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Pattern, process and the evolution of the African antelope (mammalia: bovidae)

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To

Marie Caithness, *née* Plewman

Hugh E. H. Paterson

and

Sheila T. Rock

"...free at last, to enjoy the present, unfettered by the future which is history."

(approximately) Tom Robins

Declaration

I declare that this thesis is my own work. It is being submitted for the degree of Doctor of Philosophy, in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

Signature: Neil Caithness

Date: 5 Oct, 1995

Abstract

The methods of vicariance biogeography are in general rendered equivocal by widespread taxa. Standard methods resort to *ad hoc* assumptions in their treatment of widespread cases, and the results are always subordinate to the addition of new data on endemic sister taxa. I introduce an alternative method for the analysis of widespread taxa based on the vicariance model. The method requires first the development of a habitat model for each species included in the analysis. I analyse the actual and "potential" distributions by cladistic methods, employing a weighting system designed to factor out the influence of ecological similarity. The resolution of the inferred area relationships is seen to increases with the application of the weighting—compelling evidence that the pattern reflects historical relationship. I review current approaches to the modelling of habitats. All seem to be based on an ecological model of equilibrium, where the limits of actual species distributions are thought to reflect habitat, as if historical contingency played no significant part in determining the shape of real distributions. Under this model all approaches are group discrimination methods. I reject these methods and develop a new method based on principal component analysis. I analyse the distributions of all extant endemic African antelope and derive probability surfaces for each species. The model output can be interpreted as species distribution free of history—its potential distribution. This is different from assuming that actual distributions are free of history. Areas of endemism are seen to be historical entities, not simply distributional ones, and the resulting area cladogram is interpreted as the hierarchical pattern of endemism. A striking feature of the inferred pattern of endemism is the intersection of an east-west equatorial biota, and a north-south savanna biota. These bisect in East Africa at the centre of highest antelope diversity. I predict that this feature will be seen to be the most persistent feature of endemic structuring in other African taxa with high East African diversity.

Pattern, Process and the Evolution of the African Antelope (Mammalia: Bovidae)

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October, 1995.

Humphries (1989) adopted the same position as Nelson and Platnick (1988), stating clearly and emphatically that it is impossible to determine area relationships based on distributions, without first knowing the phylogenetic relationships among the taxa.

> A more recent and worrying development has been the attempt to rid biogeography of biological relationship and simply consider distributions based on existing taxonomy. Parsimony analysis of endemicity (PAE) (Rosen, 1988) is one such method. To overcome the problem that few fossil groups have been analysed cladistically, Rosen (1988) devised a method that uses parsimony, but species or genera are the 'characters' and sampled areas the 'taxa'. In PAE, parsimony analysis is applied to the shared taxa of sampled localities in order to obtain the 'relationships' of those areas in terms of the species which occur in them. There is no guarantee that the organisms or categories utilised as 'characters' are monophyletic in the first place, and areas are nested in terms of the relative widespread distribution of taxa. Thus, the lower [sic.] the node of the area cladogram the more widespread the taxon. This method has many of the same faults as panbiogeography where considerations of distribution are considered more important than biotic relationships. There is no way of evaluating the results because the critical empirical information, the distribution of characters is missing.
>
> (Humphries, 1989, p. 102)

Humphries concluded:

> To suggest that cladistic biogeography is sterile or that there are substitutes for cladistic information is unfounded. Because of problems with extinction, widespread distribution and vicariance there can be no direct correspondence between phyletic and geographic information, and hence no quick shortcut around assumption 2 [see later]. It is not possible to determine area relationships based on biotic distributions unless the relationships of the taxa are known at the beginning. It makes no difference whether spatio-temporal considerations precede or follow taxonomic analysis, the monophyletic requirement is indispensable. Systematics has one property, homology, and one criterion of choice, parsimony or congruence, and as these are the fundamentals of systematics then ultimately characters and taxa are the empirical components of historical biogeography.
>
> (Humphries, 1989, p. 102)

The ordering of the synthesis "Space, Time, Form" (Croizat, 1964) (read: (pan)biogeography, history, phylogeny) or "Form, Time, Space" (Nelson and

recent revival of panbiogeography (Craw and Page, 1988; Page, 1987; see refs. in Platnick and Nelson, 1988) as a methodology distinct from other biogeographies serves also to highlight the primary nature of *vicariance* biogeography in the cogent rebuttals of its proponents.

Platnick and Nelson critically reviewed the "spanning-tree biogeography" (=panbiogeography) of Craw and Page (1988):

> This method differs from other modern approaches most notably in allowing historical biogeographic conclusions to be drawn even when little or no cladistic information is available about the relationships of the taxa being analyzed. Spanning-tree biogeography resolves such relationships, in effect, on the basis of relative geographic proximity.
>
> (Platnick and Nelson, 1988, p. 410)

They concluded:

> We predict only that the results of spanning-tree biogeography ultimately will be judged by their congruence, or lack of it, with cladistic analysis of characters. In other words, its results will not prove decisive in and of themselves, regardless of their mutual congruence, or congruence with geology in a particular case. Whatever congruence spanning-trees deliver will always be haunted by the possibility that it is an artifact of present geographic proximity.
>
> (Platnick and Nelson, 1988, p. 414)

Although Platnick and Nelson (1988) argued that Craw and Page (1988) presented a much simplified and erroneous interpretation of Croizat, it is clear that Craw and Page were consistent with Croizat in at least one respect: rejecting the inferential priority of phylogeny over biogeography. Croizat was emphatic:

> Even less do I agree [Ferris, 1980, p. 67] that phylogenetic analysis, achieved by means of Hennigian methods, is to precede biogeographic inference. This notion belongs to times and minds when dispersalism ruled the roost, and no concrete analysis of dispersal was possible in the light of its flimsy theories. With biogeography in the saddle, concrete analysis of a biogeographic equation is answerable to a precise method of inquiry; it ascertains the facts in play, and as such comes first before hazy form of theoretical "phylogeny".
>
> (Croizat, 1982, p. 299 [underlining mine])

traditional dispersalist and ecological biogeographies, and also from other historical biogeographies (e.g. phylogenetic biogeography, Hennig, 1966a, b; Brundin, 1966, 1972, 1981; and panbiogeography, Croizat, 1952, 1958, 1964). It is now almost synonymous with the cladistic biogeography of Nelson and Platnick (1981; see also Humphries and Parenti, 1986) (Humphries, 1989), though several divergent methodologies (e.g. Craeraft, 1988a; Kluge, 1988; Mayden, 1988; Wiley, 1987, 1988a, b) compete for the attention of historical biogeographers (Wiley, 1988a), and must be included in the general class of vicariance (=cladistic) methods.

Dismissing alternatives

Although Croizat's panbiogeography, and the newer vicariance biogeography that derived from the works of Hennig and Brundin (e.g. Rosen, 1974, 1975 [sic.], 1978, 1979) did converge for a time (Nelson and Platnick, 1981; Platnick and Nelson, 1988; cf. Croizat, 1982), the sociology of their acrimonious interaction is all but incomprehensible given recourse only to the scientific literature (but see Croizat, 1982; Platnick and Nelson, 1988). The two are best regarded as separate formulations, with whatever mutual development they may have enjoyed being now of philosophical interest (Hull, 1988).

The major difference between the two disciplines seems to have been that vicariance biogeographers wanted to use only monophyletic groups (*sensu* Hennig, 1966a) (Wiley, 1988a), and Croizat rejected any alliance with Hennig on personal and political grounds (Platnick and Nelson, 1988).

Panbiogeographers continued to develop methods independently, but the

(Hennig, 1966a), biogeography has undergone a revolution of equal proportion, but nowhere has a methodological consensus emerged that parallels the simplicity of the one in systematics: search for the most parsimonious interpretation of the distribution of homologies, (Patterson, 1981). In 1969 Gareth Nelson complained:

> [E]ven today there is no generally accepted methodology that enables biogeographers, when faced with the same data, to reach approximately the same answer to a given problem.
>
> (Nelson, 1969, p. 243).

Now past its 25th anniversary, this statement is still true today, and vicariance biogeography seems persistently irreducible to simple statements.

Vicariance biogeography was introduced in the 1970's as a critical alternative to traditional thinking in biogeography (Craeraft, 1988b) That tradition held ecology, vagility, and dispersal as primary in explanations of the distributions of taxa (e.g. the "Wallacean synthesis" of Darwin, Wallace, Matthew, Simpson, Mayr and Darlington, with its focus on centres of origin (e.g. Darlington, 1957, 1965; see Brundin, 1966) and the immigration/emigration and speciation/extinction balances of MacArthur and Wilson (1963, 1967) as a model for all biogeographic explanation, (but see also MacArthur, 1965; Pianka, 1966; Whittaker, 1977)).

In the first substantial application of the new ideas to a real biogeographic problem, Donn Rosen suggested that the history of salmoniform fishes was better explained by vicariance than by dispersal (Rosen, 1974), a theme that continued in the critical examination of many of the conceptual foundations of dispersalist biogeography (e.g. Croizat et al., 1974; Platnick and Nelson, 1978; Nelson and Platnick, 1981).

Vicariance biogeography is now a separate discipline, distinct from both

fragmentation of a distribution (e.g. Brown and Gibson, 1983) rather than to make explicit reference also to the products of cladogenesis that result from fragmentation, the use of *vicar* to refer to those results (i.e sister taxa with disjunct distributions in sister areas) is less common.

Through this usage, vicariance has lost something of its essential meaning, i.e. the production of taxonomic substitutes. This meaning can be restored, if by vicariance we understand explicitly the production of vicars by the fragmentation of formerly cosmopolitan taxon distributions. However, the former usage of vicariance to refer primarily to collective range fragmentation is well entrenched in the literature, and while keeping in mind the meaning of *vicar*, the meaning of vicariance can be inferred from the context.

Vicariance, as the collective fragmentation, and subsequent taxonomic differentiation of even some of a biota's constituent species, will result in distinct areas whose endemic species show phylogenetic relationships that reflect the historical area relationships. Vicariance then, is a structuring agent of biogeographic history, creating areas of endemism, and leaving its historical ordering in the shape of the phylogeny of taxa. The relationships among areas of endemism, and their historical ordering, is addressed by the methods of vicariance biogeography. However, there are also destructuring agents that confound interpretation, and threaten the utility of vicariance methods.

Breaking ties

In the three decades since the start of the cladistic revolution in systematics

species, with generalists showing cosmopolitan distributions.

Tests of these explanations are often assumed to lie in phylogenetic explanations, but they rest equally in biogeographic analysis; this thesis addresses some of the fundamental aspects of that analysis. As biogeographers, we hope to reveal the patterns that structure biotic endemism, and the processes that produce the pattern; ultimately the synthesis of spatial and genealogical pattern, in explanations of general process.

1.2 Vicariance biogeography

Prologue

Vicariance is the making of vicars (**vi'cars**). In biogeography, a vicar is a taxon in one area, that *substitutes* for its sister taxon, or homologue, in another (Cracraft, 1983, 1994). The implication of vicar here is slightly different from common usage; a biogeographic vicar is a taxon that substitutes for its sister taxon, horizontally in the hierarchy of taxa; in common use a vicar is a substitute for an entity *up* the hierarchy.

Vicariance has also the added implication of passive and collective fragmentation of taxon distributions by some agent of earth history (e.g. continental drift, mountain building, climate change), rather than individual and independent dispersal of organisms from one area to another.

Perhaps because of the common use of *vicariance* to refer to just the

1.1 Questions worth answering

Although this thesis deals principally with *how* to go about answering certain kinds of questions, it is important to bear in mind what those questions might be.

Ultimately, the question of how the earth's biotas came to be spatially structured is a question worth answering; what is the pattern of the structure, and what processes produced the pattern? Proximately we might ask how the patterns of phylogeny are related to processes of biogeography? Or, How are particular patterns and structures in phylogeny and biogeography produced?

Vrba (1980) for example, has asked how the phylogenetic pattern of speciose clades, as sisters of non-speciose clades arises. One explanation has been that of "species selection" (see Cracraft, 1982; Stanley, 1979; Vrba, 1983); an hierarchical analogue of natural selection within populations, that refers to emergent properties of species, and consequent differential speciation and extinction. Vrba's (1980, 1983) own explanation, the "effect hypothesis", attributes the pattern to differences in the spatial response of species distributions to changing environments, responses attributable more to the features of organisms, than to emergent properties of species; trophic or environmental generalists (i.e. eurotopic species) will in general be less affected spatially than specialists (i.e. stenotopic species); the specialists will, in effect, be subject to vicariance at a higher frequency than generalists, and the pattern that emerges will be one of speciose vs. non-speciose sister clades (Vrba, 1980, 1983). Areas of endemism will also then be characterised by the narrower endemism of specialist

methods is warranted by the arguments of many critics (Cracraft, 1988a; Kluge, 1988; Page, 1988; Wiley, 1988a; Zandee and Roos, 1987) but most especially by the realisation that while the process of vicariance writes its spatial pattern in the phylogeny of species, the widespread distributions of undifferentiated populations are shadows of that same pattern (Cracraft, 1994). The distributions of widespread species are as much a consequence of the historical pattern of vicariance, as are the disjunctions of sister species; they just don't carry its phylogenetic mark.

Both patterns, of sister species disjunctions, and of widespread species disjunctions, are the products of common cause, and singular event distortions. By searching for repeated pattern in the disjunct distributions of phylogenetic sisters, vicariance biogeographers attempt to infer common cause (vicariance), as distinct from singular events (dispersal) in the history of biotas. If we can tell apart the influence that vicariance has on the distributions of widespread species, from the influence that other factors or processes may have, then we can infer the history of biotas, within the time-frame for which undifferentiated species may be relevant, independently of phylogeny.

The method of ecological induction applies the same principle of corroboration by repeated pattern, but operates over a near time-frame relative to the extended time-frame of vicariance methods. As such it represents a complementary method in historical biogeography and relieves the burden of inference imposed on vicariance methods by undifferentiated and phylogenetically uninformative distributions.

solve their respective problems? These questions structure much of what follows and I have adopted as an on-going theme the integration of cladistic theory into the study of biogeography, and the methodological complexities that pertain to the different contexts of cladogenesis and vicariance. A second structuring theme is the change in context from which we see pattern, or process. I take the position that pattern over time is equivalent to process, and that our concepts of pattern and process are therefore contextual.

Cracraft (1988a) has questioned the tacit expectation in vicariance biogeography that a single pattern underlies biogeographic history, suggesting instead that we recognise the possibility of multiple historical patterns, and that current methods in vicariance biogeography are insufficient to recover the patterns of these multiple histories (cf. Platnick and Nelson, 1984).

Other authors (e.g. Kluge, 1988; Wiley, 1988a) have identified a more immediate problem: the central dictum of vicariance biogeography is the priority given to phylogeny over biogeographic inference; consequently a central problem is how to deal with widespread species whose spatial disjunctions carry no apparent information relevant to the historical relationships among areas. Not wishing to discard the potential information contained in these distributions, current methods advocate a choice of one of several more-or-less constraining assumptions (1 and 2 of Nelson and Platnick, 1981; 0 of Zandee and Roos, 1987) to alleviate the incorporation of potentially misleading information.

I address here the formulation of an alternative method for the treatment of widespread species: the method of ecological induction. The search for alternative

1. Introduction

> **vic'ar,** n. Parson of parish of which the tithes have been impropriated (cf. RECTOR); (poet. &c.) person's deputy or agent. ~ *apostolic*, R.-C. missionary or titular bishop; ~ *choral*, person assisting in musical parts of cathedral service; ~ *general*, (arch)bishop's assistant in ecclesiastical causes &c.; ~ *of Bray*, systematic turncoat (w. ref. to the song); *V~ of Christ* (a title of the Pope).
>
> **vicar'ious** a., deputed, acting as substitute, done or suffered by one person on behalf of another, (*~ious authority, victim, atonement, punishment*). [AN f. L *vicarius* substitute]
>
> (Fowler and Fowler, 1969)

> Biogeographic patterns within continental biotas are produced by cycles of vicariance of widespread species, followed by narrow endemism, followed by population dispersion of descendant species to produce more widespread forms, followed by new cycles of vicariance. Vicariance of biotas produces areas of endemism. Yet the historical tendency within a biota will be to lose those areas over time, although as biogeographers we hope their traces will persist in the histories of the different biotic elements.
>
> (Cracraft, 1988a, p. 233)

Historical biogeography seeks ultimately to understand the construction of the earth's biotas. Proximately, it is the search for common cause in the spatial distributions of taxa, and an attempt to resolve the historical relationships among areas of endemism. The common cause is the vicariance of primitively cosmopolitan biotas, which imposes a descent-like hierarchy on area relationships. Thus there is an analogous context for investigations in phylogeny and biogeography.

What are the implications of this analogous context? Just how parallel are the two fields, and to what extent does a single methodology underlie attempts to

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between "affinity" due to current ecology and close proximity, and "relationship" due to vicariance history. We need the taxonomic information of sister group relationships, taxonomic component (B,C) in (A,(B,C)), in order to say that areas (2) and (3) are synapomorphic (=syn-taxic of Kluge, 1988) and related as (1,(2,3)). If any taxon is widespread, area relationships inferred from these data become equivocal. (If any taxon is widespread, then in this example at least, one area is not characterised by an endemic taxon.)

Perhaps it's not surprising that so much attention has been directed towards interpreting the distributions of widespread taxa.

Methodological prescriptions

Kluge (1988, p. 318) has examined all the types of distributions that can be observed: (i) all terminal taxa are endemic; (ii) there is a missing taxon, i.e. a recognised area is unoccupied by any terminal taxon; (iii) a terminal taxon is widespread, occurring in more than one area; (iv) two or more terminal taxa are sympatric, occurring in the same area. Only the first type provides unambiguous and relevant area evidence, the other three are all problematical to some degree.

The dominant methodological prescription that addresses the problems of widespread taxa, missing taxa (=missing areas), and sympatric taxa (=redundant distributions) (Nelson, 1984; Page, 1988), is "component analysis" (Platnick and Nelson, 1978; Nelson and Platnick, 1981). (The earlier cladogram reduction methods of Rosen (1978, 1979) have been abandoned as general methods; see Humphries and Parenti (1986)).

Titular vicars

Thus, widespread taxa actually pose two separate problems: (i) that individually they are "everywhere the same" (not vicars) and therefore uninformative of possible character state transformations that might resolve area relationships (their widespread sameness is only a measure of similarity), and (ii) as one of the sisters in sister groups, they confound the interpretation of area history by seeming to break from the established pattern of endemism, because of the failure of cladogenesis (failure to become vicars), and therefore show plesiomorphic distributions (Nelson and Platnick, 1978).

The difference is subtle (*not being a vicar* vs. *failure to become a vicar*), but it matters because our methods do not allow us to tell the difference in any specific case. Widespread species of the first kind may have distributional histories that are independent of vicariance; widespread species of the second kind have distributional histories congruent with the general vicariance history, but they don't carry any cladogenic mark of that history. Explained another way, widespread distributions are *putatively* caused by the first, or spatial component of vicariance, i.e. range fragmentation, but are rendered equivocal because they show nothing of the second, or cladogenic component of vicariance; the putative cause cannot be corroborated by phylogenetic pattern. Populations in the different areas of a widespread distribution are *titular* vicars, such in name only without the reality, i.e. not substitutes for sister taxa, but the *same* taxon in different areas.

For the areas spanned by widespread taxa, we cannot tell the difference

following either vicariance or jump-dispersal. Presumably it is this second possibility that prompted Nelson and Platnick (1978) to characterise widespread taxa as plesiomorphic characters of areas, and therefore not evidence of sister group relationships (a plesiomorphic character in systematics is a character that fails to respond to cladogenesis; but see Page, 1988).

Another way of saying this is that widespread taxa might be widespread because of either their current ecology (dispersion), or their past history (failure of cladogenesis). Vicariance is the common cause of endemic structuring, and as widespread taxa carry no mark of that history, because of their failure to respond to it by cladogenesis, they are uninformative. Taxa that *do* show a cladogenic response to isolation, caused by either vicariance (producing vicars), or jump-dispersal (producing false vicars), will collectively carry the signature of the *vicariance* history, i.e. the pattern due to common cause will overwhelm that due to uncorrelated singular events.

The different contributions of vicariance and dispersal are resolvable by cladistic methods, treating vicariance as a common cause, first-order event, and dispersal as a parallel or convergent, second-order event. We assume that vicariant events can explain cladogenesis simultaneously in more than one taxon, but that dispersal events are independent, and that incongruences are likely to be incongruent with the main vicariance pattern, and also incongruent among themselves. Again, spatially correlated dispersal (but not dispersion) in different taxa is not considered impossible, only unlikely.

relationships among the *taxa* are primary, not their current distributions, whatever they may be. So, the kinds of data are the monophyletic sister group relationships among taxa.

The kinds of hypotheses considered relate areas by the vicariance history of their *endemic* taxa, exhausting all possible vicariant relationships as first-order explanations, before resorting to *ad hoc* second-order explanations (Wiley, 1988b).

Nelson and Platnick (1978) point out that the critical point of departure of vicariance biogeography, from traditional biogeographies, is inferring sister group relationship among areas by synapomorphy, not overall similarity; analogous to the point of departure of cladistics from phenetics. Traditional biogeographies would infer a close relationship between two areas if they share a common taxon not found in the third, i.e. inferring relationship by similarity. For example, inferring (1,(2,3)) if a taxon is found to be distributed in area (2) and (3), but not in area (1), regardless of the relationships among the taxa themselves. However, the *similarity* of areas with respect to their constituent taxa is uninformative regarding their historical relationships, being based as it is on the distributions of widespread taxa (Platnick, 1981; Platnick and Nelson, 1978; Nelson and Platnick, 1981).

Widespread taxa

Several factors contribute to this interpretation of widespread taxa. A taxon might have a widespread distribution across several areas of endemism because of (i) close geographic proximity and dispersion (cf. dispersal; Platnick, 1976) from one area to the other, or (ii) a failure to respond (by cladogenesis) to isolation

Implementing phylogenetic priority

What principle guides the development of method to a point beyond the pessimistic realisation that the mark of biogeographic history may be all but obliterated in complex reticulation? Just after the passage quoted earlier, Nelson concluded:

> ... a biogeographer is obliged to use all of the known distributional data to construct the most parsimonious hypothesis of earlier distributions. Historical biogeography deserves a place in science only to the extent that its methods, given the same distributional data, can lead to such an hypothesis, and produce agreement that in fact the hypothesis is the most parsimonious.
>
> (Nelson, 1969, p. 246)

Use all the data, and construct parsimonious hypotheses! The same principle that guides phylogenetic systematics (Eernisse and Kluge, 1993; cf. Bull et.al., 1993). But what kinds of data, and what kinds of hypotheses?

Platnick and Nelson provide us with one of the earliest statements of method in vicariance biogeography:

> ... the method outlined here allows us to choose any set of three or more areas of the world that can each be delimited by the presence of two or more endemic taxa (of any rank) and, by comparing the patterns of interrelationships of the various groups with taxa endemic to those areas, test hypotheses of the interconnections of the areas themselves.
>
> (Platnick and Nelson, 1978, p. 16)

Minimally, we require sister group relationships for a monophyletic taxonomic group with members endemic in at least three separate areas. For example, consider three taxa (A), (B) and (C), respectively endemic in areas (1), (2), and (3), and related as (A,(B,C)): the hypothesis of area relationships (1,(2,3)) is the most parsimonious, uses all the data, and is unproblematic. The sister group

differentiation occurs until (A^2) is again sub-divided, and speciation occurs in one of these secondary disjunctions. The genealogical relationship is (A^1,(A^2,B)), although cladistically no synapomorphy unites (A^2,B) to the exclusion of (A^1). On mitigation of the barriers, dispersion results in secondary sympatry (=distributional reticulation), and reproductive recombination results in genealogical reticulation, leaving just two sister species (A^{1+2},B).

Speciation has ensured the genealogical integrity of (B), even after secondary sympatry and the reticulation of (A^{1+2}). In the absence of diagnosable apomorphies, cladistics is insensitive to genealogical history below the boundary of reticulation. Baum and Shaw (1995; see also Shaw, 1993) have recently described a species concept recognising basal taxa at the (fuzzy) boundary between divergence and reticulation. Basal taxa are the smallest (=lowest) units appropriate for cladistic analysis, but there is no analogue in biogeography, and no acquired integrity for a basal area.

Area reticulation by biotic dispersion can occur at any level of the area hierarchy, and between any adjoining areas. Historical signal is present only to the extent that vicariance structuring overwhelms reticulate destructuring. The level to which dispersion is itself structured is less significant because dispersion is not followed by taxonomic differentiation to the extent that differentiation occurs in vicariance. Biotic dispersion is, in effect, the same as genealogical reticulation described in the above example, and vicariance methods are insensitive to the former histories of hybrid areas, just as cladistic methods are insensitive to the former histories of reticulated lineages.

paradoxically, we would never know, as our only recourse to inference about phylogenetic relationship is our ability to tell the historically structured pattern of homology from the historically unstructured noise of homoplasy.)

The biogeographic formulation that opposes vicariance, as the structuring agent creating a nested hierarchy of endemism, against dispersal, as random and particulate destructuring events, is the analogue of phylogenetic systematics. Correlated dispersal, and the creation of biotas with structure historically independent of vicariance, is not considered impossible, only unlikely (Kluge, 1988). However, there is an agent of endemic destructuring other than random dispersal, i.e. dispersion. If dispersion is itself structured, then the true hierarchy of endemism is obscured not only by noise, but by an independent, and possibly alternative structuring.

As an agent of endemic randomisation (e.g. Cracraft, '988a), dispersion poses no more of a problem than dispersal, but as an agent of non-random endemic destructuring, its effects must be carefully analysed. If dispersion does create an alternative structuring, and if existing methods cannot distinguish which of these reflects the historical ordering of vicariance, then phylogenetic priority will deliver a false inference about biogeographic history. Equally, the integrity of the areas will not be maintained, and our reading of history will be blind to them.

Reticulate destructuring

Consider again the situation as it pertains in systematics: a widespread species (A) is divided into two disjunct populations (A^1) and (A^2), but no taxonomic

to biotic randomisation.

Homology and homoplasy: signal and noise

Biotic dispersion raises two potentially critical problems for vicariance biogeography and the priority given to phylogeny as the marker of spatial history: (i) the possibility of multiple biogeographic histories as a consequence of reticulate destructuring (=area-hybridization; Cracraft, 1988a), and (ii) the possibility that a destructuring agent may itself be structured (=historically constrained; Cracraft, 1994).

Consider the argument in phylogenetic systematics: cladogenesis is the structuring agent creating a nested hierarchy of homologies. With only cladogenesis acting as the agent of genealogical form-making, i.e. in the absence of lineage reticulation, taxa can experience only single histories with respect to their attributes. The sources of homoplasy that destructure the hierarchy are themselves argued to be unstructured, i.e. random and particulate events with respect to the structuring of cladogenesis. The nested hierarchy of homologies is the *true* taxonomy, obscured sometimes, and only slightly, by the random noise of homoplasy.

A fundamental assumption of phylogenetic systematics is that homoplasies do not covary more than do homologies. We have reasonable expectation that homologies are hierarchically structured, and little expectation that homoplasies covary significantly. If this is not so, then there is as much signal in non-history, as there is in history, and our inferences of phylogeny are false. (If this is true, then

Dispersal and dispersion must be clearly distinguished. Platnick (1976) argued that dispersal is best identified as a property of taxa, and dispersion as a property of individuals. Though dispersal involves the movements of individuals, it is the introduction of individuals into entirely new regions, not before occupied by that taxon, and thus fundamentally changes distributions at the level of taxa. In contrast, dispersion *maintains* the established range of a taxon by the continual movement of individuals.

Cracraft (1994) distinguished dispersion, as a population-level phenomenon describing changes in species distributions in contiguous space, either individually, or jointly (biotic dispersion), from dispersal, a phenomenon of colonisation across a barrier by small numbers of individuals rather than populations. It is the latter sense that I adopt here: dispersion describes advancement of the boundary of a species distribution; biotic dispersion is the simultaneous and correlated advancement of the boundaries of all or many of the species of a regional biota; and (jump-)dispersal describes the colonisation of a new, disjunct region.

Dispersal and dispersion have different taxonomic implications. Dispersal may lead to speciation in newly isolated populations, resulting in disjunct sister taxa (false vicars), but dispersion involves range expansion, continuous in space, and so no isolated populations are produced, and in general no taxonomic differentiation occurs. In this sense, dispersal promotes endemic randomisation, both in producing widespread disjunctions of species populations, and in producing disjunct sister taxa. In contrast, Cracraft (1994; cf. 1988a) has argued that dispersion may itself be historically structured, and may not contribute significantly

rendered even impossible.

(Nelson, 1969, p. 246)

It is evident then that there are structuring, and destructuring agents of historical biogeography. Cracraft's (1988a, p. 233) statement, quoted earlier, portrays the dominant interaction as "cycles of vicariance" (structuring), "followed by population dispersion of descendant species" (destructuring), "followed by new cycles of vicariance". The implication is the historical tendency to lose older endemic structuring as newer cycles accumulate.

The destructuring of endemism

Whereas vicariance acts historically to increase endemic structuring, there are three processes that act to destructure endemism: (i) dispersal, (ii) dispersion, and (iii) extinction (cf. Cracraft's (1994) four processes, incl. speciation, that add or subtract species from a region).

These four processes, vicariance (*sensu stricto*), dispersion, dispersal, and extinction, are central to understanding the construction of biotas; to the ontology of space and form; to the epistemology of inferential priority; and to understanding the nature and transfer of theory, in and between systematics and biogeography.

Extinction, either of all populations of a species, or of just those populations within a local area of endemism, will tend to erode the endemic structuring of a biota. In general we assume that extinction is itself historically and taxonomically unstructured, but the possibility that this may not be so is little appreciated; extinction as a process is always a local phenomenon (Cracraft, 1994) which seems also to support this assumption.

This is simply a methodological deduction from the general consequences of vicariance: the historical ordering of biotic division is written in the historical ordering of cladogenesis; disjunct sister taxa (i.e. vicars) show the historical ordering of space in their phylogenies.

In other words, vicariance is historically constrained by the prior structure of existing biotas. It is the *en masse* fragmentation of a biota, and the subsequent differentiation into vicars of its biotic elements in opposite fragments. Narrow endemism and the uniqueness of biotas follows. The historical ordering of biotic fragmentation, and hence the historical relationships between areas of endemism is contained in the ordering of cladogenesis; phylogenetic priority is a contingent fact of vicariance!

This contingent fact leads to an epistemological rule: that the best first order explanation for the disjunct distribution of sister taxa is that it is a consequence of the past fragmentation of the range of a formerly widespread ancestral taxon, rather than a dispersal phenomenon from a restricted centre of origin (Wiley, 1988b).

Just how faithful over time is the biotic st. .g written by vicariance? Does endemism persist in the face of all the other processes that impinge on the integrity of areas? Anticipating the tremendous problems, Nelson continued:

> It is a complicating fact that the distribution of organisms changes with time, either expanding or contracting in response to physical and biological factors of the environment. There is little likelihood, therefore that Recent distributions are a very accurate mirror of past distributions of the same species or groups. In addition, Recent distributions of closely related species often are very complex, with ranges partially or completely overlapping. In such cases, very detailed geographic analyses become complicated or are

Platnick, 1981) (read: form = cladistics, cladistics + time = phylogeny, phylogeny + space = vicariance biogeography) is significant, as it pertains directly to the *epistemological* necessity that, in vicariance biogeography, phylogenetic inference precedes biogeographic inference. But, synthesis is concerned more with ontology than epistemology; what of the interdependence of genealogical form-making (cladogenesis), and spatio-temporal form-making (vicariance)? The dual context of Form and Space, united in Time as macroevolutionary process, seems to me as worthy of a synthesis.

Nonetheless, at least as concerns epistemology in vicariance biogeography, the congruence of biogeographic pattern with cladistic character analysis is the final arbiter of relevance! This apparently simple prescription belies a methodology that is dauntingly complex.

The logic of phylogenetic priority

The realisation that investigations of phylogeny *must* be prior to investigations of biogeography was probably the fundamental realisation that allowed the emergence of vicariance biogeography, and the reason it could not emerge during ~300 years of biogeography any time before Hennigian phylogenetics (cf. Nelson's (1978) contention that the intellectual roots of vicariance biogeography go back to Candolle).

Inferential priority was first made explicit in 1969:

> As conceived here, a biogeographic analysis implies, logically follows from, and at best can be no more reliable than, a prior phylogenetic analysis.
> (Nelson, 1969, p. 246)

Recent studies of African faunas

Two recent studies have purported to investigate endemism in African faunas: (i) Coe and Skinner (1993), and Turpie and Crowe (1994).

Coe and Skinner (1993) noted that many mammals have distributions more or less continuous between southern Africa and East Africa, some are endemic to one or the other region, and some occur in both but not in the intervening area. These authors proceed to discuss individual instances of distributions, describing past and present environments, and attempting to account for the distributions as consequences of environmental changes. Nowhere did they infer common history by the evidence of endemic distributions of sister taxa. Although they went to great length to discuss a history of environmental change, the emphasis is entirely on equilibrium response, rather than on common distributional history:

> In terms of the total species, the ratio of the numbers recorded in eastern Africa and southern Africa is 369:284, 168 of which exhibit a continuous or disjunct distribution between them, leaving respectively 201 isolates in the north and 116 in the south.
>
> A study of the species that share their distributions between the two study regions is far more instructive, for it demonstrates marked differences between the major mammal groups. Here we note that the insectivores share 39% and 37% of their species respectively, between eastern and southern Africa; bats 48% and 81%; primates 25% and 90%; rodents 35% and 40%; carnivores 80% in both regions and the large herbivores 52% and 84%. What this seems to indicate, in general terms is that the absence of tropical habitats, or those with high primary productivity in the south, results in the fact that many of its species are shared, while those in East Africa are boosted by species that are either restricted to humid or even northern arid habitats.
>
> (Coe and Skinner, 1993, p. 242)

Considering only two regions in a study one can make no relevant statements about historical relationships; one requires a minimum of three regions

demarcation of monophyly being a conclusion of a systematic analysis, as much as it is a prior requirement. These are hypotheses, and as such are not indelible! Research is iterative; new elements of the analysis being added as they become available. The paradox is not an obstacle to further research, though few, if any, studies of endemism meet Harold and Mooi's (1994) stringent requirement of phylogenetic *and* distributional congruence.

2.2 Congruence of distribution: congruence of ecology

The distributions of species within continents often form complex patterns of intersecting regions; the antelope are no exception. In Figure 1(i), I show the outlines of all the species included in the study (see Table 1) on a single map to illustrate the complexity. There is a general congruence of outlines in certain narrow regions, e.g. at the Sahara/Sahel boundary, and the equatorial rain-forest/savanna boundary. However, the complexity is overwhelming and one cannot discern any more detailed patterns in this map beyond a few narrow regions of congruent edges.

Anderson (1994) suggested plotting the geometric centres of each distribution, and looking for clusters of points as indicative of areas of endemism. Figure 1(ii) illustrates that this is of little use; species with cosmopolitan distributions may have the same geometric centres as narrowly endemic ones, distributions that circumscribe the equatorial rain-forest may even have the same centres as ones occurring exclusively in the rain-forest. Such a map indicates little of distributional interest, and nothing about endemism.

"extensive sympatry at some scale must surely be a requirement". These requirements are too restrictive; Harold and Mooi (1994) refer to the different ecological requirements of the diverse groups that should be included in biogeographic analyses as precluding syntopy among species. Similarly, distributional fluctuations preclude sympatry as a defining criterion (Harold and Mooi 1994).

If endemism is not principally a distributional phenomenon, how then can we demarcate areas of endemism for the purposes of further analysis? Harold and Mooi defined an area of endemism:

> [A] geographic region comprising the distributions of two or more monophyletic taxa that exhibit a phylogenetic and distributional congruence and having their respective relatives occurring in other such-defined regions.
> (Harold and Mooi, 1994, p. 262)

This definition leads to two phases of research: the first is basic taxonomic and distributional analysis; the second identifies possible areas of endemism, and tests their historical reality.

They continued:

> There is more to defining areas of endemism than merely looking for congruence of distribution. Most importantly, designated areas are hypotheses, and as such are not indelible. Incongruence in the array of cladograms may be caused by ill-defined areas (e.g., the result of lack of endemism or composite origin) (Platnick and Nelson, 1984). Area delimitations should be reexamined, and the implications for the general area cladogram should be studied. This is analogous to the testing of the homology of characters in phylogenetic analysis, but here we are testing the origins of species distributions
> (Harold and Mooi, 1994, p. 265)

Paradoxically, the demarcation of endemism seems to be as much a conclusion of a biogeographic analysis as it is a prior requirement, much like the

to structure or destructure endemism that I discussed in the introduction: (i) vicariance (in the strict sense, i.e. fragmentation of an ancestral distribution, followed by taxonomic differentiation), (ii) dispersion, (iii) dispersal, and (iv) extinction; or equivalently, by changing (i) to speciation, that add or subtract species from a region (Cracraft, 1994).

It seems that ecological concerns revolve around explaining a dynamic equilibrium as a product of many interacting forces, whereas historical concerns revolve around explaining the way in which general patterns emerge over time; the terms of the phenomenon are similar, e.g. the events that add or subtract species from a region, yet the concepts of process are quite different. Expressed a different way, it seems ecological concerns are with explaining the maintenance of diversity and endemism, and historical concerns are with explaining their origins.

2.1 Endemism as history

Harold and Mooi addressed the definition and recognition criteria of areas of endemism as functional units in a vicariance analysis:

> [A]reas of endemism are fundamentally historical entities, not distributional ones, and their definition should take history into account. General distributional congruence among taxa (e.g., Croizat, 1962) may suggest regions of concentrated endemism, but they are not necessarily relevant to delimiting areas for analysis. Distributional patterns are only sources of biogeographic information in the context of the relationships of the inhabiting organisms.
>
> (Harold and Mooi, 1994, p. 262)

They further criticised Platnick's (1991) contention that areas of endemism are minimally, the "congruent distributional limits of two or more species" and that

(the "mass effect" of Schmida and Wilson 1985).

(Ricklefs, 1989, p. 599, [underlining mine])

Ricklefs (1989) continued to argue that the paradox of contrasting the apparent asymmetry between rates of local and regional processes, with the relative symmetry of their effects, is resolved by considering factors that prolong the exclusion of species to evolutionary, rather than ecological time scales, and so to time scales that approach those of speciation and dispersal. Ricklefs, although at other times critical of ecology (e.g. Ricklefs, 1987) displays here a preoccupation with equilibrium and the ultimate balance of effects, that elsewhere he criticises.

This discussion of diversity is in terms very similar to those used in a recent review of endemism by Anderson (1994). Anderson listed six processes that change the number of species in a given area:

(1) *Splitting of one species in an area into two species* (by whatever evolutionary mechanism). If one (or both) of the resulting species is confined to the area specified (i.e., is endemic thereto), this generally increases both the percentage of endemism and the species density in that area.
(2) *Expansion of the range of an endemic species beyond the area, so that the species is no longer endemic.* This reduces the percentage of endemism but does not change the species density (defined as the number of species present) in this area.
(3) *Contraction of the extralimital part of the range of a species whose range initially extended beyond the area, to such a degree that the species becomes endemic to an area.* This increases the percentage of endemism but, again, does not change the species density in the area.
(4) *Extinction of an endemic species.* Extinction may be regarded as a special case of range reduction to zero. This decreases both the percentage of endemism and the species density.
(5) *Extinction within a specified area of one of the nonendemic species.* This increases the percentage of endemism and reduces the species density.
(6) *Expansion into a specified area of a species whose range was initially entirely outside the area.* This decreases the percentage of endemism and adds to the number of species present.

Anderson (1994, p. 456)

This list, in turn, appears quite similar to the list of four processes that act

2. Areas of Endemism

Like many concepts in biogeography, endemism is a contentious one, and the divisions seem most clearly understood as divisions of ecological and historical biogeography. Researchers in these different fields seem to describe the same biological patterns, but with quite different concepts of process in mind.

The classic literature of ecological biogeography (e.g. MacArthur, 1965; Pianka, 1966; Whittaker, 1972, 1977) explains all of the phenomena of diversity and endemism as processes of dynamic equilibrium; different degrees of these are related to properties of regions, (e.g. environmental stability; harshness; productivity) and to maintenance by the balance of speciation and extinction, or of immigration and emigration.

This tradition continues in the modern literature. Ricklefs (1989), for example, has distinguished between local and regional processes that influence the spatial structure of biological diversity:

> Local processes include various physical disturbances and catastrophes that reduce the number of individuals in populations, stochastic variation, whose force increases as population size decreases, and such interactions between species as competition and predation, which may lead to exclusion of one or more species (MacArthur 1972). These local processes, which tend to reduce diversity, are balanced by long term, regional processes that either facilitate the coexistence of species or bring new species upon the local scene. Movement of individuals between habitats and through the geographic range of the population lessens the probability of extinction or exclusion. As a consequence of such movements individuals may recolonize an area of local extinction or augment a population in a habitat unproductive for the species

methods to derive a factorial weighting scheme to distinguish the effects of ecological similarity, from those of historical contingency, on the widespread distributions of species. I apply the weighting system in a conventional cladistic analysis of a taxon-area matrix. The result is an area cladogram, but one whose terminals are point localities, not areas. I then reconsider endemism and apply the results to the demarcation of areas.

In **Chapter 5,** I attempt briefly to consolidate the findings of the thesis in the broader context of biogeography. I consider some of the strengths and shortcomings of the methods I develop, and briefly consider prospects for future research.

columns covering Africa south of 24°N latitude.

1.4 Overview of the thesis

I have discussed in this chapter the general aims of historical biogeography, and the justification for vicariance methodology. I also argued that widespread taxa share, in general, the same spatial history as vicariated taxa, but without taxonomic differentiation, and that they may be as useful in revealing that history over a short time-frame, as vicars are over an extended time-frame. To make full use of widespread taxa in historical inference we must devise a method to tell the difference between the ecological and historical causes of widespread distributions.

In **Chapter 2,** I review briefly the concept of endemism, drawing a distinction between ecological and historical concepts of endemism. I argue that endemism is more a conclusion of historical analysis than its starting point, and suggest deferring the demarcation of areas of endemism, as the units of historical analysis, till after the historical analysis has been done.

In **Chapter 3,** I review methods for the analysis of distributions, and the spatial modelling of habitats. I reject them all, developing instead my own method. I apply this to species distributions of the African antelope, and present detailed maps of the model outputs for each species. I look briefly for general patterns of spatial similarity by applying a cluster analysis, and map the resulting ecological regions.

In **Chapter 4,** I present a method of historical inference that is based on the vicariance model, but not on current vicariance methodology. I use compatibility

Data Capture

Reay Smithers kindly made the original ink plates prepared for his book available to me. I made photostat copies of these, and scanned the copies using a digital photo scanner (IBM 3117 SCANNER). I then applied edge tracing algorithms to the digital "picture" files to produce a stream of X–Y co-ordinates defining each species range outline.

Conventional equatorial equal area projections of Africa (i.e. Lambert's projection) have the centre of the projection at the equator and 18° East longitude. The scale decreases in concentric circles radiating from this point. The co-ordinate system adopted in this study has its origin at the centre of the projection, and an arbitrary linear scale, equal in the X and Y directions, of approximately one unit per 50 km at the projection centre. This gives 10 590 unit cells, of equal area, covering Africa south of the Sahara which is taken arbitrarily as south of 24°N latitude.

I was unable to identify the projection used by Dorst and Dandelot (1970) but I followed essentially the same procedure, making photostat enlargements of the maps, and then fitting the continental outlines to an equal area projection manually.

