971	1	1		0		0
Chipinge 1978	9	11		0		0
Marondera 1979	9	31		1		1 (cat)
Mount Darwin 1979		0		0		0
Marondera 1991		20		0		2 (cats)
Rusape 1991	18	29		2	2	2 (cats)
Karoi 1991	14	17		0		0
Chinhoyi 1992	2	15		22	1	6 (civet, mongoose, cat)
Centenary 1993		2		28		2 (civet, hyaena)
Mhangura 1993	2	12	1	11		3 (civet, mongoose)

Cat = *Felis domestica*
Civet = *Civettictis civetta*
Hyaena = *Crocuta crocuta*
Mongooses = *Herpestes ichneumon, Ichneumia albicauda* and one unidentified species

areas. Of the eight jackal cases reported from protected (wildlife and forest) areas from all three species zones, only one was from a large national park and this case was from near the boundary with commercial farmland. The remainder were reported from small parks surrounded predominantly by commercial farmland.

The positions of the fronts of the four major *C. adustus* outbreaks were plotted over intervals (Fig. 7). During the 1965–1968 outbreak the front moved up to a maximum of 56 km in one year, with the fastest movement being during the April to June period when it advanced 43 km in some areas. During the epidemic of north Mashonaland during and after 1979 the front moved up to 140 km during 1980 and up to 93 km during 1981. The fastest movement was reported during July to September 1981, when the front moved 58 km in one region. The maximum front progression during the years 1991 to 1993 in the Mashonaland East areas varied from 38–51 km per year with the periods of greatest movement being during January to March 1992 when it moved 26 km and October to December 1993 when it moved 23 km.

All the major outbreaks progressed not only as gradually advancing fronts but also by establishment of foci ahead of the front. This phenomenon was responsible for most of the fastest movement described above. During the epidemics of 1965 and the early 1980s, foci established 19–30 km away from the nearest other reported jackal cases. These foci all grew to become large clusters of cases which merged with the main epidemic. In the post-1991 epidemic in northern Mashonaland (Fig. 7C) foci, listed as separate epidemics in Table 2, started 48, 50 and 68 km from the nearest other jackal cases.

