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The historic ranges of three equid species in north-east Africa: a quantitative comparison of environmental tolerances

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Abstract. The historic ranges of three equid species native to north-east Africa are analysed with respect to annual rainfall, several temperature parameters and a satellite-derived multispectral index of primary productivity. *Equus africanus* Fitzinger, *Equus grevyi* Oustalet and *Equus burchelli* Gray used to largely replace each other, geographically, with narrow zones of range overlap occurring between *E. africanus* and *E. grevyi* in the Awash valley, and between *E. grevyi* and *E. burchelli* in southern Ethiopia and northern Kenya. The three species are shown to succeed each other along an environmental gradient. The position of each species on this gradient and the resulting location and extent of its range are discussed. Competitive exclusion, specific adaptations and historic events are likely determinants of equid distribution. In the area of sympatry between *E. grevyi* and *E. burchelli*, mixed habitat characters as well as environmental fluctuations seem to prevent either species from excluding the other. Different social organizations of *E. grevyi* and *E. burchelli* and the resulting migratory patterns may be adaptations to the environment in their allopatric ranges; in their sympatric range they could alleviate competition.

Key words. Wild ass, Grevy's zebra, Burchell's zebra, vegetation index, north-east Africa, NOAA-AVHRR.

INTRODUCTION

Three equid species are native to an area of north-east Africa extending over the modern countries of Somalia, Ethiopia and Kenya. Within this region, the historic ranges of the African Wild ass (*Equus africanus* Fitzinger, 1857), Grevy's zebra (*Equus grevyi* Oustalet, 1882) and Burchell's or Common zebra (*Equus burchelli* Gray, 1824) used to succeed each other roughly from north to south. They were largely allopatric ranges, but narrow zones of sympatry occurred between *E. africanus* and *E. grevyi* in the Awash valley (at the northern end of the Great African Rift) and between *E. grevyi* and *E. burchelli* in an area extending from the southern end of the Ethiopian part of the Rift and along Lake Turkana to the edge of the Eastern Highlands far into Kenya.

Several authors have made efforts to reconstruct the historic ranges of some or all of the three species (Kingdon, 1979; Sidney, 1965; Yalden, Largen & Kock, 1986). Their published maps, however, show little agreement in detail, a fact which reflects the difficulties involved. Figures 1–3 are an attempt at a 'conservative estimate': they show individual records from the literature to which geographic coordinates could be assigned with some degree of certainty.

The present distributions of at least *E. africanus* and *E. grevyi* bear little resemblance to these maps, as anthropogenic influences have led to marked contractions of their ranges since the last century. *E. africanus* is critically endangered; the IUCN estimates that there may only be a few hundreds of individuals left in the wild (Moehlman, 1992). *E. grevyi* is also classed as endangered; it is now probably restricted to the southern part of its former range, and even here its numbers have declined severely in recent years; there may remain only 5000 in Kenya and a few in Ethiopia (Rowen & Ginsberg, 1992). Initial declines were probably due to hunting, but more recently the principal cause has often been competition with livestock and people for space, food and water (Fisher, Simon & Vincent, 1969; Klingel, 1974; Clark, 1983; Yalden *et al.*, 1986; Duncan, 1992). *E. burchelli* is still common in Kenya today, but there may be only 2000 left in Ethiopia (Duncan & Gakahu, 1992).

Climatically, north-east Africa is characterized by a decrease in temperature and aridity from north to south: *E.*

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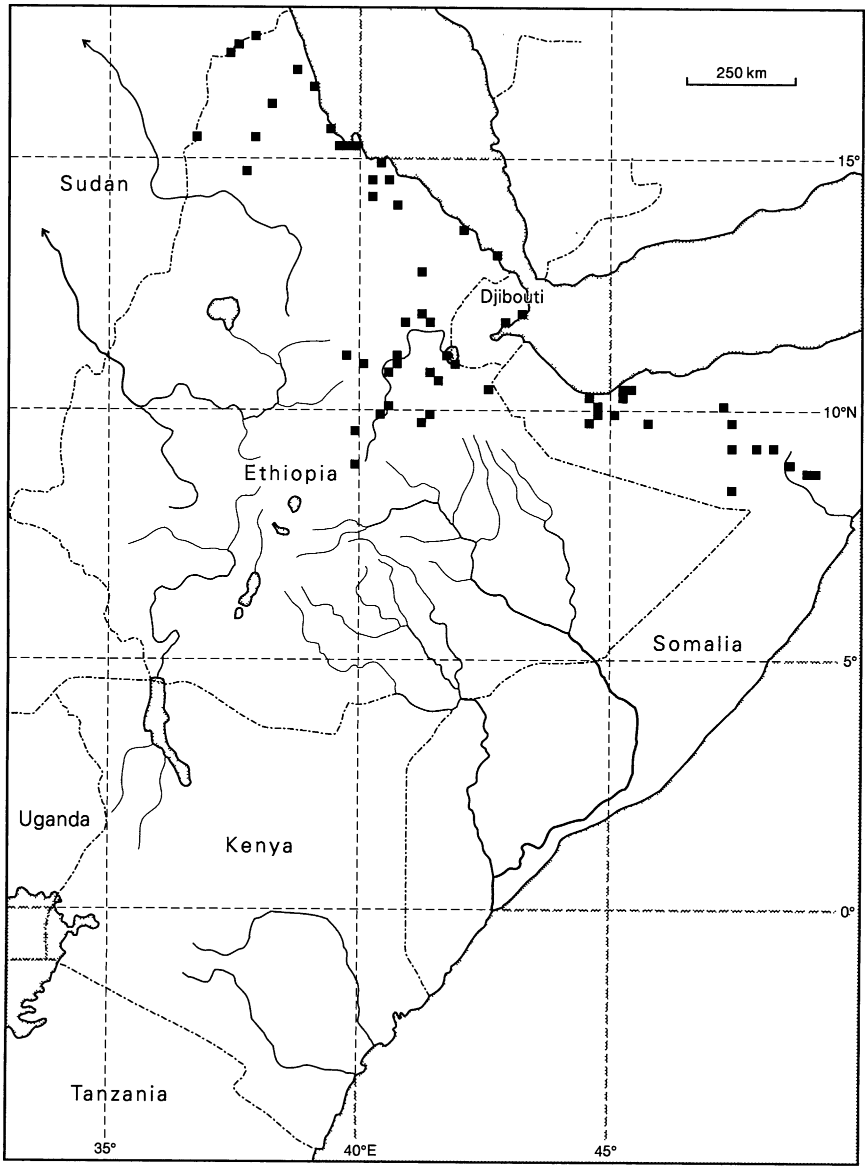

FIG. 1. Recorded distribution of *E. africanus* Fitzinger in north-east Africa.

africanus is an animal of desert country whereas *E. grevyi* occurs in semi-arid areas and *E. burchelli* is a member of the East African grassland fauna (e.g. Keast, 1965; Kingdon, 1979; Yalden *et al.*, 1986). The different habitat preferences of the three species are likely to arise from differences in their biology, but experimental data are scarce, and the precise mechanisms of niche separation, particularly between the two zebra species, are controversial.

Physiological adaptations to an arid climate have been experimentally demonstrated in *E. africanus* (Maloiy, 1970, 1971; Maloiy & Boarer, 1971) and different tolerances to temperature, aridity or the concomitant changes in food availability have also been observed or implied for the two zebras (Klingel, 1974; Foose, 1972 in Ginsberg, 1988; Ginsberg, 1988). There is no agreement about the adaptive significance of differences between the social systems of *E. grevyi* and *E. burchelli* (Klingel, 1974; Ginsberg, 1988), with Klingel even claiming that the social system of *E. grevyi* is maladaptive in its semi-arid habitat.