Finally, for each of the 71 species, unit cells of the co-ordinate system were given a score of "present" if the cell falls entirely within the species distribution, or a score of "absent" if the cell falls partially (except along continental edges) or entirely outside the distribution. This gives a data matrix of 10 590 rows by 71

African sub-region (south of the Cunene and Zambezi rivers), though he did give the Africa-wide distribution for the 33 species occurring in the sub-region. For species not covered in Smithers (1983) I have used Dorst and Dandelot's (1970) older *Field Guide* for the distributions of a further 38 species. Both of these sources present maps of a boundary line circumscribing the species range.

Estimates of species distributions on a continental scale are clearly inaccurate in many respects. Smithers (1983), and Dorst and Dandelot (1970) compiled extensive bibliographies of source references for distribution data, and it is from these that they compiled their maps. Although there are more recent sources of information covering sub-regions in Africa, and I look forward to improvements in the overall accuracy of available data, I accept for the moment that Smithers (1983), and Dorst and Dandelot (1970) provide the most accurate of any comprehensive data sources covering the whole of Africa.

Taxonomy

I have followed as closely as possible the taxonomic conventions for the family Bovidae established by Honacki et.al., (1982), and modified, where appropriate, according to Meester et.al., (1986). Considering only the African endemic species within the Bovidae, this taxonomy gives account for 9 sub-families, 12 tribes, 28 genera, and 71 species. Table 1 contains further details of the taxonomies of species included in the study.

imposed by undifferentiated distributions. This would leave us free to apply component analysis to the exclusion of widespread taxa, having analysed their distributions independently by the method of ecological induction.

1.3 An African example

Africa, and the African antelope of the family Bovidae, provide a good test case for a detailed exploration of the methods that I develop here. As a landmass, Africa is large, old, and discrete; the bovidae are speciose, almost certainly monophyletic (following Ansell, 1971), and almost exclusively African (see Honacki et.al., 1982); all appealing circumstances for the application of new methods investigating the construction of continental biotas.

The northern continents have complex continental margins, substantial incontiguity, apparently complex histories of biotic interchange, and biotic distribution patterns that have been undoubtedly much disturbed in recent times. Of the great southern continents, Antarctica is biotically depauperate, South America is biotically linked to North America, Australia is linked by archipelagos to Asia, and India *is* Asian; only Africa seems to retain a unique integrity.

Data sources

The most comprehensive source of data for distributions of antelope in Africa is Smithers (1983). East's (1988) compilations for East Africa are not as yet matched for other regions. Smithers (1983) included only species that occur in the southern

If widespread taxa are uninformative, then why not simply ignore them as suggested by Kluge (1988)? If cladogenesis is the overwhelming consequence of vicariance, then what possible relevance do the non-cladogenic components, the titular vicars, of a biota have for investigating vicariance history?; only that failure to respond to vicariance does not mean that the non-cladogenic components do not share the same vicariance history, just that they don't have its *cladistic* signature. Component analysis recognises the unequivocal contribution of the sister group relationships of monophyletic groups of taxa that have members endemic in all the areas being studied. But, then assuming that widespread taxa are *actually* vicars, it proceeds to invent, "out of thin air" as it were (Wiley, 1988a, p. 277) components in all their possible configurations, given one of several more-or-less constraining assumptions.

Ecological induction

At the risk of contributing still further to methodological escalation, I suggest an altogether different approach that I call the method of "ecological induction". Looked at a different way, the problem of widespread taxa is that we cannot tell the difference between the consequences of ecological contingencies on the one hand (dispersion), and historical contingencies on the other (vicariance and dispersal).

If we could develop a method capable of differentiating the historical aspects of biotic distribution, from the ecological aspects, then this would be a powerful addition to component analysis, relieving it of the burden of inference

> is my belief that many wildlife ecologists have often mistakenly confused biological with statistical significance. Multivariate models have generally not yielded great insights into the relationships between population processes and habitat structure.
>
> (Noon, 1986, p. 199)

The correctness of a model, and the procedures commonly used to validate a model should be distinguished: correctness refers to the insights that the model yields about the real phenomenon that the model represents; validation refers to the statistical accuracy and significance of the model output, as measured against a supposedly correct set of observations. In Noon's (1986) sense, a model may have little "correctness", despite being highly "validated".

Group-discrimination models are readily validated because they are always based on an initial set of observations that the model output has simply to replicate. Quite apart from correctness, the models reviewed in the following sections are extremely difficult to validate. We have to ask: validate against what?

Profile construction procedures

In an alternative approach, profile methods attempt to build a description of the habitat of a species from observations of environmental variables at localities of species presence only--a significant departure from discriminant procedures. The profile is then used to classify any locality for which the same habitat predictors are known. The important difference is that putative absence plays no part in the profile construction, and the asymmetry of contingent causes that renders discriminant procedures inappropriate, does not pertain.

Two such procedures have been reported:

all times of observation, i.e. that habitations and habitats are at all times in equilibrium, and (ii) that the predictors considered provide a complete, adequate, and necessary, description of the habitat of the species. Part of the reason for wishing to estimate the extent of suitable habitat for a species is precisely because it is *not* directly observable. These expectations cannot be maintained, and clearly we need a different approach.

Noon (1986) continued his review of methods with a brief discussion of principal component analysis:

> The principal components model is most often used for data exploration. The concepts of dependent and independent variables are not relevant; there is no attempt at statistical inference or tests of hypothesis (sic.); and the data have no group substructure. The researcher seeks one or more linear composites of the data that recapture most of its original variance, but in fewer dimensions. Dimension reduction is straightforward, as the principal components are ordered in terms of the amount of variance they explain. Principal components, as regression equations and canonical variates, can be given biological interpretations in terms of those variables with large associated coefficients.
>
> (Noon, 1986, p. 197)

It seems that ecologists are prevented from using a "data exploration" technique in the context of habitat modelling, because it lacks group substructure, and the concepts of dependent and independent variables, i e. it lacks the properties of group discrimination. This is, however, precisely what we require in procedures for exploring habitats and habitations—I return to PCA shortly.

Model validation

Noon (1986) also discussed the limitations of biometric models:

> At the outset we need to recognize that multivariate techniques are essentially correlational. That is, they do not necessarily yield insights into the true causal relationships that exist between animals and their habitats. It

discrimination procedures that were applied are inappropriate in this case, not because of possible errors in sampling (of used vs. available), but because of errors in the assumption (of used vs. unused = suitable vs. unsuitable).

In support of these procedures, proponents may argue that success in achieving significant between-group discrimination attests to their appropriate use, and that this in turn serves as justification to examine the classification results (Noon, 1986). I suggest instead that the procedures tell us about environmental structure and the differences between sets of localities, but nothing about the habitat relationships of the species under study.

In most cases where significant discrimination for prior group membership is achieved, almost any arbitrary regional subdivision will also achieve significance; this reveals more about the smooth spatial structure of the independent variables, than it does about habitat.

Williams et. al., (1994) have reviewed other methods for the statistical modelling of georeferenced data, including: linear discrimination; non-linear discrimination; decision tree induction; k-nearest neighbour analysis; and neural networks. These are all sophisticated methods, and have been used with varying, but generally high degrees of success (Williams et. al., 1994). A common feature of these methods is the prior classification of a training set of observations of species presence or absence; this renders them inappropriate in the application of habitat modelling.

Between-group discriminant approaches to the study of habitats require (i) that species distributions expand always to fill all appropriate habitat space, at

> interpretation of DFA is in the context of classification. The researcher is interested in determining the probable group membership of an observation given a vector of predictive variables. The two contexts of DFA are often combined; rejection of the null hypothesis of no difference serves as a justification to examine the classification results. Also, given a significant result, the linear canonical functions are interpreted in terms of those variables whose coefficients suggest a strong contribution to group separation. This is the step at which biological inferences are made (see Tatsuoka 1971; Williams 1981, 1983).
>
> (Noon, 1986, p. 197)

Interpreting rejection of the null hypothesis of no difference, as indicative of habitat, assumes *causal* symmetry in prior group membership. However, if the groups are, for example, categories of species occurrence, "present" indicates tolerance, at least, of the habitat parameters that pertain, but "absent" indicates only absence, for what-ever reason. So again the procedure is reasonable only given the implicit assumption of equilibrium of habitation and habitat. Biological inferences based on this kind of group discrimination, will, in general, be false.

The paper by Brennan et. al. (1986) illustrates this point further:

> We measured 15 habitat variables on organism-centered (used) and randomly located (available) 0.02-ha (15-m diameter) plots. Organism-centered plots were obtained by walking transects and using the location of the first quail seen in a covey as the center of a plot. Thus, it is possible our estimate of habitat use may be biased in favor of the habitat structure used by the most conspicuous individuals rather than the entire population. An estimate of available habitat structure was obtained from a random sample of plots stratified by cover type. We acknowledge that the available habitat sample possibly contained an unknown amount of suitable habitat. It was impossible, however, to map the spatial limitation of mountain quail territories to obtain a used/unused habitat contrast.
>
> (Brennan et. al., 1986, p. 177-178)

Thus, an accurate map of the spatial limitation of mountain quail territories *would* allow a used/unused habitat contrast, which in turn would relate exactly to habitat suitability or unsuitability! This assumption cannot be maintained, and the

Group-discrimination procedures

Noon (1986) reviewed the popular methods:

> A survey of wildlife-habitat literature reveals two facts: (1) the past decade has seen a large-scale trend to quantify habitat patterns in terms of multivariate, biometric models; and (2) most biometric approaches have been restricted to multiple regression (MR), discriminant function analysis (DFA), or principal component analysis (PCA). Multiple regression is usually framed in the context of explaining the variance of a dependent variable (e.g., breeding density) by considering its relationship with two or more independent (habitat) variables (e.g., shrub density, tree basal area). The resulting model is a linear function of the independent variables, each weighted by their partial degree of association with the dependent variable. Multiple regression is often viewed as having applications beyond the immediate curve fitting procedure because it can be interpreted in terms of a model that predicts the value of the dependent variable conditioned on a new vector of independent variables. Its appeal to wildlife managers is obvious.
>
> (Noon, 1986, p. 197)

Only the expectations of ecology, where populations move always towards equilibrium with habitats, make this a reasonable procedure. There is no guarantee that a value of 0 for the population parameter taken as the putative dependent variable (e.g. breeding density) is in fact related to the independent variables in any causal way; a breeding density of 0 at some locality, may be quite unrelated to any of the habitat parameters chosen, being perhaps a incidental fact of history, while for a breeding density greater than 0, the habitat parameters chosen are at least tolerable. It is an assumption of the above procedure that every locality is at all times occupied if suitable, and unoccupied always, only if unsuitable; that habitation is in equilibrium with habitat; an assumption that cannot be maintained.

Noon (1986) continued with discriminant functions:

> Discriminant function analysis (DFA) is often framed in the context of testing the null hypothesis of no difference in the position of two or more group centroids in some multivariable space. An equally popular use and

"habitations" may not be in equilibrium with "stations"; that distributions are not mirrors of habitats. Still, Rotenberry (1986) saw the problem as one of a species not being able to track shifting resource abundance fast enough:

> It is usually assumed that natural selection for some sort of optimal habitat response is relatively strong and continuous and that populations are generally in equilibrium with respect to the resources that the habitat provides. But both population and environment vary in time and space, and as variation increases, pressure favoring selection of optimal habitat may not always be intense. Thus, species may not be able to track shifting resource abundance, and population densities may become uncoupled from habitat parameters that otherwise might have influenced changes in population size (Wiens 1977).
>
> (Rotenberry, 1986, p. 217)

The role of contingency, not of what would happen in an equilibrium world, but what did happen, of history, in the structuring of distributions, of biotas in general, is lost. The aims and interests of ecology, are not those of historical biogeography, but the modelling of habitats, when based on observations of distributions, requires some cognisance that distributions are not entirely the consequences of habitats.

3.2 From habitation to habitat

Given some measure of the geographical distribution of a species, its "habitation" in Candolle's terminology, how can we best characterise its "habitat", such that we might estimate the spatial extent of its *potential* distribution, independently of the contingencies that have created its *actual* distribution? In other words, how can we best estimate the spatial extent of habitat, based on an observation of habitation?

(ii) everything has its place; and (iii) everything has a cost. Writing the epigraph for the proceedings of the 1984 symposium, *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates* (Verner et. al., 1986), Thomas (1986) described the whole of biology as leading just to the recognition of these insights (with a fourth for good measure):

> Studies in the realm of biology started with descriptive biology of individual species, then moved on to the examination of interspecific relationships, and from there to consideration of the entire community (i.e., ecology). This led to the recognition, as Barry Commoner (1971) put it, that (i) everything is connected to everything else; (ii) everything has to go somewhere; (iii) there is no free lunch; and (iv) nature knows best.
>
> (Thomas. 1986, p. xix)

Thomas continued:

> As these insights developed and gained widespread acceptance, pressure increased to see this knowledge applied to natural resource management
>
> (Thomas. 1986, p. xix)

This is environmental spiritualism, and it has, if anything, strengthened over the past decades. To put it bluntly, ecology has developed down the road of bio-centrism, to become a sophisticated justification for whatever policy about our environmental indifference.

The 60 papers contained in the *Wildlife 2000* conference proceedings (Verner et. al., 1986) are replete with concerns only of abundance, carrying capacity, and equilibrium. This, despite Thomas' own admonitions regarding modelling:

> "You are dealing only with an essence of what is—nature seen *through a glass darkly*." It is not real—it is but a shimmering image of the moment that will change as the viewer's perspective and need change.
>
> (Thomas, 1986, p. xxii)

Only one of those 60 contributions (Rotenberry, 1986) recognised that

of history.

I find it surprising that ecology, with its strength in numerical analysis, modelling, and estimation, has paid so little attention to the spatial analysis of stations—that at the same time takes cognisance of the historical contingencies implicit in Candolle's concept of habitations. The study of habitats (=stations) in ecology is too often assumed to be synonymous with the study of biogeography, as if habitat is of overwhelming importance in determining actual distributions (=habitations). This has led to the equally incorrect practice of assuming the converse: that the study of distribution is synonymous with the study of habitat.

In this chapter I review some of the methods used by other researchers, and support the claim that little had been done in the field of ecology that is of relevance to historical biogeography. Further, I develop a more rigorous method for the analysis of distributions leading to the spatial estimation of habitats. By this I mean developing a model of the *potential* distribution of a species, as if distributions do depended only on habitat suitability, regardless of distance, disjunction, or any of the other contingencies that influence their actual distributions. The difference between the s, between potential and actual distributions, is of relevance in historical biogeography. However, seeing this difference requires a more rigorous approach to spatial estimation than is current in ecology.

3.1 Ecology, and the eclipse of history

Ecology is the embodiment of three concepts: (i) everything is connected;

3. Habitations and Stations: Distributions and Habitats

> It might not, perhaps, be difficult, to find two points, in the United States and in Europe, or in equinoctial America and Africa, which present all the same circumstances: as, for example, the same temperature, the same height above the sea, a similar soil, an equal dose of humidity, yet nearly all, *perhaps all*, the plants in these two similar localities shall be distinct. A certain degree of analogy, indeed, of aspect, and even of structure, might very possibly be discoverable between the plants of the two localities in question, but the *species* would in general be different. Circumstances, therefore, different from those which now determine the *stations*, have had an influence on the *habitations* of plants.
>
> (Candolle, 1820, cited in Lyell, 1832, p. 68)

> The terms "stations" and "habitations" are not familiar in modern usage. In this combination Candolle used them for the first time. His usage was followed by Lyell, but not by Darwin. Alfred Wallace (1823-1913) used the terms, but he abbreviated "habitations" to "habitats," which today is understood in a different sense—that of Candolle's term "station." Even so, the terms, as used by Candolle, have modern counterparts: ecological and historical biogeography. Ecological biogeography is the study of stations (Candolle's "botanical topography"); historical biogeography, the study of habitations (Candolle's "botanical geography").
>
> (Nelson and Platnick, 1981, p. 365)

That historical and ecological biogeography were distinguished so clearly, so long ago, must be provocative to the modern reader, especially as these continue to be conflated (Nelson and Platnick, 1981). Even more provocative is the realisation that modern ecology, as the study (at least in part) of Candolle's "stations", and Wallace's "habitats", has discovered almost nothing of relevance to the study of historical biogeography. Perhaps this is due to the pervasive bio-centrism in ecology, expressed as a preoccupation with system economies, carrying capacity, competition, optimisation, and equilibrium, but more directly it is due to the eclipse

this in Chapter 4). That the identified areas are well-defined is subject to test by evidence presented in Chapter 4.

Turpie and Crowe (1994) simply equate congruence of distributions (clusters in their analysis), with congruence of ecological requirements, and call it endemism.

2.3 Demarcation deferred

To-date there have been no studies of endemism in Africa that are not overshadowed by assessments of ecological similarity. Historical inference based on these areas is compromised as they may all lack endemic taxa, or be of composite origin (Platnick and Nelson, 1984).

The requirement for endemic taxa and areas of endemism is one of vicariance methodology. Taxa with distributions that are widespread across hypothesised areas of endemism are problematic, and the only unambiguous inference comes from the analysis of the endemic taxa alone. As the methodology that I develop in this thesis concerns exclusively widespread taxa, prior concerns regarding endemism are unnecessary.

In the analysis that follows I propose to use samples of point localities, instead of any prior hypotheses of areas of endemism. Then, with the results, i.e. a cladogram of the historical relationships among localities, I'll return to the question of hypotheses of areas of endemism.

Such areas as are discovered are historical entities, and not merely distributional or ecological ones. Although phylogeny is not considered, and these areas therefore do not meet Harold and Mooi's (1994) strict definition, I do anticipate them to be true reflections of endemic structure (see the discussion of

to say that two are more closely related to each other, than either is to the third; their study is in fact limited to historical scenarios.

Despite their concern for identifying past events to account for current patterns, Coe and Skinner (1993) are concerned more with ecological similarity than with historical process in their explanations of distributional patterns. Their study rests on counting species, and posing scenarios of environmental change, rather than on inferring historical relationship from biogeographic evidence:

> If we are to explain the presence of these disjunct distributions patterns, restricted distributions and local endemicity it is necessary for us to look for the factors which may in part have led to the fragmentation and subsequent coalescence of these areas, not once but several times. At the present state of our knowledge, tectonic activity and climate change would seem to provide the most plausible historical explanation for the isolating factors that must have given rise to the mammalian distributions patterns that we observe today.
>
> (Coe and Skinner, 1993, p. 242)

In the other recent study, Turpie and Crowe (1994) applied quantitative methods to the analysis of distributional patterns. Although their methods are sophisticated, and their scope continental, this study shows the same ecological constraint as the previous one; identified regions have more to do with "faunal zones" of ecological similarity, than with history and the origins of regional biotas.

Turpie and Crowe (1994) used cluster methods to group localities of similar species composition. Although they purport to interpret patterns of distribution, diversity, and endemism, their conclusions were essentially ecological:

> Distributional patterns generally correspond well with those of present-day vegetation types and of resident non-aquatic birds. However, the precise locations of zonal boundaries and the degree of zonation differ between groups, primarily reflecting their different ecological requirements.
>
> (Turpie and Crowe, 1994, p. 19)

directional bias, so all interpolation was performed isotropically.

Summaries of predictor variables

Shaded contour maps of the interpolated mean monthly maximum, and mean monthly minimum temperature (bi-monthly), and monthly total rainfall are presented in Figures 2.1–2.24. These are the 24 predictors that were used in developing the habitat models. Annual rainfall is shown in Figure 2.25, but annual rainfall was not used as a separate variable in addition to the monthly rainfalls.

3.5 Model output

I have calculated habitat models for the 71 species listed in Table 1, using the 24 variables of climate as described above. Table 2 lists the eigenvalues for the first eight of the 24 components of each model, indicating which components were included by the "broken stick" criterion.

Figures 3.1–3.71 show details of the habitat models for each of the 71 species; (i) a contour map shows probability values of the habitat model; (ii) the inset map shows the intersection of the given distribution, and the habitat model at $p \geq 0.2$; (iii, iv, v) show generalised climate diagrams (Walter, 1955) of the regions formed by the intersection in (ii). These climate diagrams are based on mean values for the region, and do not show any multivariate structural analysis as contained in the habitat models; they are presented simply as visual aids to comparisons between species.

0.001 inches with 0.001 inch repeatability and ± 0.010 inch accuracy; well within the 0.1 mm conventional limit of cartographic accuracy. All the data in Jackson's (1961) atlas are presented on azimuthal equal area projections, with the centre of the projection at the equator and 18° East longitude, so transformation to a linear co-ordinate system was straightforward.

Interpolation of irregular data

Spatial interpolation is the procedure of estimating the value of a regional variable at some locality based on observations of that variable at other localities. Spatial interpolation is necessary if one wishes to compare unmatched regional variables on a point by point basis. We wish here to interpolate average values for unit cells on the desired co-ordinate system.

Spatial interpolation can be achieved "optimally" by the method known as "Kriging" (Clark, 1979). The interpolation is optimal in the sense that the result is unbiased and has minimum variance. Also, the variance of the estimates can itself be estimated so the interpolated values can be used with known. I have used this method for interpolating unevenly distributed observations into unit cells of a "flat" co-ordinate system. All interpolation was performed using the GeoEAS software package commissioned by the US Environmental Protection Agency (GeoEAS, 1989). Kriging cross-validation, the procedure of comparing each known value with its kriging estimate, revealed an unbiased and acceptably low average error (<2%, whereas the average error of interpolation using an inverse distance method (Matlab, 1992) was ~10%). A search for anisotropy revealed no consistent

show some of the pattern. Because of this "shortcoming", point locality values are presented at a much higher density (some seven hundred station localities). This puts us in the advantageous position of being able to use more advanced interpolation methods than were available then, with a higher observation density than would have been available otherwise. Furthermore, minimum temperatures are topographically far more complex than mean or maximum temperatures; at the time of day when the maximum occurs the air is usually turbulent, causing a more uniform distribution of surface observations. Minimum temperatures are also thought to be more important with respect to plant and animal habitat relations than are mean or maximum temperatures; so the opportunity to perform the more complex interpolation with data of greater density is significant.

Mean temperatures as presented in the atlas are usually the average of minimum and maximum, and therefore carry no addition information not contained in the information of the extremes; the maps for mean daily temperature can be safely ignored. Mean daily maximum temperature is presented on isotherm maps which also show surface observations for some three hundred major localities; as maximum temperatures are more uniformly distributed and interpolation is therefore less complex I accepted these data as probably the best available.

Data capture

Data capture was achieved using a large electronic flat bed digitiser (GTCO DIGI-PAD) recording the X-Y co-ordinate pair for each observation presented on the map along with its value. This digitiser is reported to have a resolution of

daily minimum temperature. A further eighteen maps show atmospheric conditions of humidity and circulation; six maps show bi-monthly mean humidity mixing ratio and twelve show quarterly contours of millibar surfaces

Of all these, the maps of rainfall are the most comprehensive, though the distribution of recording stations is uneven resulting in maps of uneven quality. In addition to those showing patterns of isohyets, a series of six maps show the monthly distribution of mean annual rainfall for sub-regions of the continent by showing histograms plotted at nearly eight hundred localities. These six maps present the best summary data for rainfall yet compiled for the whole continent.

Temperature proved more difficult to present on a map than rainfall (Jackson, 1961); partly because fewer reliable records were available, and partly because temperature in free air decreases with altitude. Although isotherms of surface temperatures would be the best way to present temperature data, Jackson (1961) found that the low density of observations and the existing methods for spatial interpolation combined to produce unreliable estimates of surface temperatures. He resorted to a rather coarse isotherm interval (5°C), and adjusted surface observations to a standard altitude of 1 250 m using a lapse rate of 0.75°C per 100 m for maximum temperature and 0.5°C for mean temperature.

Attempts to prepare isotherm maps of mean daily minimum temperatures were a failure, as no basis could be found for adjusting surface observations to any standard altitude, and interpolation using the actual observations proved too difficult (Jackson, 1961). Instead Jackson adopted the unconventional device of printing actual i.. ires directly on the map using different colours in an attempt to

the spatial history of the relatively recent African antelope biota (Ford, 1982), I have chosen in this study, to consider only variables of climate as putative predictors of habitat. As I argued earlier, validation of habitat models rests on the success of their application, and not on appeals to "experts" or to spurious "cross-validation".

3.4 Climate data for Africa

Jackson's (1961) *Climatological Atlas of Africa* is a comprehensive data source for the climates of Africa. The atlas was commissioned in 1954 by the *Commission for Technical Co-operation in Africa South of the Sahara* (CCTA [sic.]) and completed in 1961. The CCTA's first and only undertaking, it was intended both as a work of reference on the climates of Africa and as a regional contribution to a *World Atlas* planned by the *World Meteorological Organisation*. (The *World Atlas* was never produced). Thirty years on, and despite the shortcomings noted by Jackson (1961), the work remains the most complete and detailed compilation of climatic information available for the whole continent, the information of remote sensing from orbiting satellites not-with-standing.

The collection contains seventy-two maps devoted to important climatic elements. The maps are presented at scales appropriate to the resolution of the primary information; usually 1 : 15 000 000. Thirty-six maps show patterns in the distribution of rainfall; mean annual, monthly distribution of mean annual, mean monthly, , nd the monthly percentage of mean annual rainfall. Eighteen maps are devoted to temperature; bi-monthly mean daily maximum, mean daily, and mean

response surface, the habitat model, for any region represented by vectors of the predictor variables.

3.3 Design criteria

To attempt to predict the spatial extent of habitat for a species, based on an estimate of current distribution, and some collection of putative predictor variables, implies that one has an expectation that the "predictors" are adequate to make the prediction.

It may seem reasonable to assert that the distribution of large herbivores is strongly dependent on the distribution of acceptable food plants, and that the distribution of these is more strongly influenced by the pluvio-thermic components of climate than by herbivory, and therefore that antelope habitats are well predicted by climatic features. On the other hand, climatic components may be relatively minor factors among those determining actual habitats, principal among which may be factors such as soil nutrients, vegetation cover, or photo-period, or biotic factors such as predation, competition, etc. I suggest that any of these single cause explanations of the limits to a species distribution are in fact based on correlation and temporary association (Walter and Paterson, 1994) and should be accorded no more weight as putative predictors of habitat than any others we may think important.

The purpose of this study is to unlock the historical richness of species distributions by discovering the historically-free potential range. As there is good reason to think that climate change has been the most significant agent affecting

effective method reviewed by Jackson (1993), but his equation of the BS model (Jackson, 1993, p. 2207) is misleading because the eigenvalues are also sensitive to the number of observations in a dataset, yet this is not a parameter of the equation he presented. Estimating the distribution of eigenvalues for randomly generated datasets of the same size as the training set is simple enough. I suggest that one then admit only components whose eigenvalues exceed the mean plus two standard deviations of the estimates, rather than just those that exceed the mean. This ensures that components are admitted only if one anticipates them to be significantly outside the range expected for spurious random covariance (cf. Horn, 1965).

Alternatively, I note that the mean value of the model surface for the sample of "present" observations generally increases as I increase the number of components admitted to the model. The maximum is often reached after many more components are admitted than is indicated by any of the conventional stopping rules. This gives the impression of a "closer" fit to the observed distribution. However, with no evidence to the contrary, we should regard this as an over-interpretation of the model, similar to what can be achieved by a sufficiently large decision tree (see Williams et. al., 1994). If the data surfaces are complex, any arbitrary domain is well recovered, but the model has no statistical support or justification; we should not be led astray from the statistically reasonable, by subjective assessments.

In summary, the model I have developed here takes a training dataset of localities of species presence, and produces a statistically justifiable probability

Stopping rules

There are *n* principal components, but because of the covariance structure of the original *n* variables, the "information" content is generally contained in just the first few components. This is indicated by eigenvalues much greater than one for a few components, and much less than one for most components. To consider those components with small eigenvalues as meaningful would be to over-interpret the model. It is important to determine the number of meaningful components before obtaining probability values.

Jackson (1993) investigated several criteria for such "stopping rules" by analysing the eigenvalue distribution of simulated datasets with known covariance structure. His principal finding was that most commonly used criteria overestimate the number of useful components.

The most popular criterion used in ecology, i.e. Kaiser-Guttman (KG) (Jackson, 1993) admits only components with eigenvalues greater than one, arguing that components with smaller eigenvalues "explain" even less of the variance of the original data than any one of the original variables. The method has been criticised (see references in Jackson (1993)) as even a dataset of random values will produce eigenvalues greater than one, because of spurious covariance structure.

An alternative is the "broken-stick" model (BS) (Jackson, 1993) which estimates the distribution of eigenvalues obtained from random data, and admits only components whose eigenvalues exceed these estimates. This was the most

To apply PCA to the problem of modelling habitats, we first centre and standardise observations from the training dataset, i.e. the distribution of a species, represented by vectors of predictor variables. The matrix of transformed values (column variables, and row observations) is the matrix **U**, and the columns of **V** are then the component loadings for the model. Next, the same centring and standardisation applied to the training set is now applied to the prediction set, i.e. vectors of predictor variables at localities of putative "absence" are shifted and scaled by the means and standard deviations of observations in the training set. If this is the matrix **W**, then **W*V** is the matrix of scores for the habitat model.

The model can be described as first deriving a hyperspace of orthogonal (=unrelated) dimensions containing observations from the training dataset, and then mapping observations from the prediction set into that space. In this observation space, the distance from the multivariate origin to any observation is a measure of its "centrality" in the habitat space defined by the values of observations in the training dataset.

Probability contours, concentric about the origin, can be calculated if the variances on each component axis are first standardised (i.e. divide component scores by the eigenvalues to achieve unit variance). As the sum of squares of n standard normal random variates is distributed as chi-square, with n degrees of freedom, the probability associated with each observation (from either the training or prediction dataset) is obtained by summing the squares of the standardised component scores, and referring to the chi-square probability distribution.

multivariate statistical technique (Jackson, 1993). It is a decomposition of the covariance (or correlation) structure of variables in such a way that the variance structure of observations is preserved. The principal components (PC's) are a set of variables (there are n components, for n original variables) that are constructed out of weighted linear sums of values of the original variables. The PC's are orthogonal (i.e. uncorrelated) and "explain" the total variance of the original variables such that PC1 is the axis of the maximum variance possible on any linear axis through the original variable space, PC2 is orthogonal to PC1, and is the axis of the maximum residual variance, and so on to PCn.

PCA is essentially an eigenvalue decomposition of a covariance matrix. The eigenvalue problem is to determine the nontrivial solutions of the equation $\mathbf{A}v = \lambda v$, where $\mathbf{A}$ is an n-by-n covariance matrix, v is a length n column vector, and λ is a scalar. The n values of λ that satisfy the equation are the *eigenvalues*, and the corresponding values of v are the *eigenvectors* (Manly, 1986). In PCA, the eigenvectors are the component loadings (i.e. the linear weights applied to the observation values to obtain the component scores). If $\mathbf{U}$ is the matrix of observation values who's covariance matrix is $\mathbf{A}$, and $\mathbf{V}$ is a matrix whose n columns are the eigenvectors corresponding to the n values of λ, then $\mathbf{Z}$ is the matrix of component scores given by $\mathbf{Z} = \mathbf{U}*\mathbf{V}$ (Manly, 1986). If $\mathbf{U}$ is first mean centred and standardised to unit variance (equivalent to performing the eigenanalysis on the correlation matrix, instead of on the covariance matrix) then the sum of the eigenvalues is n, and the eigenvalues equal the variances of the columns of $\mathbf{Z}$ (i.e. the variances of the component scores).

being evaluated against the profile is excluded from the "potential" distribution if any one index value falls out of range (and excluded from the "core" if any one index value falls outside the 5th-95th % range).

Both of the profile methods discussed above are essentially non-statistical. Although they use multiple variables, they make no reference to the multivariate structure of those variables, and only superficially to the univariate structure. This makes them at most inadequate, rather than inappropriate; profile approaches are still preferable to discriminant approaches. However, profile methods do produce models that are untestable with reference to observations of distributions. The usual approach to model validation is either to refer to "expert" knowledge, or to employ a procedure of "cross-validation", where "known" values are compared to model values, and the pattern of residuals examined. We have here models with improved "correctness", but with no recourse to the usual statistical procedures of validation.

Model validation in this case must rest in the reliability of its application; in the general congruence of inferred area relationships across taxic groups. I return to this in the next chapter.

In response to the lack of any real statistical basis to either of the profile methods that have so far been reported, I have developed a multivariate statistical approach to profile modelling.

A principal components model of habitat

Principal component analysis (PCA) is the simplest and most commonly used

(i) CLIMEX (Maywald and Sutherst, 1985; Sutherst and Maywald, 1985) is intended principally as a substitute for a population dynamics model. It was developed to provide predictive information in situations where there is insufficient data for the construction of population models. Designed for predicting arthropod habitats in agricultural applications, CLIMEX derives an index of climatic suitability, (ecoclimate index EI) based on climatic data, and estimates of population responses to the combined influences of temperature, moisture, and day length (Norval et. al., 1992). It is a "profile" method, in the sense that it attempts to derive a description of the habitat requirements of a species, but is generally not concerned with the estimation of habitat, from habitatio. . CLIMEX is not applicable to species whose potential for survival and development is not specified *a priori* in terms of temperature and moisture stress (Norval et. al., 1992). (For examples of the application of CLIMEX see Lessard et. al., 1990; Maywald and Sutherst, 1987; Perry et. al., 1990.)

(ii) BIOCLIM (Nix, 1986; Busby, 1991) is another profile method that uses climatic data, this time to derive a series of "bioclimatic indices". The indices are, for example, the mean daily minimum temperature in the coldest month, or, the total rainfall in the wettest quarter, etc. The profile is calculated for a sample of localities where species presence has been observed, and is represented by arbitrary measures of the range of values of the various indices. For example, the profiles reported by Nix (1986) consist of the extremes of index values, and a "core" region lying between the 5th and 95th percentiles of index values. Each index is evaluated independently, without regard for covariance structure; any locality

probability that two character state distributions will be incompatible, given the null hypothesis of the random distribution of their apomorphic states.

The original aim of compatibility analysis, i.e. phylogenetic inference, has in general been a failure (e.g. the "clique" analysis of Estabrook et.al., 1977). It seems that a suitable procedure for implementing tree construction from the results of compatibility tests cannot be found, and the results are always subject to comparison with conventional parsimony anyway, so nothing useful is gained (Farris, 1977).

My use of character compatibility here is to derive a measure of the pair-wise consistency of the distributions of each species in turn, and to relate this to a relative weight that can be applied to the factoring out of ecological similarity, without compromising correlated evidence of historical pattern.

I first calculate the total number of pair-wise incompatibilities for each species, and then the sum of the probabilities of pair-wise incompatibility for each species. This is done independently in the two matrices of potential and actual distributions. In other words, I calculate the number of observed and expected incompatibilities for each species, compared pair-wise with every other species.

The ratio of these numbers for each species is a measure of its mutual consistency with all other species distributions: values near 0 indicate high consistency; values near 1 indicate low consistency; values much greater than 1 indicate positive inconsistency (i.e consistency increases as incompatibility decreases).

Consistency then refers to the complement of average incompatibility (the

weighting scheme that achieves the separation of pure ecological pattern, from the complex composite of causes that form the actual distributions of species. I anticipate that a weighting scheme that can be applied in standard cladistic methodology is the only effective approach to achieving the desired kind of ecological factoring, that leaves intact the correlated evidence of history.

It is difficult to imagine how such a system can be evaluated though, other than by the increasingly corroborated pattern resulting from the steady accumulation of data from diverse taxa. However, I suggest that we can proceed with growing confidence, if at each step the cladistic resolution of the weighted system of characters improves over that of the unweighted system.

We can reasonably anticipate that the endemic structuring of vicariance will persist in the patterns of real distributions, in excess of any apparent spatial structuring due only to ecological similarities among areas. So the cladistic resolution of historical patterns should be more highly resolved than purely ecological patterns.

Character compatibility

Compatibility analysis is the pair-wise comparison of character state distributions across a set of taxa. Compatibility means that both characters of a pair are consistent with the single origin of each of their apomorphic states. Incompatibility means that at least one of the characters must have multiple origins.

LeQuesne (1969) described a formal procedure for discovering character pair incompatibilities, and LeQuesne (1972) derived an equation for the exact

Factoring out the pattern of area relationships indicated by potential distributions, from that indicated by actual distributions, leaves the residual pattern of vicariance history.

Why not consensus?

In an earlier analysis (Caithness, 1994) I used cladistic methods to analyse the patterns of actual and potential distributions, and then applied consensus techniques to remove all evidence supporting common features of pattern from the data of actual distribution. I then reanalysed the sparse matrix to infer historical area relationships.

The intent was to remove the influence of ecological similarity from the evidence of geographic distribution, leaving just the influence of history. The problem is that these different influences do not fall into neat orthogonal partitions, and hence cannot be simply separated.

The procedure of removing all evidence that supported the consensus pattern was too severe. It removed also all evidence of correlated pattern, leaving only those aspects of historical pattern that were orthogonal to all others. An alternative procedure is required that will remove only the aspects of "non-history", rather than leaving only the aspects of "non-ecology".

Factorial weighting

What are the prospects for developing such a factoring system? Character compatibility (Meacham and Estabrook, 1985) provides the theoretical tools for a

accompanied by a shadow pattern of many widespread distributions (Cracraft, 1994). This may be especially marked over a near time-frame, since the pattern will be progressively lost over longer time-frames as taxonomic differentiation accumulates, and new cycles of vicariance overlay older ones.

However, dispersion confounds the application of a simple cladistic methodology. The simultaneous dispersion of multiple species destroys endemic structuring and produces correlated homoplastic similarity between areas (cf. Cracraft, 1994). Cladistics is rendered ineffective, as the result is a conflation of vicariance history, ecological similarity, and geographic proximity (Humphries, 1989); the correlated effects of dispersion need to be factored out before cladistic methods can be applied effectively.

The procedure I develop here is essentially not a vicariance method in the strict sense, as it makes no reference at all to the information of phylogeny, though it is still based on the vicariance model. Instead, I address explicitly the distributions of widespread taxa as the "shadow markers" of vicariance history.

4.2 Factoring ecological similarity

I have discussed at length the development of habitat models that distinguish the ecological potential of a species distribution, from its actual distribution. Taken collectively, the habitat models represent biogeography free of history, as if only ecological similarity has an influence on where populations of a species occur. In contrast, actual distributions are a composite consequence of all the factors that influence biogeographic form-making. The two are therefore partially correlated.

Form-making in phylogeny is overwhelmingly of just two kinds: (i) similarity by relationship (homology), and (ii) similarity by independent evolution (homoplasy). The process that represents common cause of the first kind is cladogenesis: sister taxa share entire suites of characters inherited from a common ancestor in a single event. There is no process of common cause of the second kind: each and every homoplasy is marked by a particular event, and we have no expectation that homoplasies covary in any significant way. Cladistic methodology in this case will confidently recover the historical pattern of taxon relationships.

Form-making in biogeography is of the same two kinds, but there are *three* processes that account for them: (i) vicariance, (ii) dispersal, and (iii) dispersion. With just the first two, cladistic methodology would be appropriate, but the addition of the third is problematic. In the cladistic formulation of PAE (Rosen 1988, 1992), areas are taxa, taxa are characters, and cladogenesis results in autapomorphic characters, i.e. derived taxa unique to their areas of occurrence. Several processes promote increasing cosmopolitanism, i.e. increasingly widespread distribution, following cladogenesis. Vicariance (here in the loose sense of range fragmentation *not* accompanied by cladogenesis) produces homologous similarities between areas; dispersal (without cladogenesis) produces homoplastic similarities between areas. With only these two processes, cladistic analysis of a simple taxon-area matrix would recover spatial history as effectively as cladistics recovers phylogeny.

It seems quite reasonable that vicariance proper, will in general be

addition of new data of sister taxa, a criticism that echoes Platnick and Nelson's (1988) criticism of spanning-tree biogeography! Cracraft summarised the practice as follows:

> The bottom line is that a widespread species does not carry any intrinsic information about area-relationships, so why not ignore them altogether, as Kluge (1988) suggest, rather than introduce potentially spurious data into the analysis? One answer given by component analysis is that it seems preferable not to ignore data but to attempt to reconcile conflicting area-cladograms when those conflicts are derived from potentially "false" areas contributed by widespread (or missing) species. One difficulty with th ter approach, however, is that any so-called resolution of area-relationships will remain equivocal until adjudicated by phylogenetic analysis of endemic taxa.
>
> (Cracraft, 1988a, p. 226)

In alternative procedures, Kluge (1988) and Wiley (1988a) have suggested coding of the taxon cladograms in a binary matrix, followed by cladistic analysis to find the corroborating evidence of repeated pattern, instead of using the consensus among individual area cladograms. Here areas are considered analogous to taxa, and taxic relationships analogous to characters (Cracraft, 1988a). These procedures use explicitly the information of phylogenetic analysis, while widespread taxa are treated as either special cases (under assumption 0 by Wiley (1988a)) or as irrelevant (treated as missing data by Kluge (1988)).

Common cause and correlated effects

How is it that cladistic methods can be applied to collections of taxa and observations of their characters, and provide confident inference about relationships, whereas the same methods cannot be applied to directly collections of areas and observations of their taxa? To answer this I must discuss the different kinds of "form-making" in phylogeny and biogeography.

across the areas being studied. Finally, a general area cladogram is constructed from the consensus of all the individual area cladograms; this is the final estimate of area relationship.

To apply component analysis one must already have taxon cladograms, areas of endemism, and lists of taxa present in those areas. Taxon cladograms are converted into area cladograms by replacing terminal taxa with their areas of endemic occurrence. The general area cladogram represents the corroborated evidence of relationship, i.e. the consensus among individual area cladograms is the evidence of repeated pattern.

Sister groups of *endemic* taxa are unproblematical, but widespread taxa are dealt with by applying one of several assumptions about their occurrence.

- *Assumption 0* (Zandee and Roos, 1987): areas sharing the same taxa are monophyletic (Page, 1988).
- *Assumption 1* (Nelson and Platnick, 1981): whatever is true of one occurrence of a widespread taxon is true of the other occurrences of that taxon (Page, 1988); i.e. the areas of widespread occurrence are constrained to be monophyletic or paraphyletic on the area cladogram (Wiley, 1988b).
- *Assumption 2* (Nelson and Platnick, 1981): whatever is true of one occurrence of a widespread taxon need not be true of the other occurrences of that taxon (Page, 1988); i.e. the areas of widespread occurrence may be monophyletic, paraphyletic or polyphyletic on the area cladogram (Wiley, 1988b).

These special treatments of widespread taxa are always subordinate to the

4.1 Vicariance and the problem of widespread taxa

Humphries (1982) has stated that vicariance biogeography is the search for an epistemology comparable to the cladistic analysis of taxa. The analogy involves exchanging taxa with areas, and characters with sister groups of taxa (Zandee and Roos, 1987). This is significantly different from Rosen's (1988, 1992) "parsimony analysis of endemicity" (PAE), which simply exchanges taxa with areas, and characters with taxa (i.e. not with *sister* relationships).

PAE produces area cladograms of sample localities directly from geographical distributions (Rosen 1988), and thus discards the most fundamental requirement of vicariance methods: the information of sister groups contained in a phylogenetic analysis (Humphries, 1989). PAE is an analysis simply of the degree to which taxa are widespread, conflating the different causes of widespread distributions in such a way as to render a cladistic analysis historically meaningless.