In several instances jackal rabies outbreaks crossed small communal areas. In one of these instances, between 1992 and 1994, the epidemic of Mashonaland East moved through the 30 km wide Chinamora, Msana and Masembura Communal Lands northeast of Harare to reappear again, as a 30 km long front, in the commercial farming areas around the towns of Bindura and Shamva. Between the time the epidemic stopped at the southern boundary of the communal area and the time of its reappearence again north of the communal area, which was a period of
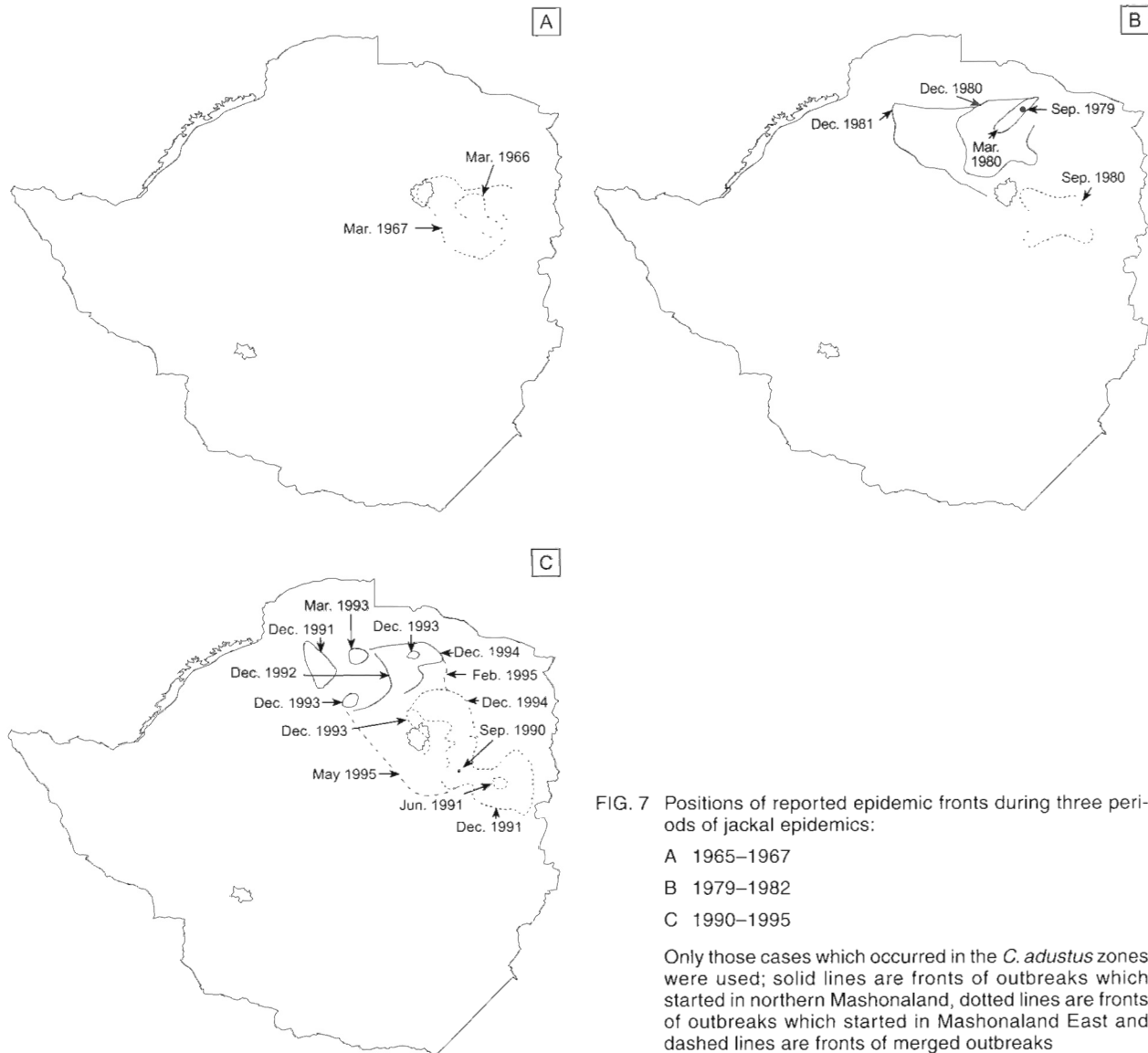
A

B

C

FIG. 7 Positions of reported epidemic fronts during three periods of jackal epidemics:

A 1965–1967

B 1979–1982

C 1990–1995

Only those cases which occurred in the *C. adustus* zones were used; solid lines are fronts of outbreaks which started in northern Mashonaland, dotted lines are fronts of outbreaks which started in Mashonaland East and dashed lines are fronts of merged outbreaks

17 months, rabies in two dogs was diagnosed within the communal area. Rabies in three jackals was also diagnosed within the communal area, but all after the disease had re-appeared at the northern boundary.

Temporal pattern of jackal rabies epidemics

Fig. 2 shows the trends of jackal rabies in the two main species zones. As the zones cover relatively large areas, these graphs obscure more definable patterns at local levels. The combined summed data for quarter degree squares showed that, within an average square, 94% of cases occurred during the first 12 months for the 1965 Mashonaland East epidemic, while the epidemic of northern Mashonaland which started in 1979 had 89% of cases in the first 12 months. In contrast, the average quarter degree square of the epidemics of the 1990s of Mashona-

land East and northern Mashonaland had 46% and 60% of cases (using cases up to June 1996) respectively occurring in the first 12 months after arrival of the disease. This lower percentage is due to the presence of secondary waves in these epidemics. Secondary waves occurred at variable times after the primary epidemic: beginning 42 months after the 1979 epidemic of Mashonaland East and between 35 and 60 months after the first cases in the 1990s epidemics. Low numbers of cases occurred sporadically in between the primary and secondary waves and after the secondary wave.