A quantitative comparison of the historic ranges of *E. africanus, E. grevyi* and *E burchelli* in terms of several environmental attributes such as precipitation, temperature and different vegetation parameters should enable us to define the precise habitat tolerances and preferences of each of the species, and might also provide some clues about mechanisms of competition and niche separation.

METHODS

Animal distribution maps

The distribution maps of *E. africanus, E. grevyi* and *E.*

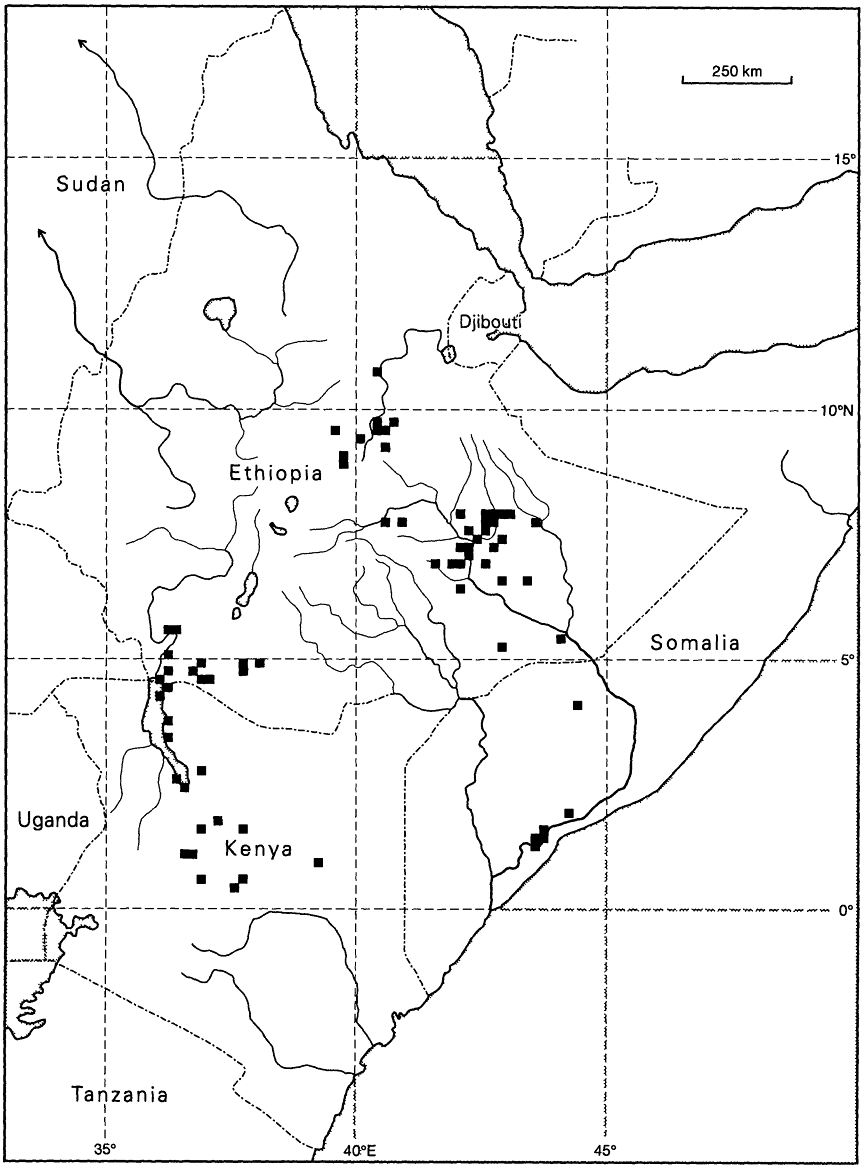

FIG. 2. Recorded distribution of *E. grevyi* Oustalet in north-east Africa.

burchelli were prepared by recording their presence in a 10-minute grid over Ethiopia, Kenya and Somalia (Figs 1–3).

For Ethiopia, recorded sightings listed in Yalden *et al.* (1986) were used. The geographical coordinates for these were taken from EWCO (1989).

For Kenya, records listed in Sidney (1965) were used, provided that their exact geographical location could be determined with reasonable confidence using the *Atlas of Kenya* (Butler, 1959). If a reference was to an area rather than to a point, the mid-point of this area was used. If a reference was to a linear feature, a point midway along this was used unless the feature itself was too long to make such an approach reasonable.

In Somalia, recorded points from the maps of Funaioli & Simonetta (1966) were used, as well as sightings listed in Yalden *et al.* (1986).

Climatic data sets

Raster image maps of climatic, topographic and vegetation parameters of Africa were available in an experimental data base compiled for the *Global Change Database Project, Pilot project for Africa, Version 1.0* (Eastman *et al.*, 1990; Kineman *et al.*, 1990)[1]. The data layers chosen had a spatial resolution of 30 or 10 minutes latitude and longitude, equivalent to approximately 50 and 17 km ground resolution at the equator, respectively. The climatic layers used were as follows:

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[1] Now available from National Geophysical Data Center, Boulder, Colorado as the 'Global Change Educational Diskette Project', price approximately US $150.

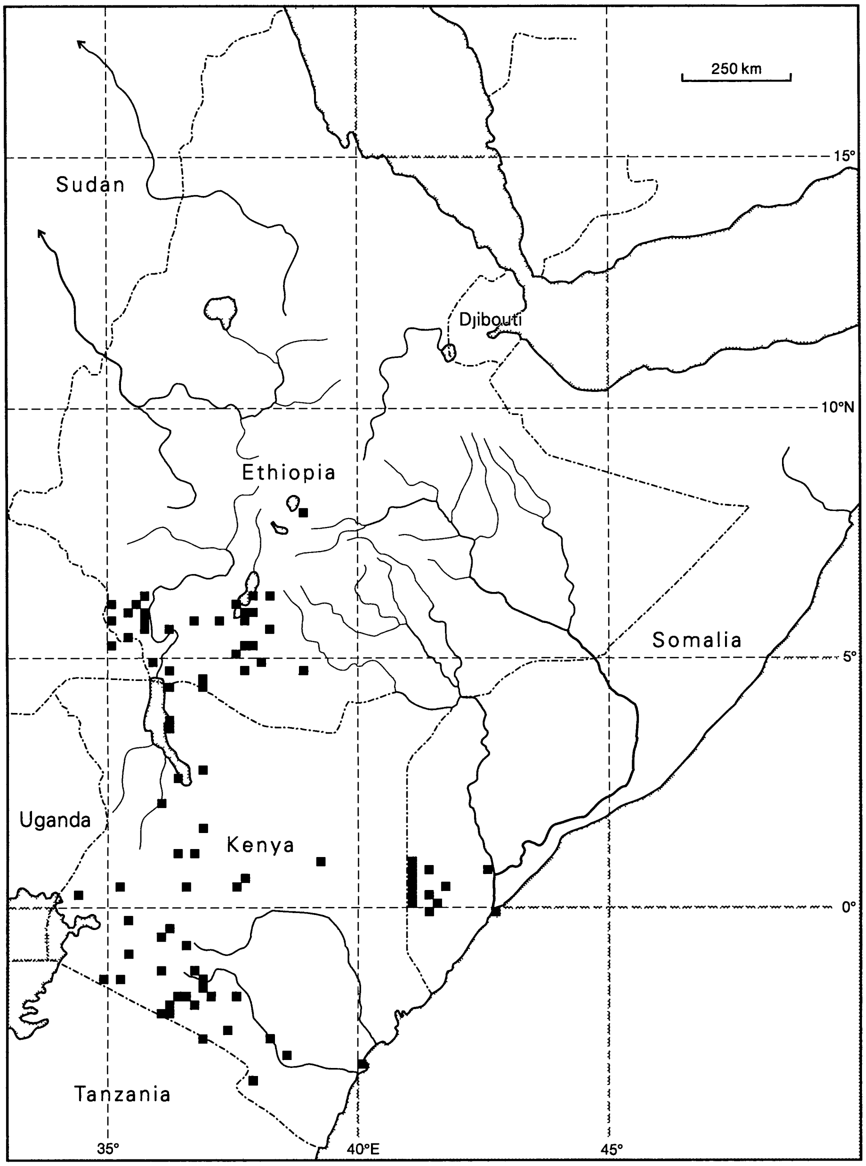

FIG. 3. Recorded distribution of *E. burchelli* Gray in north-east Africa.