Repeated pattern

Vicariance biogeography is the search for patterns of sister taxa occurring in different areas of endemism. When these patterns are found repeatedly, biogeographers infer close historical relationships among the areas (Nelson and Platnick, 1981; Humphries and Parenti, 1986).

Component analysis (Nelson and Platnick, 1981) is one procedure that can be used to find the patterns and make the historical inferences. It proceeds by first constructing separate area cladograms for each monophyletic group distributed

4. Historical Inference by Ecological Induction

Induction is to draw general inference from particular instances (Fowler and Fowler, 1969). In Chapter 3, I presented particular instances of habitat models, and looked briefly for general patterns of the kind indicated by measures of similarity (e.g. the UPGMA analysis shown in Figures 5 and 6) In this chapter I present an analysis of a different kind of general pattern, the kind from which we can infer history.

The current dominant methodology for historical inference in biogeography is based on the model of vicariance: the fragmentation of once continuous species distributions, and the subsequent taxonomic differentiation of the disjunct populations. Vicariance biogeographers use the ordering of phylogeny to infer the historical ordering of space. The treatment of widespread taxa is problematic though (Craoraft, 1988a; Kluge, 1988; Page, 1988; Wiley, 1988a) as these lack the essential phylogenetic information on which the inference is based: sister group relationships of taxa in different areas of endemism.

Here I present a method of historical inference based on induction from the accumulated ecological data of habitats, and use it to analyse the distributions of widespread species under the model of vicariance, but independently of the information of phylogeny.

"historically-free" potential distributions. Their value lies in their collective contribution to the discovery of historical patterns.

equate them with areas of endemism.

I have applied similar clustering techniques (UPGMA; Statistica, 1993) to the habitat models and report a striking similarity with Turpie and Crowe (1994). This is all the more striking because the information I used is quite different; Turpie and Crowe (1994) used the information of species occurrence in cells of a mesh-grid sub-dividing Africa into 160 cells, i.e. a species-area matrix; I used 120 eigenvectors of the first 5 principal components of the habitat models (see Table 3), i.e. a species-eigenvector matrix. The UPGMA tree is shown in Figure 5. On the tree I identify 19 clusters, calculate the mean value of the habitat models for each cluster of species, map the maximum values, and finally identify regions by the maximum clusters (see Figure 6).

This analysis, like Turpie and Crowe's (1994) is "phenetic biogeography". The patterns discovered are patterns of "affinity", resulting from a search for similarity; if one wants to interpret affinity, then the methods are appropriate. But interpret the pattern in comparison to what? The pattern is devoid of process!

In an alternative way of seeing, historical biogeography is the search for corroborated patterns of "relationship" among areas; these patterns are indicative of common cause. The search for historical pattern leads ultimately to the synthesis of spatial and genealogical process. If the results of phenetic biogeography are to be interpreted at all, it will be with reference to this historical synthesis of process.

The habitat models that I have presented show the spatial extent of habitats, and allow comparisons of actual distributions with estimates of

3.6 General patterns and ways of seeing

Particular instances of anything are interesting only in so far as one can detect a relationship to general patterns. Only by comparison can the nature of a particular instance be understood and interpreted. For things in the real world, there are usually many ways of seeing general patterns, and what one sees is largely dependent on the way one looks.

In Figures 4.1-4.5, for example I show the total number of species (diversity) for each of the five regions shown in Figures 3.1-3.71, (i.e. red, blue, green, blue + red, blue + green). These are the simplest summaries of the combined information of the actual distributions and the habitat models that I can imagine. Inspecting these patterns one asks several obvious question. Why is the highest concentration of diversity centered in East Africa? Why is there not a comparable concentration in western equatorial Africa? Why do the montane forest regions in eastern and southern Africa have diversity nearly equal to the surrounding regions, while the habitat models indicate much lower diversity? Why is South Africa so depauperate? These simple question are all comparative, but the general patterns depicted in the maps provide no answers.

One often employed way of looking for general pattern in complex data is cluster analysis. Turpie and Crowe (1994) for example, employed clustering techniques to detect general patterns in the distributions of large mammals in Africa, and reported a general similarity with the patterns of vegetation (e.g. White, 1983). They interpret these clusters as indicative of "faunal zones" and

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Ecology and biogeography: phenetics and systematics

In ecology, relationship means that two things are the same—in systematics, relationship is a statement about *when* two different things *were* the same. In this sense, ecology is phenetics, and biogeography is systematics.

The model of vicariance in biogeography is wider in scope than current vicariance methodology. We need to explore further the implications for both systematics and biogeography of the shared analogy of vertical (genealogical) process, and horizontal (reticulation) processes, i.e. the synthesis of patterns of form in time (systematics), and patterns of space in time (biogeography), united as macroevolutionary process.

phylogeny, and is applicable in vicariance methodology. I suggest that the areas identified by the method of ecological induction (Figure 8) are equivalent.

The results of analysis by conventional vicariance methods, should be congruent with these, only to the extent that relationships in the near time-frame are the same as those on the far time-frame. As these overlap to a greater or lesser degree, a general congruence is expected, and differences can be interpreted as relating to different time-frames.

Shortcomings and future research

I have argued that the increase in the resolution of relationship that results from applying a system of ecological weighting in a cladistic analysis of areas is compelling evidence in support of the method. However, the statistical properties of the result are unknown.

The weighting system is derived from the model of character compatibility (Meacham and Estabrook, 1985). The null hypothesis of that model is the random distribution of apomorphic states. This seems a severe assumption for the character of species distributions. A more appropriate null model would involve the absence of systematic structure between species distributions, but individually distributions would be more or less structured, i.e. continuous in space. An improved null model for distributional compatibility should allow an assessment of the confidence interval of increased tree resolution.

ecological potential, as if distributions have no vertical structure, only the horizontal structure of ecology.

The method derives a weighting scheme based on character compatibility (Meacham and Estabrook, 1985) that can be applied in conventional cladistic analysis of a species-area matrix. The success of the method is evidenced by the increased resolution of area relationships based on the weighted characters, over the unweighted species-area matrix.

This is a compelling result: (i) there is an intrinsic structure in the ecological potentials of species distribution; (ii) the weighting of characters systematically removes this structure from consideration; (iii) the resolution of the area relationships of the residual pattern *increases*.

The pattern of historical area relationships created by vicariance is hierarchical, the patterns of area affinity due to ecological similarity are probably not (see for example White, 1983, p. 42). The higher resolution of the tree of relationships that results from removing whatever independent ecological patterns are displayed, argues compellingly that this is indeed a way of looking at history.

We should recognise the different kinds of patterns shown by cladistic and phenetic biogeography (e.g. Turpie and Crowe, 1994), and proceed to interpret them in the context of congruence or difference.

Areas of endemism

Harold and Mool (1994) presented a concept of endemism that is historical rather than purely distributional. Their strict definition includes consideration of

biogeography: history is characterised by the vertical structuring of vicariance; ecology is characterised by the horizontal destructuring of endemism. In phylogenetic analogy: vertical structure is created by cladogenesis; horizontal destructuring is promoted by genealogical reticulation. In phylogeny, reticulation is constrained to low levels of genealogy and cladogenic pattern persists; in biogeography, reticulation is unconstrained and vicariance history is constantly rewritten.

Time-frames

The overlaying of cycles of vicariance and cosmopolitanism, by newer cycles that partially rewrite history, and overlay old patterns with new ones, means that time-frames become relevant.

Vicariance of cosmopolitan biotas is accompanied by a shadow pattern of widespread species: those *titular* vicars that fail to respond by cladogenesis. This shadow pattern will decay over time due to the slow accumulation of taxonomic divergence. Vicariance then presents patterns in different time-frames, and different methodologies can investigate these independently.

The conventional methodology of vicariance biogeography (Nelson and Platnick, 1981; Humphries and Parenti, 1986) addresses a far time-frame, the near limit of which is set by taxonomic divergence.

I have developed in this thesis a complementary methodology of ecological induction that addresses vicariance history over a near time-frame. The approach rests on telling the difference between the actual distribution of a species, and its

5. Conclusions

> [H]ypotheses about the history of organisms in time are tested by statements about their attributes, ... hypotheses about the history of organisms in space are tested by statements about their history in time.
>
> (Nelson and Platnick, 1981, p. 6)

The model of vicariance is a powerful one, leading to the methodology of vicariance biogeography, and the primacy of phylogeny in biogeographic inference (Humphries, 1989). Careful consideration of the model leads to an understanding of the structuring of biotas in space. Alternating cycles of vicariance and increasing cosmopolitanism result in endemism and regionally distinct biotas (Cracraft, 1988a). The ordering of space by vicariance is written in the phylogenies of endemic taxa.

Biotic structuring by vicariance is opposed over time by the destructuring of endemism, promoted by dispersal, dispersion, and extinction (Cracraft, 1994). Endemic destructuring is principally the result of area reticulation.

Species reside at the boundary between genealogical divergence and reticulation (Baum and Shaw, 1995). However, there is no such persistent boundary in the history of areas; biogeographic reticulation destroys endemic structuring at any level of the area hierarchy, and structure persists only to the extent that vicariance is historically constrained by the prior structure of biotas (Cracraft, 1994).

History and ecology occupy different ontological positions in

the same, i.e. the hierarchical relationships of the cladogram are the hierarchical relationships of endemism. In Figure 8 I have shown the major features of the hierarchy that can be depicted as coherent regions.

The most striking feature is the intersection of sister relationships between the north and south savannas, and the east and west montane regions of the Great Rift. This is also the region of highest antelope diversity (see Figure 4.4).

In a speculative scenario one can imagine cyclical phases in which a continuous east-west tropical biota is bisected by the coalescence of a north-south savanna biota, which in turn is bisected again by the coalescence of the east-west biota, and so on. If cycles of vicariance are repeated in the same spatial setting, then older endemism, and older sister relationships, are not necessarily eroded by newer ones, but augmented by them.

Are there places where the near and far time-frames show general congruence, in contrast to other places where they do not? I predict that the north-south/east-west intersecting relationship is the most fixed of features of many African taxonomic groups, and is fundamental to the origin of East African diversity. As always, the test lies in the discovery of repeated pattern in diverse taxa.

I then repeated the analysis on unweighted data (*ccode /[+.; mh; bb; n;*). This found in excess of 100 trees (length = 129; ci = 36; ri = 74). The consensus tree is shown in Figure 7(ii).

The tree from the unweighted analysis has 28 unresolved polychotomies, while the tree from the weighted analysis has just 18. This indicates a much higher level of agreement among the trees in the weighted analysis. The improvement in the consistency index (ci) also indicates a higher level of agreement among the characters relative to the trees. These finding are compelling evidence that the weighting system is indeed factoring out the influence of ecological similarity, and that the resulting cladogram can be interpreted as corroborated evidence of area relationships.

4.4 Areas of endemism

I ended Chapter 3 with a discussion of pattern, and ways of seeing. I distinguished phenetic (ecological) biogeography from historical biogeography on the basis of the kinds of patterns each chooses to look for: patterns of affinity, or patterns of relationship. The former is a way of seeing that is limited to pattern without process. The model on which phenetic pattern recognition is based (i.e. measures of similarity) is timeless, hence there can be no inference of process. The latter is based on a model of pattern in time, and is directly relevant to inference of process.

Endemism is a concept based on history (Harold and Mooi, 1994). The model of ecological induction that I have used to infer the relationships among localities (Figure 8) is based on the model of vicariance. The two are fundamentally

Character weighting

I have calculated observed and expected numbers of incompatibilities for each species in the matrices of actual (o_1, e_1) and potential (o_2, e_2) distributions. The ratios ($c_1 = o_1/e_1$, and $c_2 = o_2/e_2$) are the consistency scores. Factorial weights were calculated, and rescaled as above (w, and W). All these values are presented in Table 3.

Missing values indicate undefined values resulting from division by zero ($e_1 = 0$, or $e_2 = 0$). These are autapomorphic characters (the taxon occurs at only one locality) and are uninformative. There are 24 autapomorphic cases, leaving 47 informative characters for cladistic analysis.

Values of c_1 or c_2 much greater than 1, indicate positive inconsistency, and values of w are ill-formed in these cases. This occurs in only one case in the matrix of potential distributions (*Gazella granti*; row 13 of Table 3), which is also autapomorphic in the matrix of actual distributions, so the case is not problematic.

Overall consistency values do indicate a higher level of consistency among taxa in the matrix of actual distributions ($C_1 = 0.5372$; and $C_2 = 0.6136$).

Tree searching

Cladistic analysis was performed using the computer program *Hennig86* (Farris, 1988) implementing the *ccode* option to apply the weights, and *mh; bb;* to carry out tree searching. This found 11 minimum length trees (length = 4638; ci = 38; ri = 77). The strict consensus tree (found by *n;*) is shown in Figure 7(i).

These are simply the total number of incompatibilities, over the sums of the probabilities of incompatibility, for *all* species. They provide measures of the overall consistency within each data matrix, but are of no special consequence or meaning in the analysis. What really matters is the consistency of characters relative to a particular tree, which we have not yet considered.

4.3 Cladistic analysis of antelope distributions

I have selected 70 point localities (Figure 8), chosen to give reasonable cover of the major features of the UPGMA cluster map shown in Figure 6, and constructed two species-by-locality matrices:

(i) *actual distributions*; the region **a** (blue + red in Figure 3) is the given species distribution in the source data (Dorst and Dandelot, 1970; Smithers, 1983), but I have taken the region $\mathbf{a} \cap \mathbf{p}$ (blue) as a more reliable estimate of actual distribution. Excluding the region $\mathbf{a} \cap \bar{\mathbf{p}}$ (red) seems warranted by comparing these data with East's (1988) compilation for East Africa. Many of the antelope occurring in East Africa are seen on inspection of the maps to be absent from many of the "red" regions (see Chapter 5).

(ii) *potential distributions*; the region **p** (blue + green in Figure 3) is the region contained within the $\mathbf{p} \geq 0.2$ contour of the habitat model. This indicates the extent of the potential species distribution.

The two matrices then contain integer values (0 and 1) denoting absence or presence of 71 species, at 70 localities.

total number of incompatibilities over the total number expected, rather than the total number possible), and incompatibility refers to partially overlapping distributions. Incompatible distributions are indicative of probable homoplastic origin; compatible distributions (nested, or disjunct) are indicative of possible homologous origin.

If o_1 and e_1 are the observed and expected numbers of incompatibilities for the actual distributions, and o_2 and e_2 are the same for the potential distributions, then c_1 and c_2 are vectors of consistency scores for taxa in the matrices of actual and potential distributions:

$$c_1 = o_1 / e_1$$

and

$$c_2 = o_2 / e_2$$

I then derive a vector of factorial weights w:

$$w = |1 - c_1| - |1 - c_2|$$

($-1 \geq w \geq 1$, except for cases of extreme positive inconsistency)

Rescaling and rounding w to give integer values W in the range $1 \geq W \geq 100$ provides a suitable weighting scheme that can be applied in conventional cladistic analysis (e.g. Farris, 1988).

Comparing the overall consistency values for the two matrices can give a prior indication of what to expect:

$$C_1 = \Sigma o_1 / \Sigma e_1$$

and

$$C_2 = \Sigma o_2 / \Sigma e_2$$

Table 1. Species included in the study. The table shows division by sub-family and tribe. The last column on the right indicates the source of the distribution data (SM for Smithers (1983), and DD for Dorst and Dandelot (1970)).

Sub-family: **Aepyceritinae**			
01 *Aepyceros melampus*	(Lichtenstein, 1812)	Impala	SM p.647
Sub-family: **Alcelaphinae**			
02 *Alcelaphus buselaphus*	(Pallas, 1766)	Red hartebeest	SM p.608
03 *Connochaetes gnou*	(Zimmermann, 1780)	Black wildebeest	SM p.601
04 *Connochaetes taurinus*	(Burchell, 1824)	Blue wildebeest	SM p.603
05 *Damaliscus dorcas*	(Pallas, 1766)	Bontebok and Blesbok	SM p.613
06 *Damaliscus hunteri*	(Sclater, 1889)	Hunter's hartebeest	DD p.228
07 *Damaliscus lunatus*	(Burchell, 1823)	Tsessebe, Topi	SM p.617
08 *Sigmoceros lichtensteini*	(Peters, 1852)	Lichtenstein's hartebeest	SM p.606
Sub-family: **Antilopinae**			
Tribe: **Ammodorcadini**			
09 *Ammodorcas clarkei*	(Thomas, 1891)	Dibatag, Clarke's gazelle	DD p.233
Tribe: **Antilopini**			
10 *Antidorcas marsupialis*	(Zimmermann, 1780)	Springbuck	SM p.627
11 *Gazella dama*	(Pallas, 1766)	Addra gazelle	DD p.236
12 *Gazella dorcas*	(Linnaeus, 1758)	Dorcas gazelle	DD p.239
13 *Gazella granti*	(Brooke, 1872)	Grant's gazelle	DD p.238
14 *Gazella leptoceros*	(Cuvier, 1842)	Rhim, Loder's gazelle	DD p.244
15 *Gazella rufifrons*	(Gray, 1846)	Red-fronted gazelle	DD p.245
16 *Gazella soemmeringi*	(Cretzschmar, 1826)	Soemmering's gazelle	DD p.237
17 *Gazella spekei*	(Blyth, 1863)	Speke's gazelle	DD p.245
18 *Gazella thomsoni*	(Gunther, 1884)	Thomson's gazelle	DD p.246
19 *Litocranius walleri*	(Brooke, 1879)	Gerenuk	DD p.232
Tribe: **Neotragini**			
20 *Dorcatragus megalotis*	(Menges, 1894)	Beira	DD p.267
21 *Madoqua guentheri*	(Thomas, 1894)	Guenther's dik-dik	DD p.267
22 *Madoqua kirki*	(Gunther, 1880)	Kirk's dik-dik.	SM p.634
23 *Madoqua saltiana*	(Desmarest, 1816)	Salt's, Phillips'dik-dik	DD p.268
24 *Neotragus batesi*	(De Winton, 1903)	Bates' pygmy antelope	DD p.260
25 *Neotragus moschatus*	(Von Dueben, 1846)	Suni	SM p.645

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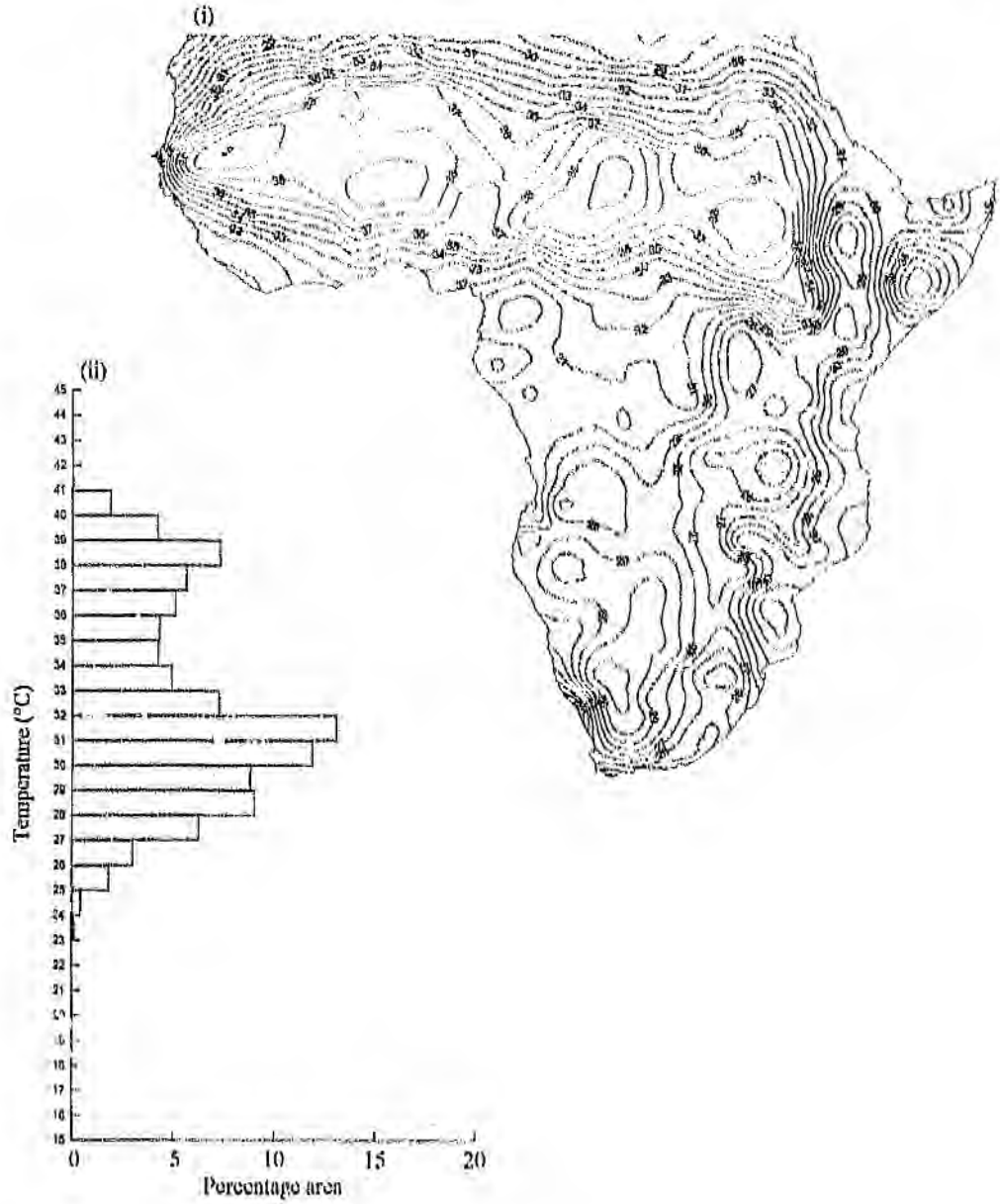


Figure 2.2. Mean Daily Maximum Temperature: March, (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

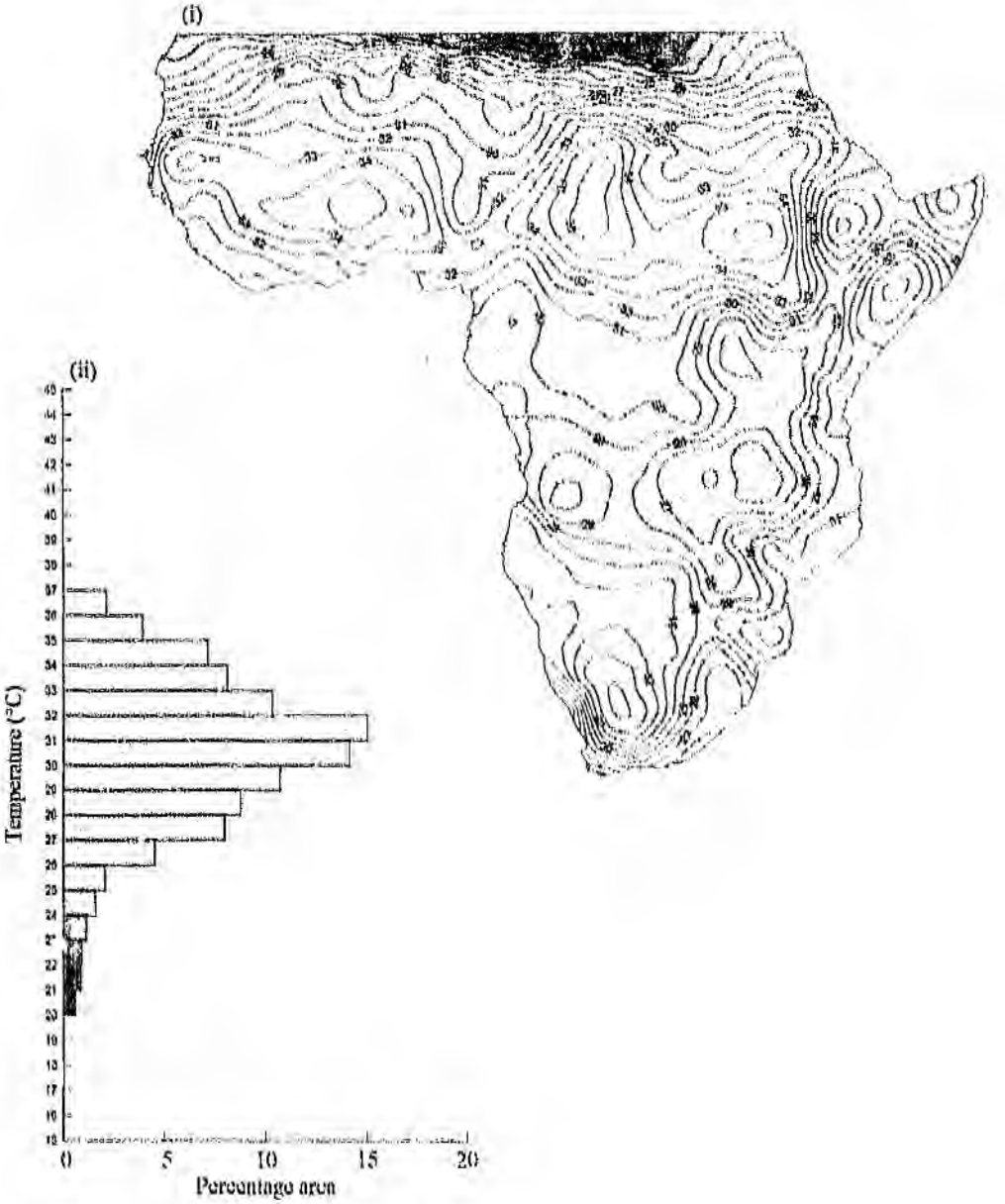


Figure 2.1. Mean Daily Maximum Temperature: January; (i) contour map of surface isotherms, (ii) histogram of percentage area by contour level.

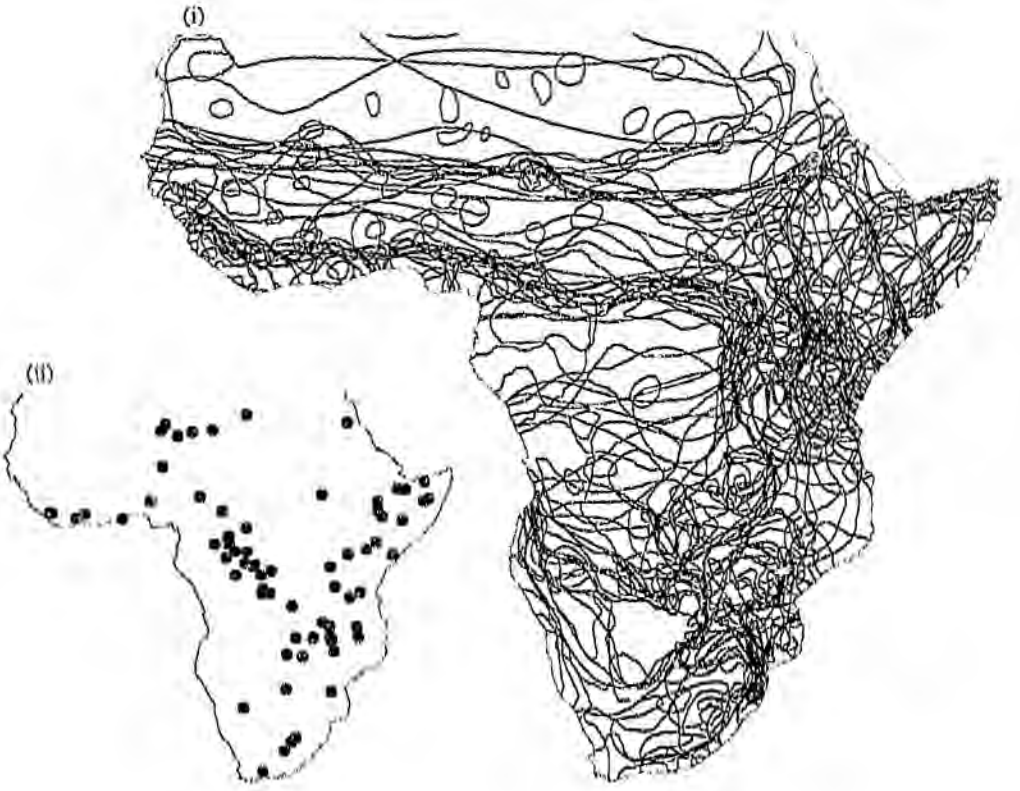


Figure 1. (i) Overlay of distribution outlines of all species included in the study (see Table 1); (ii) the geometric centres of each distribution (see Anderson, 1994).

Figures

Table 3. (Cont.)

	o_1	e_1	c_1	o_2	e_2	c_2	w	W
55	11	25.0342	0.4394	39	49.8075	0.7830	0.3436	71
56	23	40.0213	0.5747	51	61.1255	0.8343	0.2597	61
57	0	26.6251	0	4	48.2334	0.0829	0.0829	40
58	27	31.6039	0.8543	50	60.5295	0.8260	-0.0283	27
59	12	18.9262	0.6340	32	48.2334	0.6634	0.0294	34
60	2	21.2348	0.0942	5	44.3398	0.1128	0.0186	33
61	13	26.6251	0.4883	45	60.1068	0.7487	0.2604	61
62	6	16.2392	0.3695	34	44.3398	0.7668	0.3973	77
63	1	13.0087	0.0769	3	25.3609	0.1183	0.0414	36
64	7	8.7043	0.8042	36	49.8075	0.7228	-0.0814	21
65	12	29.3516	0.4088	27	53.4962	0.5047	0.0959	42
66	0	0		16	25.3609	0.6309		
67	0	0		4	16.9400	0.2361		
68	8	8.7043	0.9191	34	38.9883	0.8721	-0.0470	25
69	21	28.0562	0.7485	38	51.1905	0.7423	-0.0062	30
70	0	0		11	31.0918	0.3538		
71	11	26.6251	0.4131	38	56.0830	0.6776	0.2644	62

Table 3. (Cont.)

	o_1	e_1	c_1	o_2	e_2	c_2	w	W
26	0	0		0	0			
27	22	30.5296	0.7206	34	58.8282	0.5780	-0.1427	14
28	25	33.4821	0.7467	51	60.1068	0.8485	0.1018	43
29	19	29.3516	0.6473	41	57.3732	0.7146	0.0673	39
30	0	0		0	0			
31	13	18.9262	0.6869	31	51.1905	0.6056	-0.0813	21
32	25	37.4317	0.6679	42	61.0292	0.6882	0.0203	33
33	27	32.5852	0.8286	47	60.1068	0.7819	-0.0467	25
34	0	0		27	35.4707	0.7612		
35	0	0		13	35.4707	0.3665		
36	9	18.9262	0.4755	20	48.2334	0.4147	-0.0609	24
37	11	13.0087	0.8456	42	46.4286	0.9046	0.0590	38
38	25	39.8248	0.6277	42	61.0895	0.6875	0.0598	38
39	15	25.0342	0.5992	36	56.0830	0.6419	0.0427	36
40	18	31.6039	0.5696	33	53.4962	0.6169	0.0473	36
41	0	0		8	41.8939	0.1910		
42	0	0		14	46.4286	0.3015		
43	2	16.2392	0.1232	12	38.9883	0.3078	0.1846	52
44	10	18.9262	0.5284	18	44.3398	0.4060	-0.1224	16
45	0	0		17	16.9400	1.0035		
46	1	8.7043	0.1149	19	41.8939	0.4535	0.3386	70
47	11	13.0087	0.8456	46	55.3180	0.8316	-0.0140	29
48	0	0		0	0			
49	7	18.9262	0.3699	15	38.9883	0.3847	0.0149	32
50	0	0		10	25.3609	0.3943		
51	11	18.9262	0.5812	25	48.2334	0.5183	-0.0629	23
52	0	0		40	52.4125	0.7632		
53	19	30.5296	0.6223	36	56.7650	0.6342	0.0118	32
54	0	0		0	0			

Table 3. Compatibility scores and weights; observed, expected, and ratio of compatibility scores for given distributions ($\mathbf{a} \cap \mathbf{p}$ in Figure 3) (o_1, e_1, $c_1=o_1/e_1$), and habitat models ($\mathbf{p}$ in Figure 3) (o_2, e_2, $c_2=o_2/e_2$); $w=|1-c_1|-|1-c_2|$, and W is w rescaled from 1 to 100. Rows are numbered as in Table 1.

	o_1	e_1	c_1	o_2	e_2	c_2	w	W
01	15	25.0342	0.5992	35	53.4962	0.6543	0.0551	37
02	14	25.0342	0.5592	45	56.7650	0.7927	0.2335	58
03	1	8.7043	0.1149	1	16.9400	0.0590	-0.0559	24
04	16	18.9262	0.8454	36	48.2334	0.7464	-0.0990	19
05	1	8.7043	0.1149	1	16.9400	0.0590	-0.0559	24
06	0	0		17	16.9400	1.0035		
07	17	28.0562	0.6059	49	58.8282	0.8329	0.2270	
08	12	16.2392	0.7390	28	41.8939	0.6684	-0.0706	
09	0	0		32	48.2334	0.6634		
10	6	13.0087	0.4612	28	44.3398	0.6315	0.1703	51
11	2	18.9262	0.1057	8	41.8939	0.1910	0.0853	41
12	2	33.4821	0.0597	8	54.4599	0.1469	0.0872	41
13	0	0		29	16.9400	1.7119		
14	2	16.2392	0.1232	5	31.0918	0.1608	0.0377	35
15	11	16.2392	0.6774	18	38.9883	0.4617	-0.2157	6
16	0	0		12	16.9400	0.7084		
17	0	0		41	51.1905	0.8009		
18	0	0		47	60.5295	0.7765		
19	4	13.0087	0.3075	28	31.0918	0.9006	0.5931	100
20	0	0		33	56.0830	0.5884		
21	0	0		33	35.4707	0.9303		
22	14	13.0087	1.0762	38	56.7650	0.6693	-0.4069	1
23	0	0		29	44.3398	0.6540		
24	0	0		18	41.8939	0.4297		
25	7	8.7043	0.8042	39	48.2334	0.8086	0.0044	31

Table 2. (Cont.)

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
55	11.1773	5.8427	2.3632	1.8991	0.7676	0.5728	0.3803	0.2658
56	13.1597	4.1278	3.1977	1.1258	0.7248	0.5645	0.3619	0.1549
57	12.1107	3.2252	2.4900	1.4468	0.9782	0.7380	0.5524	0.4653
58	15.6177	3.0669	2.3446	1.3318	0.5413	0.3120	0.2192	0.0984
59	10.4835	3.7403	3.5242	2.1354	1.7318	0.6988	0.3221	0.2775
60	10.9230	3.6631	2.7105	1.7413	1.0454	0.7396	0.6361	0.5243
61	10.9170	5.2874	3.3883	1.8259	0.8718	0.3831	0.2938	0.2265
62	10.1336	5.4992	3.7343	1.7261	0.8506	0.5213	0.3966	0.2660
63	10.7118	7.4666	3.6117	0.8300	0.5415	0.3566	0.1029	0.0835
64	11.2909	4.4144	2.7464	2.0588	0.9428	0.7752	0.5138	0.3310
65	12.9270	4.6881	2.6794	1.2199	0.6247	0.4451	0.3594	0.2152
66	11.9948	4.5814	3.1603	1.7088	1.2764	0.3789	0.2741	0.1426
67	10.5822	4.3635	3.8153	2.2876	1.2214	0.4795	0.3855	0.2209
68	14.5217	2.7997	2.3504	1.6949	0.9177	0.5563	0.2718	0.2626
69	8.3925	4.6902	3.9242	2.6874	1.7350	0.6502	0.6113	0.2392
70	10.6774	5.5402	3.4799	1.6861	0.9667	0.6915	0.2874	0.2003
71	14.7504	3.6363	3.2048	0.8725	0.3687	0.2379	0.1969	0.1496

Table 2. (Cont.)

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
26	10.1493	6.7268	3.3623	2.0652	0.7475	0.3584	0.2083	0.1520
27	9.2572	6.3326	3.8564	1.3237	0.9185	0.7855	0.4354	0.2301
28	14.8375	4.1594	2.1268	0.8768	0.6707	0.4130	0.2251	0.1457
29	9.3521	6.4229	4.3552	1.2610	0.9308	0.5546	0.3311	0.2233
30	15.0991	5.0310	2.4075	0.8420	0.2215	0.1453	0.0937	0.0440
31	10.2692	4.1348	3.7901	2.4241	1.0792	0.6446	0.3267	0.3087
32	13.2768	4.5512	2.6719	1.4167	0.6338	0.3871	0.2955	0.1671
33	15.1464	2.8053	2.5696	1.4661	0.8054	0.3320	0.2649	0.1239
34	9.7236	7.6255	3.4216	1.3829	0.6677	0.3751	0.1896	0.1350
35	12.8829	8.9211	0.7568	0.5943	0.4296	0.1797	0.0700	0.0436
36	9.1423	6.8680	3.4661	2.0452	0.8717	0.5134	0.2218	0.1860
37	11.3328	4.9897	3.3237	1.6881	0.9690	0.4717	0.3185	0.2546
38	13.1500	4.4416	3.0658	1.1739	0.5632	0.5140	0.3234	0.1474
39	12.0020	5.3204	3.4740	1.4154	0.6334	0.2723	0.2490	0.2150
40	9.6516	4.9215	3.3341	2.0701	1.2948	0.8829	0.6066	0.2877
41	11.1175	4.9799	3.4055	1.4000	0.8350	0.6291	0.4208	0.3293
42	11.7463	5.9790	4.1050	1.2101	0.3019	0.1828	0.1353	0.0666
43	9.9035	9.1470	2.2886	1.1561	0.4109	0.3250	0.2679	0.1350
44	9.6697	6.3713	3.2159	2.6115	0.7344	0.3696	0.2734	0.1836
45	12.0447	9.7762	1.2201	0.4582	0.2283	0.0805	0.0710	0.0443
46	10.7570	8.1794	2.9473	0.8225	0.5252	0.2192	0.1397	0.0930
47	12.4117	5.8670	2.0343	1.4807	0.9357	0.4181	0.2872	0.1512
48	8.9572	5.7237	4.7691	2.3921	0.6661	0.4850	0.2433	0.1974
49	9.1523	7.1577	3.6850	2.0687	0.5399	0.4093	0.2035	0.1859
50	11.1913	6.6423	2.8434	1.6882	0.8868	0.2705	0.2109	0.0747
51	11.0868	5.0380	3.3041	1.5389	1.0196	0.5377	0.3454	0.2432
52	15.2423	5.3622	1.6663	0.6959	0.4089	0.2640	0.1081	0.0691
53	13.3771	3.8007	2.4266	2.1174	0.6176	0.5692	0.2691	0.2404
54	11.2820	9.9795	1.3286	0.7995	0.2763	0.1322	0.0691	0.0347

Table 2. Distribution of eigenvectors for the first eight principal components of the habitat models (PC1–PC8). Bold type indicates components admitted under the "broken stick" criterion. Rows are numbered as in Table 1.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
01	**7.7436**	**6.4835**	**3.3414**	**2.0323**	**1.4956**	0.9672	0.4440	0.3639
02	**13.8570**	**4.4783**	**2.6944**	**1.2251**	0.5755	0.3152	0.2073	0.1290
03	**11.9943**	**6.4739**	**2.5901**	1.4757	0.6157	0.2255	0.2089	0.1483
04	**9.3787**	**5.5855**	**3.6015**	**1.9387**	**1.2318**	0.7098	0.3856	0.2520
05	**9.6378**	**8.4781**	**2.3929**	**1.7540**	0.5469	0.3868	0.2386	0.2069
06	**11.2845**	**7.5716**	**2.8454**	1.0144	0.4065	0.1873	0.1704	0.1383
07	**15.2211**	**3.6729**	**2.4976**	0.9547	0.5731	0.3183	0.1460	0.1282
08	**10.6354**	**4.3372**	**3.4458**	**2.2020**	**1.2294**	0.6974	0.3045	0.2703
09	**9.3821**	**7.3096**	**1.4780**	1.3050	0.8342	0.6720	0.3354	0.2452
10	**11.0314**	**7.5560**	**2.1149**	1.0086	0.6808	0.5739	0.2696	0.1617
11	**12.1110**	**3.0624**	**2.2270**	**1.6434**	0.9885	0.8579	0.6395	0.4423
12	**11.9304**	**3.9967**	**3.1820**	**1.2219**	0.6771	0.5594	0.4187	0.3624
13	**11.4238**	**5.7173**	**2.6672**	**2.0128**	0.6970	0.5146	0.2989	0.1776
14	**11.0673**	**4.0641**	**2.1349**	**2.0130**	1.0537	0.7835	0.7340	0.4160
15	**10.6280**	**3.9351**	**3.3060**	**2.0281**	0.9324	0.6245	0.5973	0.4117
16	**11.3058**	**4.7412**	**3.2773**	**2.0848**	0.9362	0.4997	0.3097	0.2232
17	**12.0858**	**6.1560**	**2.1339**	1.4456	0.7056	0.5529	0.3331	0.2229
18	**16.5149**	**4.5544**	1.5544	0.5162	0.3757	0.1947	0.0823	0.0518
19	**10.6287**	**5.4583**	**2.9150**	**1.4449**	**1.3063**	0.6013	0.3951	0.3704
20	**11.9545**	**7.4412**	1.7547	1.0439	0.8405	0.4203	0.1548	0.1272
21	**11.7470**	**4.5104**	**4.3580**	1.1001	0.8299	0.4546	0.2547	0.1946
22	**12.4501**	**5.3008**	**2.0937**	1.2847	0.9616	0.6879	0.3618	0.2439
23	**11.0098**	**4.6853**	**3.2532**	**1.5583**	0.9544	0.6635	0.6022	0.3826
24	**10.7293**	**7.5259**	**3.3387**	0.9323	0.6223	0.2502	0.1447	0.1000
25	**8.1547**	**7.1868**	**3.1380**	**2.1755**	1.0211	0.6366	0.4817	0.2910

Table 1. (Cont.)

55 *Philantomba monticola*	(Thunberg, 1789)	Blue duiker	SM p.619
56 *Sylvicapra grimmia*	(Linnaeus, 1758)	Grimm's, grey duiker	SM p.625
Sub-family: **Hippotraginae**			
57 *Addax nasomaculatus*	(Blainville, 1816)	Addax	DD p.200
58 *Hippotragus equinus*	(Desmarest, 1804)	Roan antelope	SM p.653
59 *Hippotragus niger*	(Harris, 1838)	Sable antelope	SM p.656
60 *Oryx dammah*	(Cretzchmar, 1826)	Beisa oryx	DD p.201
61 *Oryx gazella*	(Linnaeus, 1758)	Gemsbok	SM p.660
62 *Oryx leucoryx*	(Pallas, 1777)	Beisa oryx	DD p.201
Sub-family: **Peleinae**			
63 *Pelea capreolus*	(Forster, 1790)	Vaal or grey rhebuck	SM p.652
Sub-family: **Reduncinae**			
64 *Kobus ellipsiprymnus*	(Ogilby, 1833)	Waterbuck	SM p.687
65 *Kobus kob*	(Erxleben, 1777)	Kob	DD p.210
66 *Kobus leche*	(Gray, 1850)	Lechwe	SM p.689
67 *Kobus megaceros*	(Fitzinger, 1855)	Nile lechwe	DD p.214
68 *Kobus vardoni*	(Livingstone, 1857)	Puku	SM p.692
69 *Redunca arundinum*	(Boddaert, 1785)	Southern reedbuck	SM p.682
70 *Redunca fulvorufula*	(Afzelius, 1815)	Mountain reedbuck	SM p.685
71 *Redunca redunca*	(Pallas, 1767)	Bohor reedbuck	DD p.215

Table 1. (Cont.)