Fig. 8 shows the change of *C. adustus* zone jackal rabies prevalence in three blocks of commercial farmland and the concurrent prevalence in dog rabies. This graph also demonstrates the secondary waves which occurred during some of the outbreaks.
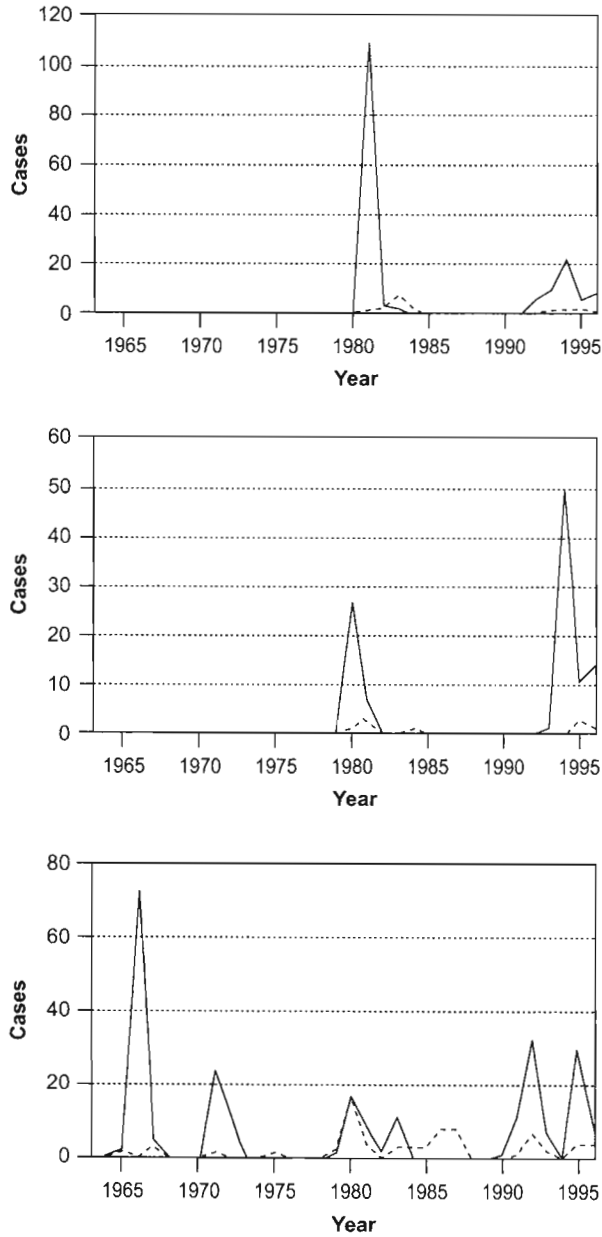
FIG. 8 The jackal (continuous lines) and dog (dotted lines) rabies cases by year in three 50 x 50 km blocks in the *C. adustus* zone centred around the towns Chinhoyi (top), Mvurwi (middle) and Marondera (bottom)
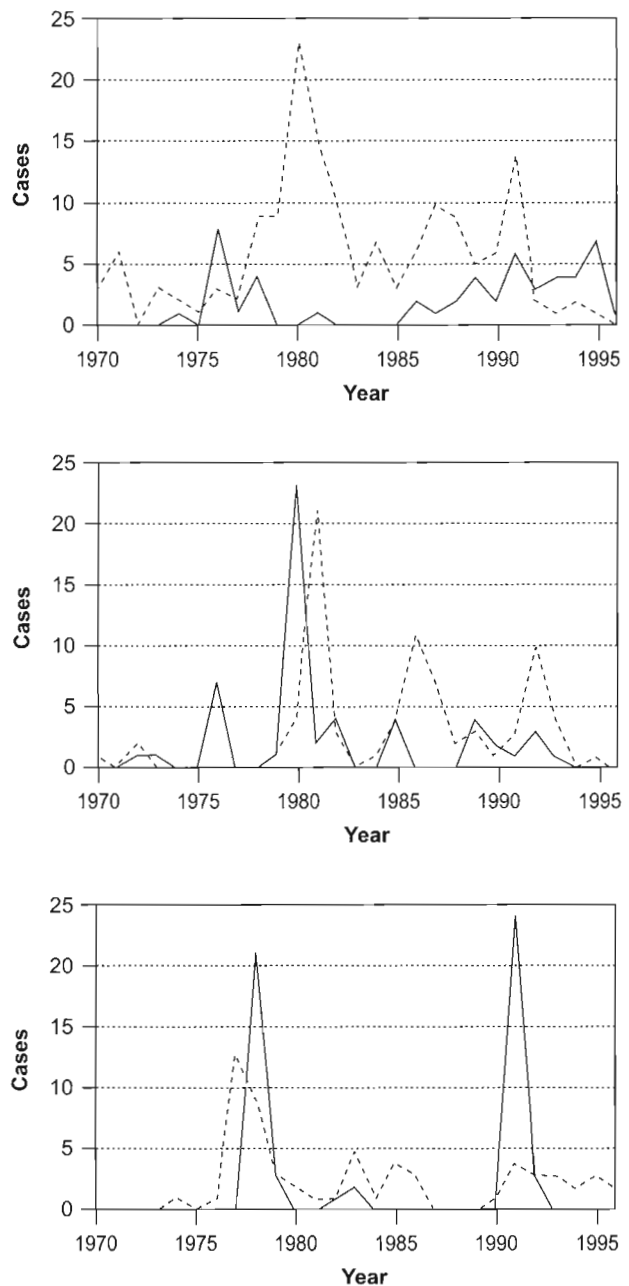
FIG. 9 Jackal (continuous lines) and dog (dotted lines) rabies cases by year in three 100 x 100 km blocks in the *C. mesomelas* zone centred around Bulawayo (top), Kwekwe (middle) and Triangle (bottom)