- Annual measured precipitation (Legates & Willmott, 1989, 1990)
- Annual average air temperature (Legates & Willmott, 1989)
- Mean temperature of the hottest month of the year (Legates & Willmott, 1989)
- Mean temperature of the coldest month of the year (Legates & Willmott, 1989)

The precipitation data set had been compiled from corrected rain gauge readings for variable periods of record, largely between 1920 and 1980. These irregularly distributed records have been interpolated to a 30×30 minute latitude/longitude grid using a spherically based interpolation algorithm as described in Legates & Willmott (1990). The temperature data were compiled in a similar manner.

Two other data layers were initially included in the analysis: elevation (Kineman, 1985) and Olson's *World Ecosystems* (Olson, 1989). Elevation was later excluded because of its strong causal connection to both temperature and precipitation, both of which are likely to have more direct effects on animal distributions in north-east Africa. Olson's ecosystem data is designed primarily for studies at global scales. The ecosystem categories were found to be too coarse for this more regional study.

Satellite-derived vegetation index

The monthly vegetation index images in the African data base are derived from the Global Vegetation Index (GVI) product compiled weekly by the National Oceanic

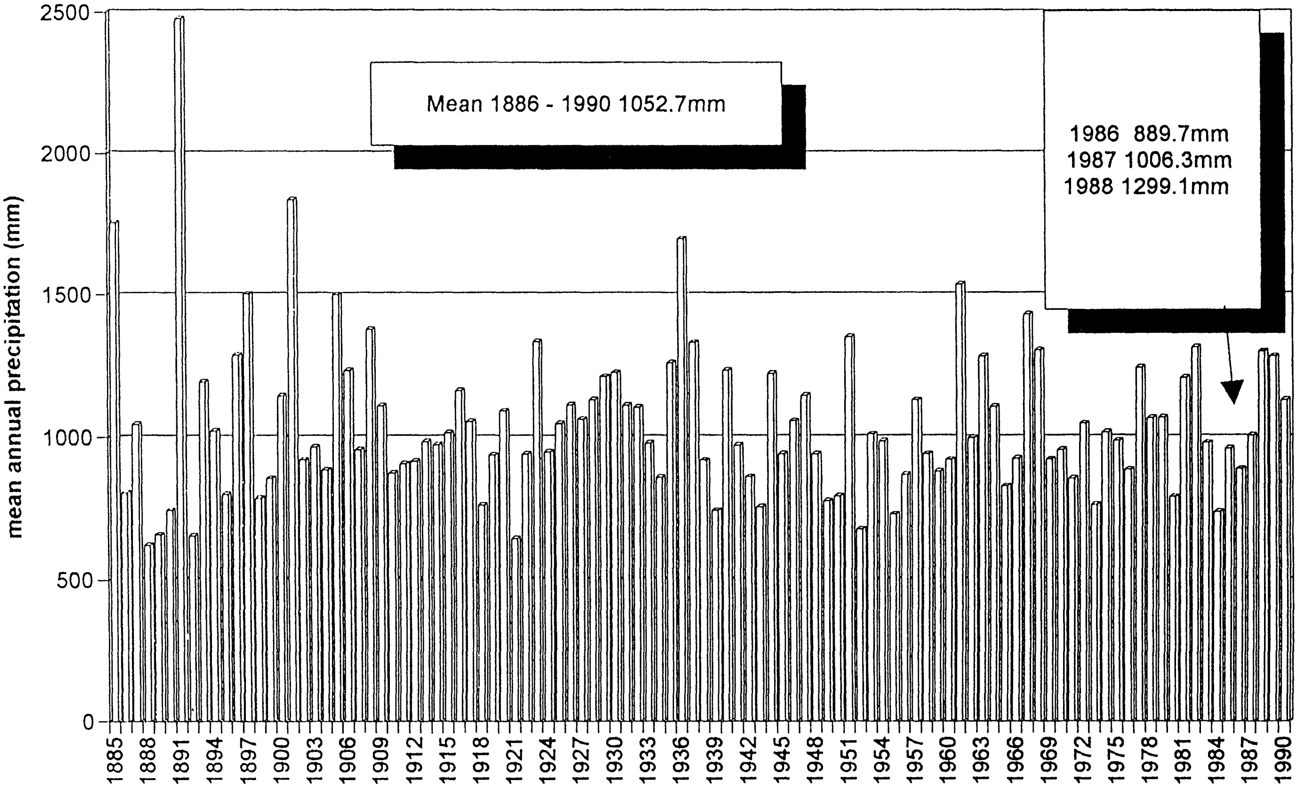

FIG. 4. E. Africa mean annual precipitation (mm) 1886–1990.

and Atmospheric Administration (NOAA). The GVI represents a spatial and temporal composite of Normalized Difference Vegetation Index (NDVI) data derived from channels 1 and 2 of the Advanced Very High Resolution Radiometer (AVHRR) aboard NOAA weather satellites.

$$\text{NDVI} = (\text{near infrared channel} - \text{red channel}) / (\text{near infrared channel} + \text{red channel})$$

For inclusion into the African data base the weekly GVI images had been further temporally averaged and resampled to a 10-minute resolution for registration with other layers in the data set. A full description of the processing is given in Kineman (1989). The result is a highly derived product, but one which is broadly indicative of the monthly vegetation activity.

The use of NDVI as a means of obtaining a relative measure of primary productivity from space is somewhat controversial. In arid rangelands, background effects from soils (Huete, 1988), scattering of radiation from senesced vegetation (Huete & Jackson, 1987) and a lack of sensitivity below a certain, very low, vegetation cover (Box, Holben & Kalb, 1989; Kennedy, 1989) are problematic.

In spite of these limitations, however, the NDVI has been extensively used in arid areas. Applications include the monitoring of the entire desert locust recession area by the Food Aid Organization (FAO) (Hielkema, 1990), the monitoring of rangelands and drought early warning (Cracknell, 1986). Justice *et al.* (1986) compared an image of annual integrated NDVI of Kenya, Uganda and Tanzania with recent vegetation maps published for the same area and found that, in arid and semi-arid areas which are strongly dependent on local rainfall, the vegetation index is a more reliable indicator of current vegetation condition than any published map.

Of the forty-five images available, thirty-six were used, covering the period from January 1986 to December 1988. Inspection of mean annual precipitation data from the World Climate Data Disk (1992) for Ethiopia, Somalia and Kenya showed that, relative to the long-term average between 1885 and 1990, the year 1986 was slightly drier, 1987 was average and 1988 was slightly wetter (Fig. 4). Thus, the 3-year sample was relatively representative with respect to mean annual precipitation and presumably, since water availability is usually the main factor limiting vegetation productivity in north-east Africa, with respect to yearly productivity.