26 *Neotragus pygmaeus*	(Linnaeus, 17 .8)	Royal antelope	DD p.260
27 *Oreotragus oreotragus*	(Zimmermann, 1783)	Klipspringer	SM p.631
28 *Ourebia ourebi*	(Zimmermann, 1783)	Oribi	SM p.638
29 *Raphicerus campestris*	(Thunberg, 1811)	Steenbok	SM p.640
30 *Raphicerus melanotis*	(Thunberg, 1811)	Grysbok	SM p.642
31 *Raphicerus sharpei*	(Thomas, 1897)	Sharpe's grysbok	SM p.643
Sub-family: **Bovinae**			
Tribe: **Bovini**			
32 *Syncerus caffer*	(Sparrman, 1779)	African buffalo	SM p.663
Tribe: **Tragelaphini**			
33 *Taurotragus oryx*	(Pallas, 1766)	Eland	SM p.679
34 *Tragelaphus angasi*	(Gray, 1849)	Nyala	SM p.671
35 *Tragelaphus buxtoni*	(Lydekker, 1910)	Mountain nyala	DD p.195
36 *Tragelaphus eurycerus*	(Ogilby, 1837)	Bongo	DD p.190
37 *Tragelaphus imberbis*	(Blyth, 1869)	Lesser kudu	DD p.194
38 *Tragelaphus scriptus*	(Pallas, 1766)	Bushbuck	SM p.674
39 *Tragelaphus spekei*	(Speke, 1863)	Sitatunga	SM p.669
40 *Tragelaphus strepsiceros*	(Pallas, 1766)	Greater kudu	SM p.666
Sub-family: **Caprinae**			
41 *Ammotragus lervia*	(Pallas, 1777)	Barbary sheep	DD p.271
42 *Capra ibex*	(Linnaeus, 1758)	Abyssinian ibex	DD p.270
Sub-family: **Cephalophinae**			
43 *Cephalophus callipygus*	(Peters, 1876)	Peters' duiker	DD p.252
44 *Cephalophus dorsalis*	(Gray, 1846)	Bay duiker	D') p.253
45 *Cephalophus jentinki*	(Thomas, 1892)	Jentink's duiker	DD p.250
46 *Cephalophus leucogaster*	(Gray, 1873)	White-bellied duiker	DD p.253
47 *Cephalophus natalensis*	(A. Smith, 1834)	Red forest duiker	SM p.623
48 *Cephalophus niger*	(Gray, 1846)	Black duiker	DD p.250
49 *Cephalophus nigrifons*	(Gray, 1871)	Black-fronted duiker	DD p.254
50 *Cephalophus ogilbyi*	(Waterhouse, 1838)	Ogilby's duiker	DD p.254
51 *Cephalophus rufilatus*	(Gray, 1846)	Red-flanked duiker	DD p.252
52 *Cephalophus spadix*	(True, 1890)	Abbot s duiker	DD p.250
53 *Cephalophus sylvicultor*	(Afzelius, 1815)	Yellow-backed duiker	DD p.250
54 *Cephalophus zebra*	(Gray, 1838)	Panded duiker	DD p.252

(1995/03/20 15:04:3 C4) C24 – 14 Mean Monthly Rainfall: February

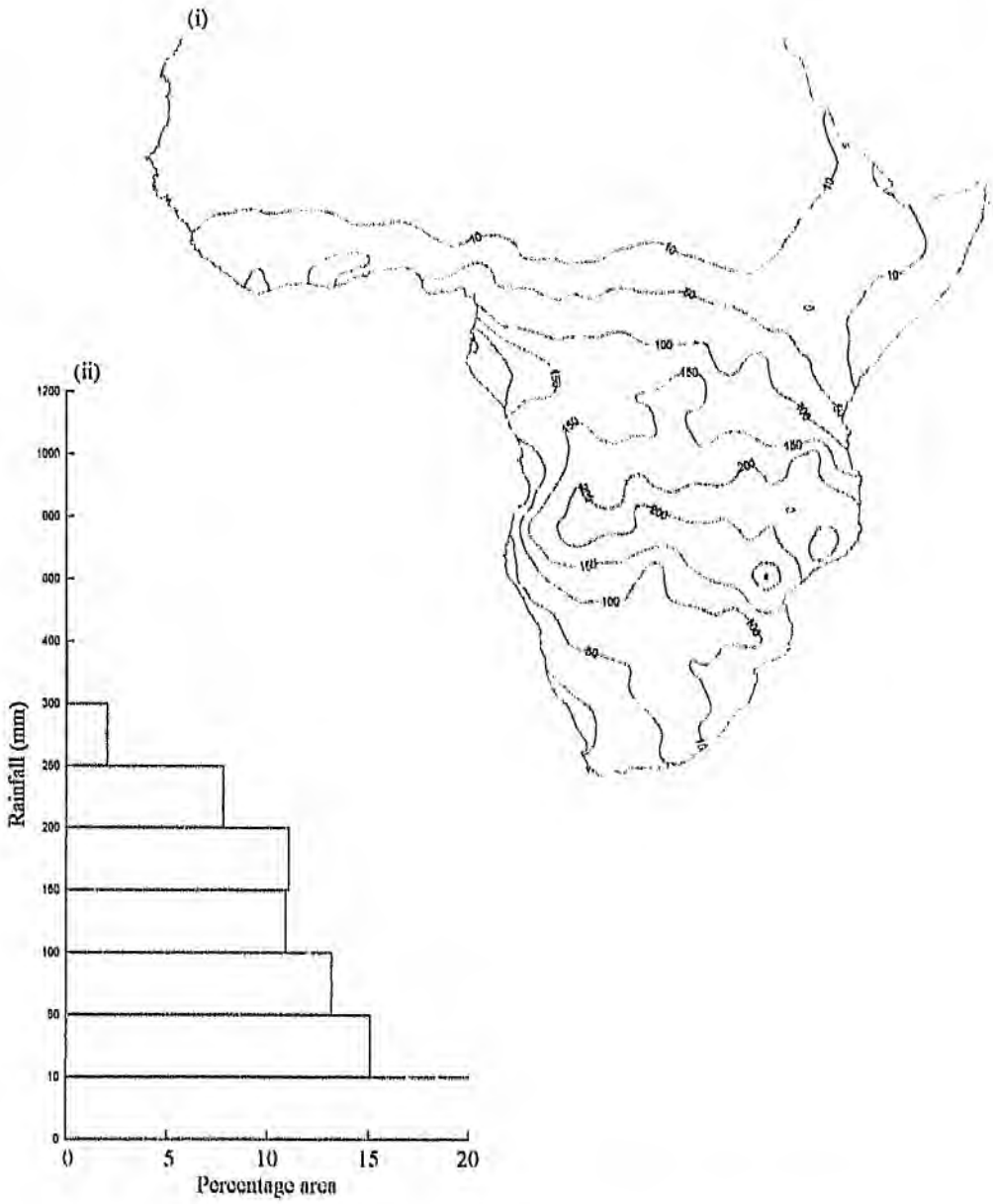


Figure 2.14. Mean Monthly Rainfall: February; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

(1985/0820) 15:04:43 76) C24 – 13 Mean Monthly Rainfall: January

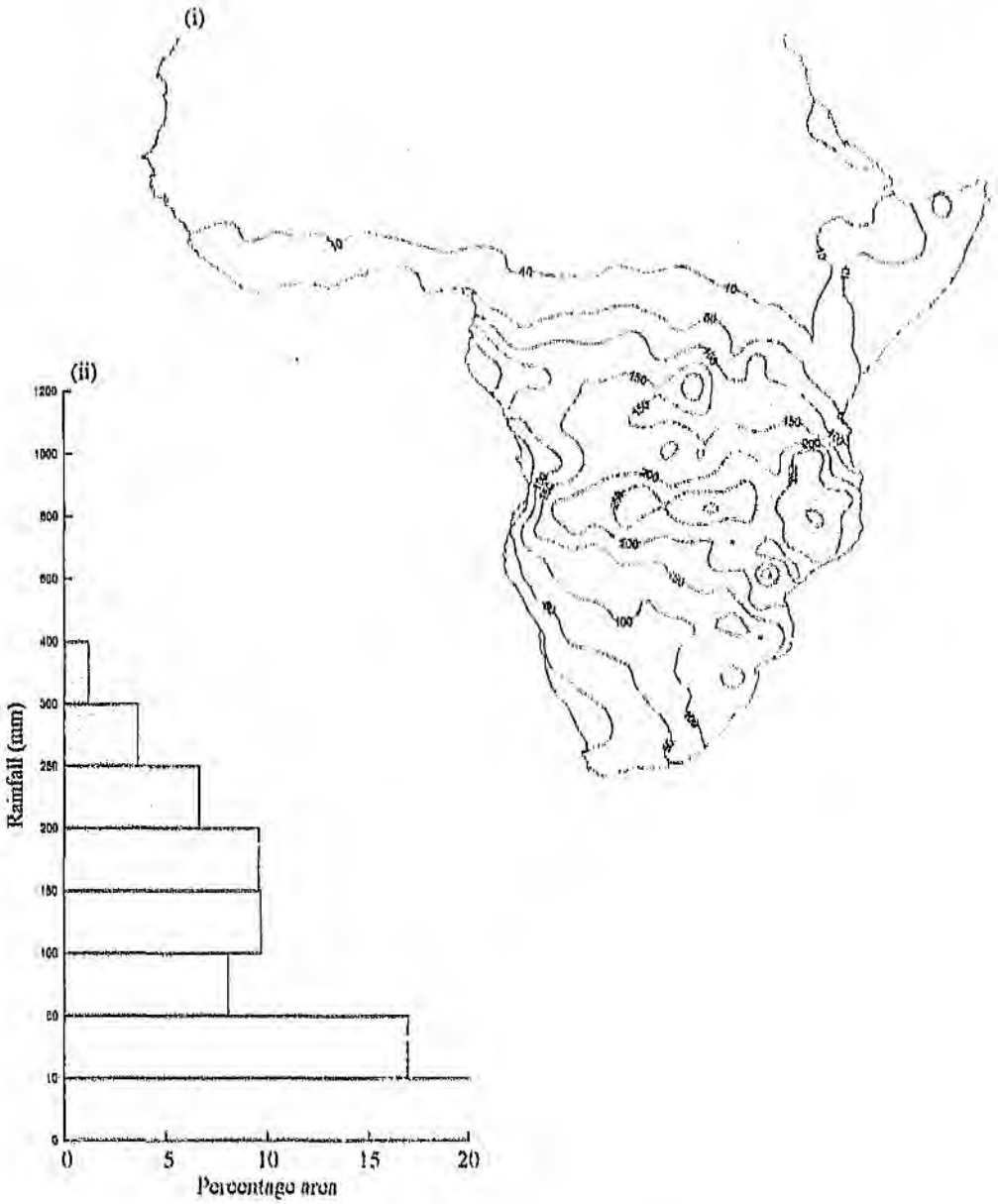


Figure 2.13. Mean Monthly Rainfall: January; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

[1995/09/18 16:06:9.75] C24 – 12 Mean Daily Minimum Temperature November

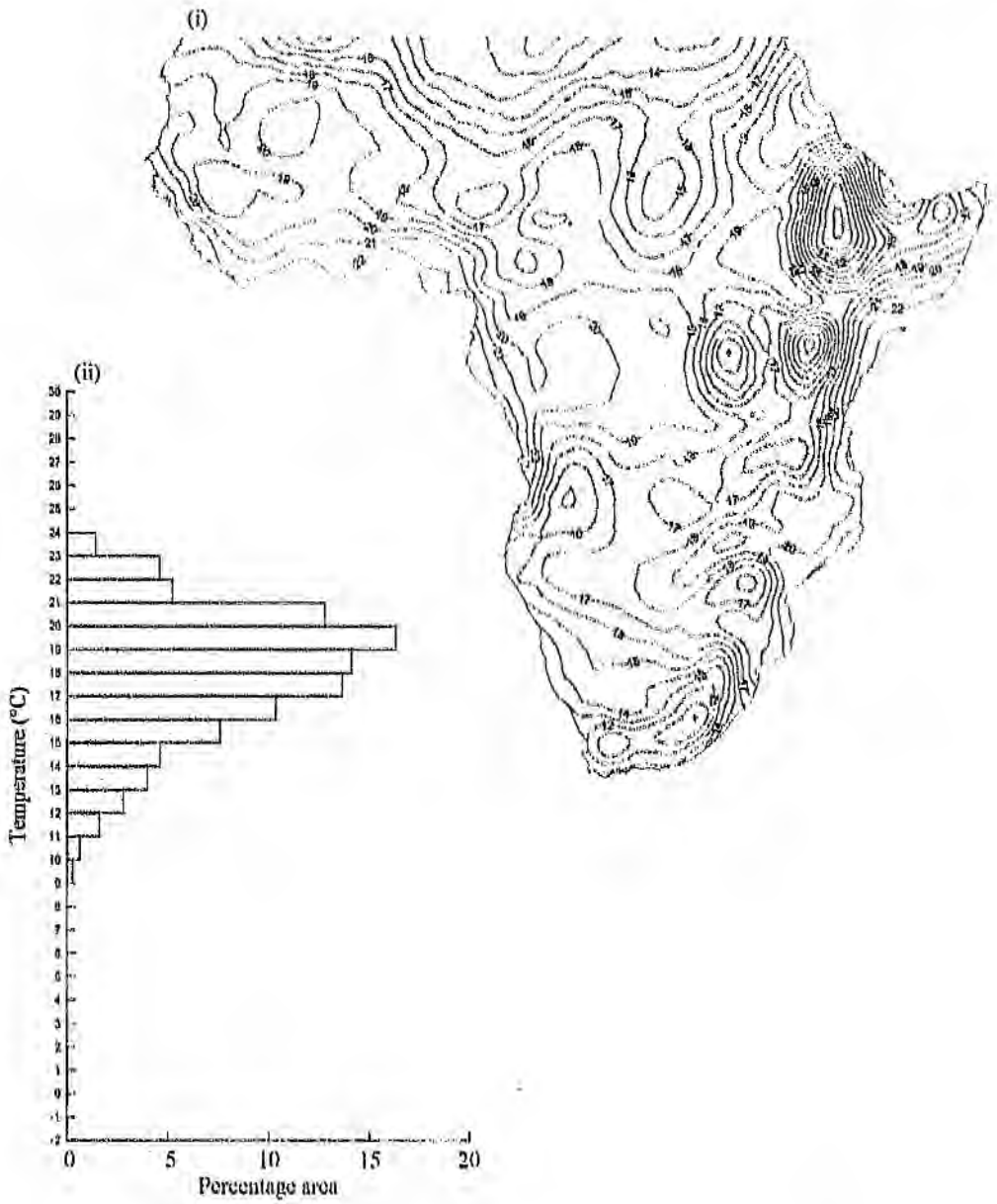


Figure 2.12. Mean Daily Minimum Temperature: November; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

(1992/05/18 16:09:20.45) C24 - 11 Mean Daily Minimum Temperature: September

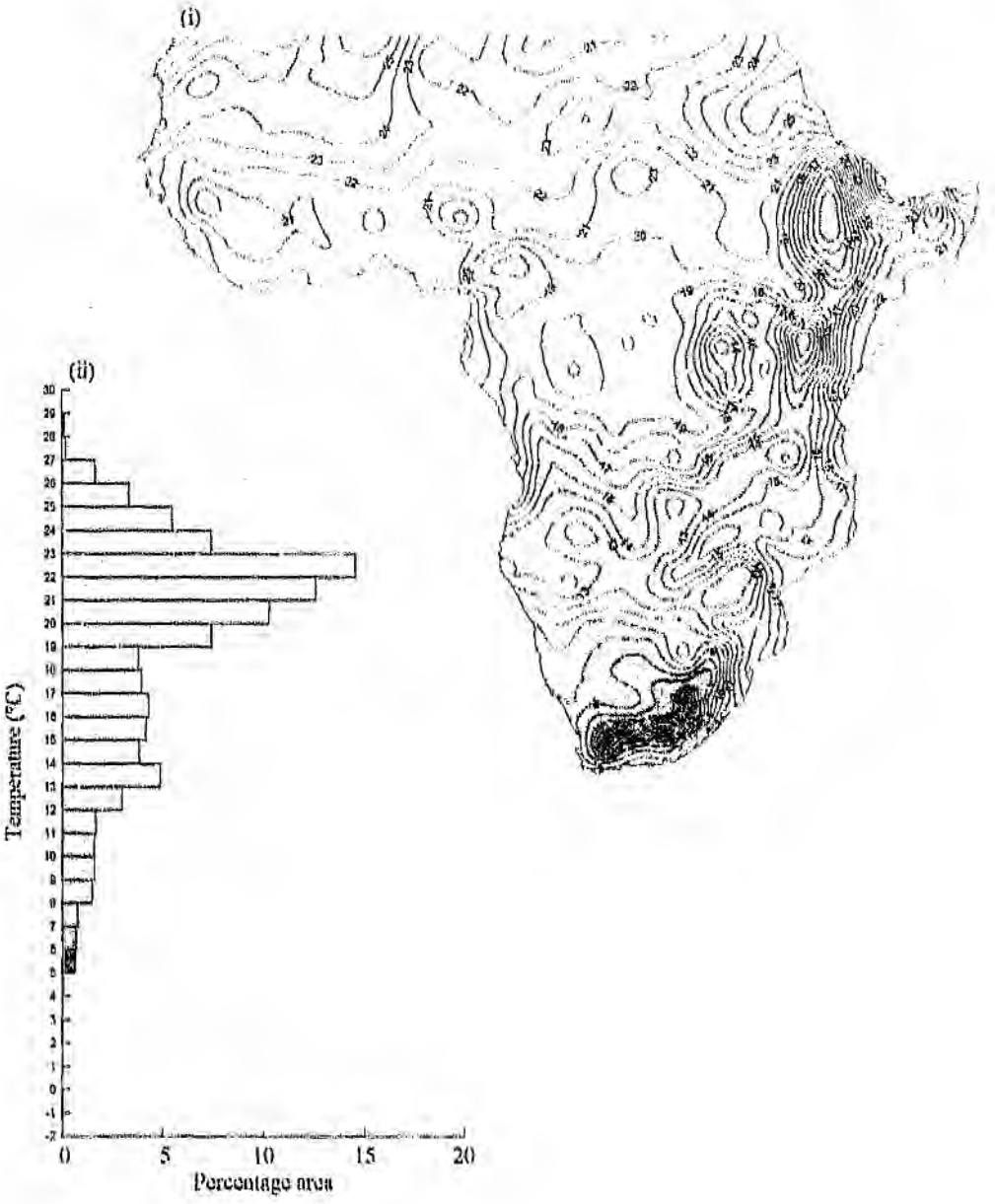


Figure 2.11. Mean Daily Minimum Temperature: September; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

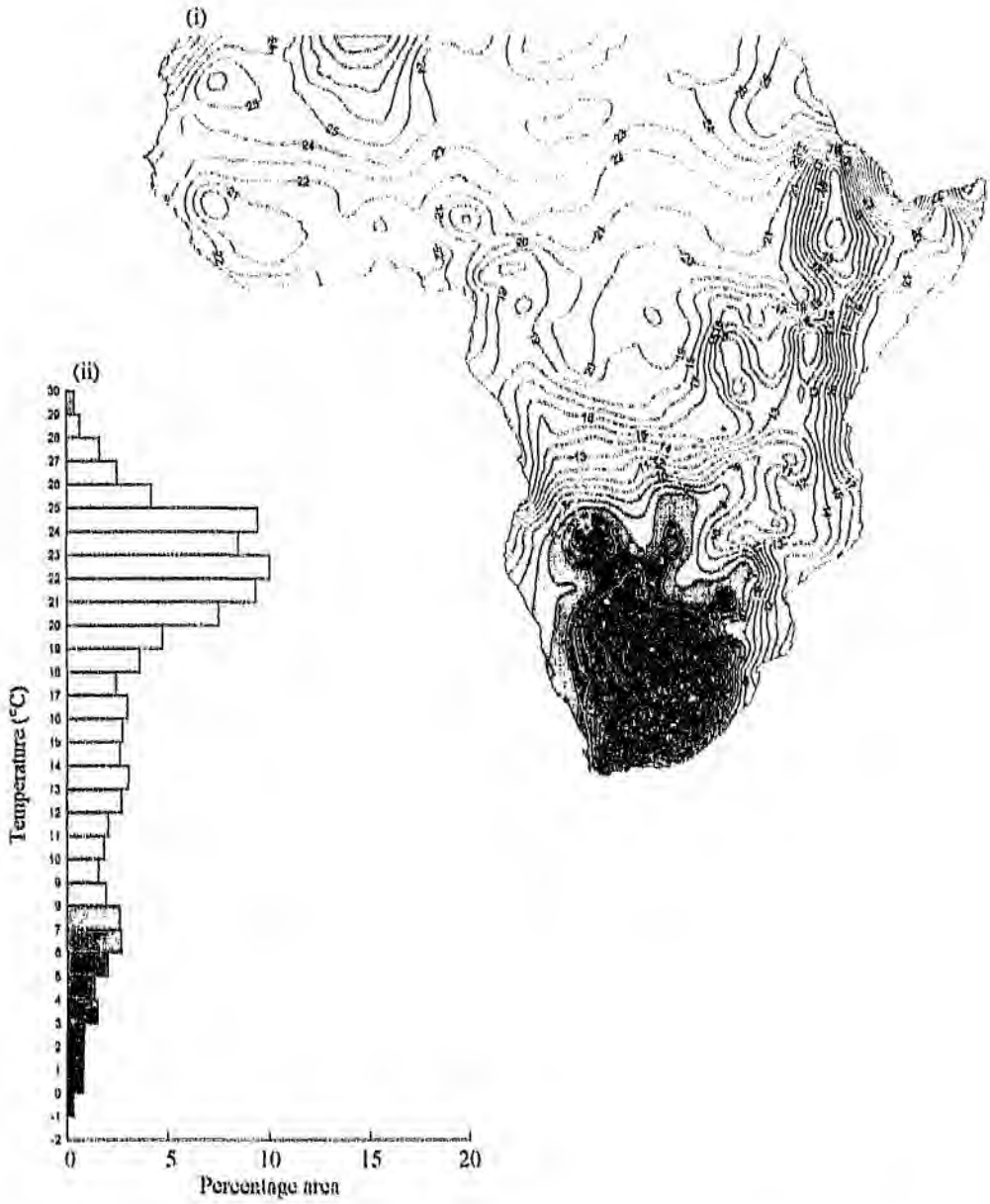


Figure 2.10. Mean Daily Minimum Temperature: July; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

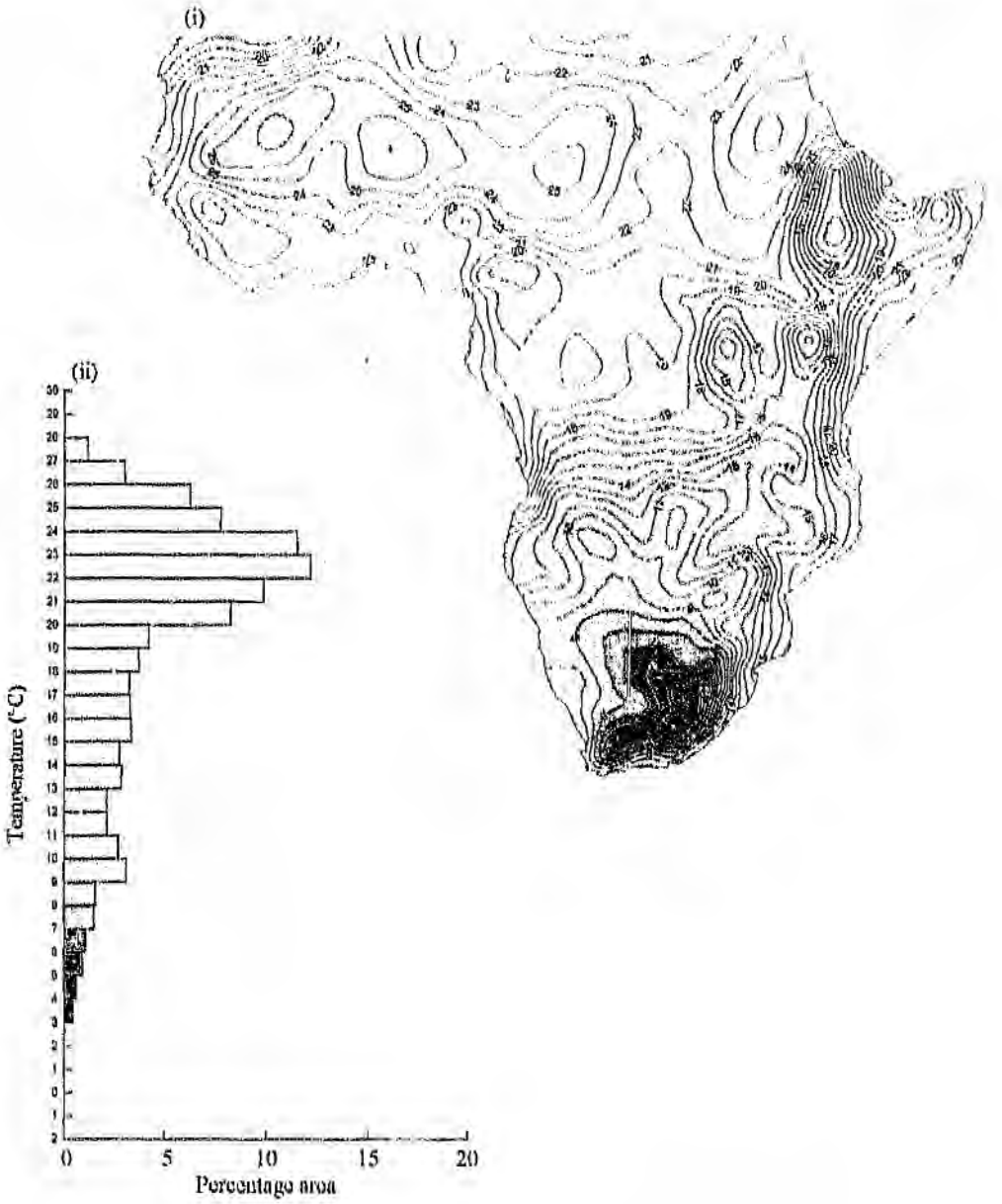


Figure 2.9. Mean Daily Minimum Temperature: May; (i) contour map of surface isotherms, (ii) histogram of percentage area by contour level.

[1995/09/18 18:14:29.85] C24 - 8 Mean Daily Minimum Temperature: March

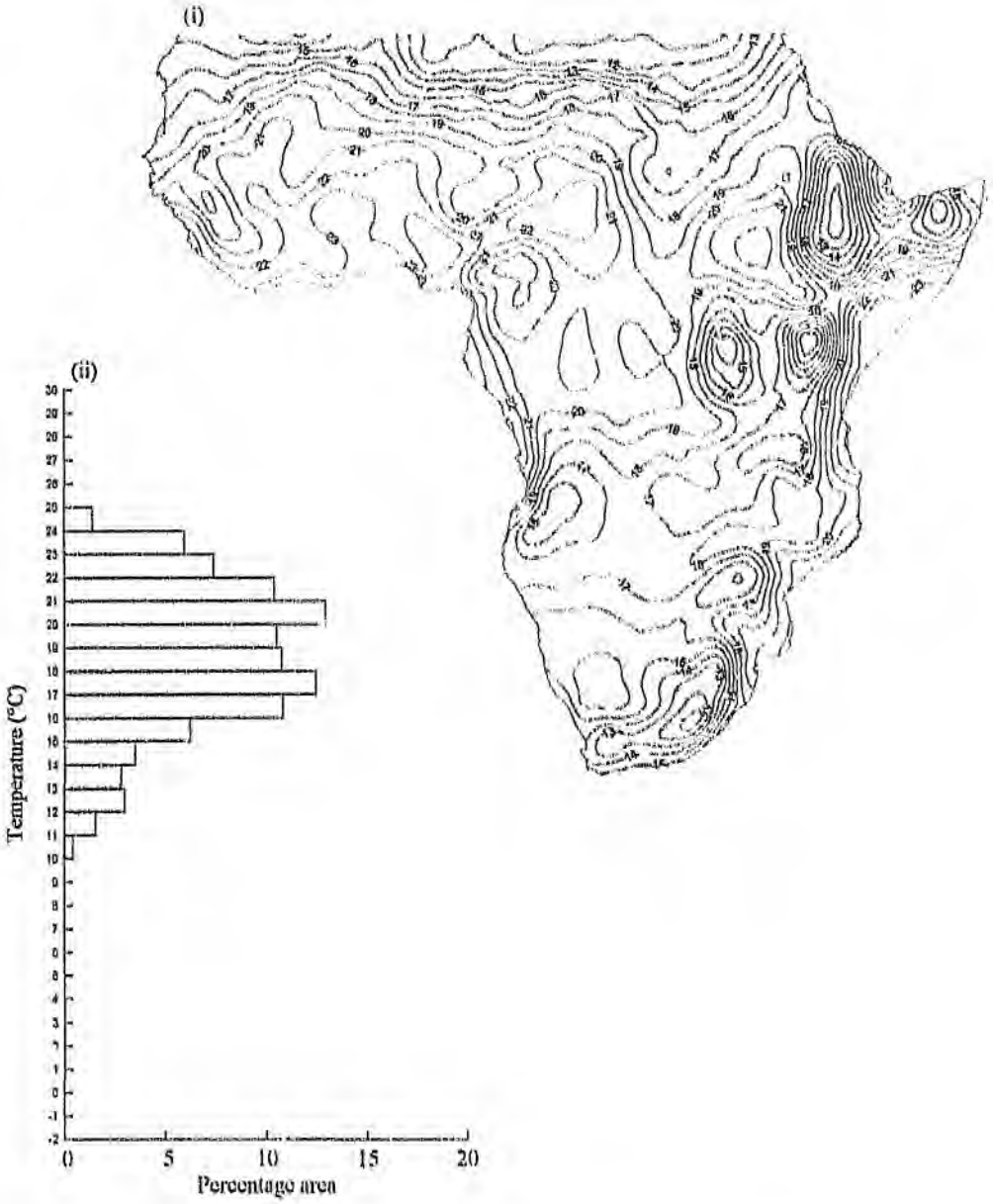


Figure 2.8. Mean Daily Minimum Temperature: March; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

(1995/03/18 16:16:36.03) C24 – 7 Mean Daily Minimum Temperature: January

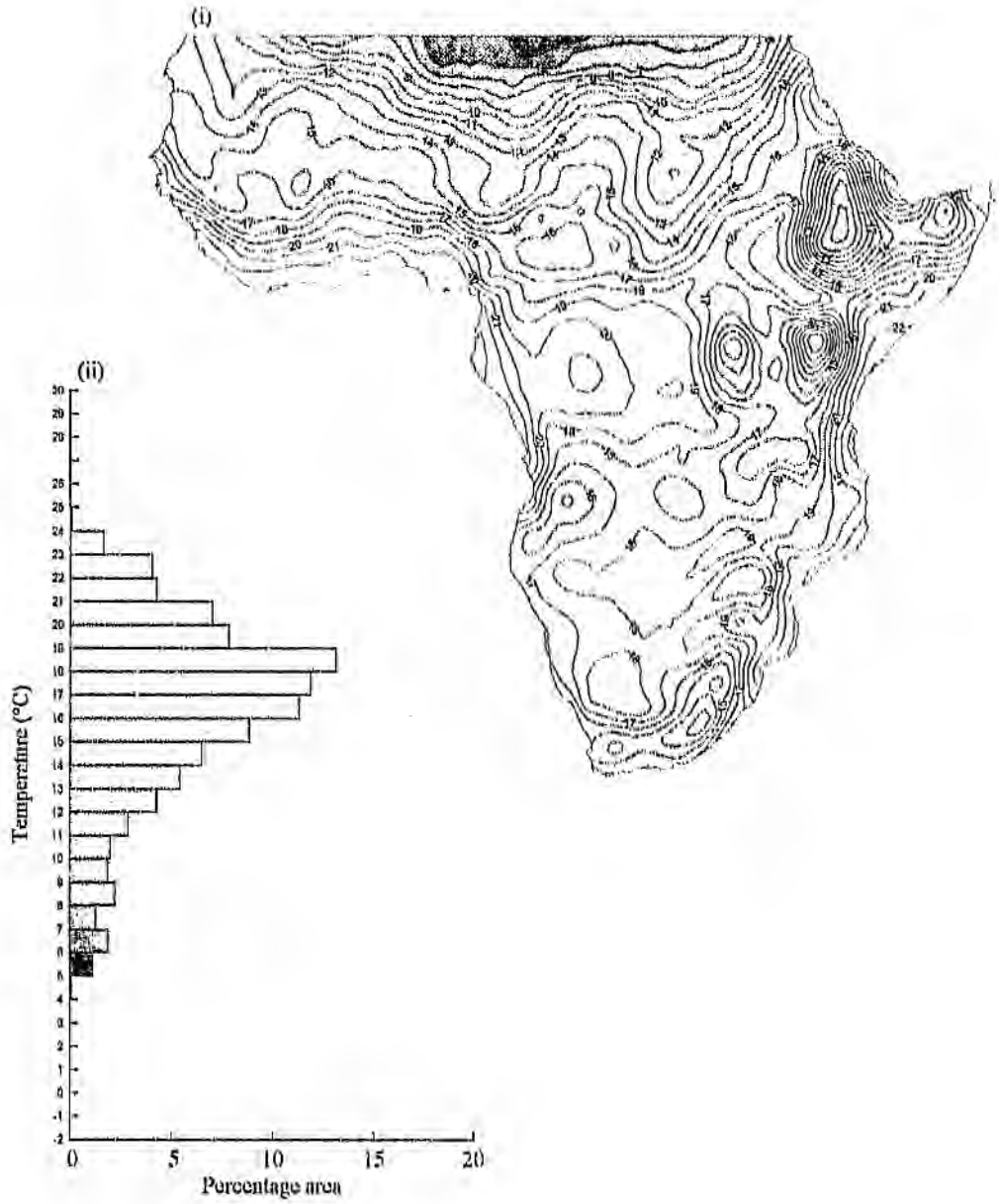


Figure 2.7. Mean Daily Minimum Temperature: January; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

[1995/09/18 16:18:24.59] C24 – 6 Mean Daily Maximum Temperature November

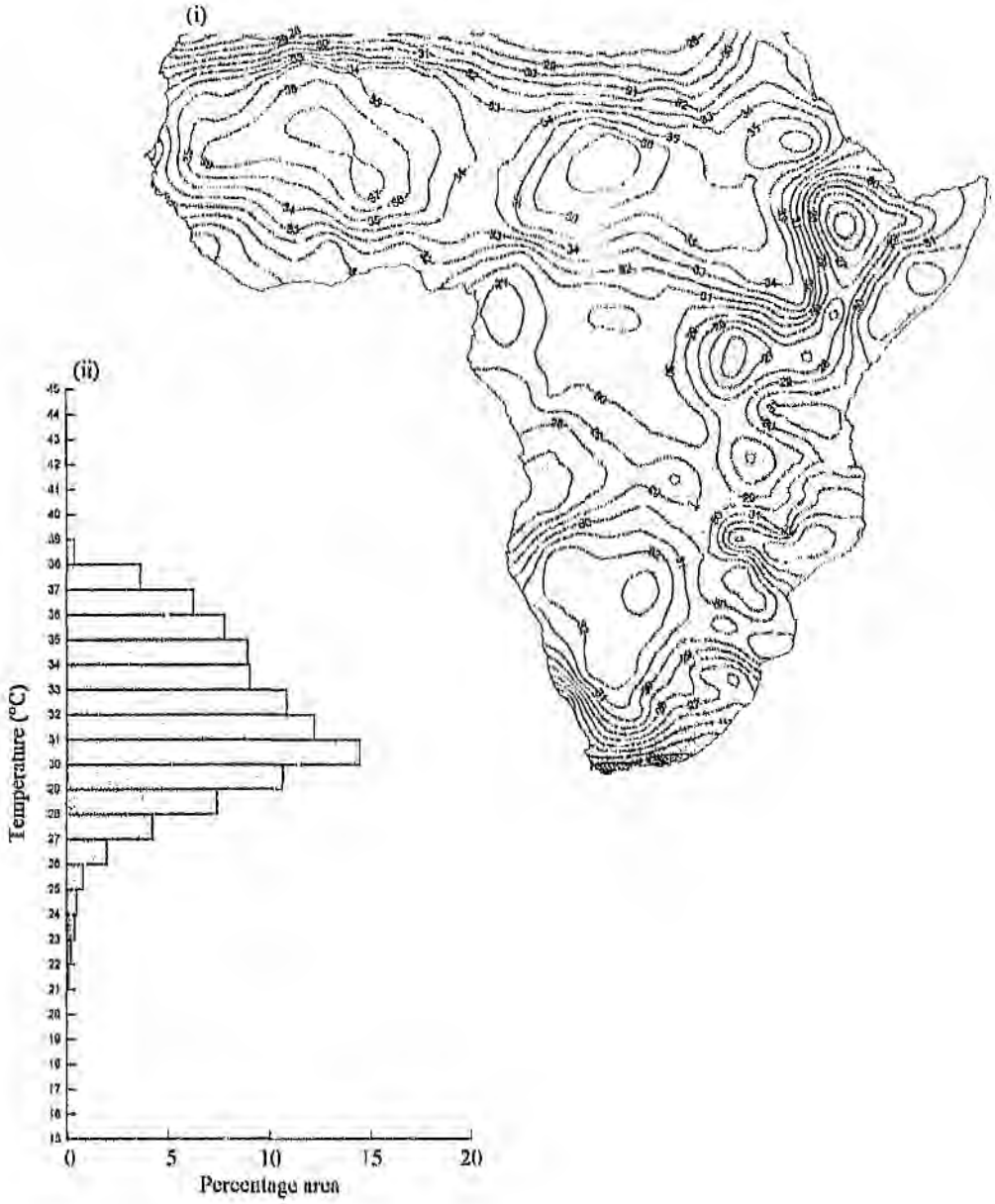


Figure 2.6. Mean Daily Maximum Temperature: November; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

(1995/09/18 18:20:18.31) C24 – 5 Mean Daily Maximum Temperature: September

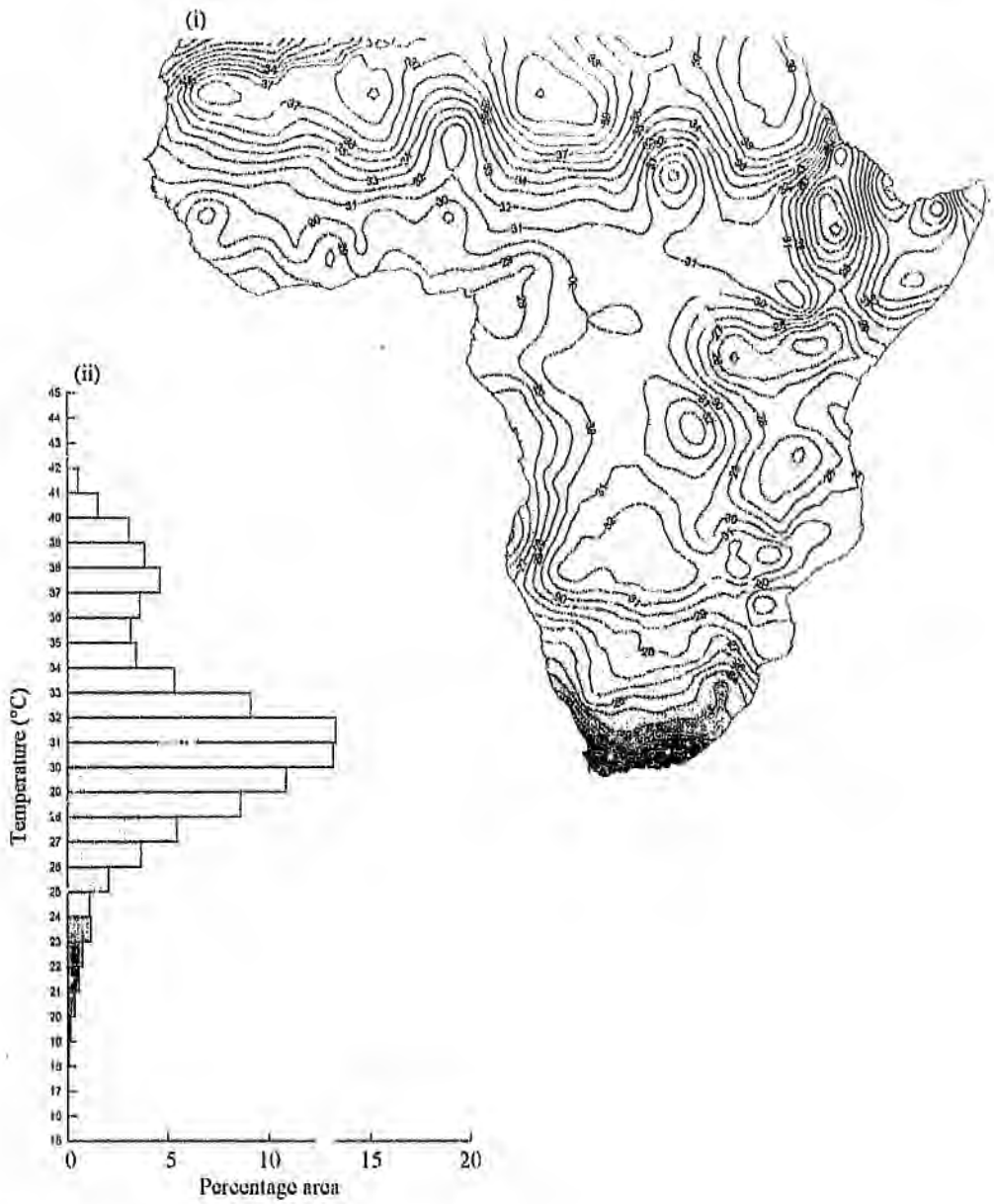


Figure 2.5. Mean Daily Maximum Temperature: September; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

[19950918 16:22:16:15] C24 – 4 Mean Daily Maximum Temperature July

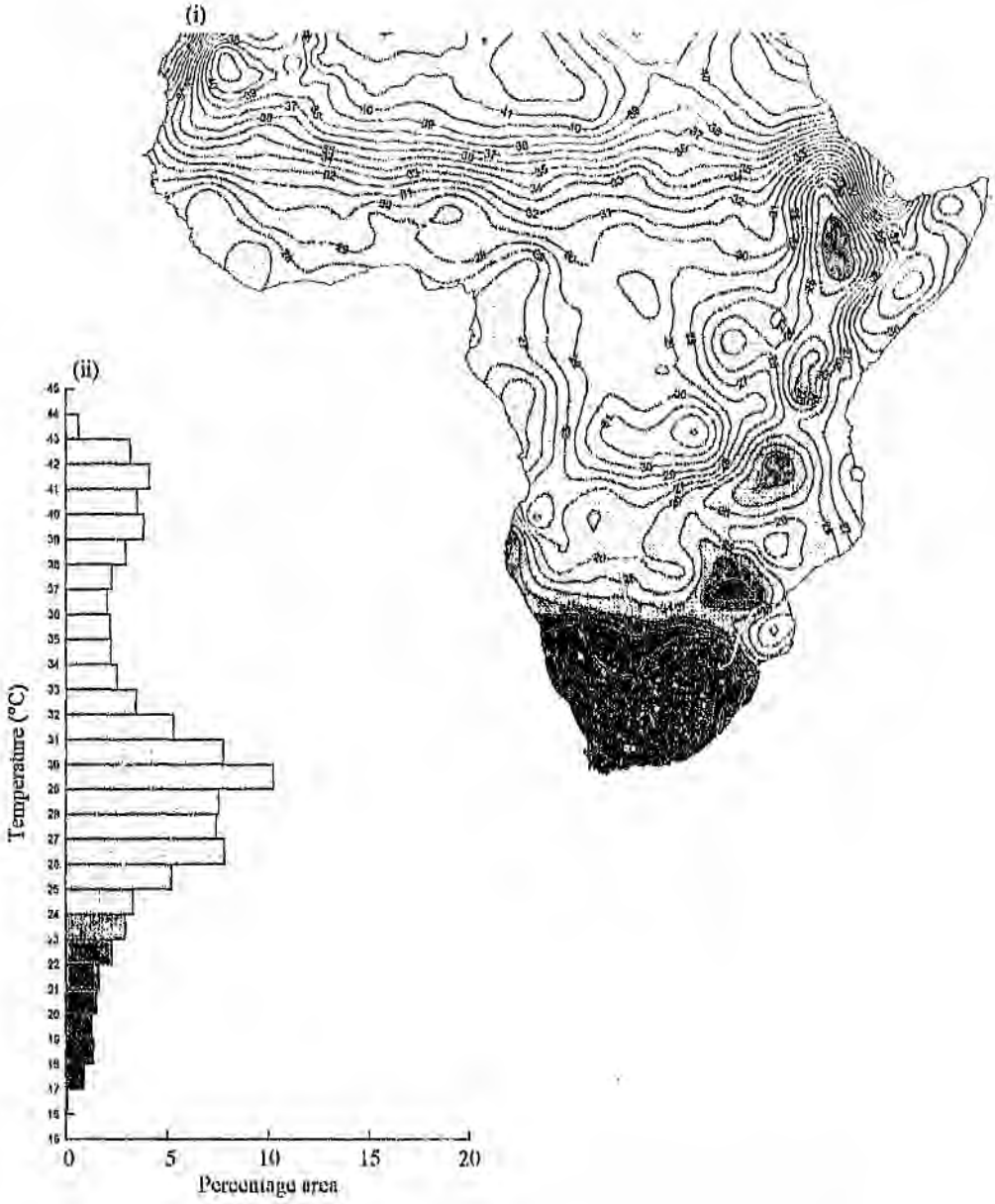


Figure 2.4. Mean Daily Maximum Temperature: July; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

(1996/09/18 16:24:15.45) C24 – 3 Mean Daily Maximum Temperature: May

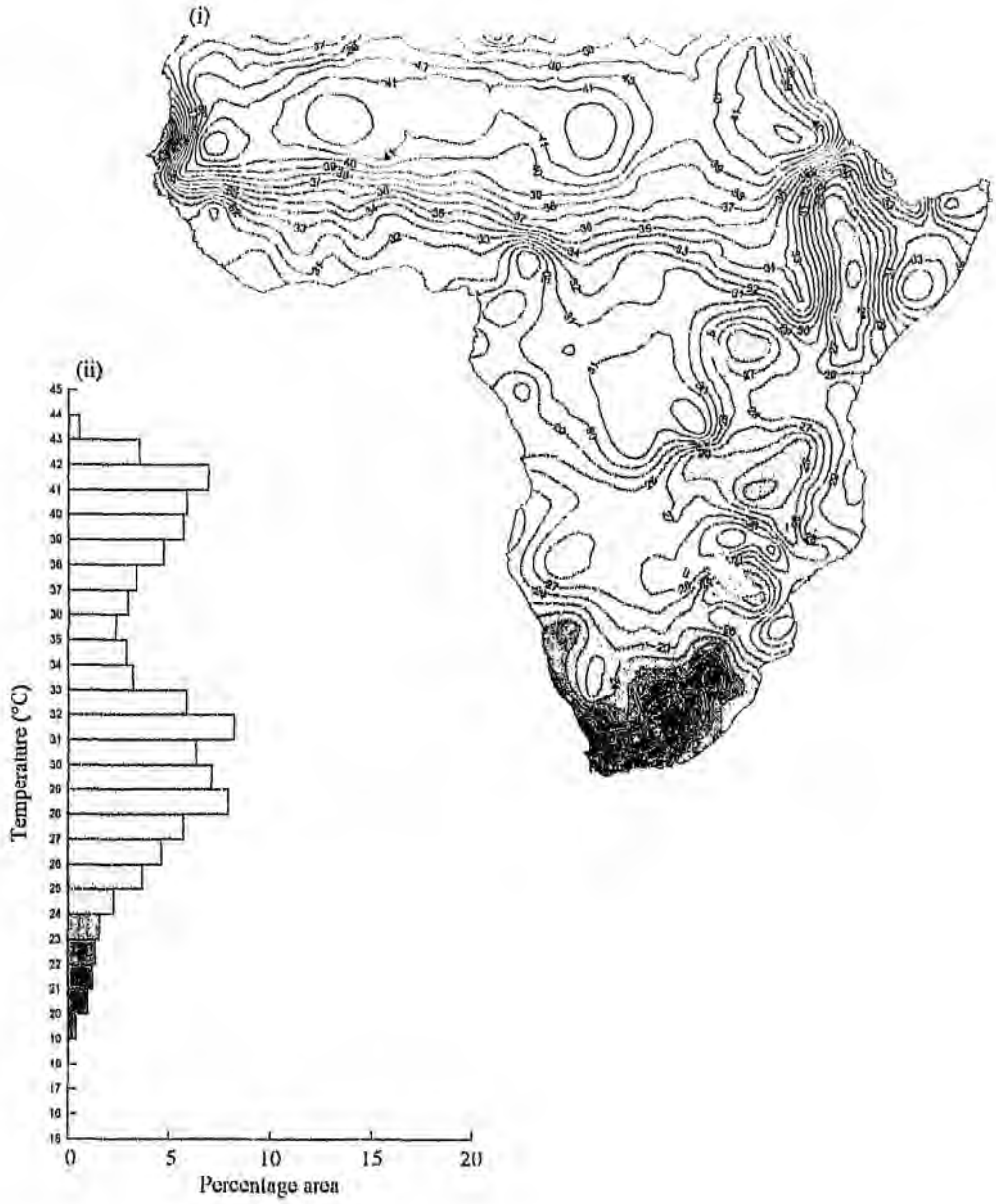


Figure [illegible]. Mean Daily Maximum Temperature: May; (i) contour map of surface isotherms; (ii) histogram of percentage area by contour level.