In addition, it demonstrates the relatively short time period in which epidemics remain in any one localized area and the long periods of absence of rabies between epidemics.

Maintenance of jackal rabies outbreaks

Fig. 8 shows that, in the defined blocks, jackal cases far exceeded dog cases during all the jackal outbreaks. Further analysis showed that of all jackal cases from the *C. adustus* zone up to 1996, 96,0% were preceded by at least one other jackal case within a period of 180 d and a radius of 50 km, while 82,7% were preceded by at least one dog case and 1,1% were not preceded by cases of any species within these limits. Only 2,6% of cases were preceded by at least one dog case without jackal cases, while 16,0% were preceded by at least one jackal case without any dog cases.

Initiation of jackal rabies epidemics

In the *C. adustus* zone a total of 13 foci which developed into epidemics was reported (Table 2). Of the 13 foci, seven had dog cases, but no jackal cases, occurring within a 50 km radius and 12 months before the jackal index case. Five of these foci had over five dog cases in the 50 km radius and six had over ten cases within 100 km. In another focus where no dog cases, or cases in any other species, were reported within 50 km and 12 months, a large number of dog cases was reported between 50–70 km from the jackal index case. In several of these instances where dog cases preceded a jackal outbreak, dog rabies had been present for several years before the jackal outbreak commenced. Dog rabies was present in most of Mashonaland during the 5 years before the beginning of the 1990s epidemics and was present, albeit at low frequency, for 3 years before the jackal epidemic of the 1960s.

In three other outbreak foci of the 1990s from Chinhoyi, Mhangura and Centenary (Fig 7C), dog cases were reported within 100 km of the jackal index case, although larger numbers of jackal cases were also reported within this distance. The jackal cases and most of the dog cases were associated with separate jackal epidemics. Hence, these outbreak foci may have been initiated either by dogs straying from the other foci of jackal rabies, or from jackals dispersing from these foci.

Two instances occurred where no other carnivore cases occurred within a 50 km radius and within 12 months of the jackal index case. The first instance was the epidemic of the early 1970s in the Marondera area. Low numbers of jackal and dog cases occurred although these were some distance from the focus of initiation. No other cases were reported within a 100 km radius of the epidemic initiated near Mount Darwin in 1979, which progressed to become the large epidemic of northern Mashonaland in the early 1980s (Foggin 1988; Kennedy 1988).

Rabid non-canid carnivores were reported within the 50 km zone associated with two outbreaks: in one, two domestic cat cases were reported, but both were associated with dog cases, and in another, rabies was confirmed in a mongoose of unrecorded species 46 km away, although in this instance this was more closely related to a different jackal epidemic than to the index case of the new epidemic.

Jackal rabies in *C. mesomelas* and sympatric zones

From 1950–1996 78,8% of 397 jackal cases from the *C. mesomelas* zone occurred in the commercial farming sector, 11,3% in the communal sector, 9,6% in urban areas and 0,3% in protected areas. A total of 107 jackals was reported from the sympatric zone

during this period and of these, 93% were from the commercial farming sector.

The seasonal prevalence is displayed in Fig. 4. Rabies reports from the *C. mesomelas* zone were of higher prevalence from June to September and the lowest prevalence was in November. Rabies in the sympatric zone (graph not shown) appeared to be similar, although the sample size was too small to draw significant conclusions.