Idrisi, a grid-based geographic analysis system (Eastman, 1990, 1992), was used to process and analyse the images. The monthly vegetation index images were further processed in two ways. First, a time series file was con-

TABLE 1. Habitat variables for the localities at which the three equids have been recorded. Though median values are all significantly different (Meddis, 1984), the ranges of values overlap extensively.

	Sample size (*n*)	Minimal value	Maximal value	Median	Rank mean	*Z*	*P*
Mean annual precipitation							
E. africanus	60	40 mm	1205 mm	337 mm	66.8		
E. grevyi	71	261 mm	1318 mm	698 mm	109.5	7.236	0
E. burchelli	84	261 mm	1709 mm	860 mm	136.1		
Average annual temperature							
E. africanus	60	17.53°C	29.96°C	24.47°C	131.9		
E. grevyi	71	14.98°C	28.6°C	22.63°C	107.9	4.039	0.00008
E. burchelli	84	15.08°C	28.95°C	20.95°C	91.1		
Mean temperature of hottest month							
E. africanus	60	20.8°C	35.8°C	27.3°C	144.1		
E. grevyi	71	16.0°C	31.4°C	24.2°C	101.9	5.378	0
E. burchelli	84	16.3°C	32.0°C	22.3°C	87.4		
Mean temperature of coldest month							
E. africanus	60	14.9°C	25.8°C	21.3°C	115.3		
E. grevyi	71	13.3°C	27.0°C	21.0°C	114.3	1.885	0.02947
E. burchelli	84	13.7°C	27.0°C	19.6°C	97.5		
NDVI							
E. africanus	60	451	3639	1346	59.6		
E. grevyi	71	626	3735	2174	107.3	8.326	0
E. burchelli	84	1000	4207	2775	143.1		

structed showing seasonal changes in vegetation index, or vegetation phenology, at grid squares where the different equid species had been historically recorded. Secondly, an accumulated vegetation index image was created by addition of all thirty-six monthly images in order to assess overall vegetation productivity over the sample 3-year period.

Data extraction

Extracts of the study area were made from each of the

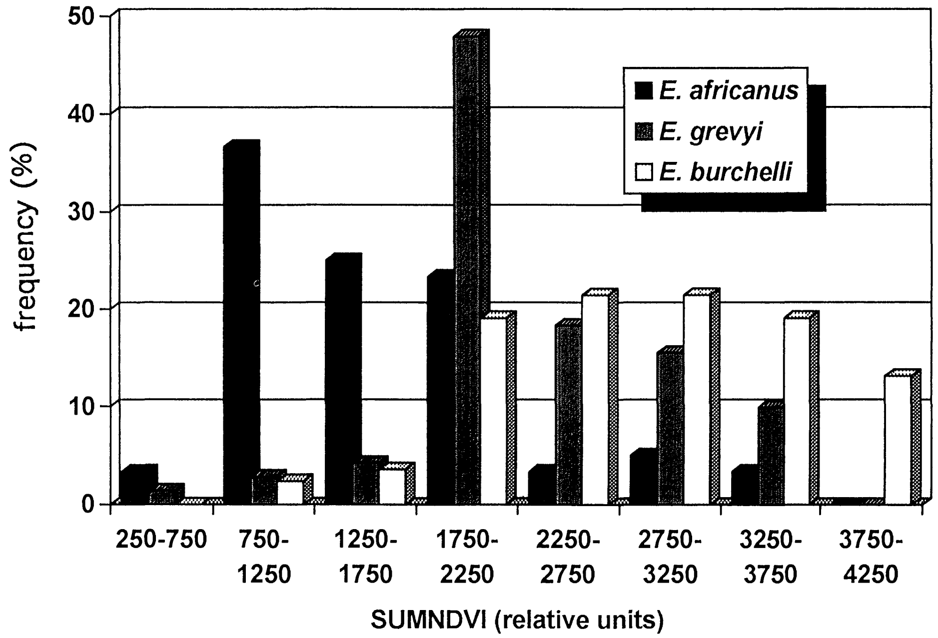

FIG. 5. Frequency distribution of sites for *E. africanus* Fitzinger, *E. grevyi* Oustalet and *E. burchelli* Gray over the total range of accumulated vegetation index values observed.

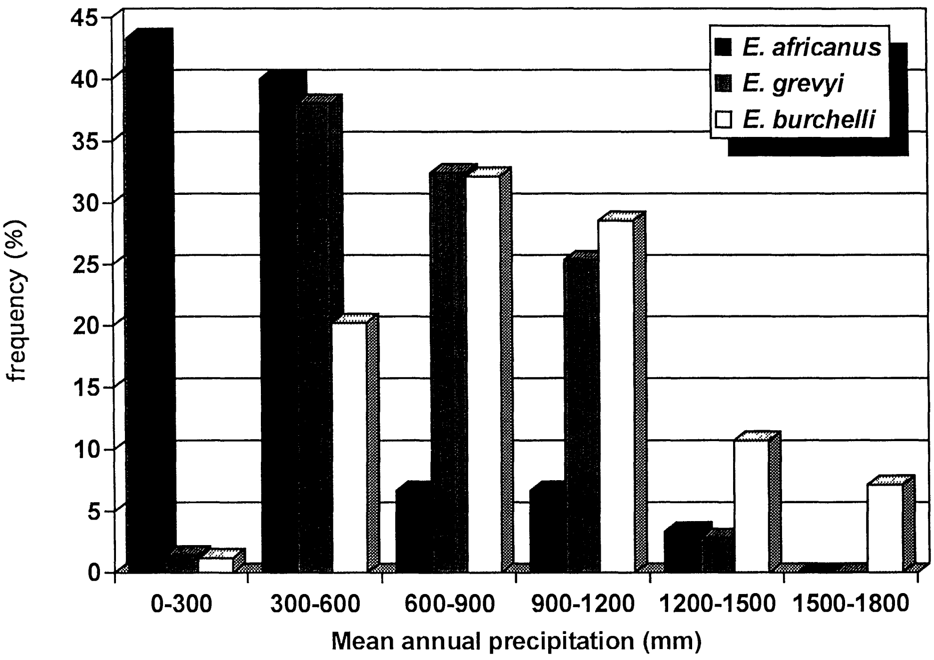

FIG. 6. Frequency distribution of sites for *E. africanus* Fitzinger, *E. grevyi* Oustalet and *E. burchelli* Gray over the total range of mean annual precipitation values observed.

environmental data sets. These new climate and vegetation images had geographic coordinates of 18°50′N, 30°00′E at the north-west corner, and 05°30′S, 51°50′E at the south-east corner.

Species distribution images were created from the distribution maps by digitising points equivalent to the centre of each 10-minute grid square in which sightings had been recorded and then converting the vector files into a series of raster images. These images were used as templates to extract values from the environmental data layers. Data extraction was first performed for the complete ranges of the three species. Subsequently, records for the sympatric and allopatric ranges of *E. grevyi* and *E. burchelli* were examined separately in order to define conditions under which the two species are able to co-exist, and to contrast these with conditions in their allopatric ranges.

Non-parametric statistics from Meddis (1984) were applied to compare data from the localities for each species.