Standard notation used in Figures 3.1 - 3.71

Habitat models

$\bar{\mathbf{a}} \cap \mathbf{p}$ is the intersection of **not a** with **p**.

$\mathbf{a} \cap \mathbf{p}$ is the intersection of **a** with **p**.

$\mathbf{a} \cap \bar{\mathbf{p}}$ is the intersection of **a** with **not p**.

It follows that

$$(\bar{\bar{\mathbf{a}}} \cap \mathbf{p}) \cup (\mathbf{a} \cap \mathbf{p}) = \mathbf{p}$$

and

$$(\mathbf{a} \cap \mathbf{p}) \cup (\mathbf{a} \cap \bar{\mathbf{p}}) = \mathbf{a}$$

a is the actual species distribution, and **p** is the model distribution ($\mathbf{p} \geq \mathbf{0.2}$).

Climate diagrams

The generalised climate diagrams shown in (iii), (iv) and (v) are based on Walter (1955). Colour intensity indicates increasingly wet conditions.

(1995/05/02) 14:55:34.05) C23 - 25 Mean Annual Rainfall

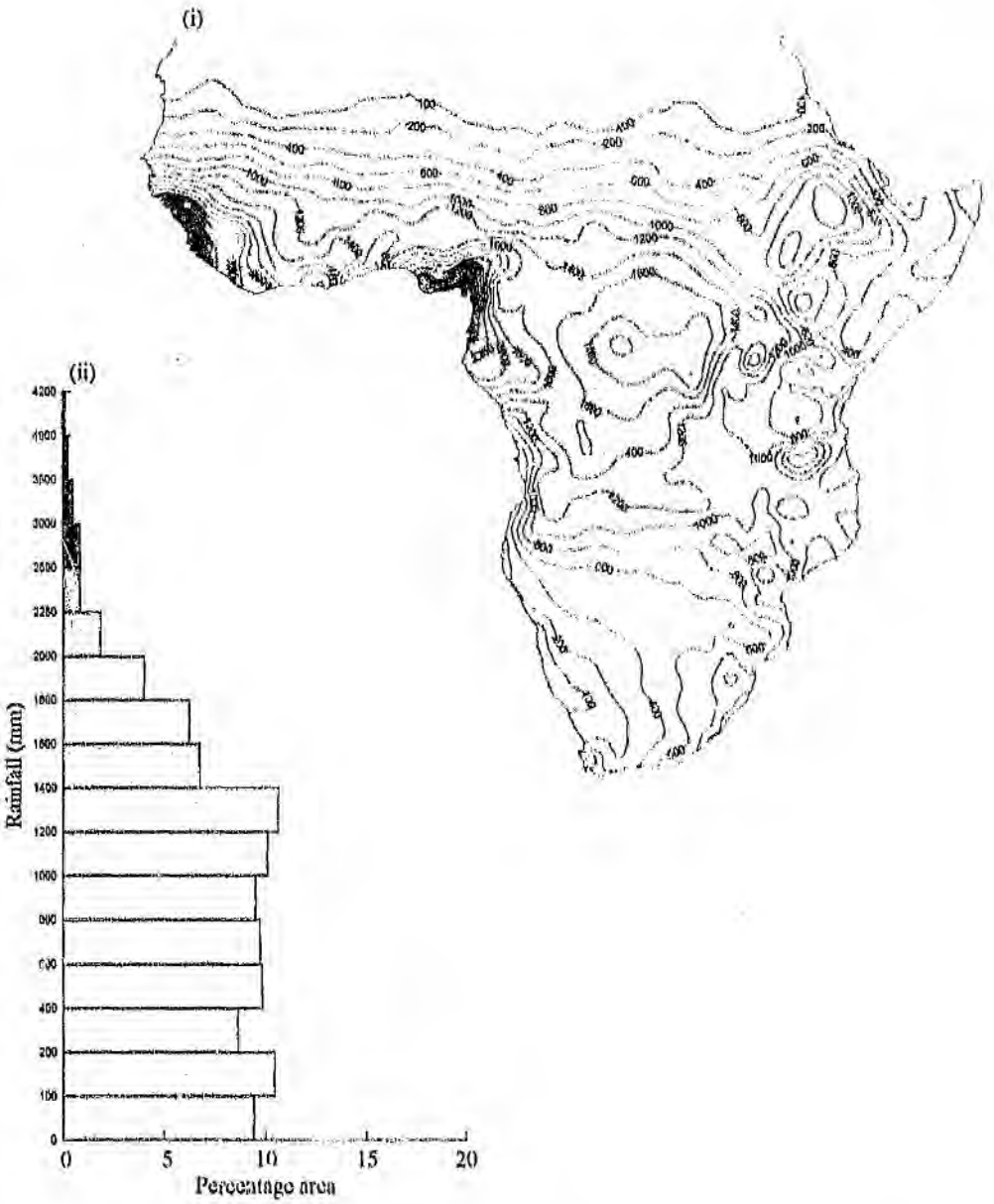


Figure 2.25. Mean Annual Rainfall; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

[1996/09/20 14:56:21.94] C24 – 24 Mean Monthly Rainfall: December

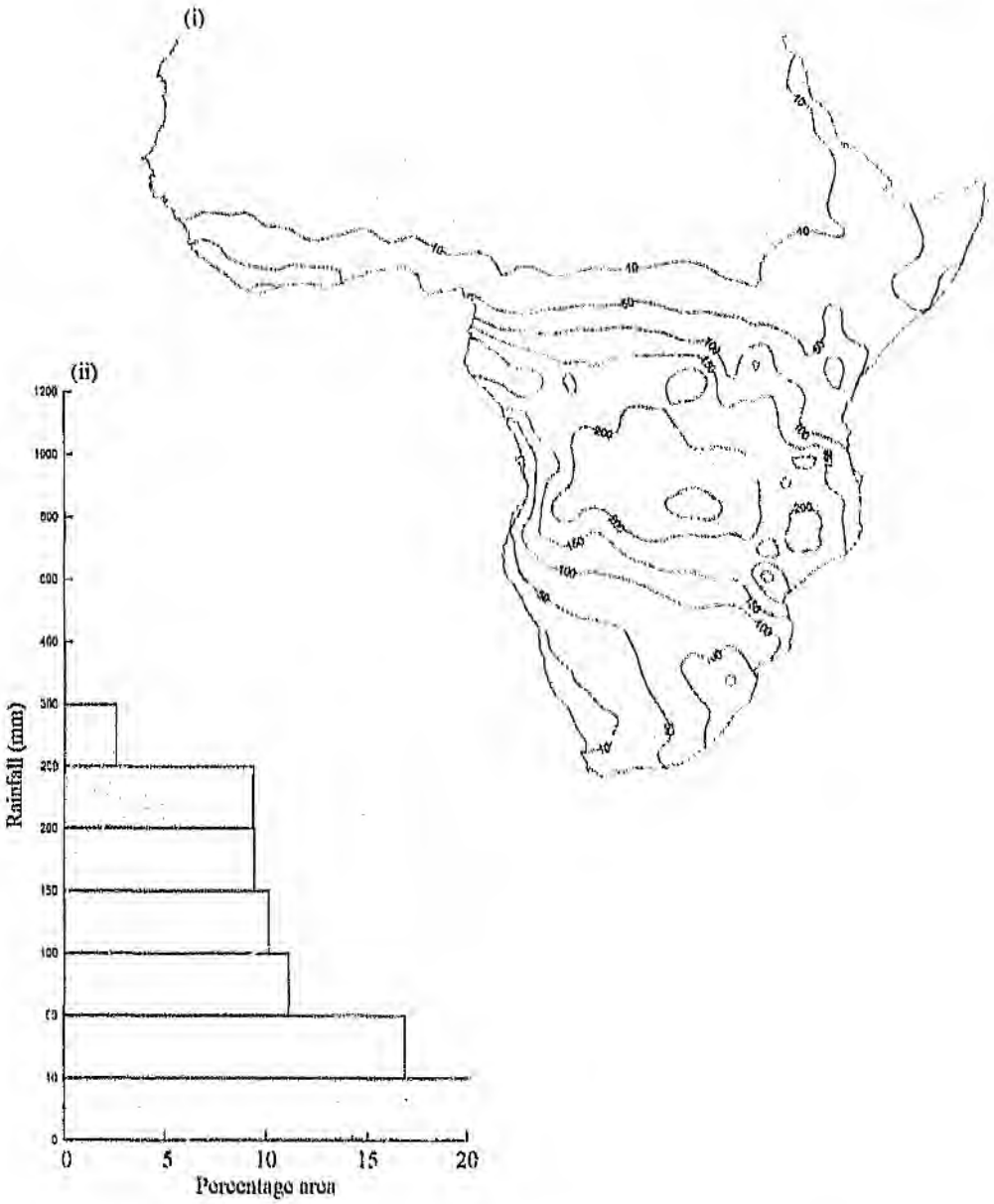


Figure 2.24. Mean Monthly Rainfall: December; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

(1995/09/20 14:57:55) C24 – 23 Mean Monthly Rainfall: November

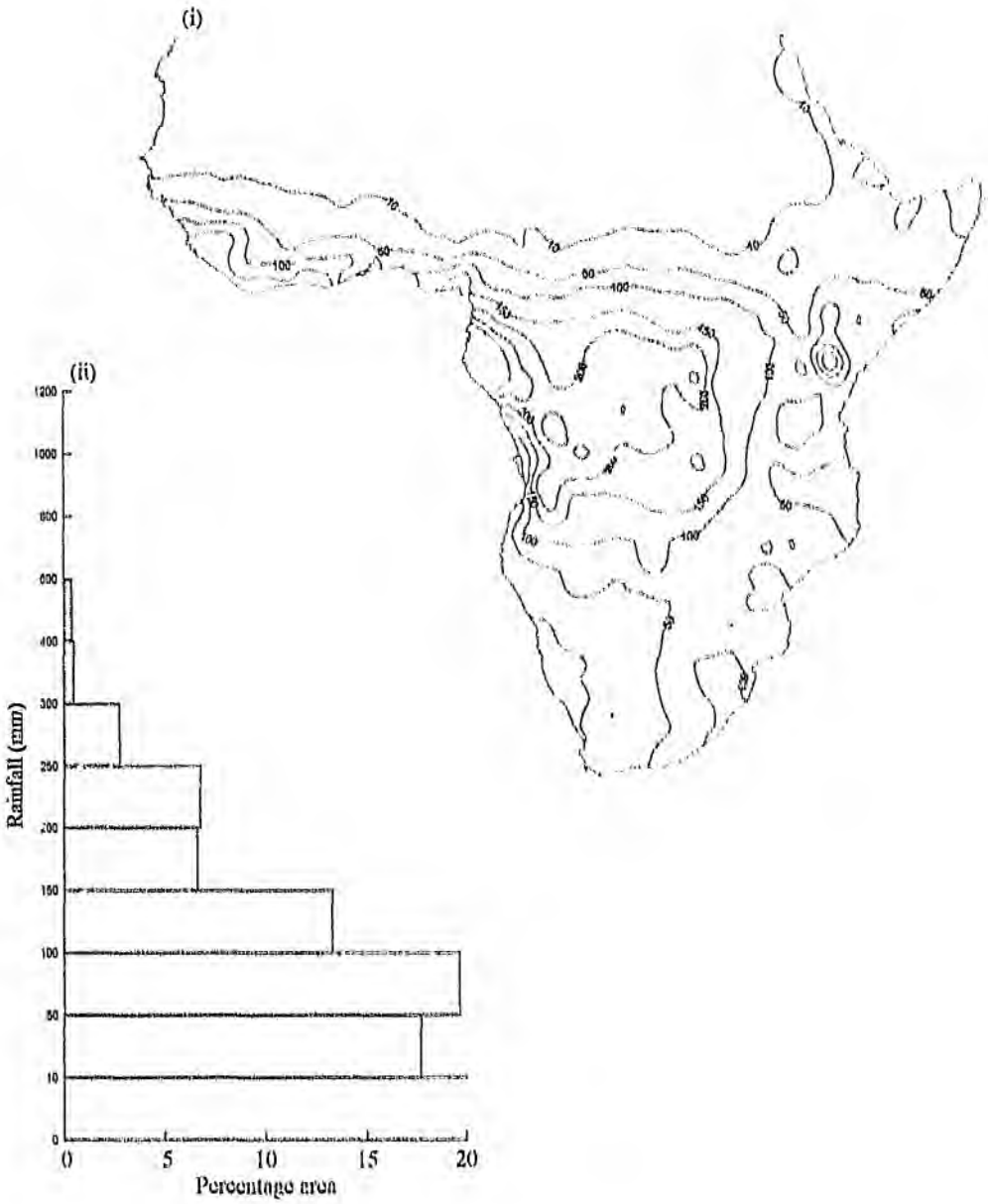


Figure 2.23. Mean Monthly Rainfall: November; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

[19920520 14:57:49:55] C24 - 22 Mean Month, Rainfall October

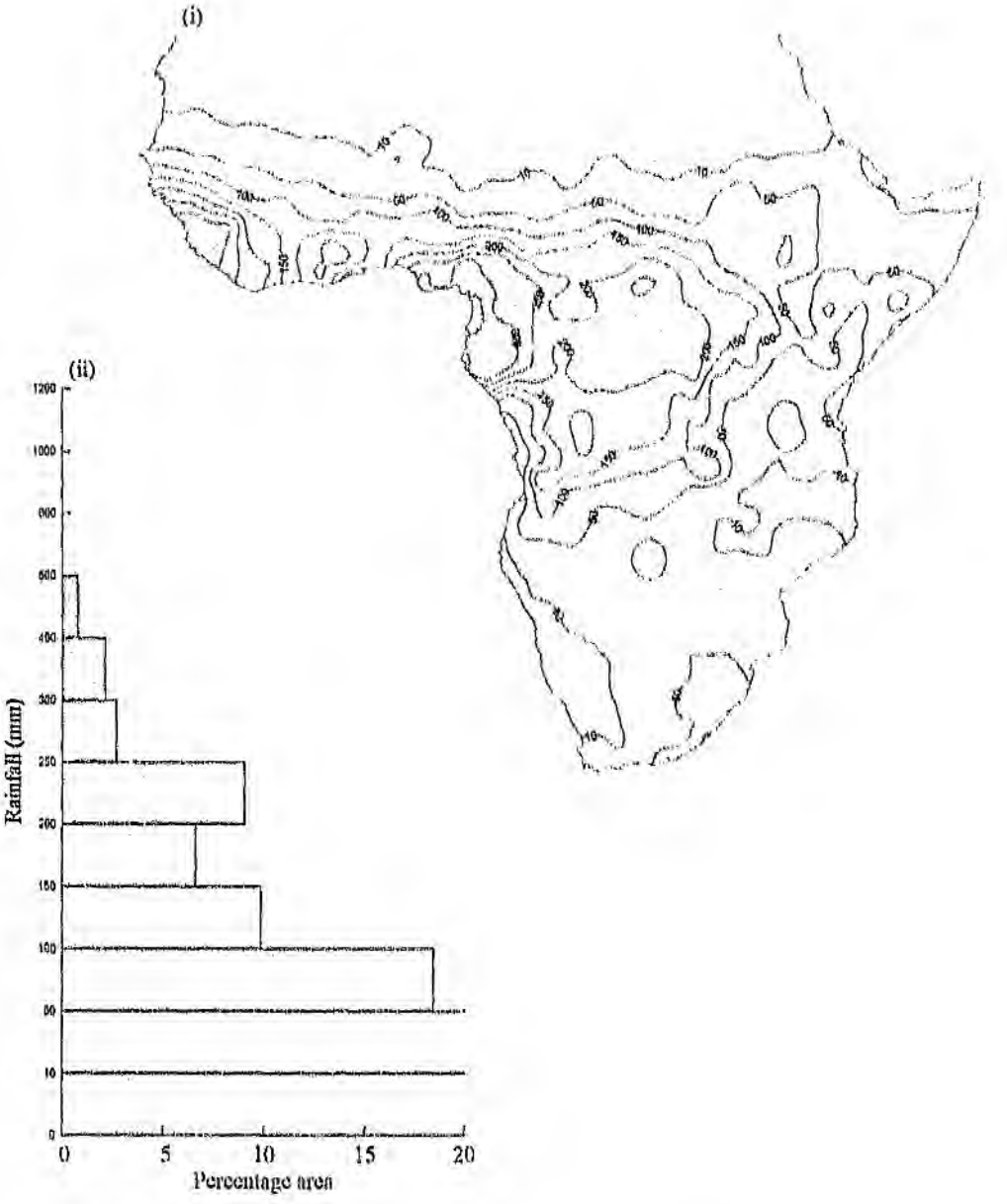


Figure 2.22. Mean Monthly Rainfall: October; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

[1995/09/20 14:58:37.11] CZ4 - 21 Mean Monthly Rainfall: September

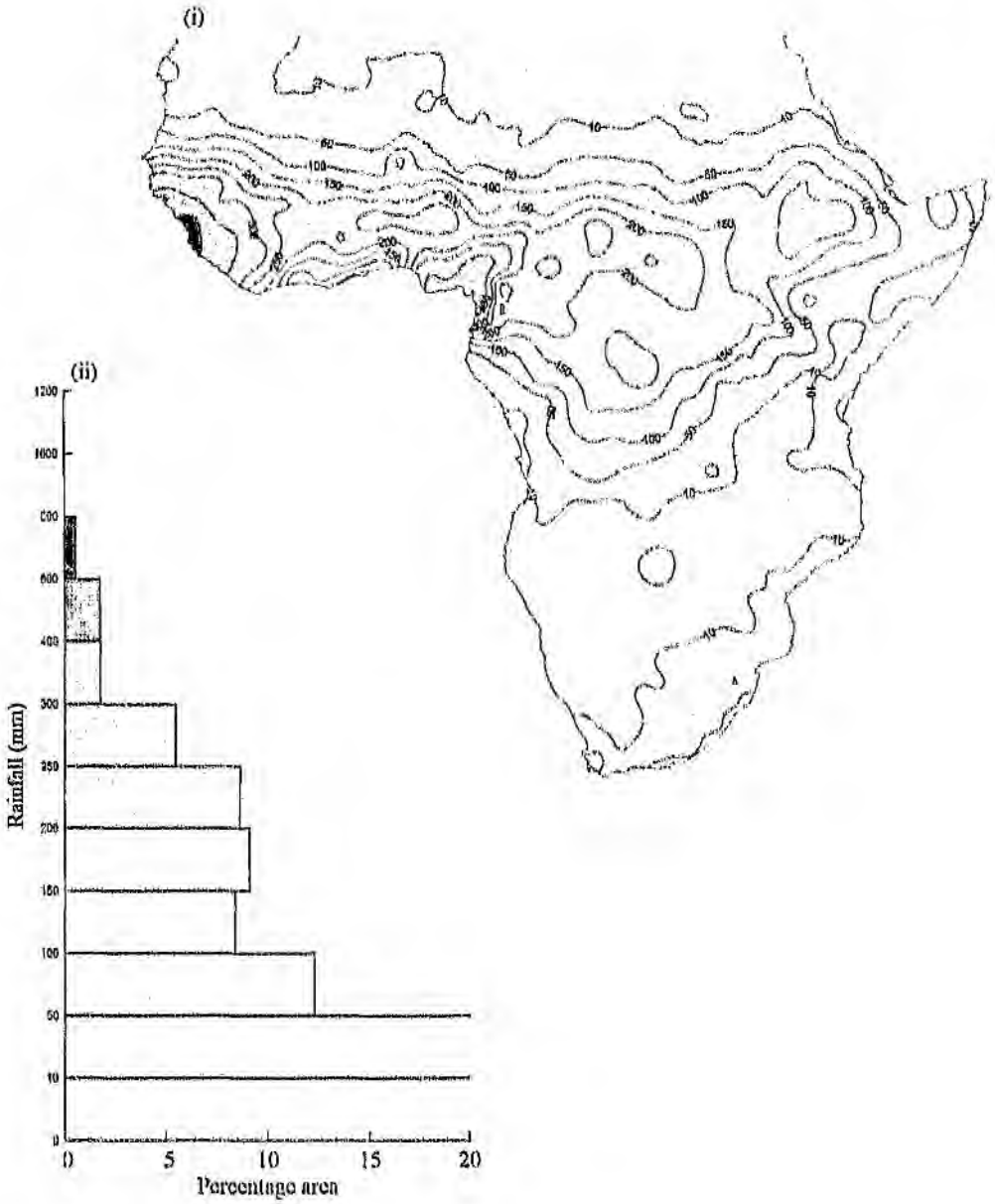


Figure 2.21. Mean Monthly Rainfall: September; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

[1995/09/20 14:59:26.67] C24 – 20 Mean Monthly Rainfall: August

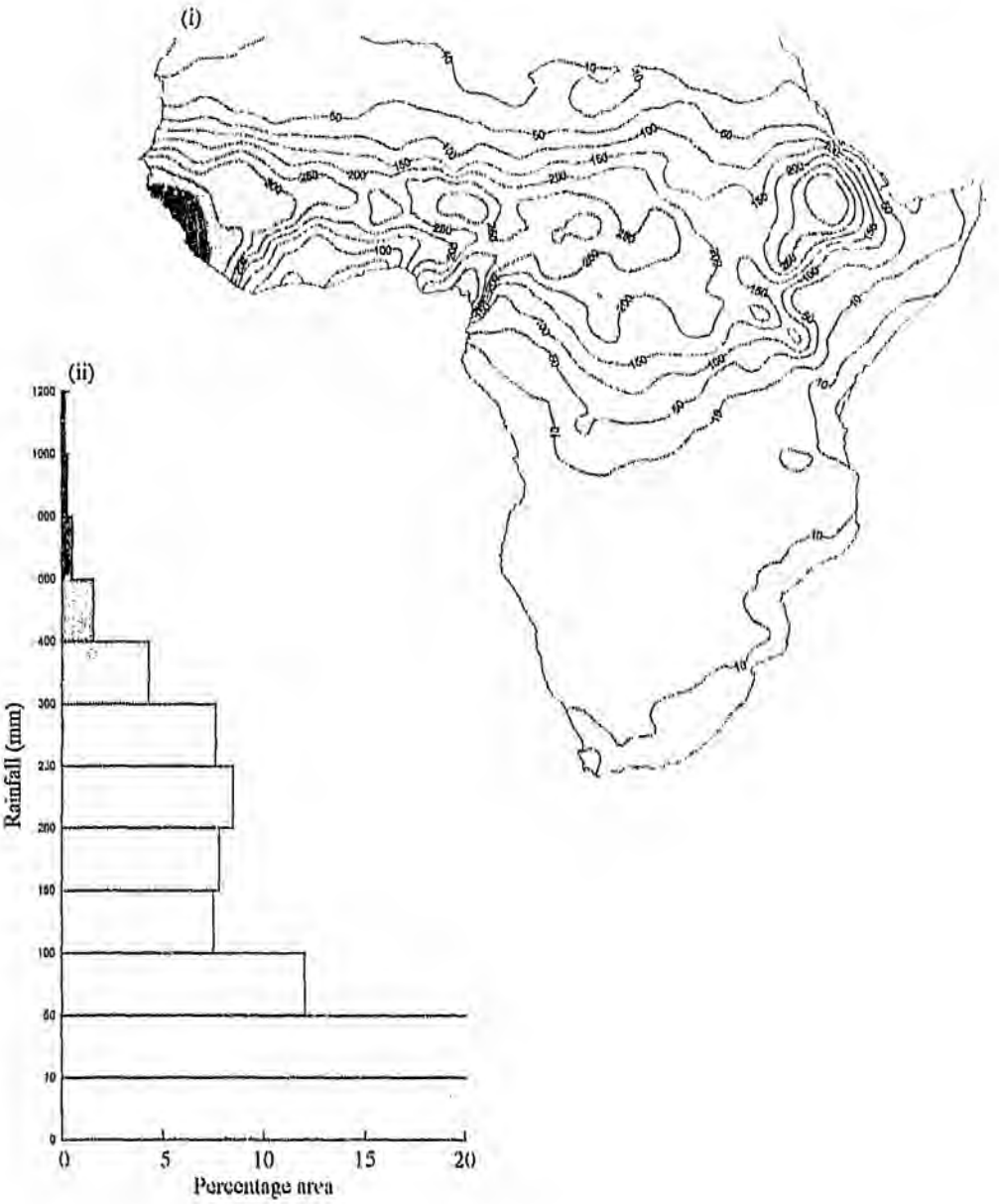


Figure 2.20. Mean Monthly Rainfall: August; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

(1995/05/20 15:00:19.63) C25 – 19 Mean Monthly Rainfall July

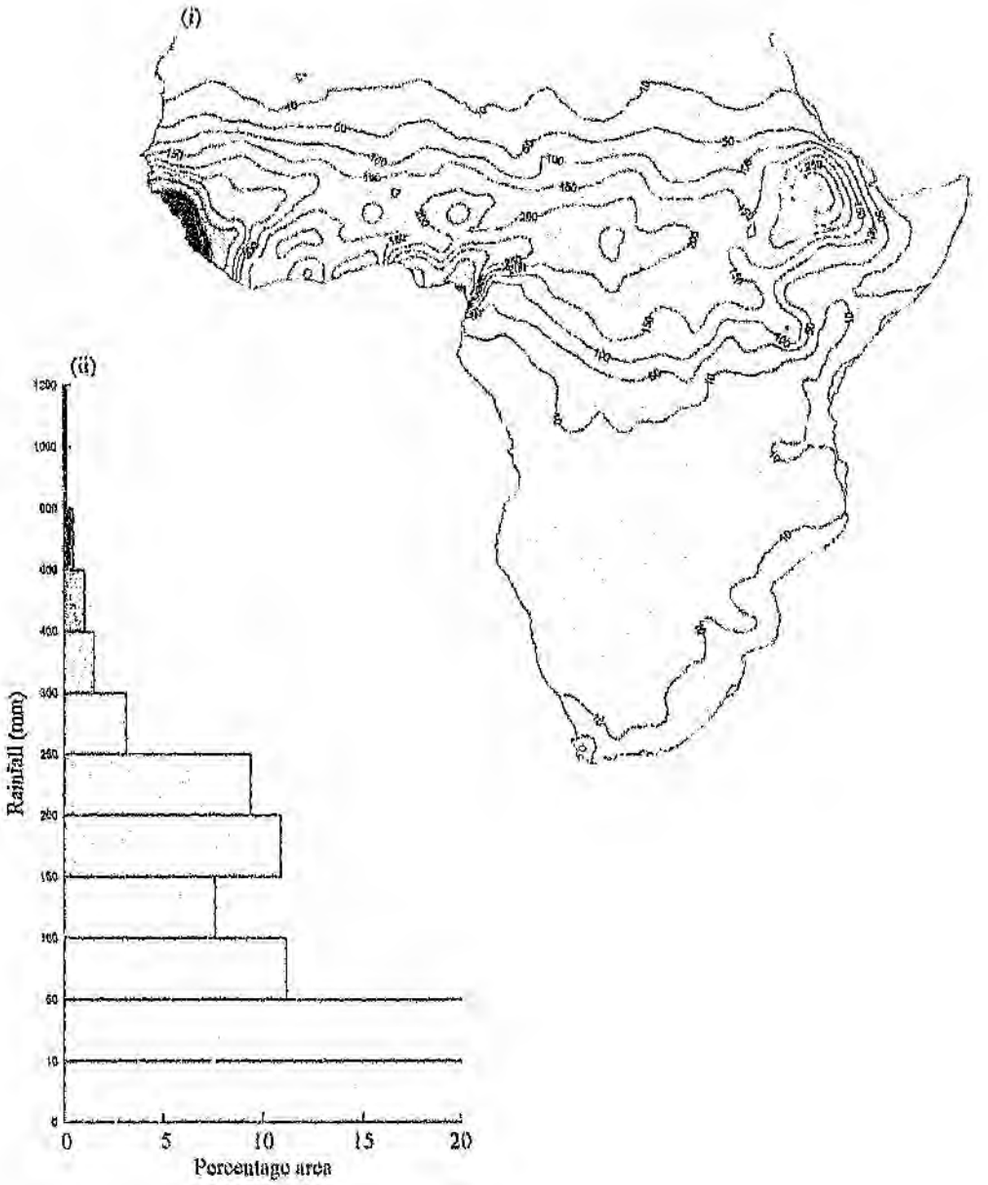


Figure 2.19. Mean Monthly Rainfall: July; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

(1995/09/20 15:01:47.75) C24 – 18 Mean Monthly Rainfall: June

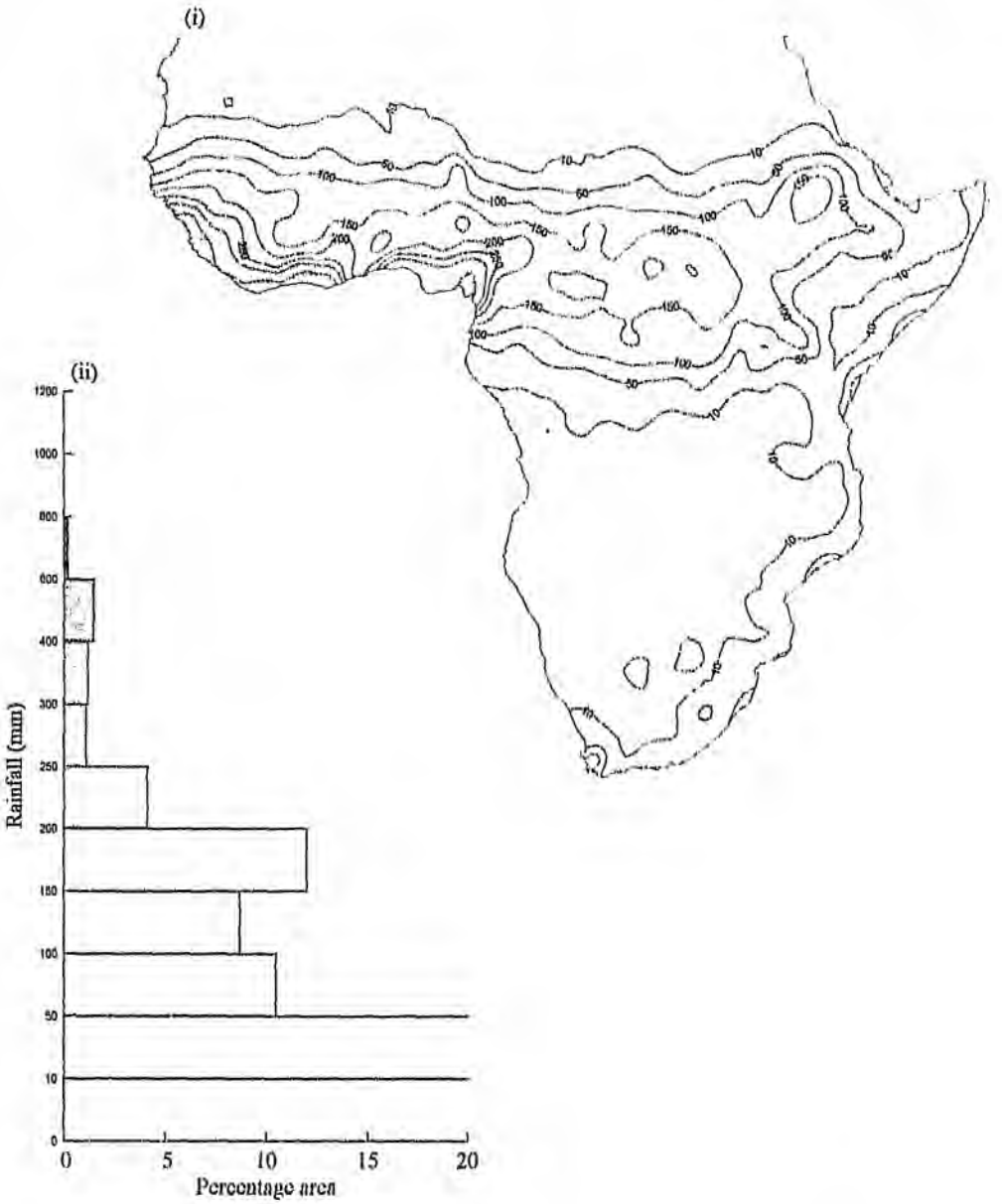


Figure 2.18. Mean Monthly Rainfall: June; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

[1995/09/20 15:01:52.37] C24 – 17 Mean Monthly Rainfall: May

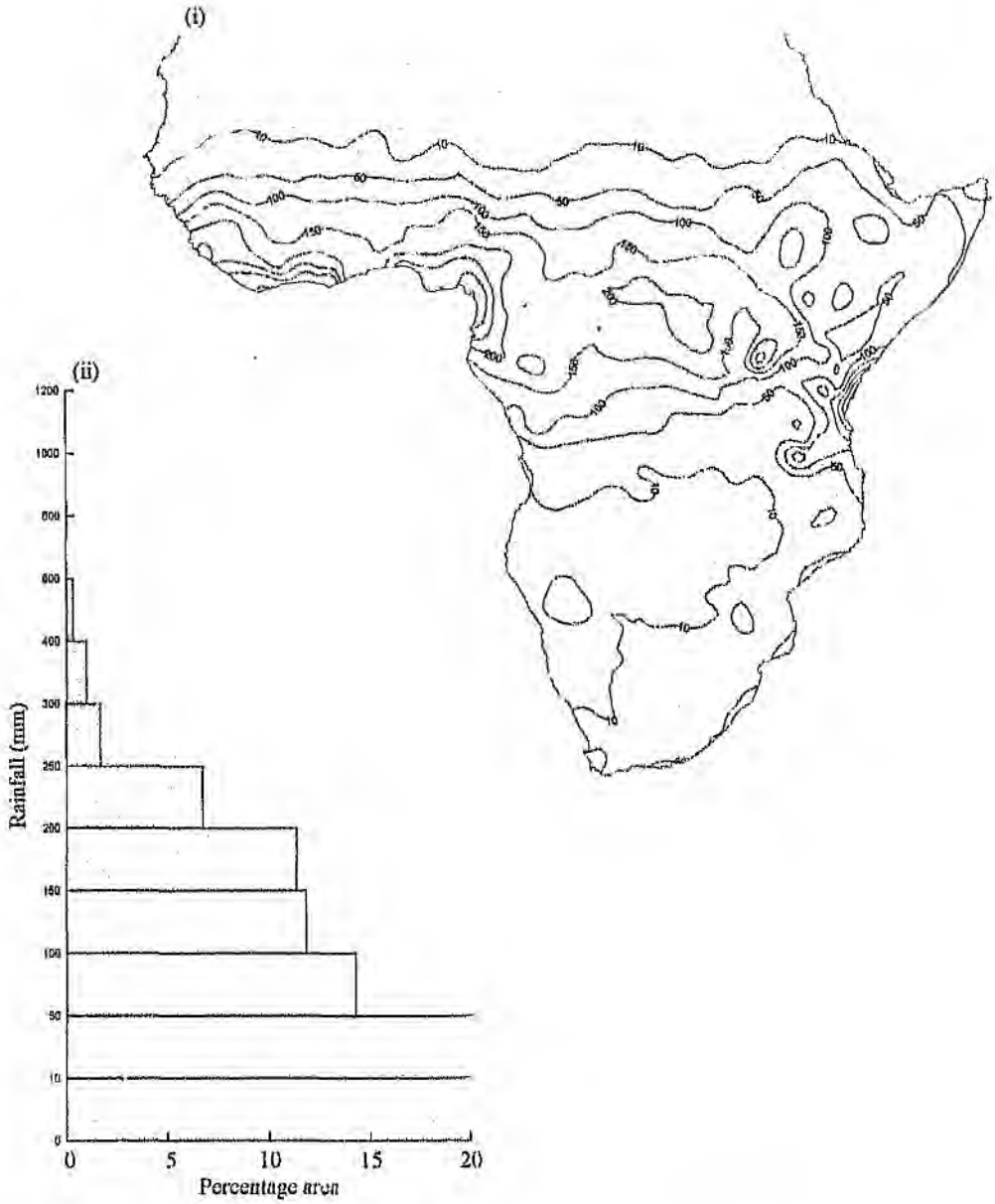


Figure 2.17. Mean Monthly Rainfall: May; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