Out of a total of 397 cases, 65,0% and 63,5% were preceded, within a radius of 50 km and a period of 180 d, by other jackal cases and dog cases respectively. Of these cases, 19,1% were preceded by jackal cases with the absence of dog cases, and 17,6% were preceded by dog cases in the absence of other jackal cases. In 7,8% of cases no other species were reported within these limits.

Fig. 9 shows the prevalence by year of jackal and dog cases around the three urban areas of Bulawayo, Kwekwe and Triangle (20 km west of Chiredzi). Jackal rabies was present at low levels in most years around Bulawayo; it was also present during most years around Kwekwe, but with one prominent epidemic in 1980; around Triangle jackal rabies was present as epidemics, with long periods of absence in between. The number of cases of rabies in jackals often exceeded those in dogs; around Kwekwe a jackal epidemic in 1980 preceded a dog epidemic, while in Triangle the reverse occurred; around Bulawayo a dog epidemic occurred in 1980 without the simultaneous increase in the prevalence of jackal cases. Cases in the two species did not necessarily coincide geographically, for example most of the dog cases from Triangle came from the communal areas nearby.

The findings of the survey conducted in the Mwenezi area are as follows. Over 7 months, two jackals, including the first reported case, were confirmed as positive in the laboratory, and rabies in another ten jackals was diagnosed on the grounds of suspicious signs only, without laboratory-confirmation. Such signs included entering homesteads, biting objects such as fences and loss of fear for people. The final, thirteenth, laboratory-confirmed jackal case was reported 15 months after the penultimate, twelfth case. In addition, rabies was laboratory-confirmed in five cases and suspected (not laboratory-confirmed) in four cases of cattle, a domestic dog, African civets (*Civettictis civetta*), honey badgers (*Mellivora capensis*), eland (*Taurotragus oryx*) and kudu (*Tragelaphus strepsiceros*). Presumptive diagnoses of rabies in the suspect cases was made on the grounds of their abnormal behaviour which included aggression and loss of fear. The first non-jackal case, a civet, was reported after the eighth jackal case: non-jackal cases occurred between 4 and 16 months after the first reported jackal case. During this outbreak a

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few cases of rabies were confirmed on other properties 10–30 km distant. Most cases of all species were observed around homesteads. During the outbreak, the density of the jackal population declined noticeably, as evidenced by reduced sightings and calling. According to the residents no similar incidents of such behaviour by jackals or other animals had been reported during the previous 10 years, however, rabies cases were confirmed in several species, mainly cattle, 6 months to 2 years before the outbreak on different ranches up to 50 km away and two cattle cases were confirmed on a neighbouring ranch about 18 months before the first jackal case of this study. This outbreak also coincided with an outbreak of jackal rabies in the Triangle area in 1991 (Fig. 9), about 90 km northeast. No suspicious dog cases were reported before the jackal cases occurred. Few dogs were present on the ranches and most of these would have been vaccinated. The ranch where this survey was conducted is 25 km from the nearest communal areas where unvaccinated dogs would have been present, although the prevalence of rabies in dogs has never been high in these areas.

Movement of rabies between different species zones

In 7 instances, jackal rabies outbreaks approached or crossed the *C. adustus* and sympatric zone divide. In 1982 and 1991 epidemics moved northeast from the Midlands area into the *C. adustus* zone northeast of Chegutu, while in five other instances outbreaks have moved from the Harare area southwards or from the Marondera area westwards. In all instances, the outbreaks dissipated around the boundary between the zones, with few cases reported up to 30 km beyond. No instance was reported where the prevalence of jackal rabies increased after crossing the boundary.

DISCUSSION

In order to study the role of the two jackal species in the epidemiology of rabies, jackal rabies cases were classified according to species zones. As most of the *C. adustus* zone cases fell outside the *C. mesomelas* distribution, almost all are likely to have been *C. adustus*. This was found to be the case when jackal cases were identified accurately, as around Harare between 1990 and 1996. Cases in the *C. mesomelas* zone, however, might not necessarily all have been *C. mesomelas* as most of this zone has the two species occurring in sympatry. But given that *C. mesomelas* are more common in their zone, most of the rabies cases from this zone are likely to have been in this species. This was found to be the case in one study where the jackals involved were reliably identified (Foggin 1988).