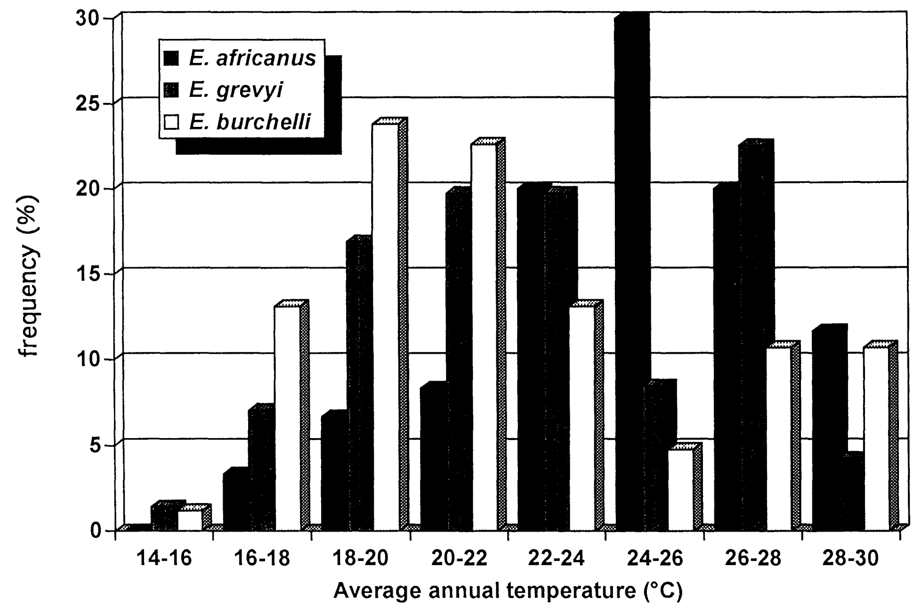

FIG. 7. Frequency distribution of sites for *E. africanus* Fitzinger, *E. grevyi* Oustalet and *E. burchelli* Gray over the range of average annual temperature values observed.

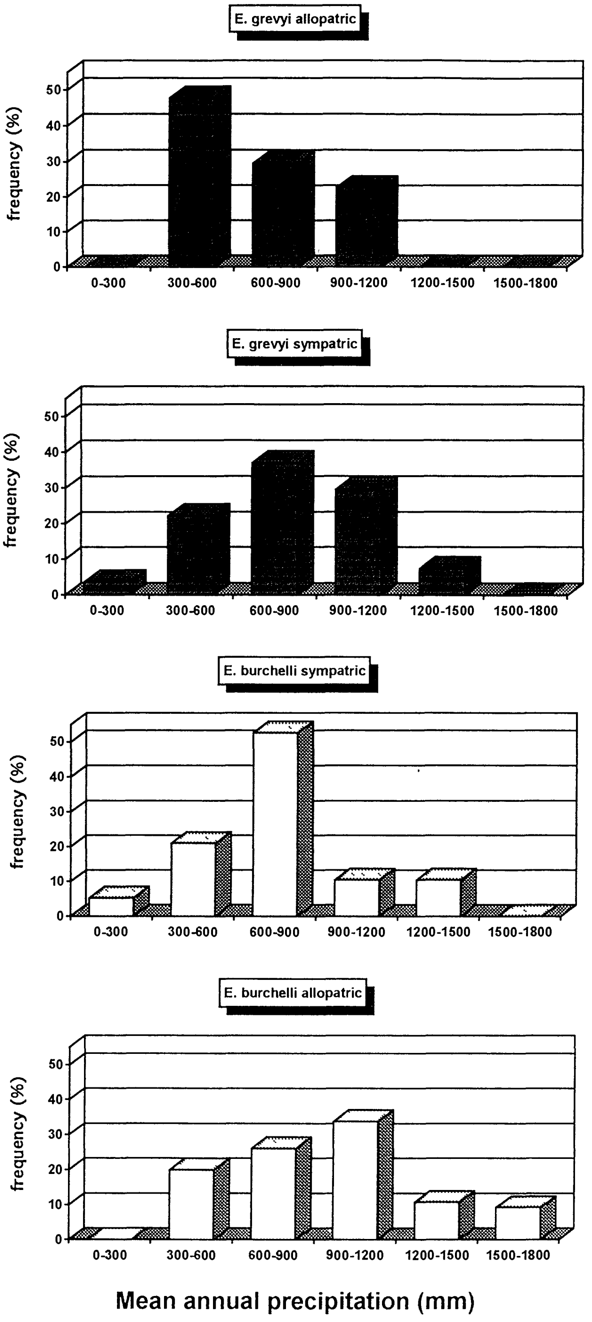

FIG. 8. Average temperature of the hottest month of the year in the allopatric and sympatric ranges of *E. grevyi* Oustalet and *E. burchelli* Gray.

RESULTS

Complete ranges

The analysis demonstrated significant differences between the ranges of *E. africanus, E. grevyi* and *E. burchelli* (Figs 1–3) with regard to annual precipitation, temperature and accumulated vegetation index: as expected there is a gradient in climate and food availability from hot, dry conditions and low vegetation index values in the range of *E. africanus*, via an environment of intermediate character in the range of *E. grevyi*, to relatively cool conditions with more annual rainfall and higher vegetation index values in the range of *E. burchelli* (Table 1).

Within each environmental variable examined there is a strong overlap between *E. africanus, E. grevyi* and *E. burchelli* in terms of the absolute range of the variable that can apparently be tolerated; the three species contrast primarily in their relative preferences for different parts of this tolerated range.

The frequency distribution of sites for *E. africanus* is of a markedly skewed shape over both the vegetation index and preciptation data, with values accumulating in each case close to the low end of the species' tolerance spectrum (Figs 5 and 6). *E. grevyi* and *E. burchelli* show bimodal distributions in all three sets of temperature data (e.g. Figs 7 and 8).

Sympatric/allopatric comparisons

Comparison of records of *E. grevyi* and *E. burchelli* from their sympatric range revealed no significant differences between the habitat preferences of the two species in this area. In the sources used for this study there are frequent records of both species from the same location within the area of range overlap, and the animals are known to form seasonal mixed herds (Keast, 1965; Klingel, 1974); the lack of demonstrable differences is therefore not surprising.

There are, however, several significant differences between records from the sympatric and allopatric ranges of both *E. grevyi* and *E. burchelli* (Table 2).

Precipitation. The allopatric range of *E. grevyi* receives a significantly lower amount of annual rainfall than the area in which the species is sympatric with *E. burchelli* (Fig. 9). No statistical differences in the amount of annual rainfall received could be demonstrated between records from the sympatric and allopatric ranges of *E. burchelli*. The shape of the two lower charts, however, suggests that this failure to demonstrate significant differences could in part be a reflection of limited sample size. Meddis, as other non-parametric tests, is not as sensitive as comparable parametric methods, and the use of a larger sample would be desirable.

The records of *E. grevyi* from the sympatric zone are spread over a wider range of values than those from the much larger allopatric zone, indicating that areas used in the overlap zone are more diverse with respect to precipitation than those utilized in the allopatric range of this species.

Accumulated vegetation index. Records from the allopatric range of *E. burchelli* showed higher values of accumulated vegetation index than those from the overlap zone (Fig. 10), whereas statistically the entire range of *E. grevyi* is uniform with respect to this variable.

Areas used in the sympatric zone show a wider range of

TABLE 2. Habitat variables compared for sites at which the two zebra species occur either separately or sympatrically.