(1995/09/20 15:02:38.95) C24 – 16 Mean Monthly Rainfall: April

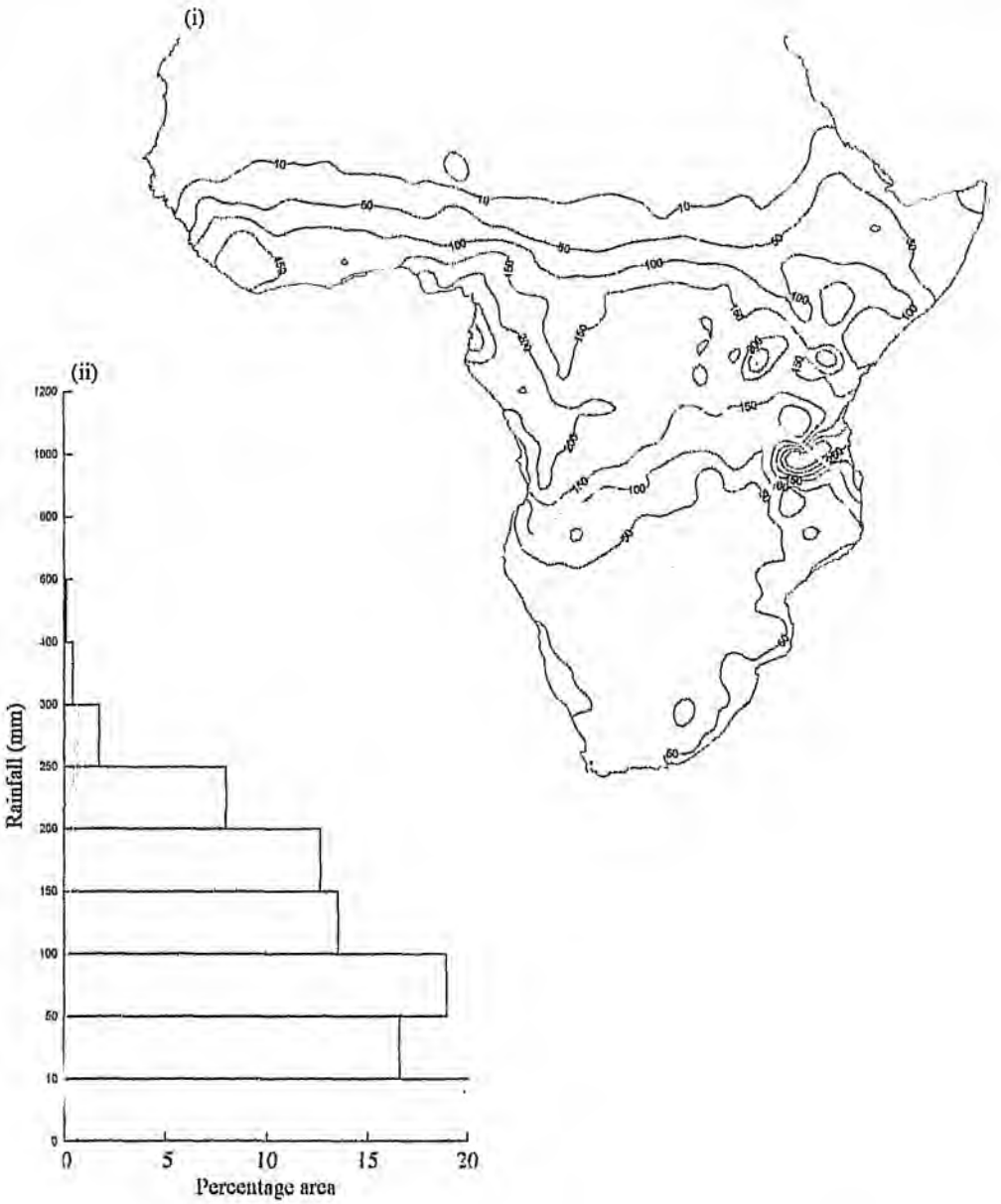


Figure 2.16. Mean Monthly Rainfall: April; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

(19950920 15:03:23.11) C24 – 15. Mean Monthly Rainfall: March

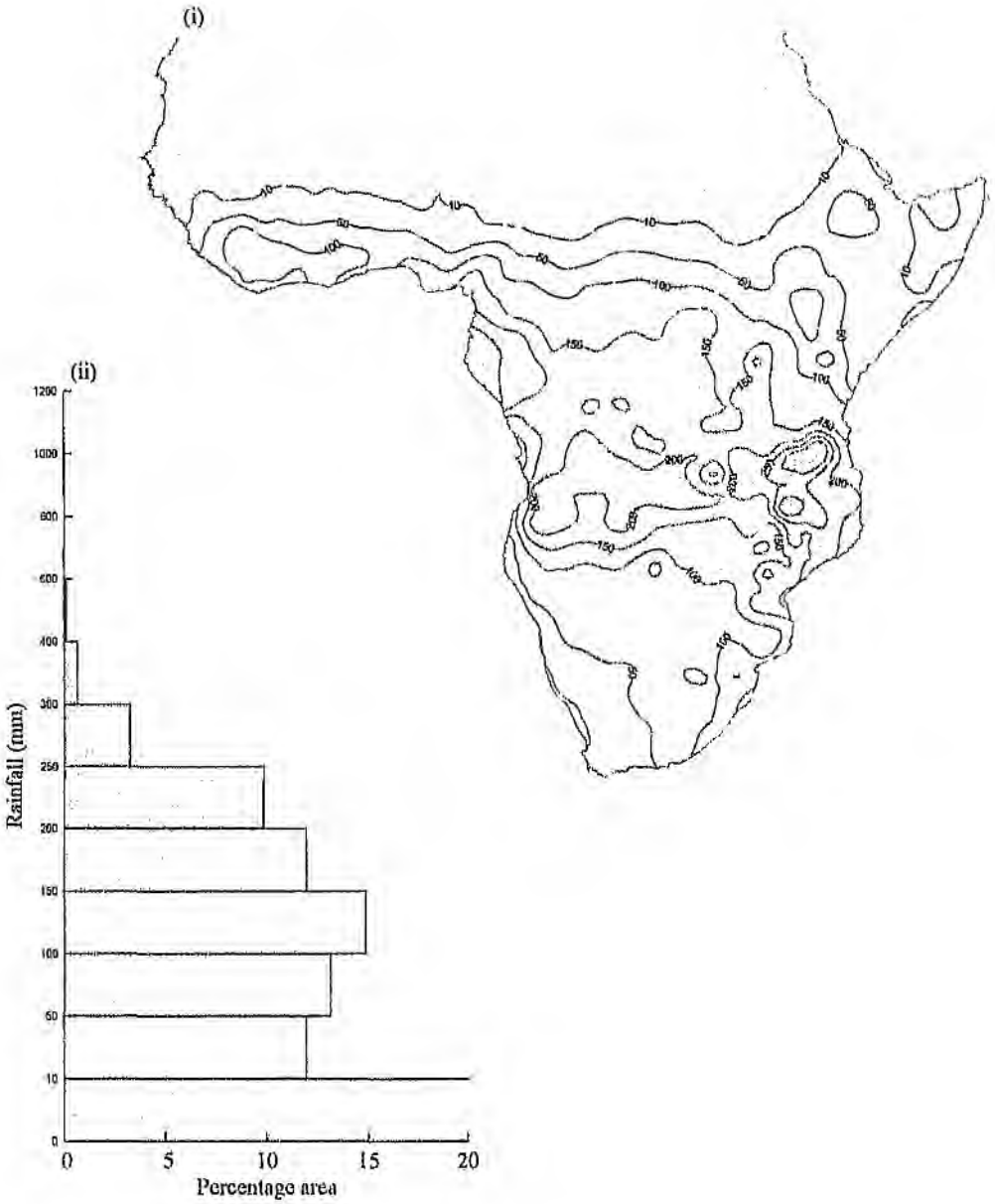


Figure 2.15. Mean Monthly Rainfall: March; (i) contour map of isohyets; (ii) histogram of percentage area by contour level.

(1998/09/09 15:03:21.45) #12 Gazella dorcas (Dorcas gazelle)

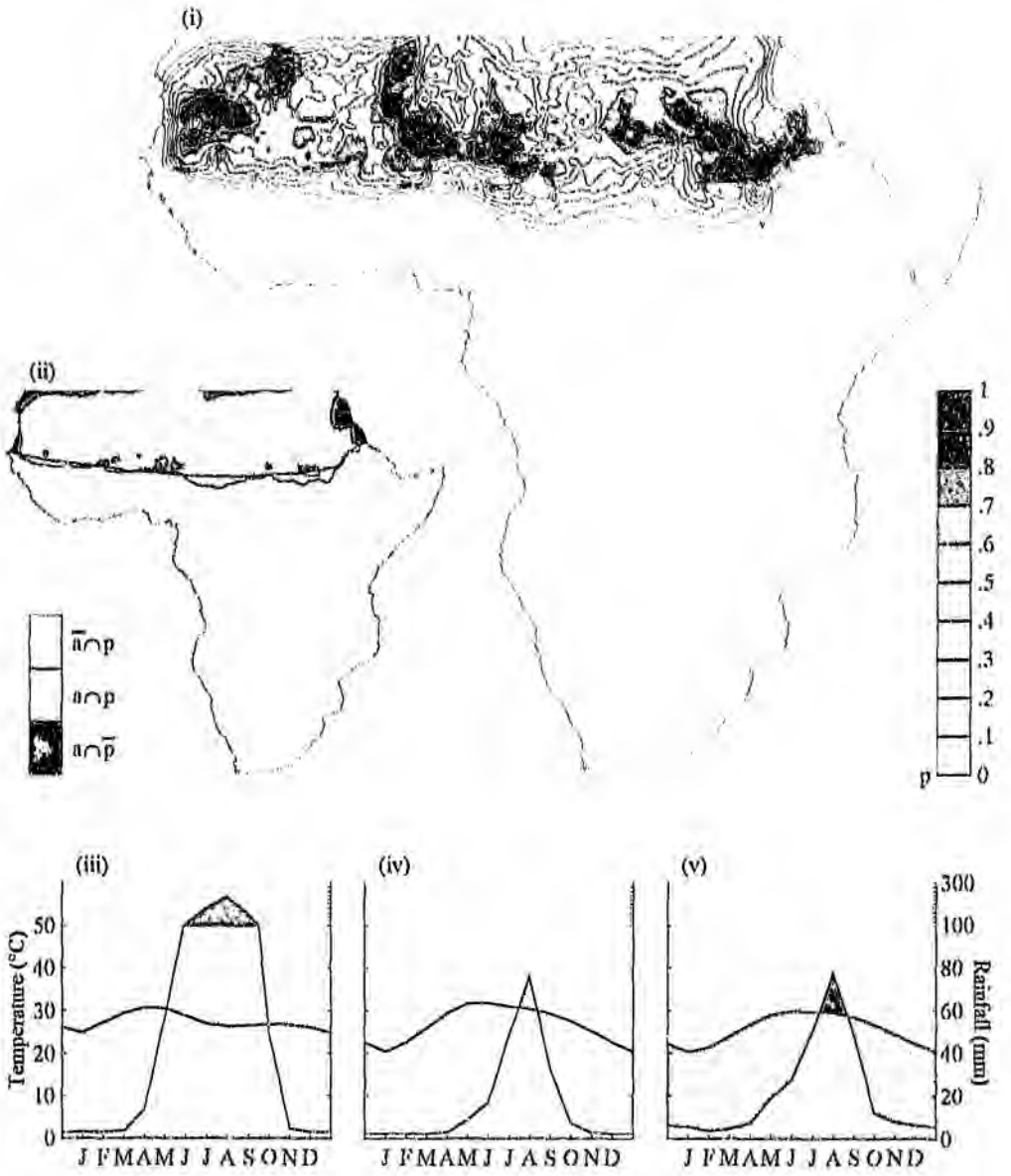


Figure 3.12. *Gazella dorcas*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/05/05 15:10:29.22) #11 Gazella dama (Addra gazelle)

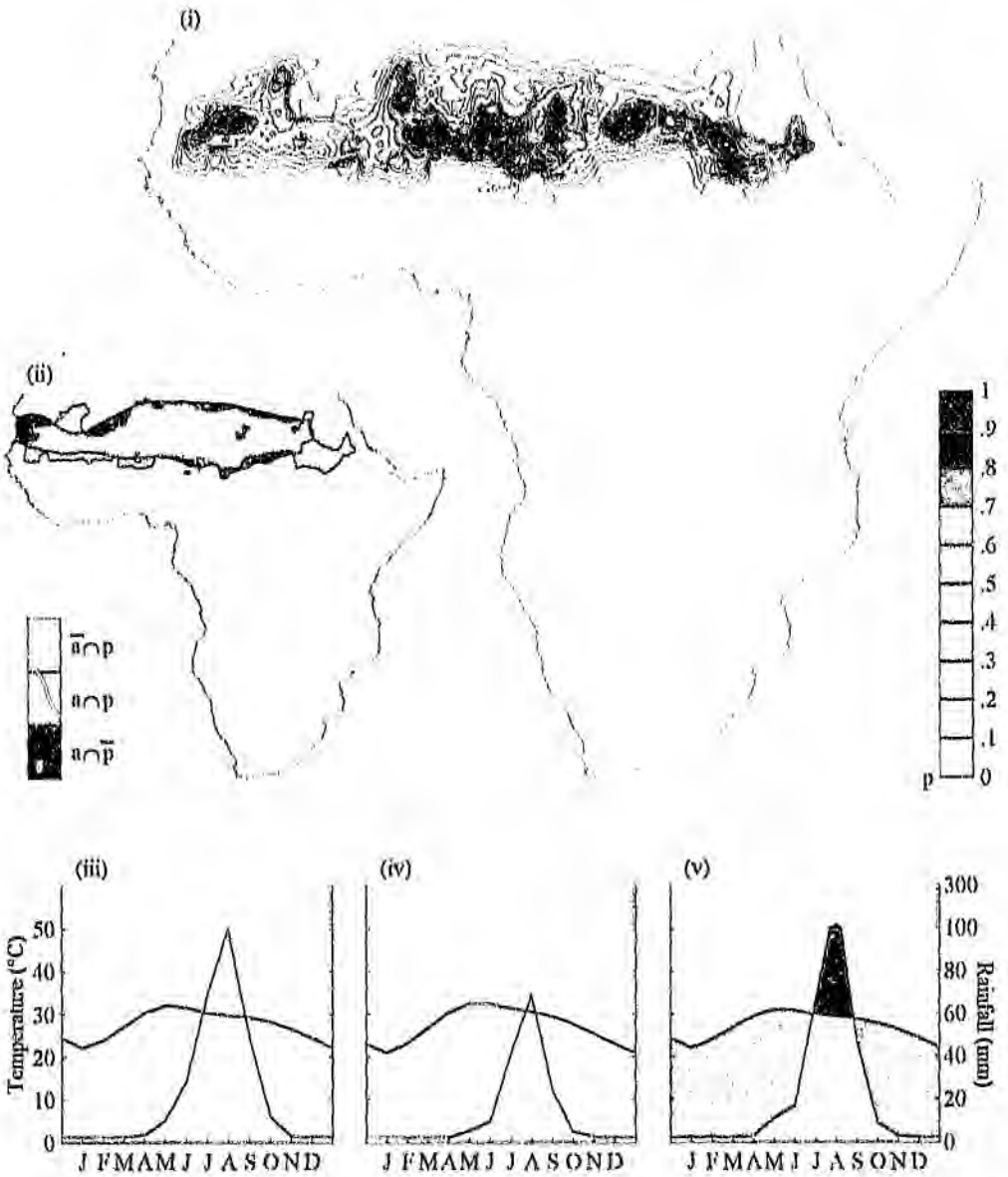


Figure 3.11. *Gazella dama*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19950908 18:02:35 BST) #10 Antidorcas marsupialis (Springbuck)

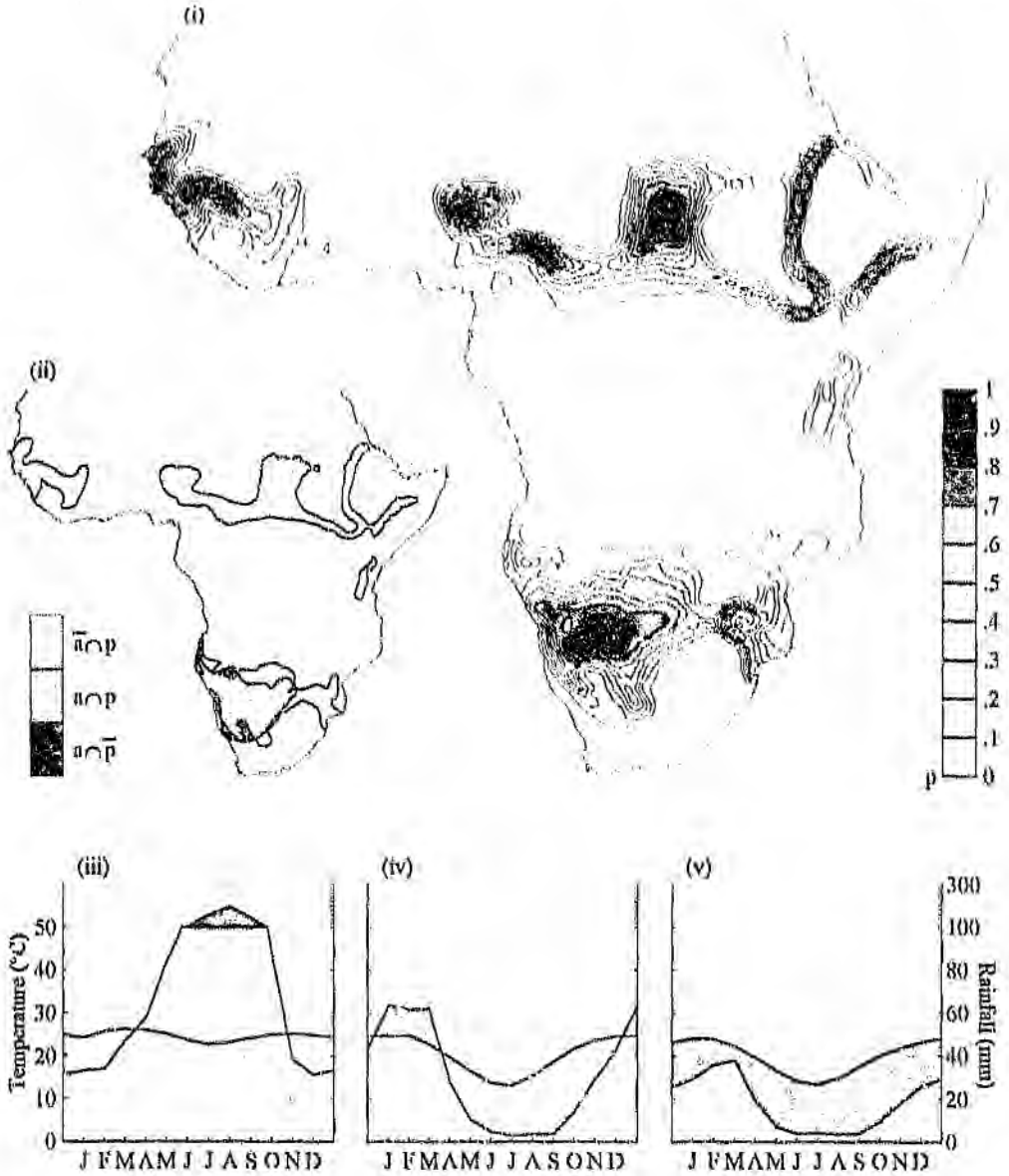


Figure 3.10. *Antidorcas marsupialis*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

{1B6D5B76-1433-22 65} #9 Ammodorcas clarkei (Dibatag, Clarke's gazelle)

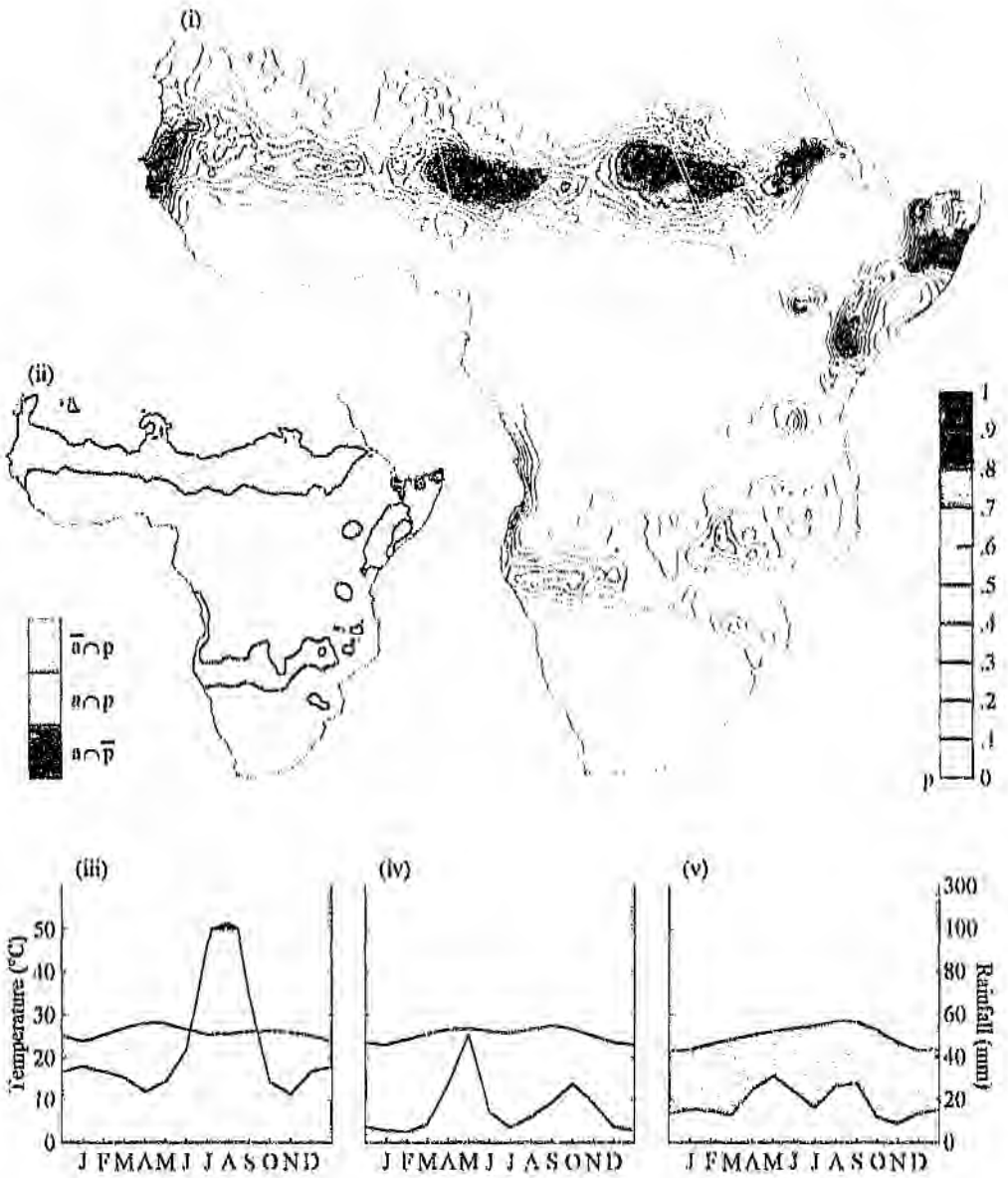


Figure 3.9. *Ammodorcas clarkei*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

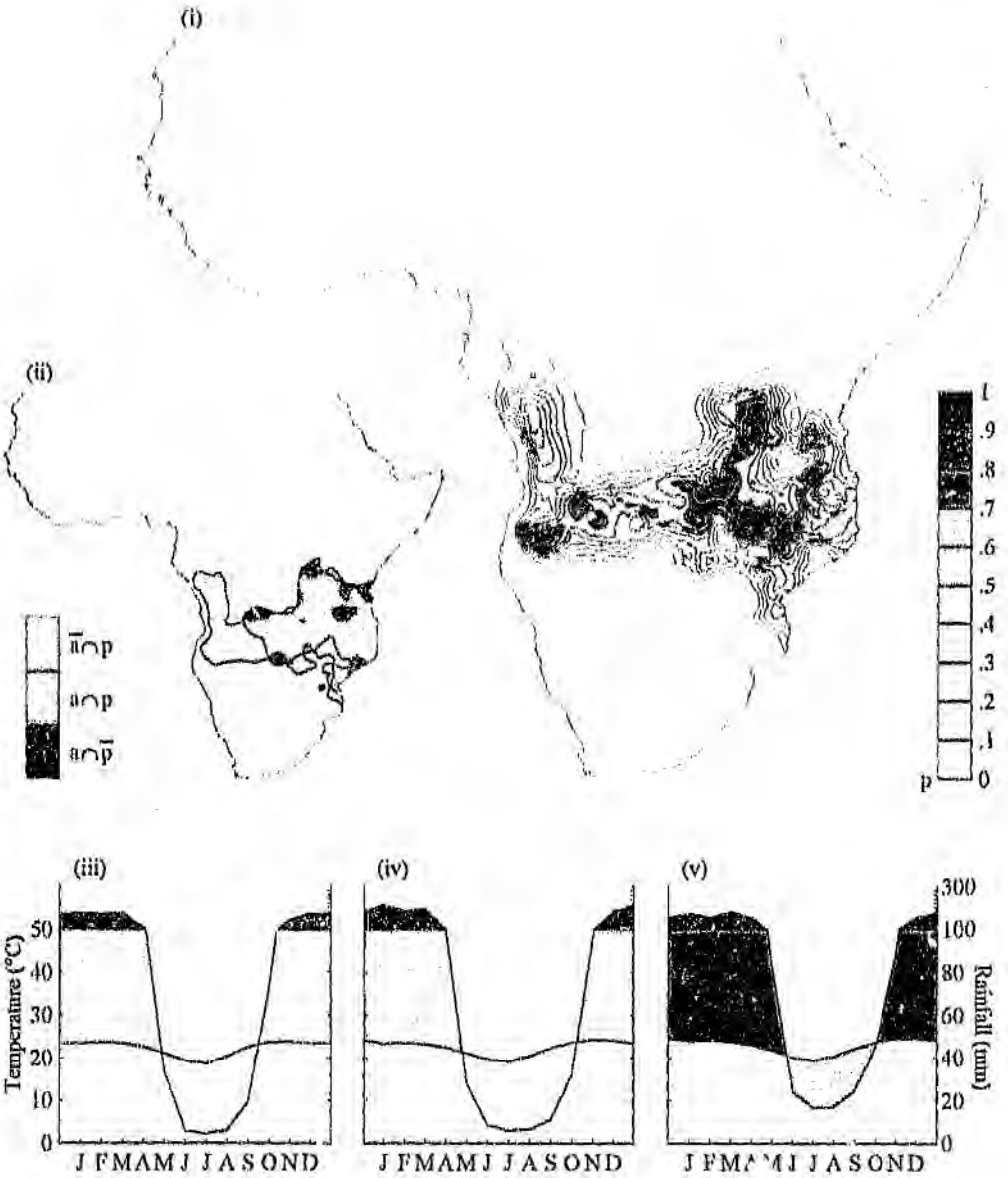


Figure 3.8. *Sigmocerus lichtensteini*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[19950908 13:32:59 44] #7 Damalscus lunatus (Isaaske, Kongjum, Topi, Tang)

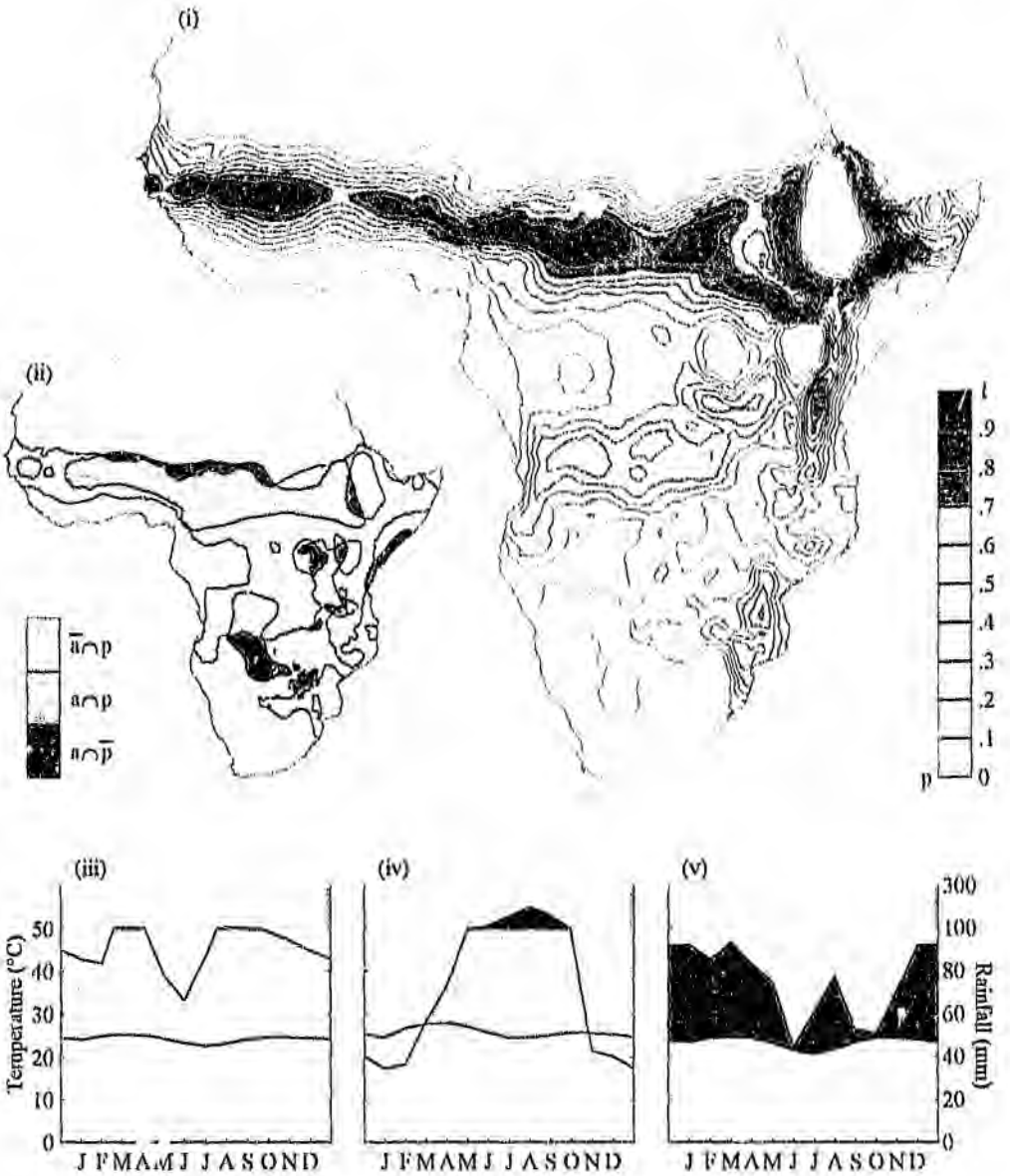


Figure 3.7. *Damaliscus lunatus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

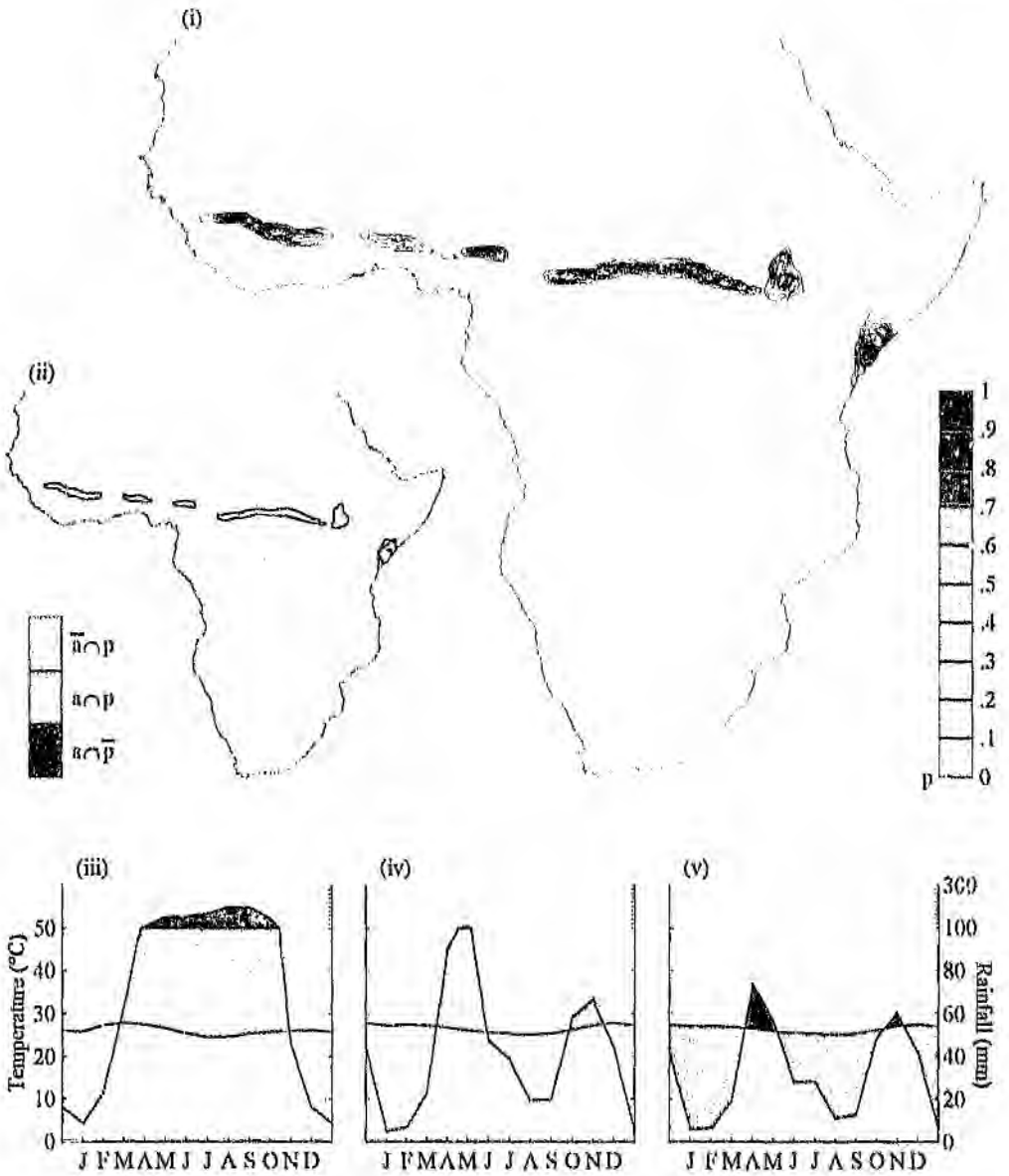


Figure 3.6. *Damaliscus hunteri*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

19980508 11:37:40:31
#D Damaliscus dorcas (Bontebok and Blesbok)

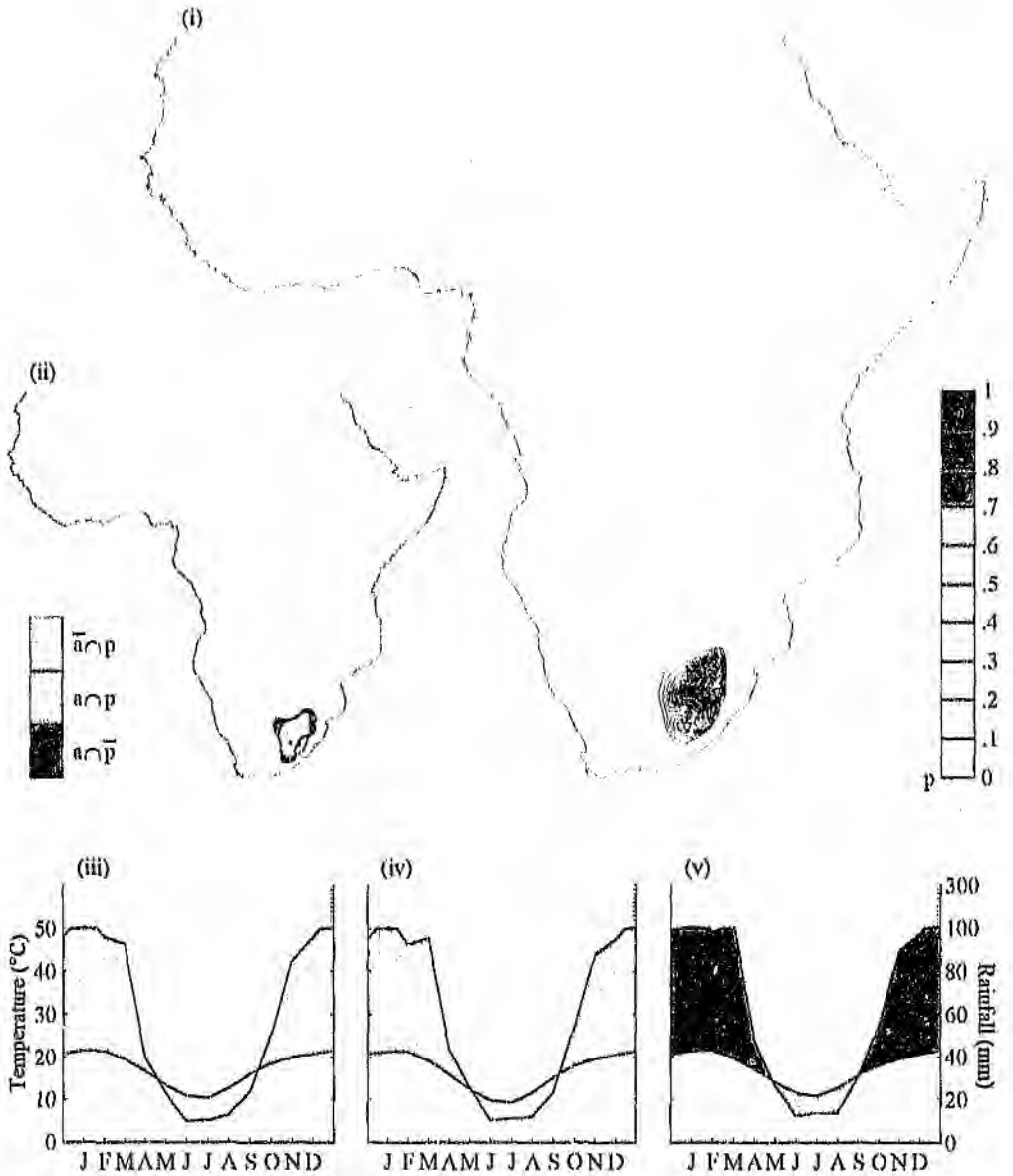


Figure 3.5. *Damaliscus dorcas*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/08 11:36:15.67) #4 Connochaetes taurinus (Blue wildebeest or brindled gnu)

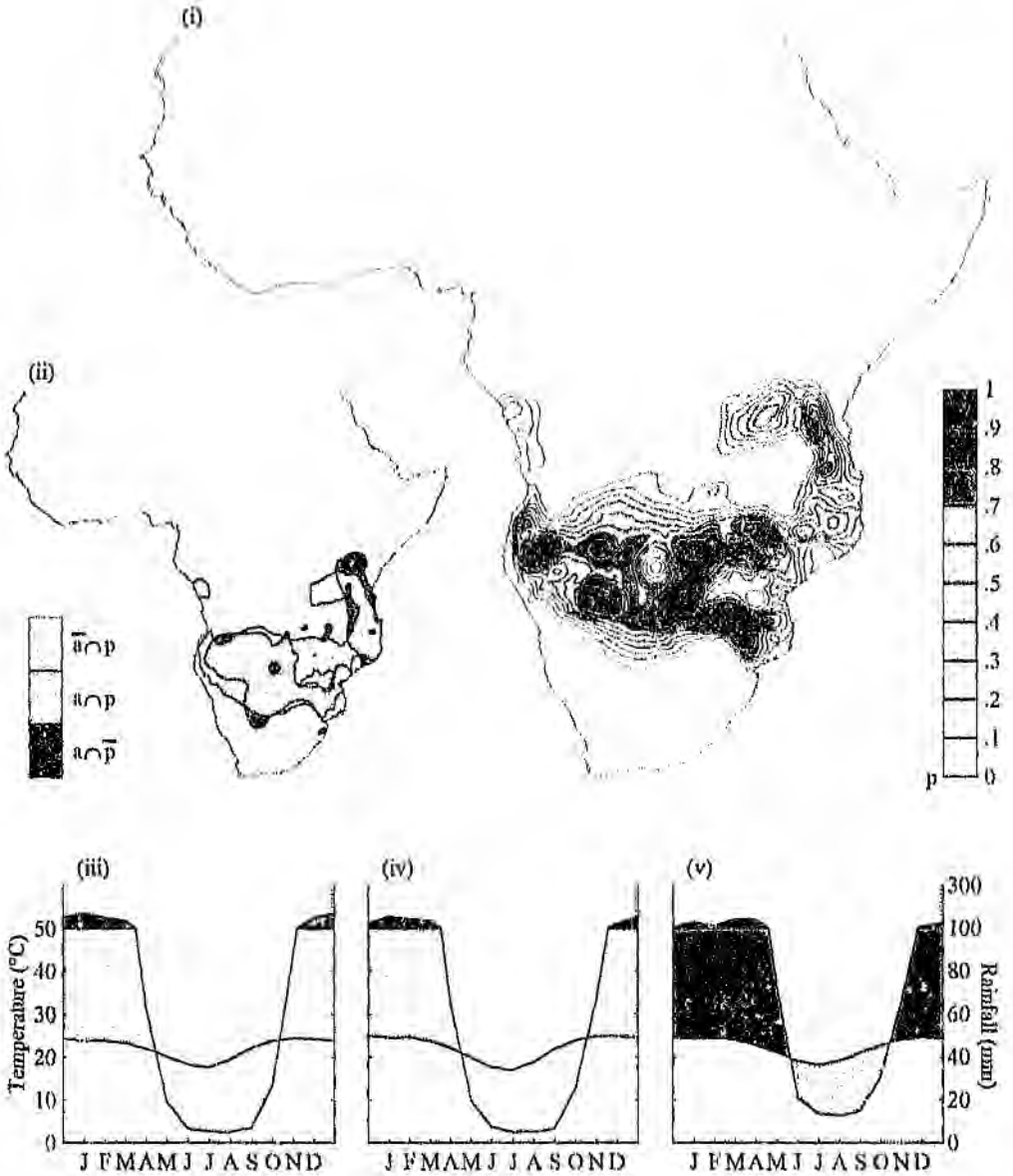


Figure 3.4. *Connochaetes taurinus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/06 11:22:14.98) #3 Connochaetes gnou (Black wildebeest or white-tailed gnu)