Jackal rabies reported in the *C. mesomelas* and sympatric zones has been of lower density than that reported in the *C. adustus* zone (Fig. 3). This may be caused to a large extent by lower surveillance coverage in the *C. mesomelas* zone. Farming practices in much of the commercial farming areas of this zone consist mainly of extensive livestock ranching, with low labour input. Hence, reporting of cases is poor due to low human densities and large distances between farms and veterinary centres.

Protected areas do not appear to support rabies in jackals or other species. This is not due only to poor surveillance as it is considered that the large numbers of tourists and biologists would report at least some rabies cases should they occur there. Although surveillance differences between commercial and communal areas could account for some of the difference in reported cases of both jackal species between these landuse sectors, during the large jackal epidemics of the 1990s, by which time communal land surveillance had improved, the pattern was essentially similar with only 8,7 % of reported jackal cases originating from communal areas. The communal landuse sector supports a large dog population (Brooks 1990) which probably competes ecologically with jackals, hence resulting in low jackal densities in this sector.

Jackals of both species give birth to their young during September and early October (Bingham, unpublished data). Young jackals leave their dens and begin foraging by December. Seasonally-restricted breeding causes large seasonal fluctuations in the population density. The January to March peak in the *C. adustus* zone cases is therefore probably related to the high density of independent, mobile juveniles. The point of lowest frequency in October may be related to low adult population density. The July/August peak of the *C. adustus* zone and the June to September peak for the *C. mesomelas* zone may be associated with the increased contact rate between adult jackals during the breeding season. A similar breeding season peak in rabies prevalence occurs in the European red fox (*Vulpes vulpes*), although this species does not have any summer peak corresponding to the emergence of young foxes (Blancou, Aubert & Artois 1991; Aubert 1992). In the outbreaks of the 1960s and 1980s high prevalence of jackal rabies from the *C. adustus* zone occurred from January to August, with what appears to be two peaks (Fig. 5). This suggests that these outbreaks were maintained by contacts caused by both high juvenile densities and breeding season interactions. In contrast, the outbreaks of the 1990s have a more pronounced January to April peak than a breeding season peak, indicating that recent *C. adustus* outbreaks were maintained mainly by high juvenile densities.

This study has demonstrated that young adult *C. adustus*, i.e. those approximately one year of age,

appear to suffer from rabies less frequently than jackals in all other age categories, both younger and older. Yearlings constitute a markedly lower proportion of rabid red foxes than older foxes (Wandeler, Wachendorfer, Forster, Krekel, Schale, Muller & Steck 1974; Artois & Aubert 1982). Wandeler et al. (1974) hypothesize that this may be because young foxes have lower contact rates with rabid individuals. Similar mechanisms may operate in jackals: juveniles, sub-adults and adults may have greater contact with one another through social affiliative or antagonistic interactions, whereas young adults, which are more independent of their family groups and are less likely to have home ranges to defend, have fewer social interactions. They are therefore less prone to contracting rabies.

As jackal cases from the C. adustus zone were the dominant, and sometimes the only reported carnivore cases within outbreaks and were more often preceded by the disease in other jackals rather than in dogs, it appears that jackals play the dominant if not the only role in maintaining C. adustus outbreaks. Within jackal outbreaks, rabies in dogs and other animal species appears to be spill-over from the disease in jackals. This does not, however, indicate how jackal rabies outbreaks are initiated. Are they initiated by other species, or by jackal cases which occur at levels too low for detection?

As there were dog or jackal cases preceding all but one of the major outbreaks studied, it is reasonable to assume that these species initiated the outbreaks. Dog cases appear to have initiated at least eight of 13 foci of jackal rabies. Foci of jackal rabies may spread to establish other geographically-distinct jackal rabies epidemics. There was only one instance where an outbreak was not preceded by either dog or jackal cases and this was in the outbreak that started near Mount Darwin in 1979. This, however, was during a period of civil unrest and the surveillance structure was not functioning in many areas (Lawrence, Foggin & Norval 1980), particularly in this instance where the initial focus was remote. As all 13 outbreak foci examined were within the C. adustus zone, it is unlikely that C. mesomelas initiated these outbreaks.