	E. grevyi				*E. burchelli*			
	Sample size (n)	Rank mean	*Z*	*P*	Sample size (n)	Rank mean	*Z*	*P*
Mean annual rainfall								
sympatric	27	41.6	2.091	0.01813	19	38.4	0.956	NS
allopatric	44	32.5			65	43.7		
Average annual temperature								
sympatric	27	30.8	1.733	0.04132	19	39.2	− 0.717	NS
allopatric	44	39.2			65	43.5		
Mean temperature of hottest month								
sympatric	27	30.0	1.971	0.02416	19	42.1	− 0.094	NS
allopatric	44	39.7			65	42.6		
Mean temperature of coldest month								
sympatric	27	34.1	0.640	NS	19	44.6	0.444	NS
allopatric	44	37.2			65	41.9		
NDVI								
sympatric	27	41.9	1.464	NS	19	28.9	2.952	0.00181
allopatric	44	35.0			65	46.5		

accumulated vegetation index values than those which are utilized by either species in its allopatric range; it is this overlap area in which both species get closest to their apparent tolerance minimum (Fig. 10). The similarity in the shape of the bar charts between Figs. 9 and 10 reflects the strong link between the amount of rainfall and vegetation abundance in north-east Africa.

Temperature. Of the three variables examined, only two yielded significant differences: average annual temperature and mean temperature of the hottest month (MTHM) are higher in the allopatric range of *E. grevyi* than they are in areas used by this species in the zone of range overlap. No significant differences were found in these parameters between the sympatric and allopatric ranges of *E. burchelli*.

All three temperature variables are of course strongly interrelated, but they differ in their importance: in north-east Africa the average temperature of the coldest month (MTCM) is unlikely to have a limiting effect (the lowest value obtained for either of the two species was 13.3°C in the allopatric range of *E. grevyi*). High temperatures, however, particularly in combination with low rainfall, could be strongly limiting. It is therefore not surprising that the differences between the sympatric and allopatric ranges of *E. grevyi* are most significant in the MTHM data (Fig. 8).

Phenology

The fluctuations of monthly vegetation index values (January 1986–December 1988) in the ranges of *E. africanus, E. grevyi* and *E. burchelli* are shown in Fig. 11. All three curves are moving in phase (Meddis correlation/concordance: Kendall's $W = 0.65681$, $H = 68.97$, $P = 0.00074$), with peaks in May and December 1986, April–July 1987, December 1987 and May 1988. Productivity within the range of *E. africanus* is lower and more consistent, whereas it is higher and more variable for the two zebras.

DISCUSSION

General considerations

There are two possible extreme explanations for the largely allopatric character of the historic ranges of *E. africanus, E. grevyi* and *E. burchelli*: competitive exclusion between species too similar to co-exist; or definite differences in habitat requirements, with each species being able to survive in its own range only, regardless of presence or absence of the other two. Slight adaptive differences between otherwise very similar species would allow for a number of intermediate scenarios, and the data obtained in this study, viewed in conjunction with information about the ecology of the animals concerned, can help to understand the actual processes at work in each case.

Our knowledge of the actual historic distributions of the three species, though imperfect and probably imperfectly represented by the 246 recorded sightings considered in this study, covers their overall geographical ranges in north-east Africa quite well. The images of animal distributions used may therefore be assumed to provide adequate coverage of the geographic attributes selected for analysis. The overlap between species is, surely, real, and better geographical knowledge would not alter this. More ecological knowledge might, if, for instance, the

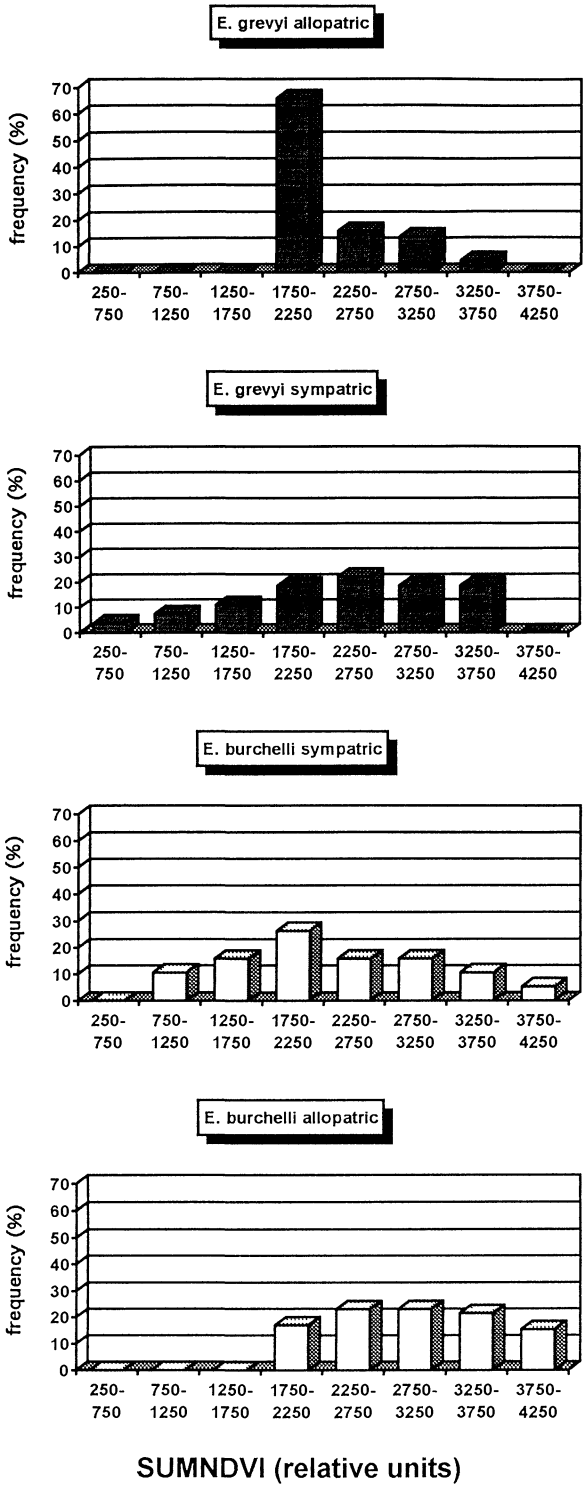

FIG. 9. Mean annual precipitation in the allopatric and sympatric ranges of *E. grevyi* Oustalet and *E. burchelli* Gray. The arrangement of bar charts from top to bottom is a reflection of the most logical arrangement of the four different animal groups along the expected environmental gradient and roughly corresponds to a move from north to south.

different species separate during dry seasons, have different breeding seasons or behave differently with respect to shade or water.

Morphologically, *E. africanus, E. grevyi* and *E. burchelli* are very similar (Forsten, 1992). The same is true for some of their basic resource requirements: all three species need access to drinking water and suitable pasture. To our knowledge, only the diet of *E. burchelli* has been studied in detail in the field (e.g. Lamprey, 1963; Gwynne & Bell, 1968; Bell, 1971; Owaga, 1975). The species feeds almost exclusively on grass, taking different species essentially in the proportion in which they are available in the pasture. The animal can also be described as a bulk feeder selecting its pasture on the basis of food quantity rather than quality, as is indicated by a selectivity for sheath and stem rather than leaves. This strategy is largely a result of digestive morphology: *E. burchelli* is much more tolerant of high amounts of cellulose in its diet than a ruminant of comparable size, but it has to maintain a high intake of this type of food in order to meet its protein requirements.

Having the same digestive morphology, the other two species are likely to have similar feeding strategies; the information that is available suggests that both, like *E. burchelli*, feed largely or even exclusively on grass (Klingel, 1972, 1974; Ginsberg, 1989). One author has reported wild *E. africanus* to browse if pasture conditions are poor (Menges, 1887 in Klingel, 1974) and Moehlman (1992) says the same for feral donkeys, but it seems justified to argue that under normal circumstances all three species exploit the same food source in a similar way. Thus, dietary competition should be intense.