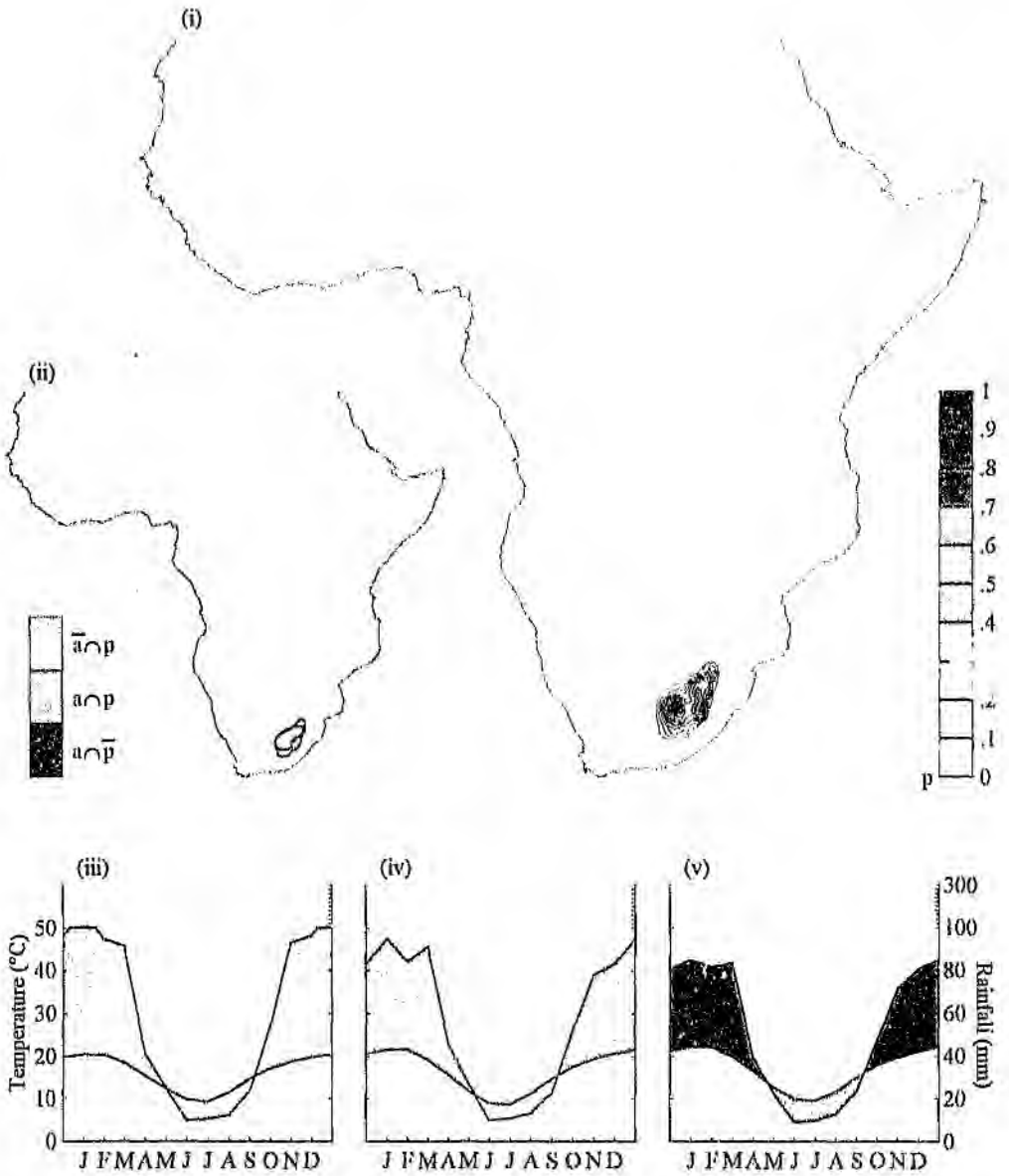


Figure 3.3. *Connochaetes gnou*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/09 11:10:57.69) #2 Alcelaphus buselaphus (Red Hartebeest)

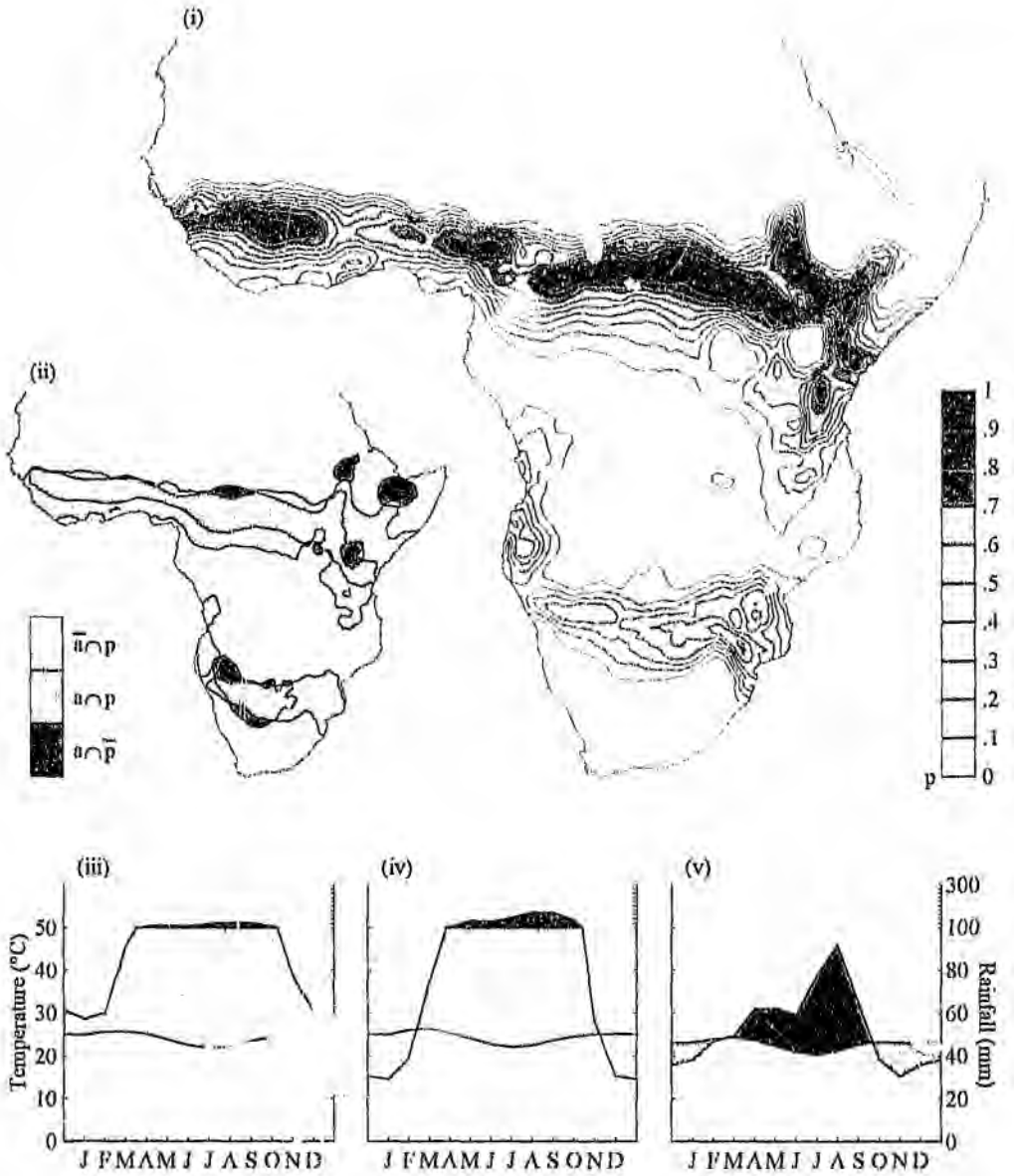


Figure 3.2. *Alcelaphus buselaphus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19950909 11:00:58 12) #1 Aepyceros melampus (impala)

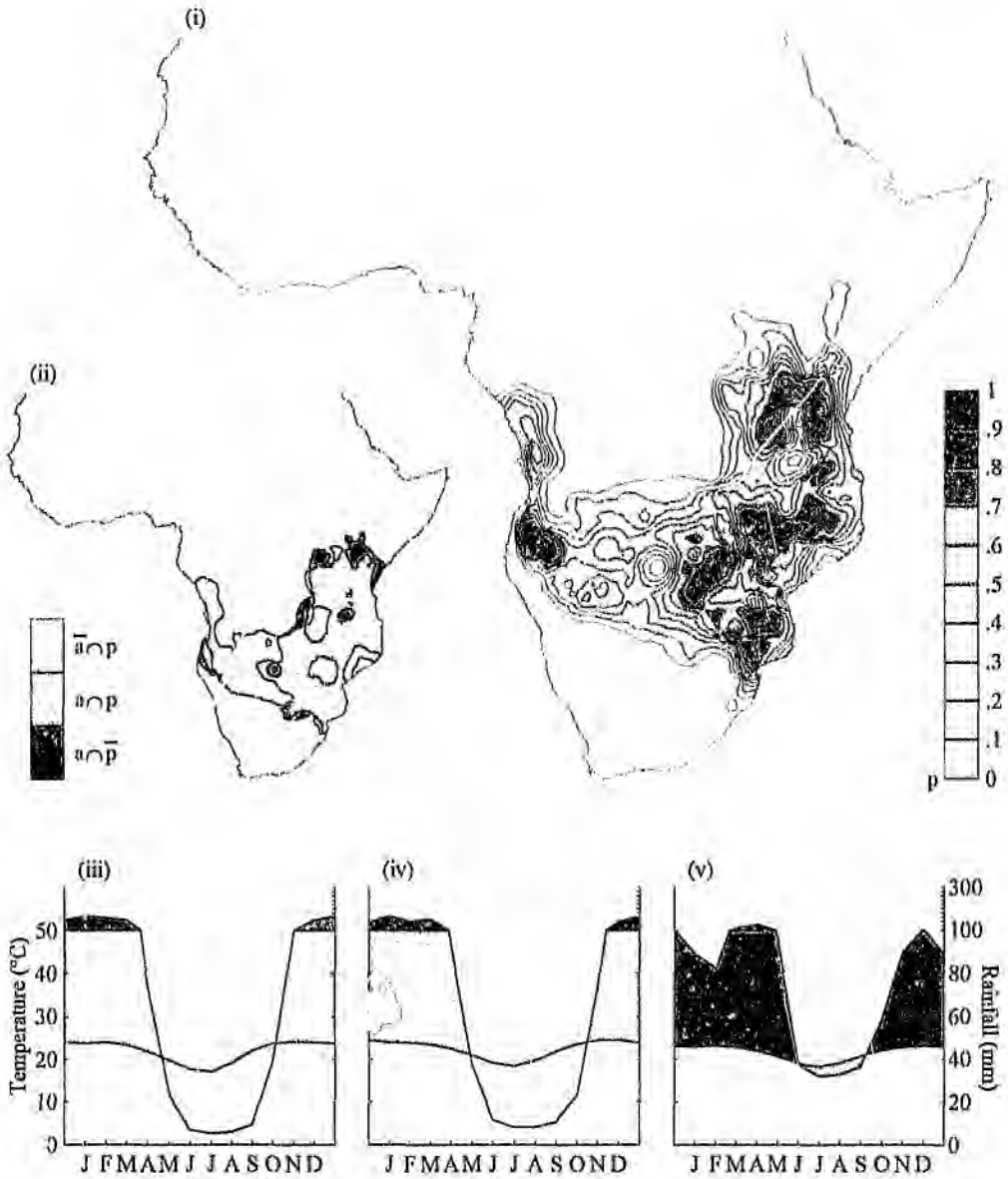


Figure 3.1. *Aepyceros melampus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[1995/05/07 13:01:23.22] #21 Madoqua guentheri (Guenther's dik-dik)

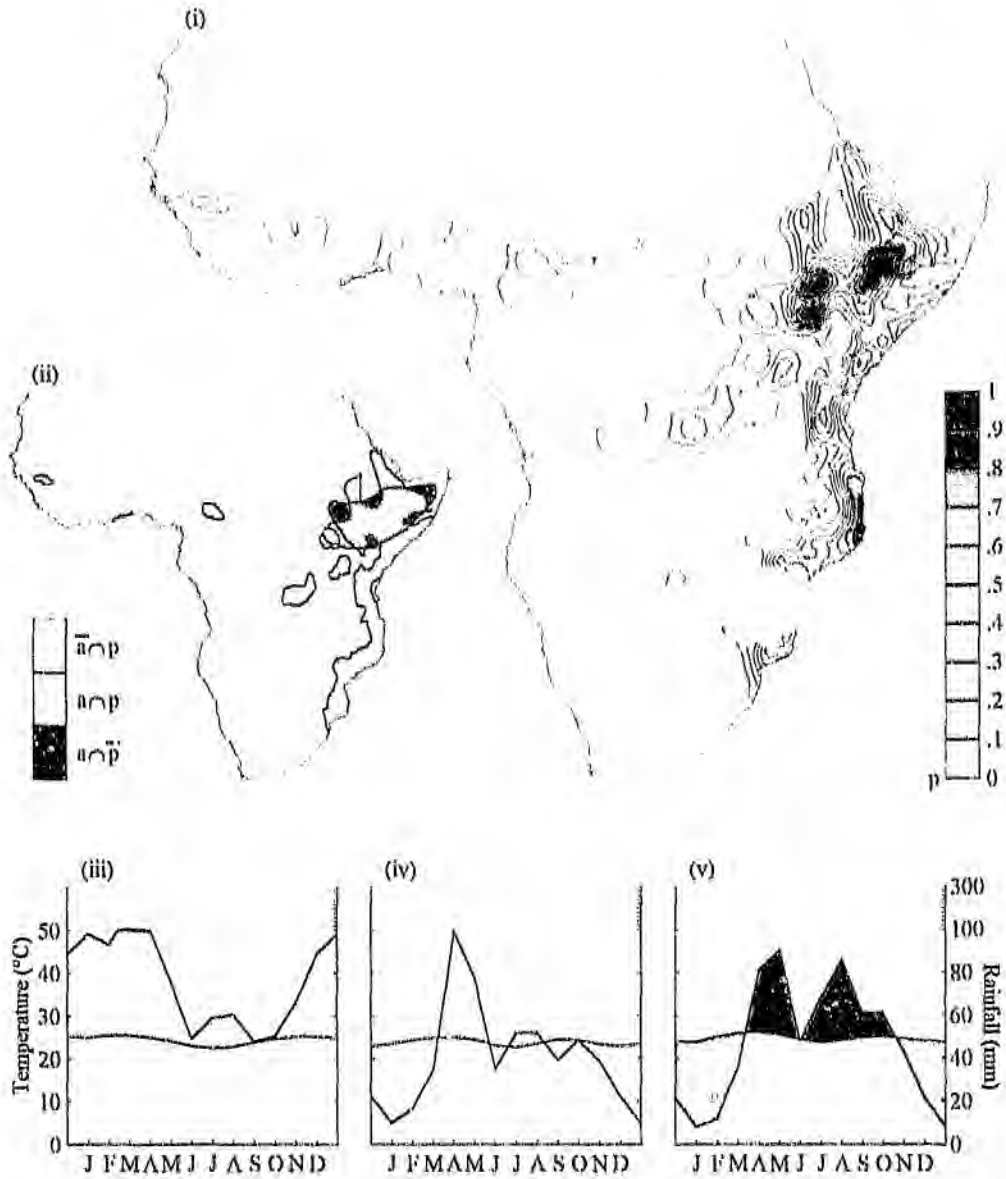


Figure 3.21. *Madoqua guentheri*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

19960306 16:53:4 06)

#20 Dorcatragus megalotis (Beis)

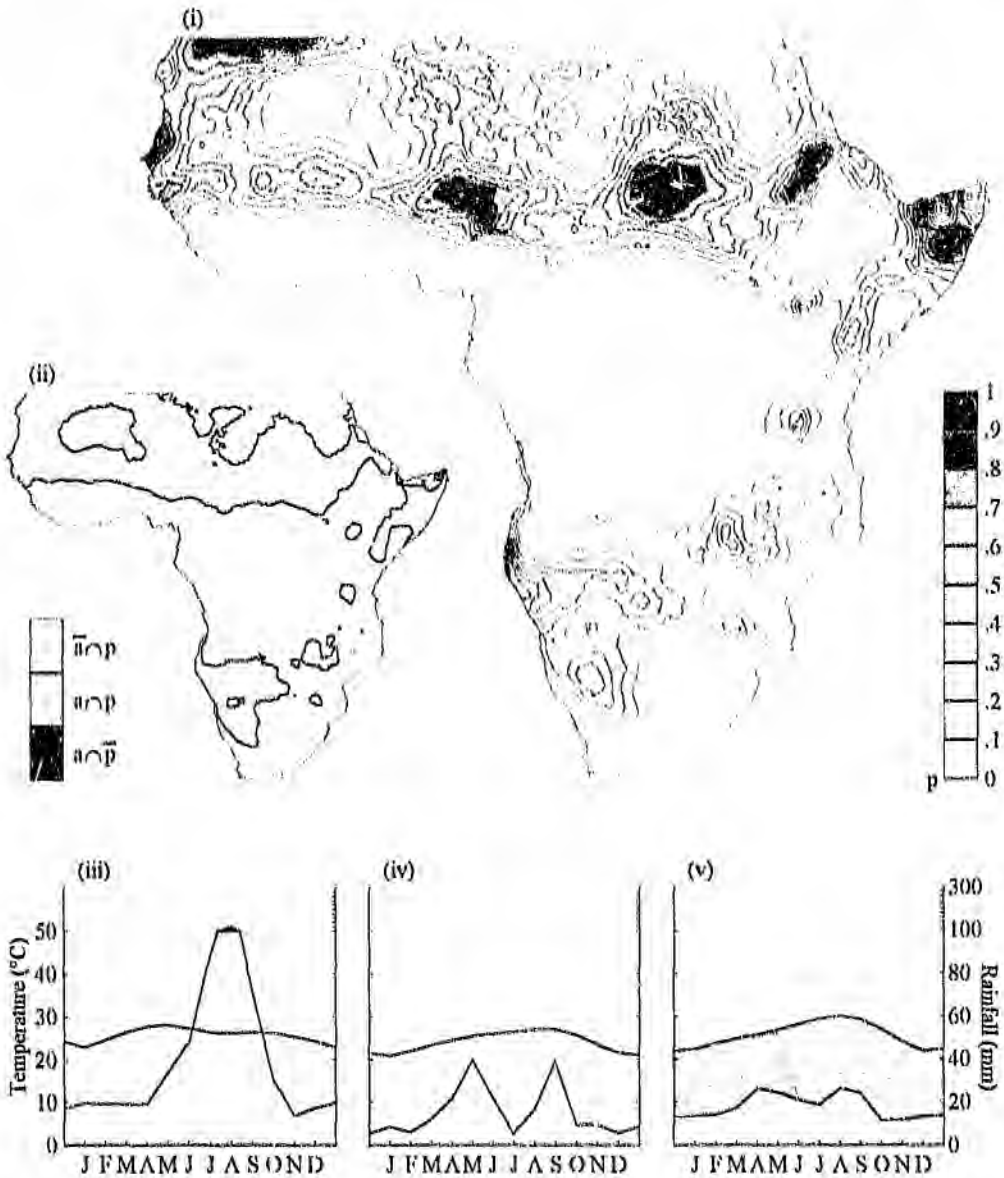


Figure 3.20. *Dorcatragus megalotis*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

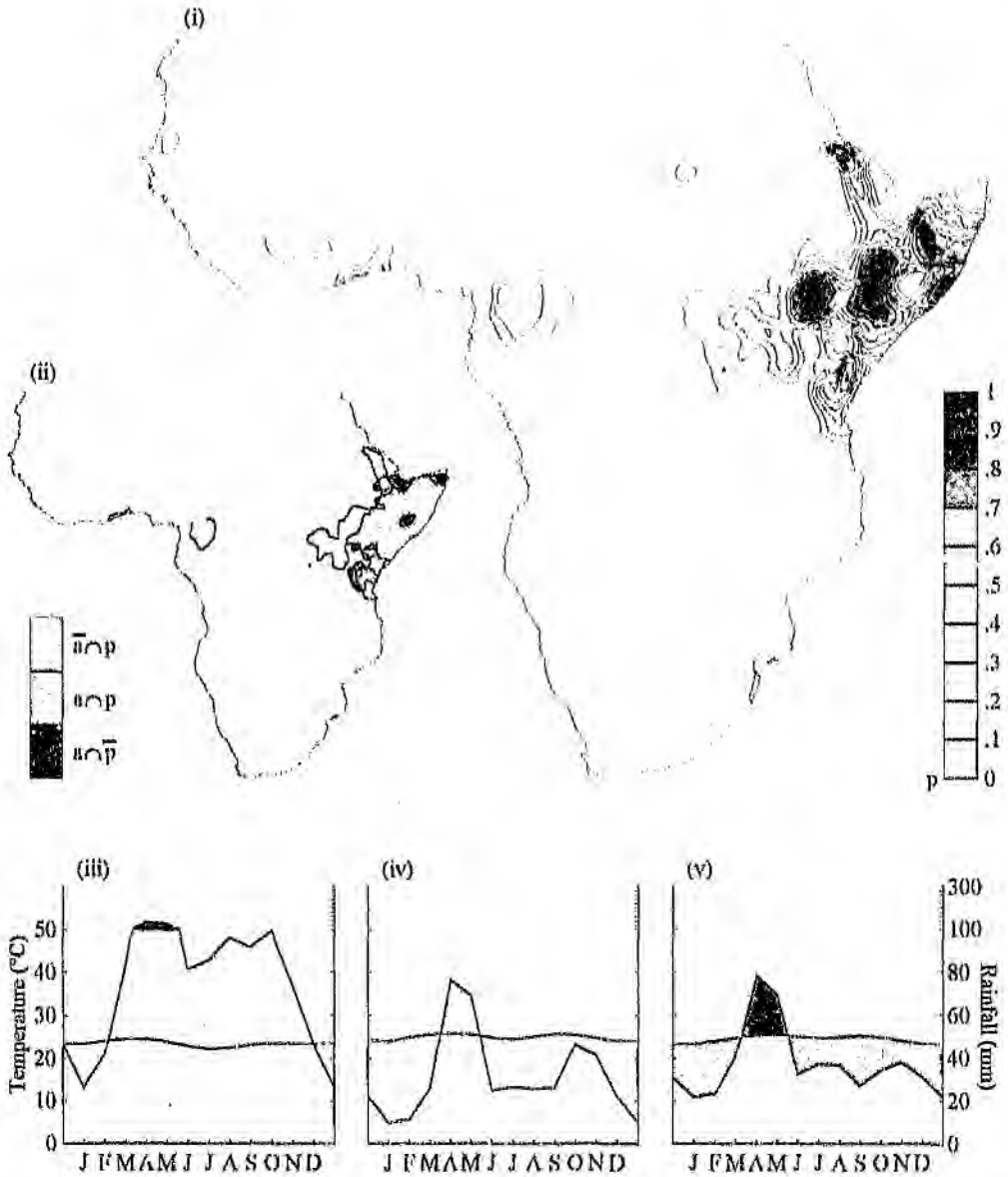


Figure 3.19. *Litocranius walleri*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/08 16:06:36.26) #18 Gazella thomsoni (Thomson's gazelle)

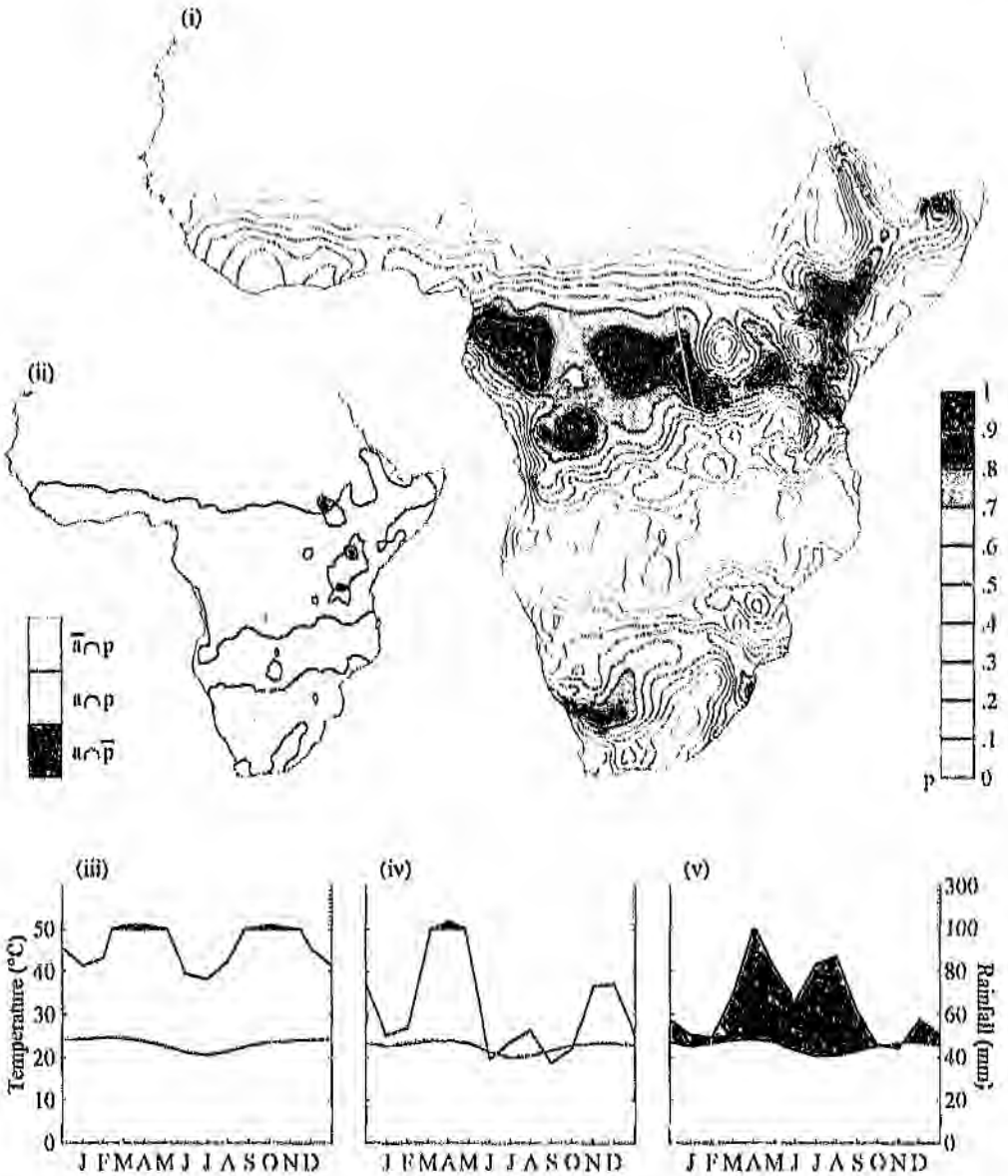


Figure 3.18. *Gazella thomsoni*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

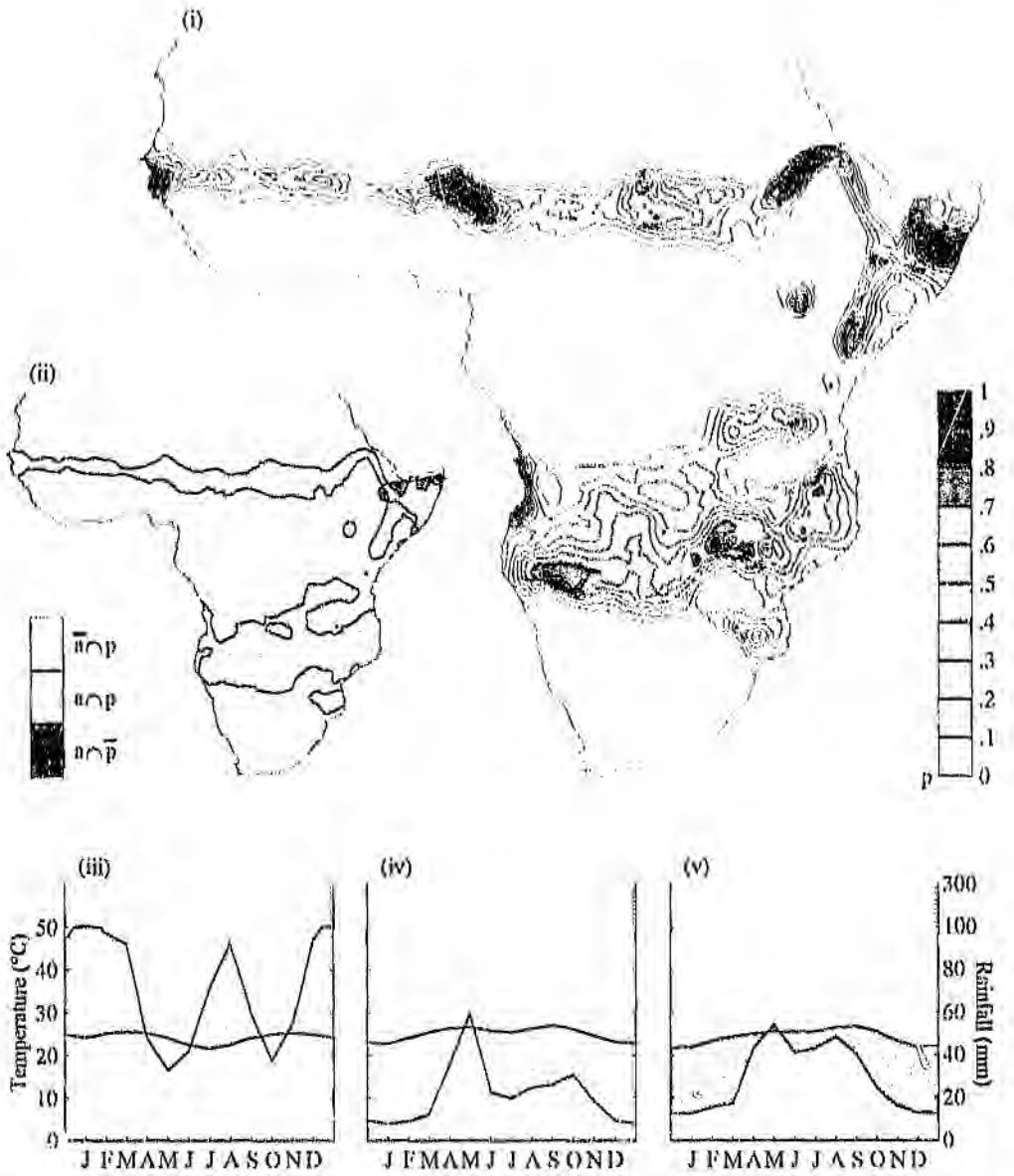


Figure 3.17. *Gazella spekei*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, a (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(ISSDNX06 15:54:15 76) #17 Gazella spekei (Speke's gazelle)

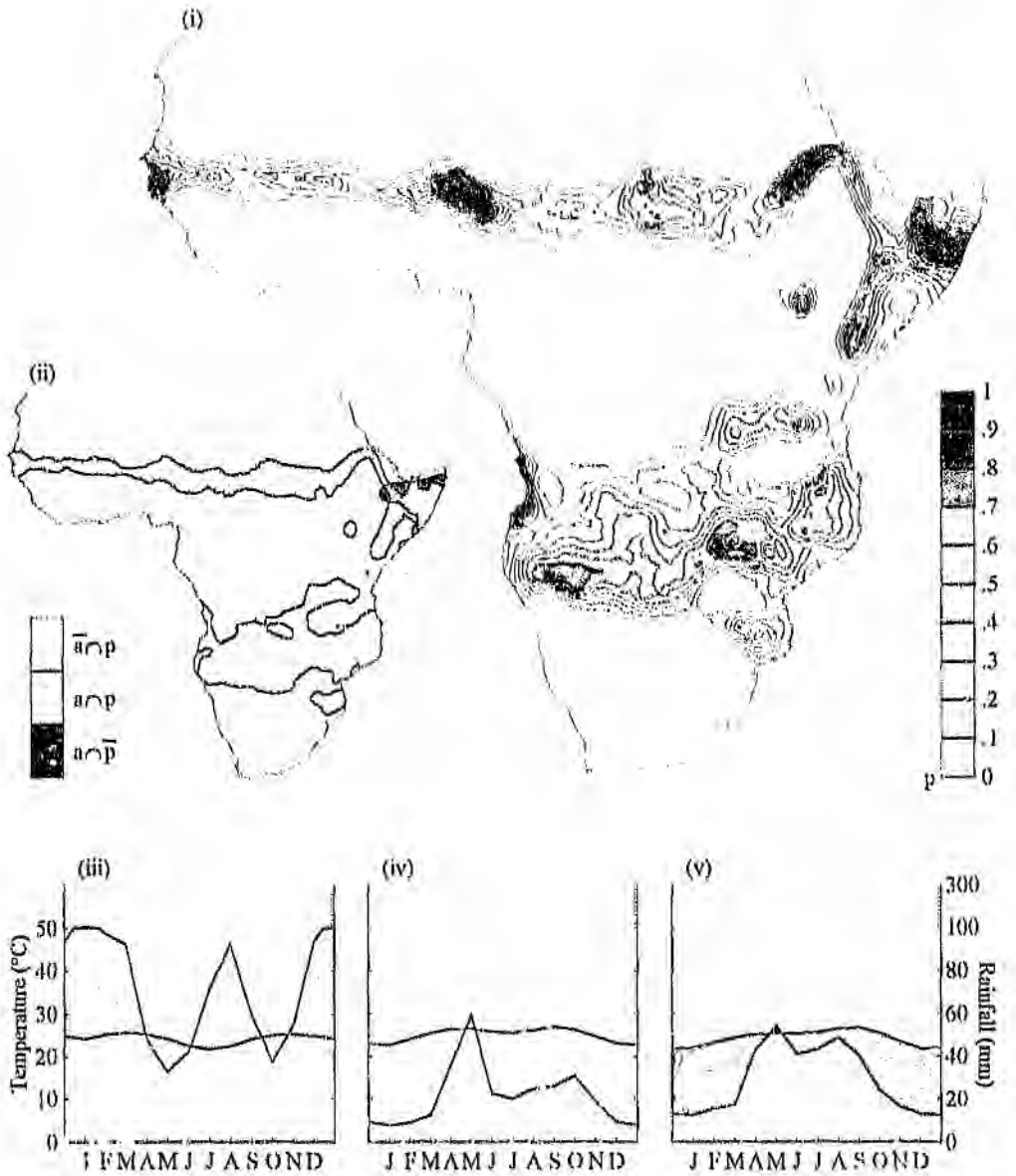


Figure 3.17. *Gazella spekei*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[1955]0006 15:44:37 17] #16 Gazella soemmeringi (Soemmering's gazelle)

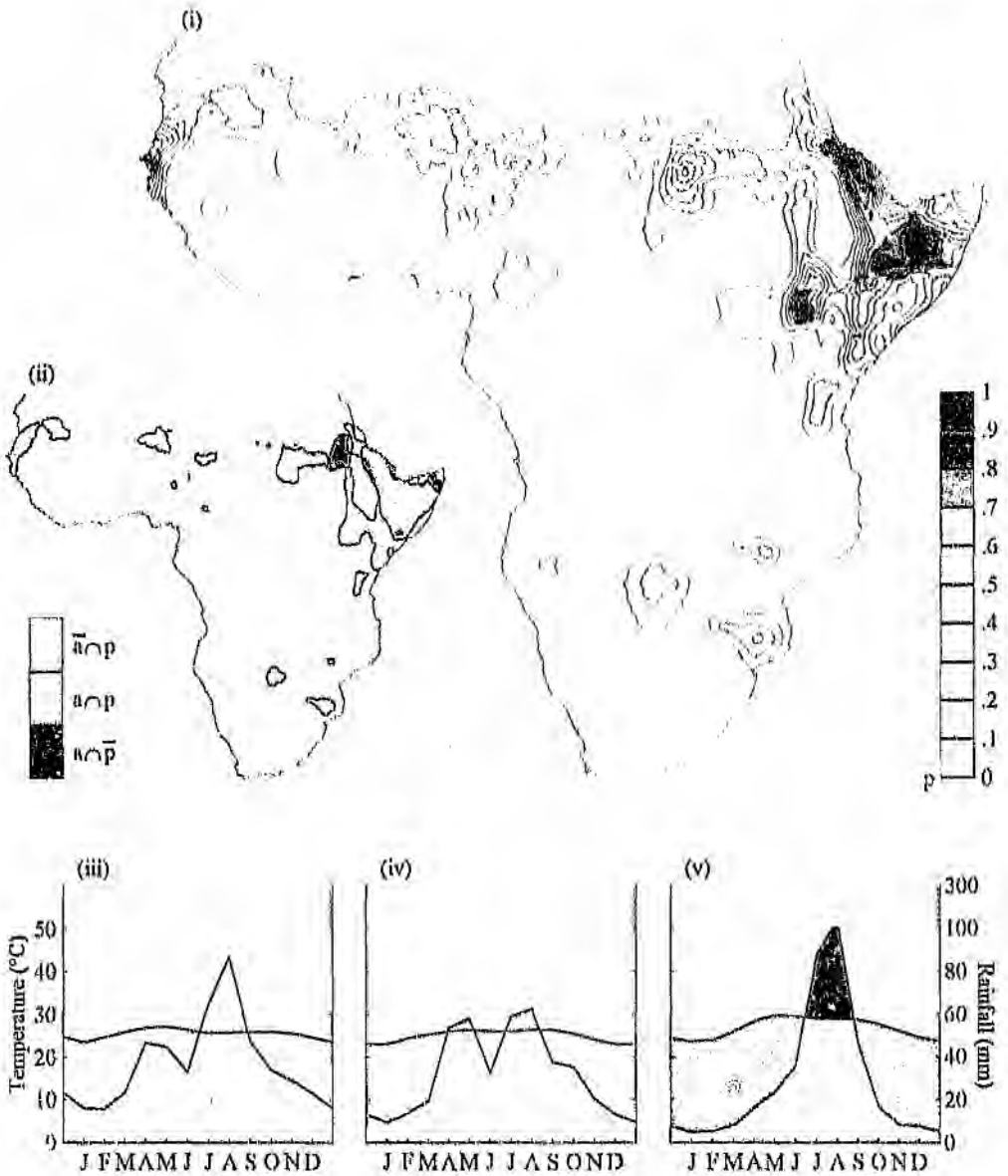


Figure 3.16. *Gazella soemmeringi*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/06 15:44:37.17) #18 Gazella soemmeringi (Soemmering's gazelle)

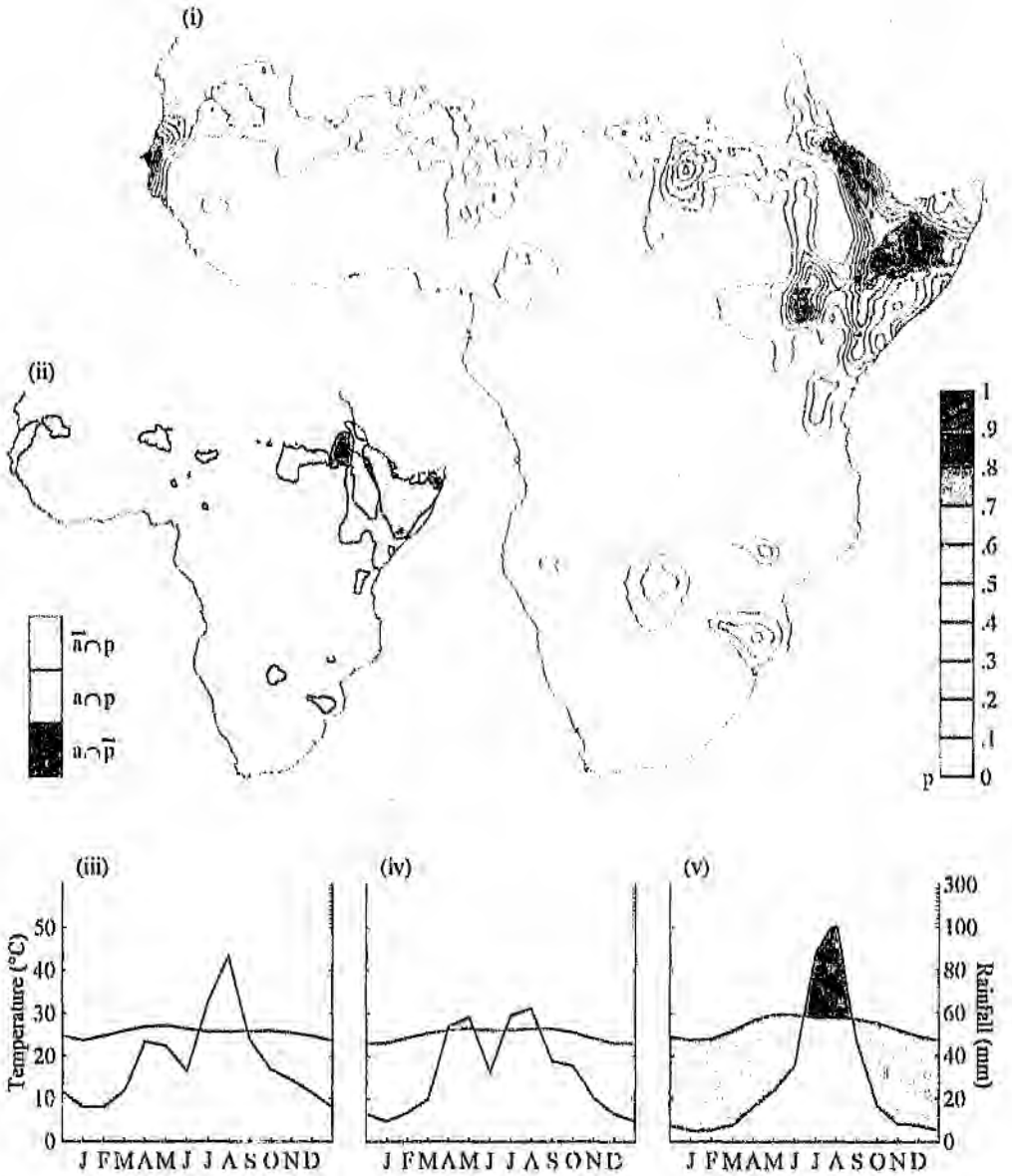


Figure 3.16. *Gazella soemmeringi*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[1995/09/08 15:35:8.83] #15 Gazella rufifrons (Red-fronted gazelle)

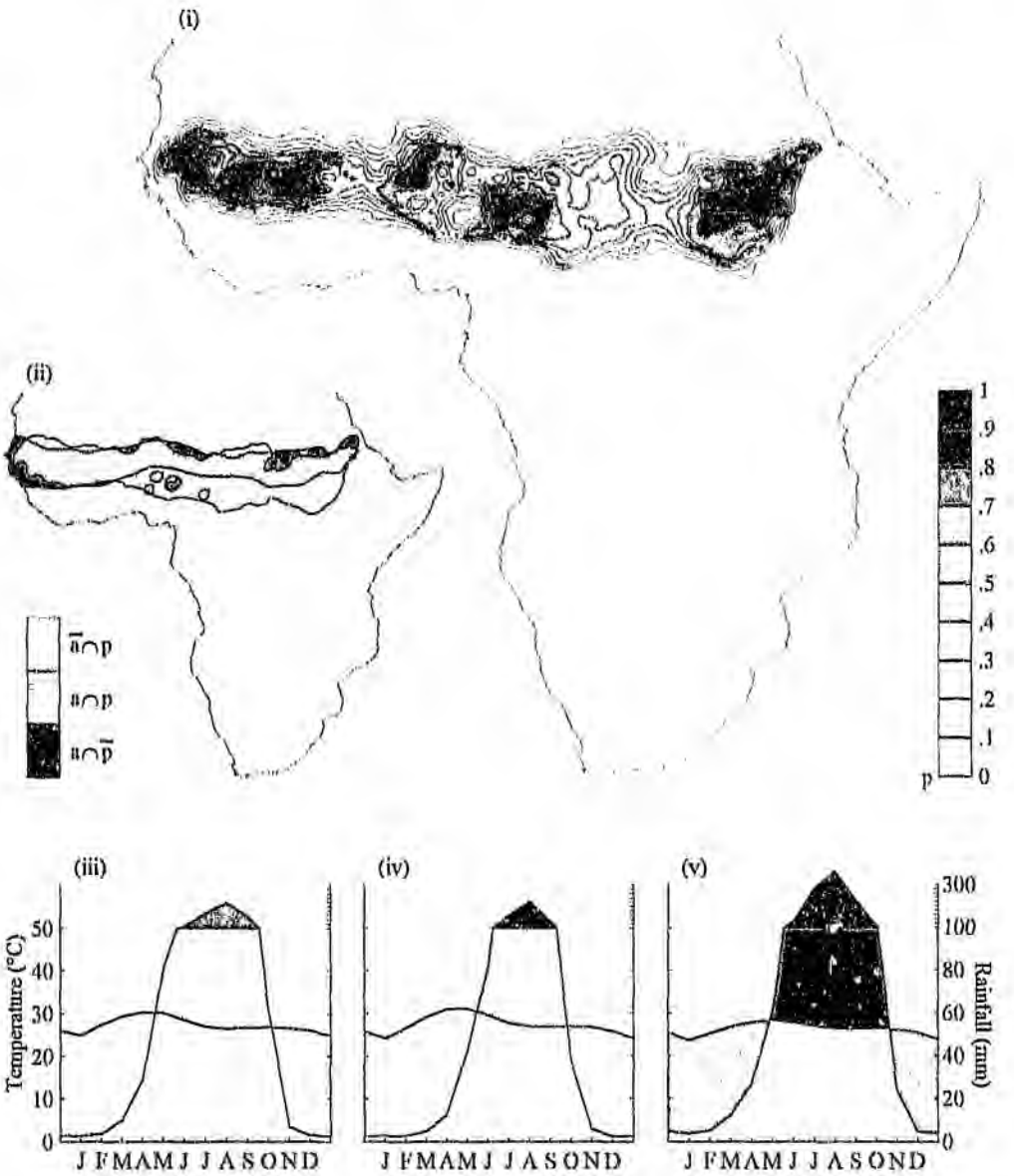


Figure 3.15. *Gazella rufifrons*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/05 15:26:29.59) #14 Gazella leptoceros (Rim or Loder's gazelle)