The rate of front movement is thought to be influenced mainly by vector home range size and not by vector density (Toma & Andral 1977). Hence, dense populations with small home range sizes will have dense but slow-moving epidemics, due to the braking effect of the vector's sedentary social structure combined with the relatively long incubation period of the disease. Itinerant vectors which do not have fixed home ranges may transmit the disease faster, although they are thought not to have any effect on the overall front movement (Blancou et al. 1991). Interestingly, while the rates of front movement of the

jackal epidemics of the 1960s and the 1990s were similar and remarkably like those of the red fox rabies in Europe, which is 30–60 km per year (Toma & Andral 1977), that for the epidemic of the 1980s was considerably faster. There is no obvious explanation for this as there has been no change in land management practices which may be expected to affect home range sizes.

Most of the jackal cases analysed in this study occurred during primary disease waves. Subsequent waves (secondary, tertiary) occurred during the outbreaks of the 1990s and during the 1980s outbreak of Mashonaland East. Unlike the primary waves, which occurred after a long absence of the disease, subsequent waves usually occurred after a lull period of about 1–3 years. In addition, cases within subsequent waves were of lower density than of the primary wave; they occurred over dispersed areas simultaneously; and they did not begin from a single focus and spread as a front.

Although data from the C. mesomelas zone is more sparse than that from the C. adustus zone, it is sufficient to determine that C. mesomelas can maintain rabies independently of other species. Dense outbreaks of rabies can occur in C. mesomelas populations, as evidenced by active surveillance, albeit in a small area, carried out in the Mwenezi District in the southeast of the country. In this instance it is unlikely that any other host was responsible for the maintenance of the outbreak, particularly as jackals were the most frequently diagnosed carnivore species and they were the first cases reported. The pattern of jackal and dog prevalence in the 100 x 100 km blocks implies that the two species had rabies cycles which are largely independent of each other, with the disease in either species preceding it in the other. There were frequent occurrences where the rate of jackal rabies exceeded that of rabies in dogs, despite the expected more efficient detection of dog rabies.

From the data available, it was not possible to determine the geographical origin of C. mesomelas rabies outbreaks. Unlike the data from the C. adustus zone, data from jackal outbreaks in the C. mesomelas zone is too scanty to determine trends with accuracy. Given the epidemic nature of some of the reported outbreaks, it is likely that they progress from foci. Although front movement was detected in some outbreaks, for example those of the Midlands, this movement could not be traced back to defined foci or index cases as in the case of C. adustus outbreaks.

Rabies outbreaks do not appear to cross the jackal species interface. The observation that outbreaks decline at the interface is not likely to be a surveillance artifact as the landuse pattern, which would

ensure consistency of reporting, on either side of the boundary was similar. Evidently transmission between the two jackal species does not happen readily, perhaps due to low inter-specific contact or to the pathogenetic response of the different jackal species to the virus strains.

In conclusion, the epidemiology of rabies in jackals can only be understood through consideration of the spatial dynamics of the disease. Such considerations have been neglected in recent attempts to model epidemics mathematically (Cleaveland & Dye 1995; Rhodes, Atkinson, Anderson & Macdonald 1998). Rabies in *C. adustus* occurs as dense epidemics, which begin at a single focus and spread centrifugally. The foci are initiated by rabid dogs, but once initiated the epidemic is maintained by *C. adustus* independently of other species. The epidemics terminate after expanding to geographical limits which correspond roughly with the limits of the commercial farming area. Wide communal areas, protected areas and the jackal inter-species zone interface act as barriers to the further progression of the epidemics. As the infected jackal populations are reduced by rabies to below the threshold density for rabies propagation, the number of cases may either decline to zero, as during the 1980s, or may continue with a seasonal prevalence, as after 1995. Dogs, in which rabies has been present continuously over most areas of the country since 1950, have been long-term maintenance hosts of rabies, maintaining the disease over periods when it has been absent in the *C. adustus* population and re-introducing it when jackal populations again reach threshold densities.

The dense epidemics of jackal rabies are a threat to both human and animal health. The epidemics may be effectively controlled through oral vaccination (Bingham, Schumacher, Hill & Aubert 1999), whereby vaccine placed into baits is consumed by jackals. However, without effective rabies control in domestic dogs, the threat of re-introduction of the disease into jackal populations will always be present. Long-term control of rabies in jackals will not be effective unless dog populations are properly immunized.

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