E africanus and E grevyi. In the case of these two species, which have very similar social systems (Klingel, 1974, 1977; Moehlman, 1992) and lack obvious differences in their pattern of resource utilization, geographical separation is probably the only way of alleviating the competition between them. The marked skew in the distribution of *E. africanus* records over the precipitation and accumulated vegetation index data suggests that physiological adaptation of this species to arid conditions, including a labile body temperature, an ability to reduce evaporative water loss when dehydrated, and tolerance of a loss of 30% of its body weight (Maloiy, 1970, 1971; Maloiy & Boarer, 1971), is a key factor, conferring on it a competitive advantage over *E. grevyi* in the extreme environment of northern Ethiopia and Somalia.

The environmental parameters examined in this study give no indications of the mechanisms enabling *E. grevyi* to outcompete *E. africanus* in all but the most marginal areas. Clearly, the competitive value of adaptations to extreme environments declines as the climate becomes cooler and wetter, but *E. grevyi* itself is not known to possess any specific adaptations to the climatic and vegetational conditions of its natural range which its northern competitor is lacking.

The historic order of arrival of the two species in northeast Africa might be another factor. The genus *Equus* evolved in North America, invading the Old World about 2.5 million years ago (Azzaroli, 1990). *Equus* has certainly been in Africa for 2 million years (Churcher & Richardson,

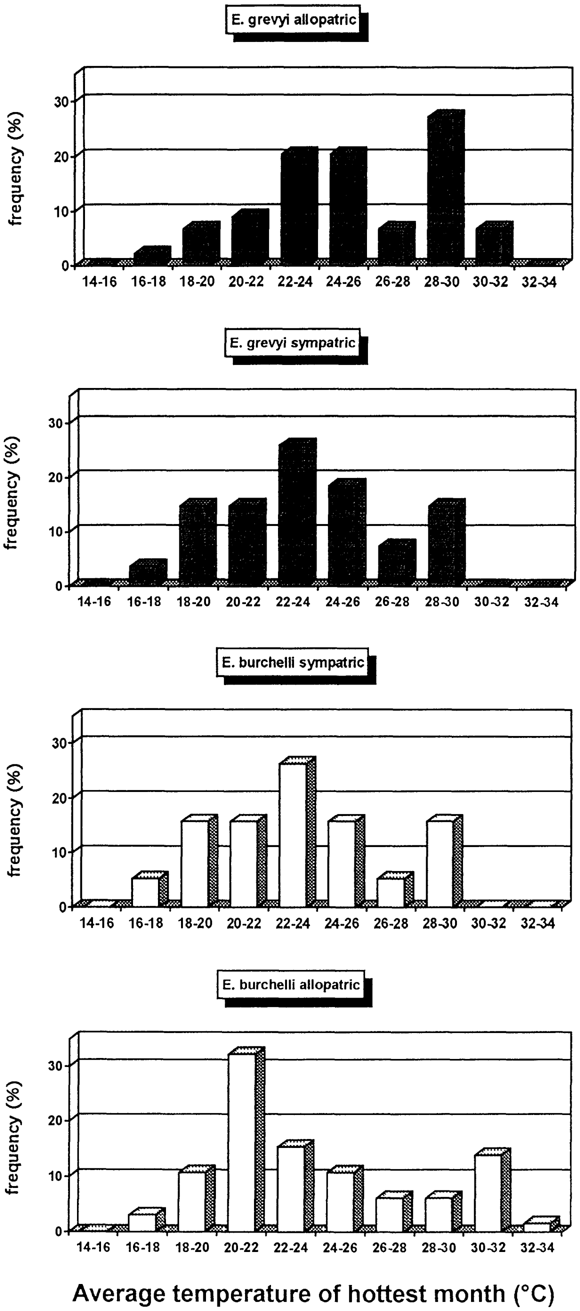

FIG. 10. Cumulative NDVI (January 1986–December 1988) in the sympatric and allopatric ranges of *E. grevyi* Oustalet and *E. burchelli* Gray.

1978; Eisenman, 1983) and the zebras probably evolved within Africa. However, there seems to be no fossil record of *E. africanus* in Africa prior to the late Pleistocene, and it seems possible that it invaded north-east Africa from Arabia in recent geological times. *E. grevyi* has certainly been present for >1 million years in north-east Africa (Marean & Gifford-Gonzales, 1991; Churcher, 1993). *E. asinus* may have managed to established itself only in areas which were so arid that its physiological adaptations outweighed any advantage that *E. grevyi* had by being already resident.

Another possible factor contributing to the failure of *E. africanus* to extend its range further south is parasite pressure: if stripes in zebras are a means of camouflage against *Glossina* flies (e.g. Reichholf, 1984), *E. africanus* could be prevented from extending its range into the tsetse belt because it lacks this defence against trypanosome infection. Other differences in the ecology of the two species yet unknown to us are, however, just as likely to be involved in determining range limits as the points mentioned here.

E. grevyi and E. burchelli. The data obtained by separate analysis of records from the allopatric and sympatric ranges of *E. burcelli* and *E. grevyi* suggest that the area in which their ranges overlap resembles climatically the allopatric range of *E. burchelli*, but it resembles the allopatric range of *E. grevyi* in terms of food availability. Simplifying, it seems as if *E. burchelli* is prevented from extending its range further north by the hot, dry climate prevailing in *E. grevyi*'s allopatric range, whereas *E. grevyi* is outcompeted in the area of high food availability further south.

E. grevyi thus seems to gain the competitive advantage in its own allopatric range by some sort of adaptation to hot, dry climate which *E. burchelli* is lacking. One factor which may be important is body size: the fact that *E. grevyi* (*c.* 400 kg) is larger than *E. burchelli* (*c.* 220 kg) would itself be advantageous in arid conditions. To our knowledge, the physiological adaptations of *E. grevyi* to drought conditions have not been examined, but several authors refer to the species as being arid-adapted (Marean & Gifford-Gonzales, 1991; Ginsberg, 1988). Klingel (1974) infers such adaptations from the species' survival in areas to which its social system is, in his opinion, maladapted. He also observed that *E. grevyi*, unlike *E. burchelli*, is capable of digging for water.

Klingel (1974) observed that pasture too poor for *E. burchelli* could still sustain *E. grevyi*. Furthermore, a study of zoo animals (Foose, 1982 in Ginsberg, 1988) showed that *E. burchelli*, when fed low-quality food, has relatively slow passage rates and reduced assimilation efficiency compared to *E. grevyi*. If *E. grevyi* is able to use and maybe even to degrade the food supply to a degree at which *E. burchelli* cannot sustain itself, the fact that it has not extended its range further south suggests that either conditions there rarely deteriorate far enough, or that *E. burchelli* possesses other superior adaptations to the environment in its allopatric range. A higher rate of reproduction could give *E. burchelli* this advantage; its gestation period of 11.5 months would allow it to exploit a regular seasonal abundance of food in a way denied to *E. grevyi*, with its gestation lasting 13.5 months.

Any such adaptations are unlikely to be explicable in terms of the environmental variables examined in this study. The higher vegetation index suggests that, of the three ranges studied, the range of *E. burchelli* contains the habitat most favourable for equines, and superior adaptations to optimal conditions are hard to demonstrate. As suggested, above, for the range limits between *E. africanus* and *E. grevyi*, the order of arrival could be an

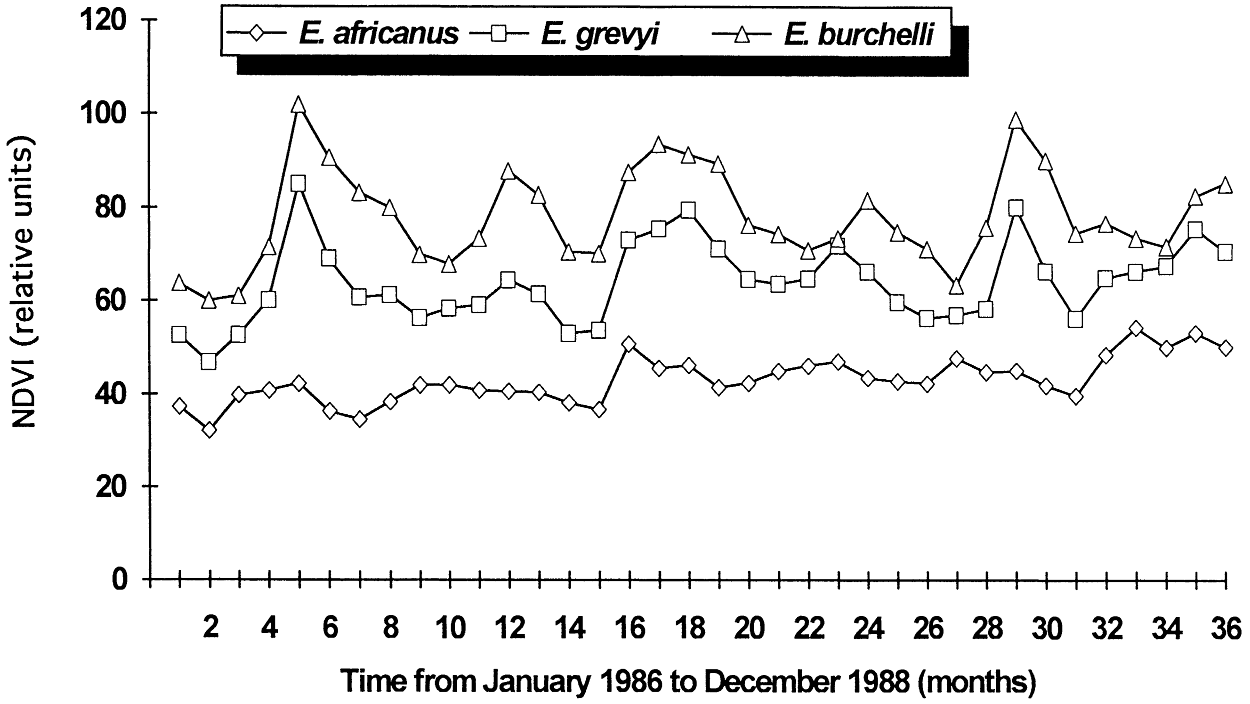

FIG. 11. Seasonal changes of productivity in the ranges of *E. africanus* Fitzinger, *E. grevyi* Oustalet and *E. burchelli* Gray.

important factor: Reichholf (1984), based on Thenius (1980), argues that the immigration of *E. burchelli* from Asia predates that of *E. grevyi*. The range extension of *E. grevyi* southwards might on this argument have been halted at the point at which its adaptation to arid conditions and low vegetation availability failed to outweigh the advantages gained by *E. burchelli* through earlier arrival.

Matters are, however, not quite that simple. First, palaeontological evidence (Churcher & Richardson, 1978; Grubb, 1981; Churcher, 1993) suggests that both species, or their forebears, have been widely distributed throughout Africa for at least 1 million years. Secondly, palaeontological data indicate that in the late Pleistocene the distribution of dry grasslands was very different from today, and the range of *E. grevyi* extended at least as far south as northern Tanzania (Marean & Gifford-Gonzales, 1991). Since that time, mean annual temperature and rainfall have increased in East Africa (Bonnefille, Roeland & Guiot, 1990), leading to changes in community distributions and probably causing the northward retreat of *E. grevyi*'s range to produce the distribution of this species as historically recorded. This clearly suggests that *E. burchelli* does possess adaptations which enable it to displace *E. grevyi* from areas in which that species had formerly been established. Our inability to explain this is probably simply a reflection of insufficient knowledge of the ecology of these two species.

The border between the ranges of *E. grevyi* and *E. burchelli* has probably shifted flexibly with climatic and environmental changes in the past, and even at present is not static. A range extension of *E. grevyi* onto the Laikipia Plateau in the 1970s has been recently reported by Rowen & Ginsberg (1992) and Churcher (1993). Although temporal analysis of vegetation index data during the years from 1986 to 1988 indicated quite regular rains during this period, north-east Africa is well-known for its irregular and often unpredictable rainfall regime. The competitive balance between *E. grevyi* and *E. burchelli* in their sympatric range is likely to shift with every season. The fact that within this area, which represents an environmental intermediate between their allopatric ranges, both species expand their niche to utilize areas of extremely low productivity, would then reflect the intense competitive pressure between them.

The sample period used might have fairly represented average annual rainfall and productivity, but clearly analysis of a longer time span, including years with irregular rains, would be desirable. Different seasonal migratory patterns are a possible way of alleviating competitive pressure, and therefore any additional climatic or vegetational data should be viewed ideally in conjunction with information about seasonal changes in animal distributional patterns. To our knowledge, however, no information on the migratory patterns of the two zebras in their sympatric zone is currently available.

Possible significance of social systems

The competitive interactions between *E. grevyi* and *E. burchelli* are further complicated because their social organizations differ.

The social system of *E. grevyi* can be described as a territorial mating system. It has been studied in detail by

Klingel (1974) and Ginsberg (1988, 1989), but these authors disagree about its adaptive significance: Klingel (1974) argues that it is poorly adapted to the unpredictable environment in its range, as mating only takes place in favourable environmental conditions, and sexes are separate for the unfavourable months. If the seasons were regular this system would be a way of maximizing reproductive success, but in the species' natural habitat it is a gamble which can result in high death rates of foals if a wet season fails, or in low birth rates despite a favourable season if the previous year was poor. Ginsberg (1988), however, observed that the basically individualistic character of *E. grevyi*'s social system allowed the animals to respond flexibly to changes in environmental conditions in situations where the organization of *E. burchelli* groups began to break down.

The basic unit of the social system of *E. burchelli* is a coherent family group (Klingel, 1967, 1969). Mating and foaling take place throughout the year, but there is a marked foaling peak coinciding with the rainy season. Productivity is correlated with rainfall. It is important to note that Klingel studied *E. burchelli* social behaviour in the Ngorongoro crater and Serengeti plains, both of which are subjected to a basically unimodal rainfall regime. In northern Kenya, however, the annual rainfall distribution is typically bimodal, but a shifting or complete failure of the rains is not uncommon. Ginsberg (1988) found that in this area the family groups of *E. burchelli* were forced to break up when conditions deteriorated. He also reports that, for harem-breeding equids such as *E. burchelli* which try to remain in groups in adverse conditions, plant biomass density limits habitat use.

A detailed comparison of the social and reproductive behaviours of the two zebras in areas such as Samburu and Meru, Kenya, where they co-exist, would greatly assist the interpretation of our results. Alternatively, the recent range extension of *E. grevyi* onto the Laikipia Plateau, at around 00°30′N, 36°30′E, would be a particularly worthwhile study. Formerly part of the allopatric range of *E. burchelli*, it is now part of the sympatric zone. The habitat variables which we can extract (mean annual temperature 17.1°C, MTHM 18.3°C, mean annual precipitation 729 mm, SUMNDVI for 1986–88 2768–2884 units) all fit this reassignment to the sympatric zone, particularly the rainfall and vegetation index (cf. Figs 5–10). Did the 8 dry years from 1969–76 (Fig. 4) give *E. grevyi* an advantage?

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