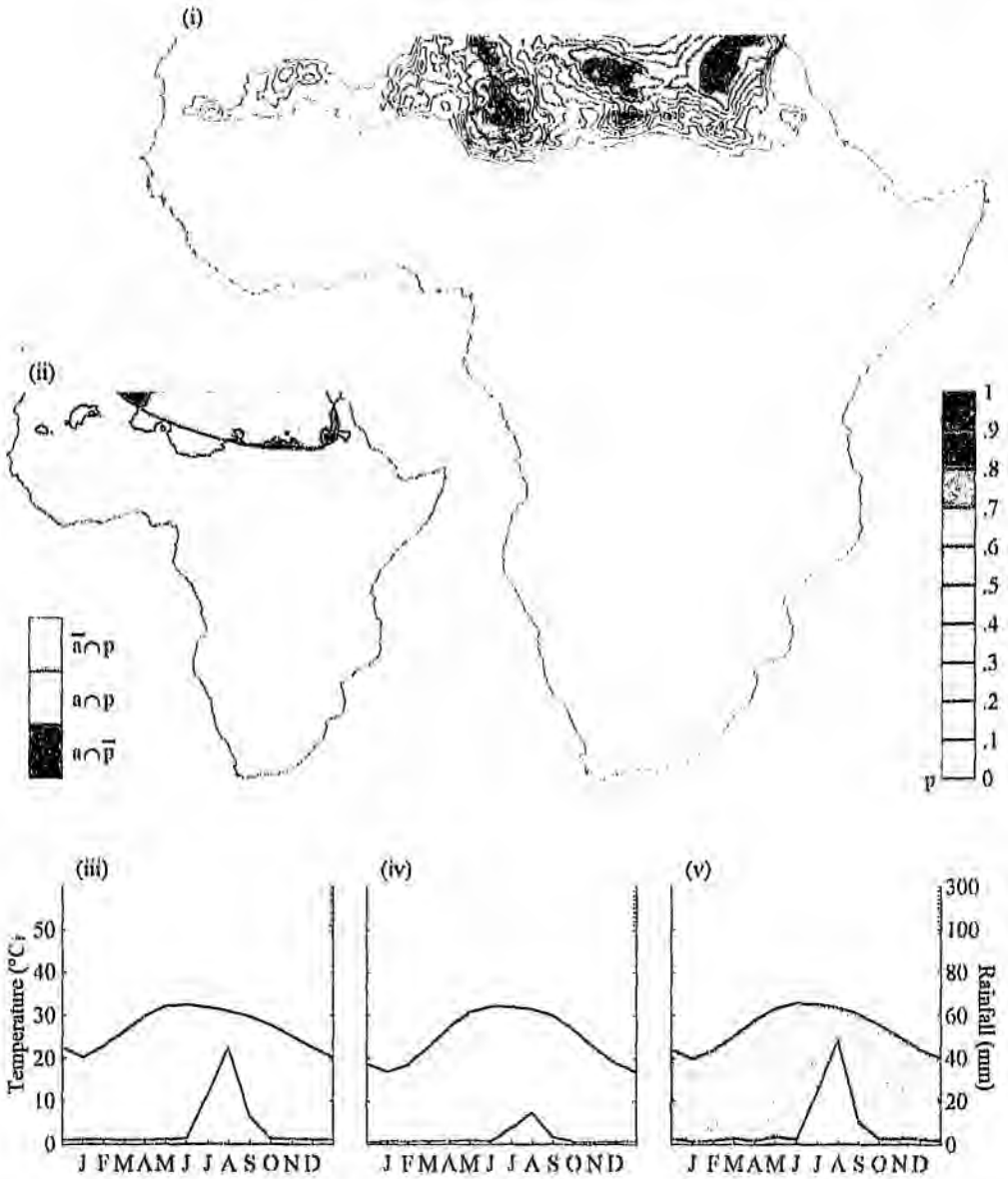


Figure 3.14. *Gazella leptoceros*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(18/06/06 16:17:53.73) #13 Gazella granti (Grant's gazelle)

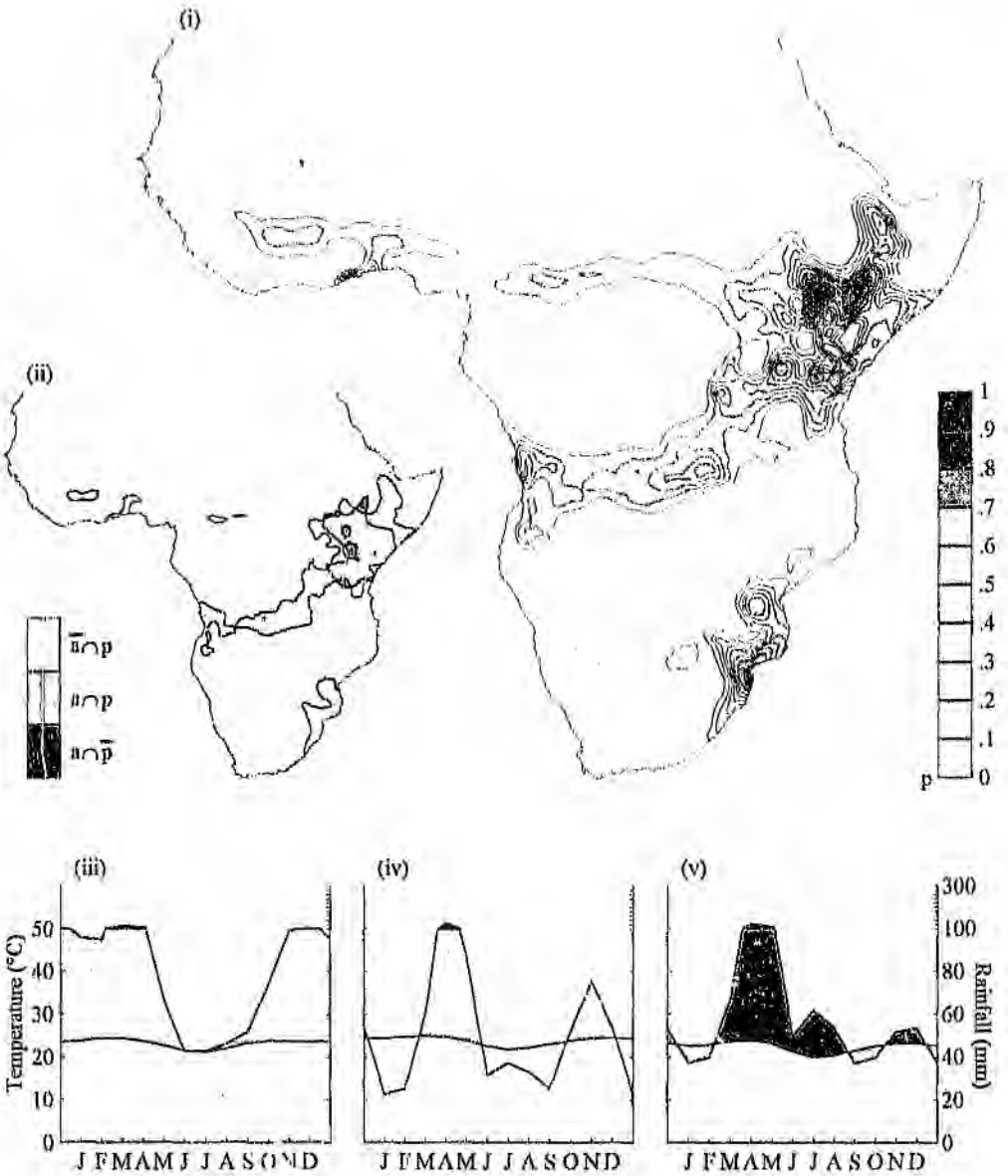


Figure 3.13. *Gazella granti*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[1995/06/06 15:06:21 45] #12 Gazella dorcas (Dorcas gazelle)

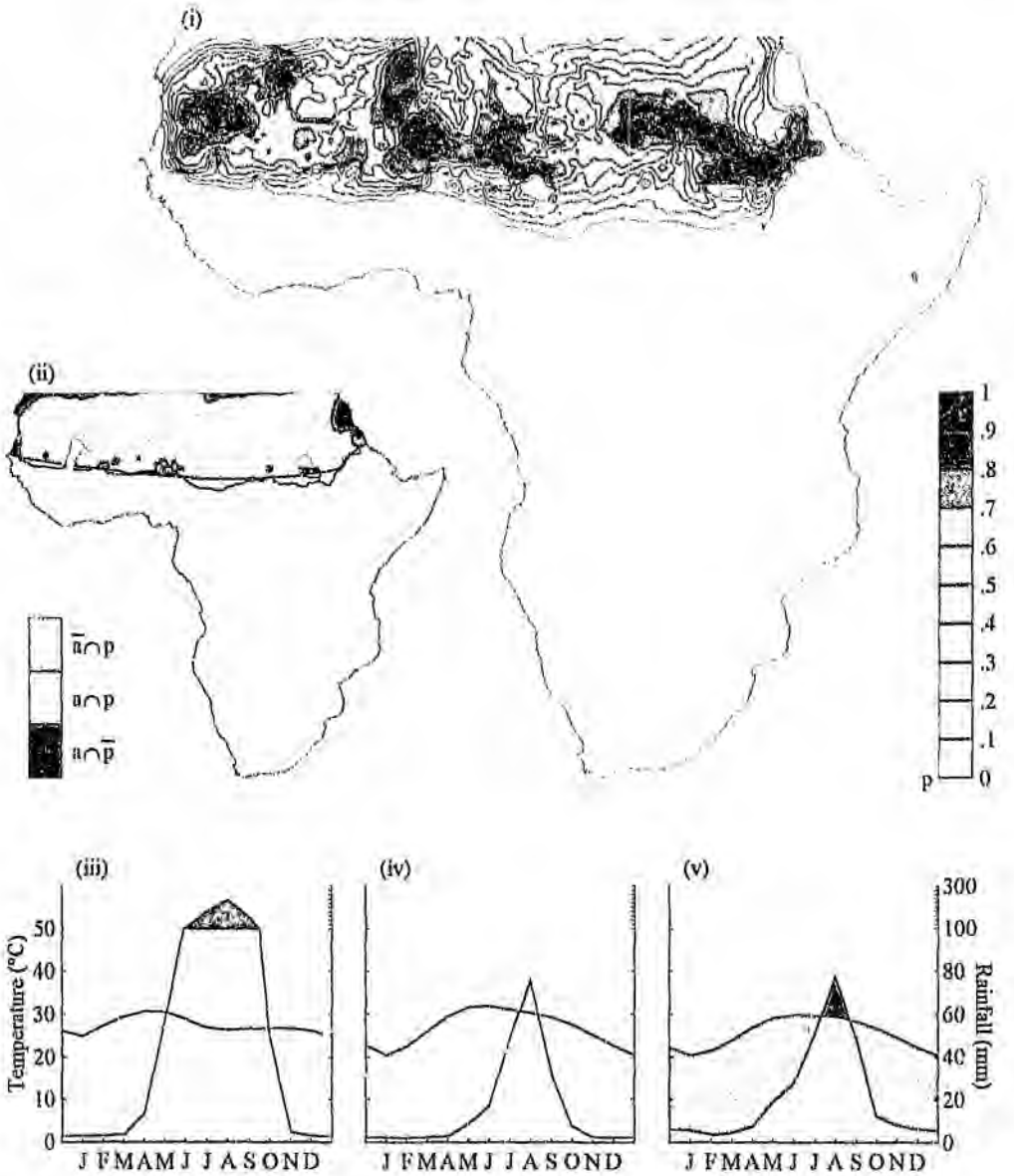


Figure 3.12. *Gazella dorcas*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

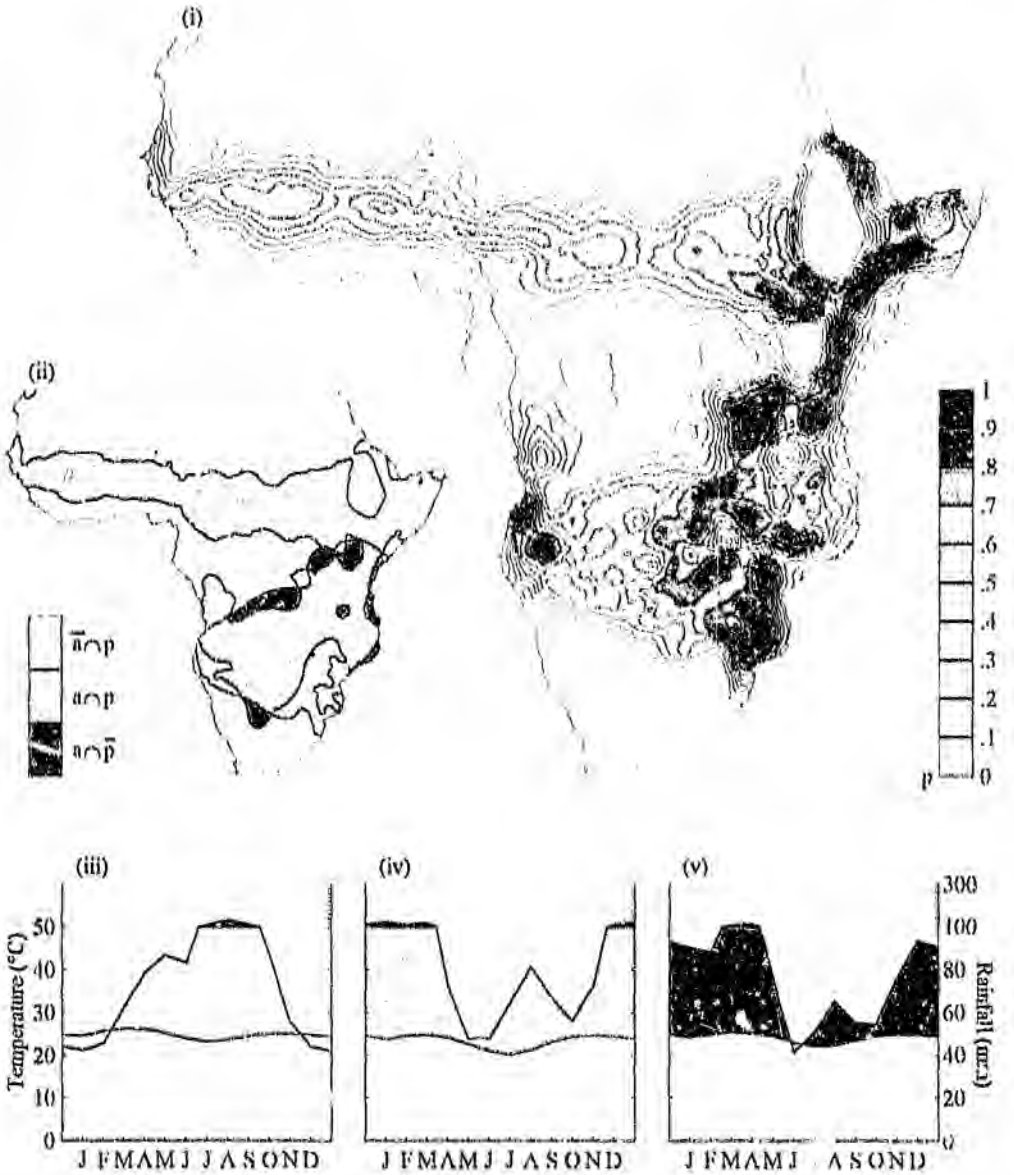


Figure 3.33. *Taurotragus oryx*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generali. d climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

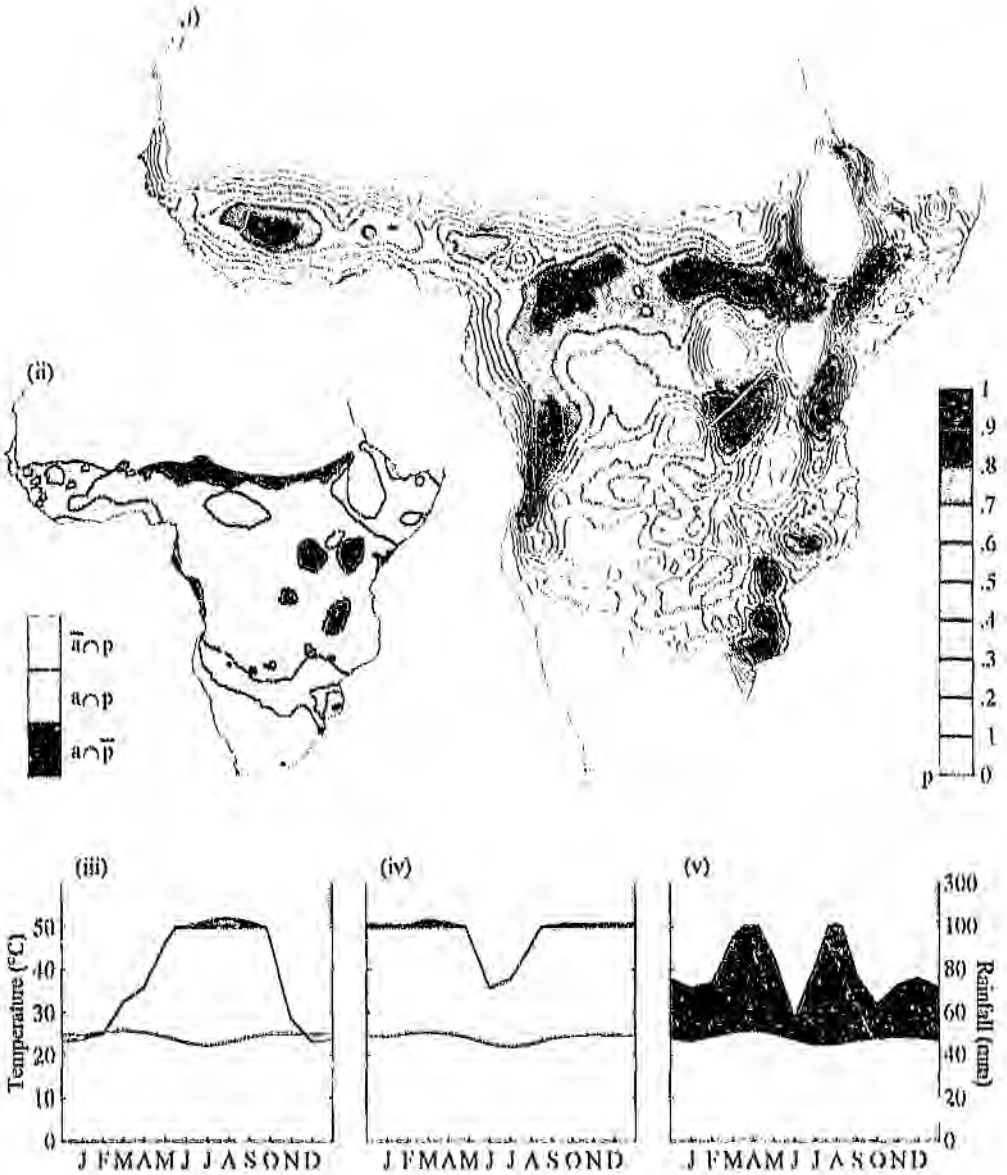


Figure 3.32. *Syncerus caffer*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

#21 Raphicerus sharpei (Sharpe's grysbok) (1985/08/07 14:53:47)

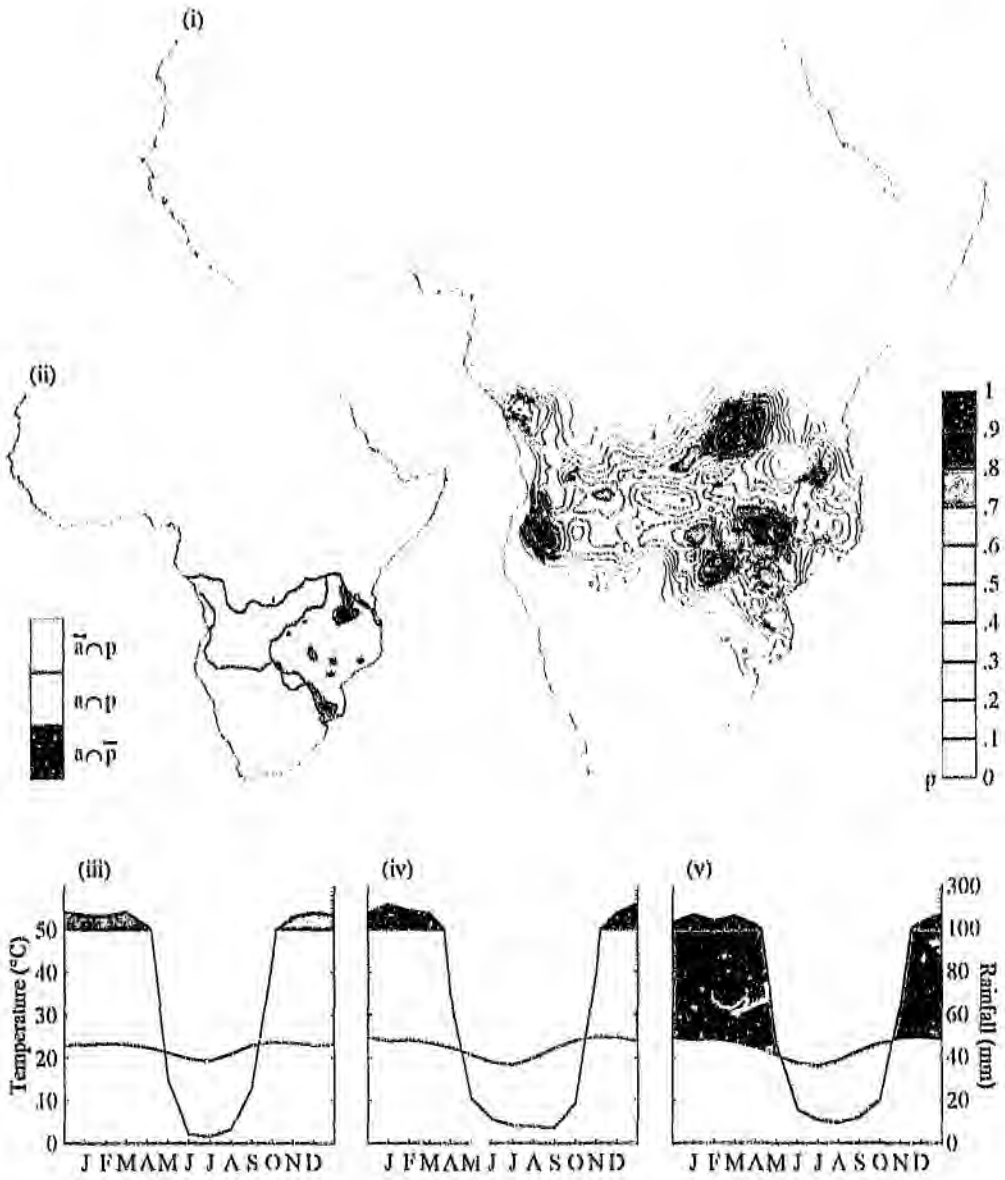


Figure 3.31. *Raphicerus sharpei*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19960507 14:44:47 41) #50 Raphicerus melanotis (Sytebok)

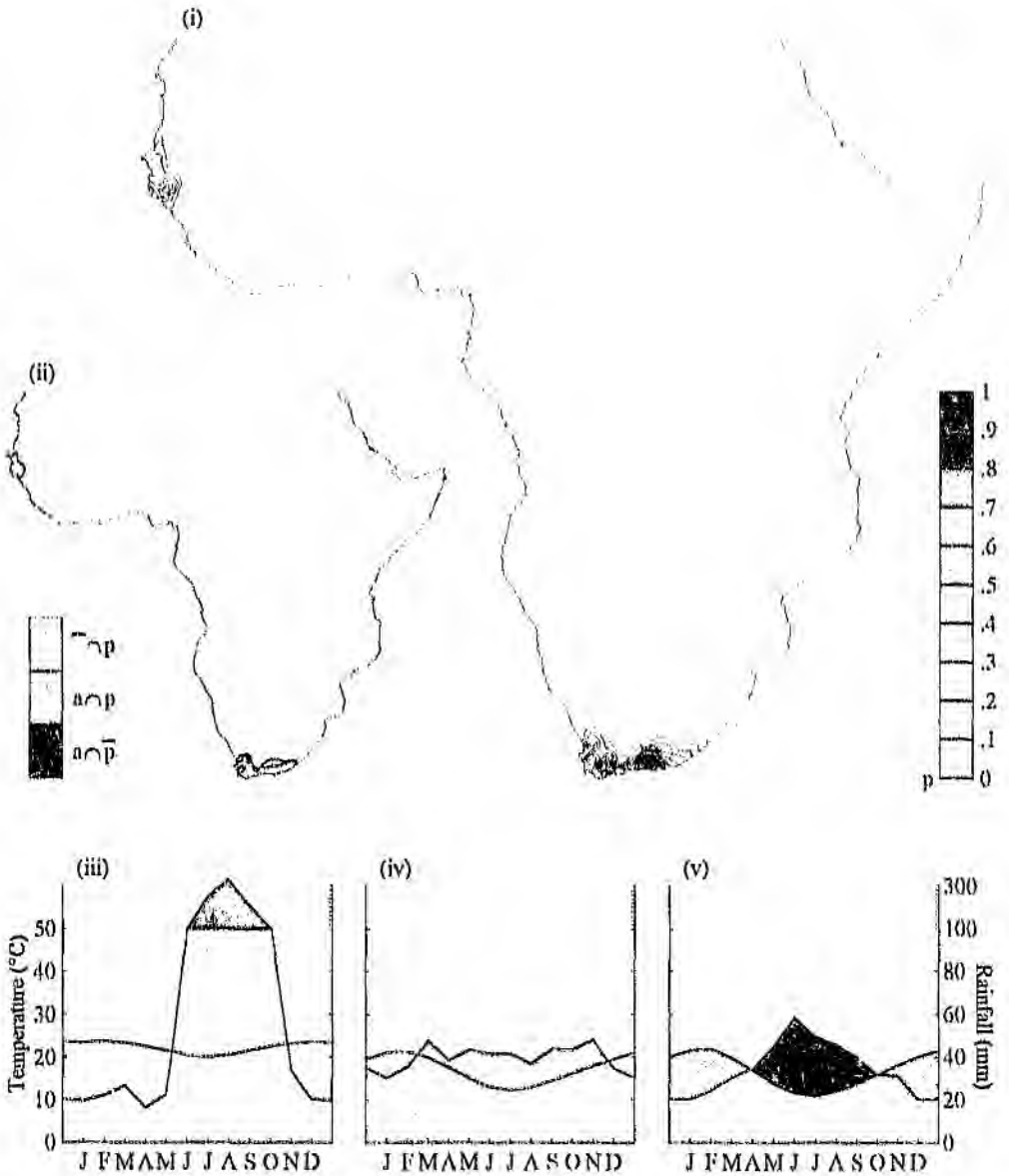


Figure 3.30. *Raphicerus melanotis*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/07 14:33:17.1) #29 Raphicerus campestris (Steenbok)

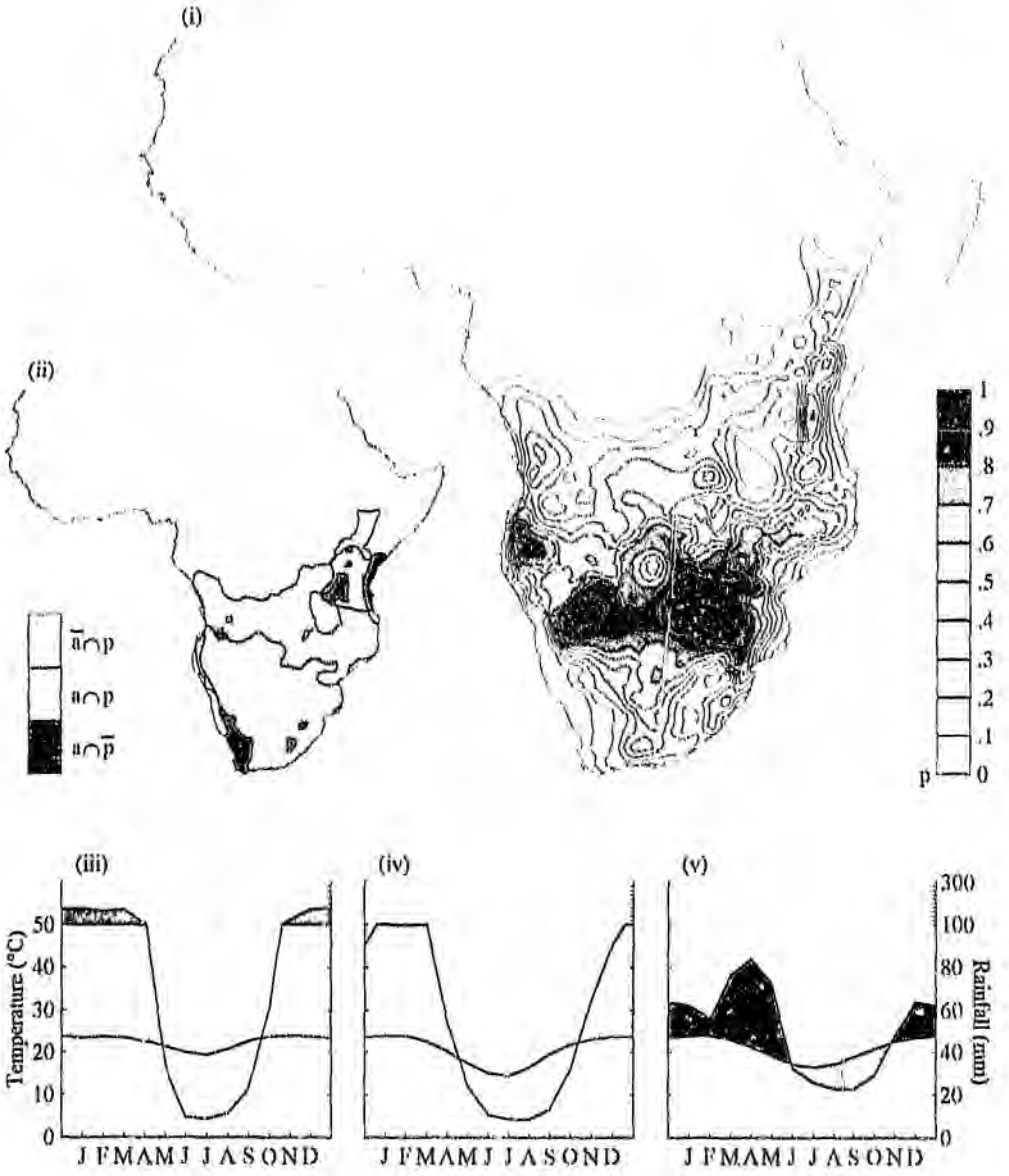


Figure 3.29. *Raphicerus campestris*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19950907) 14:12:13.05) #23 Ourebia ourebi (Oliv)

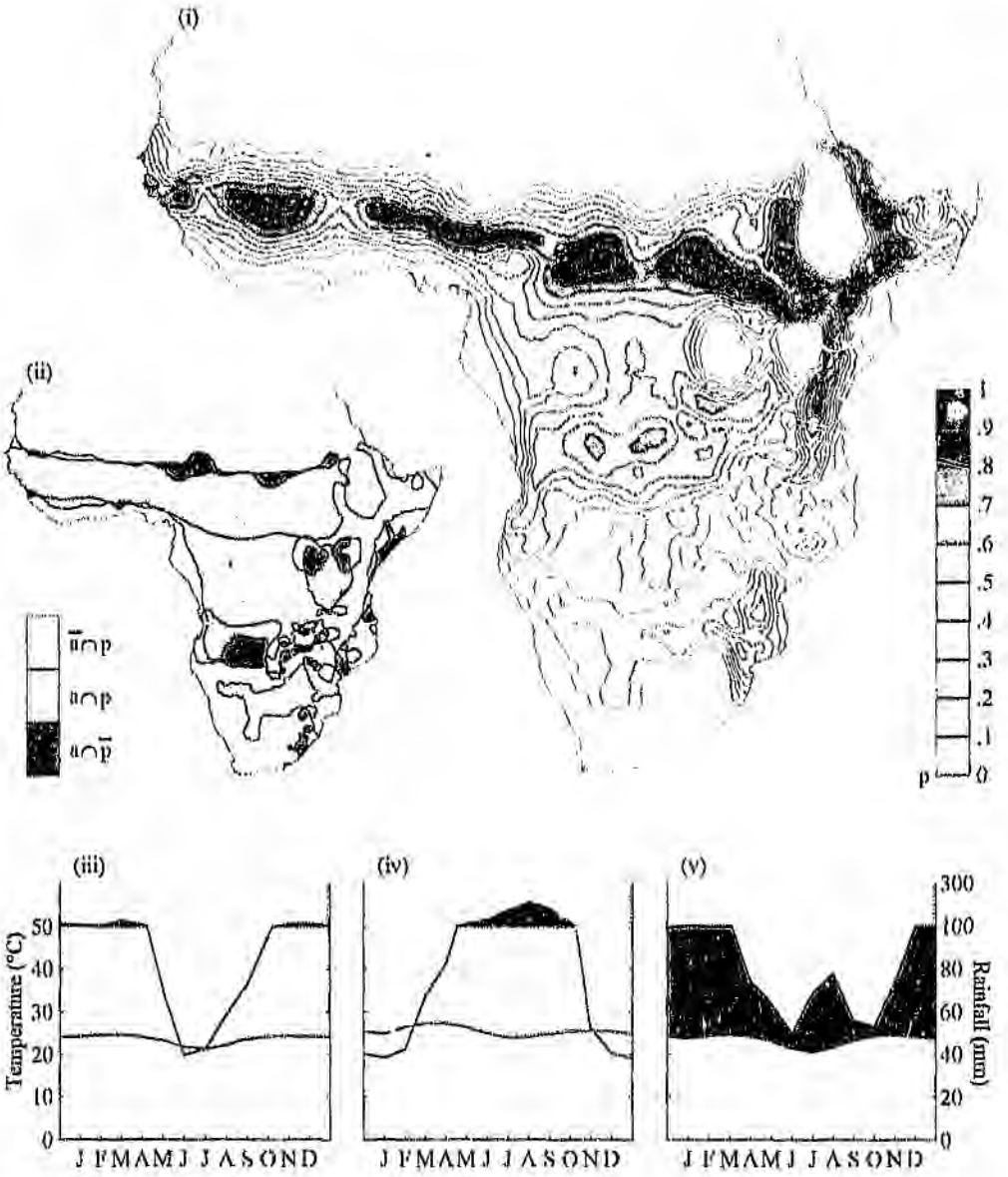


Figure 3.28. *Ourebia ourebi*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[19950607 12:56:46:63] #27 Oreotragus oreotragus (klipspringer)

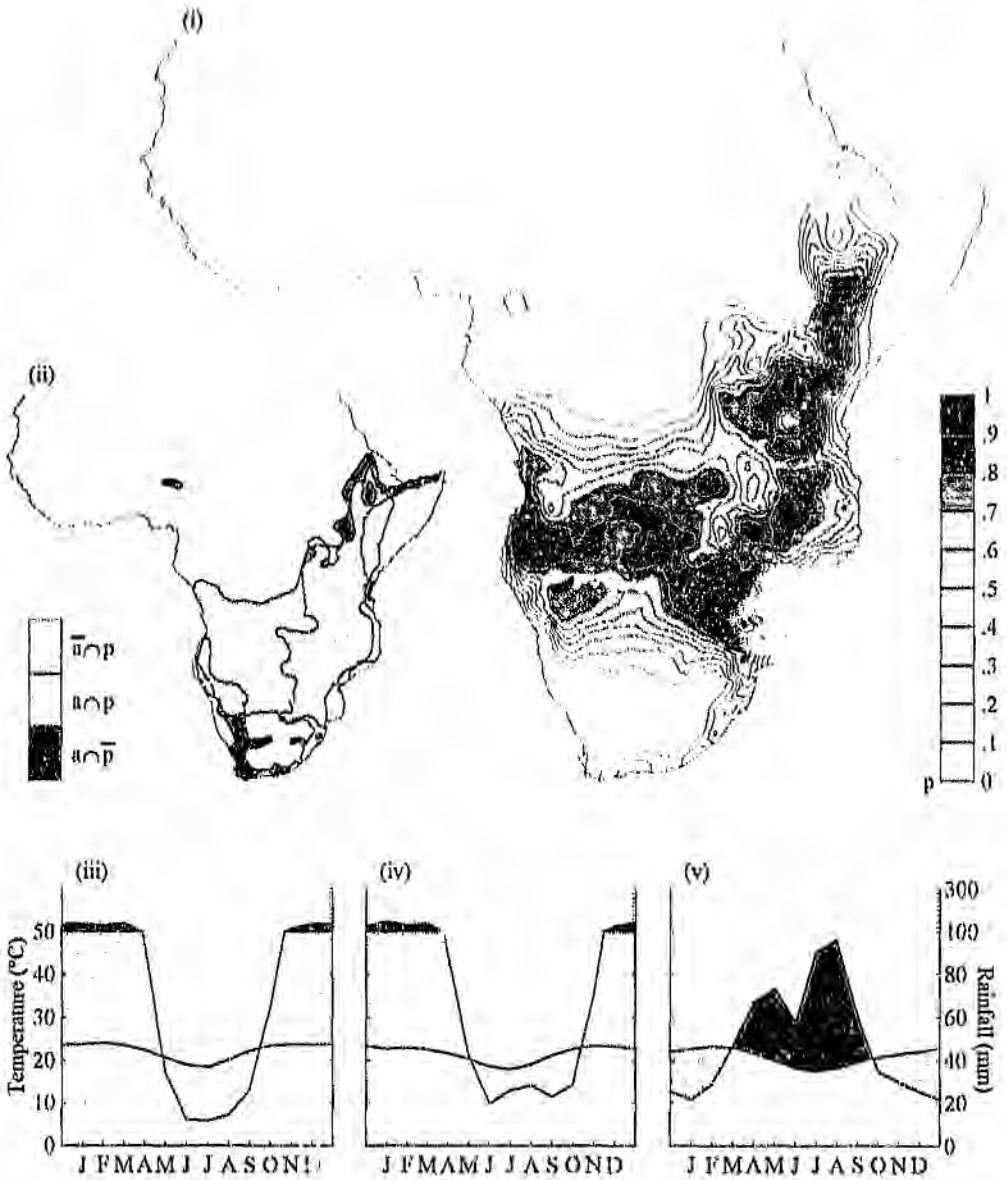


Figure 3.27. *Oreotragus oreotragus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[1996/08/07 15:50:35:56] #28 Hectragus pygmaeus (Royal antelope)

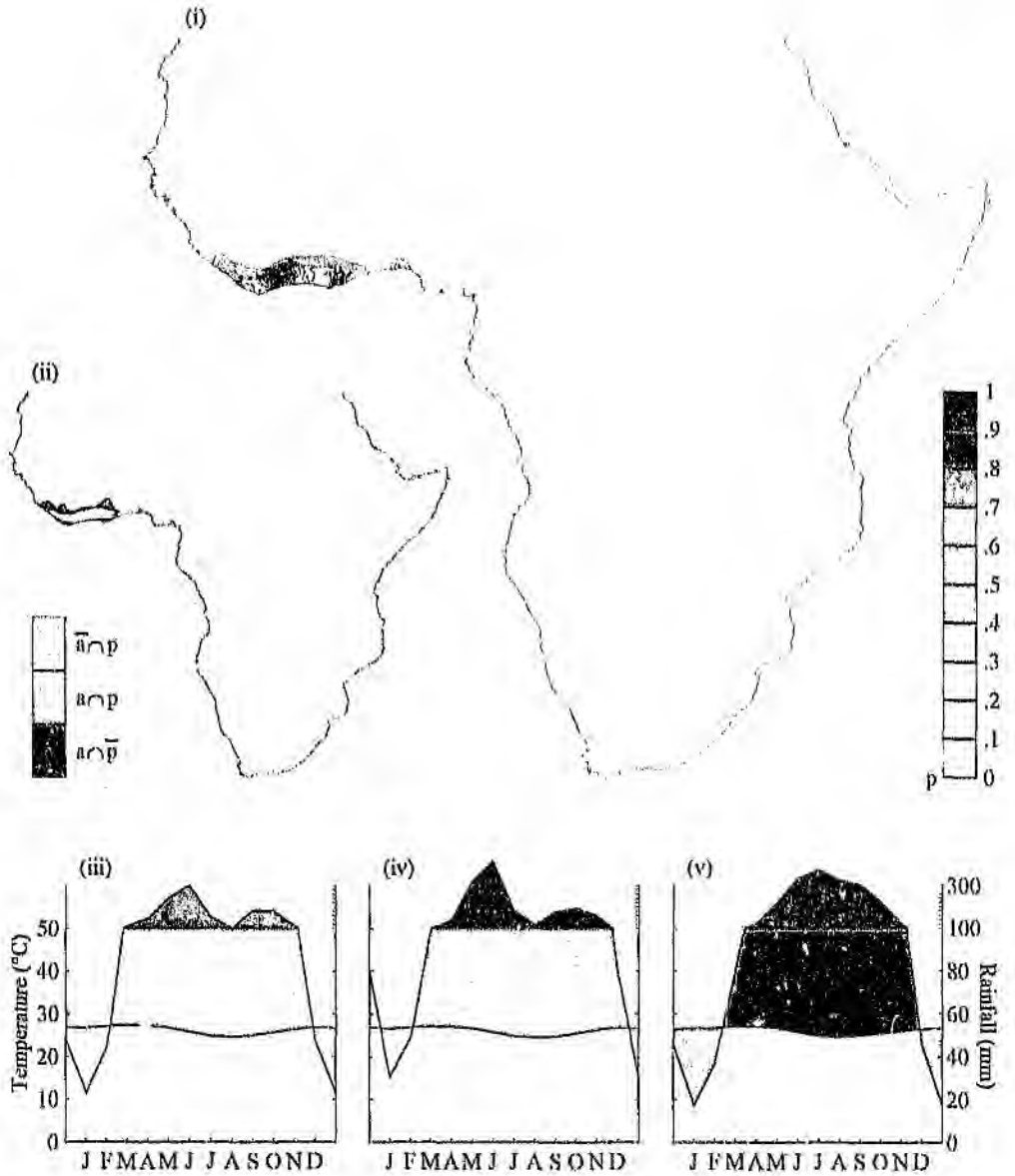


Figure 3.26. *Neotragus pygmaeus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/06/07 13:41:47.67) #25 Neotragus moschatus (Sund)

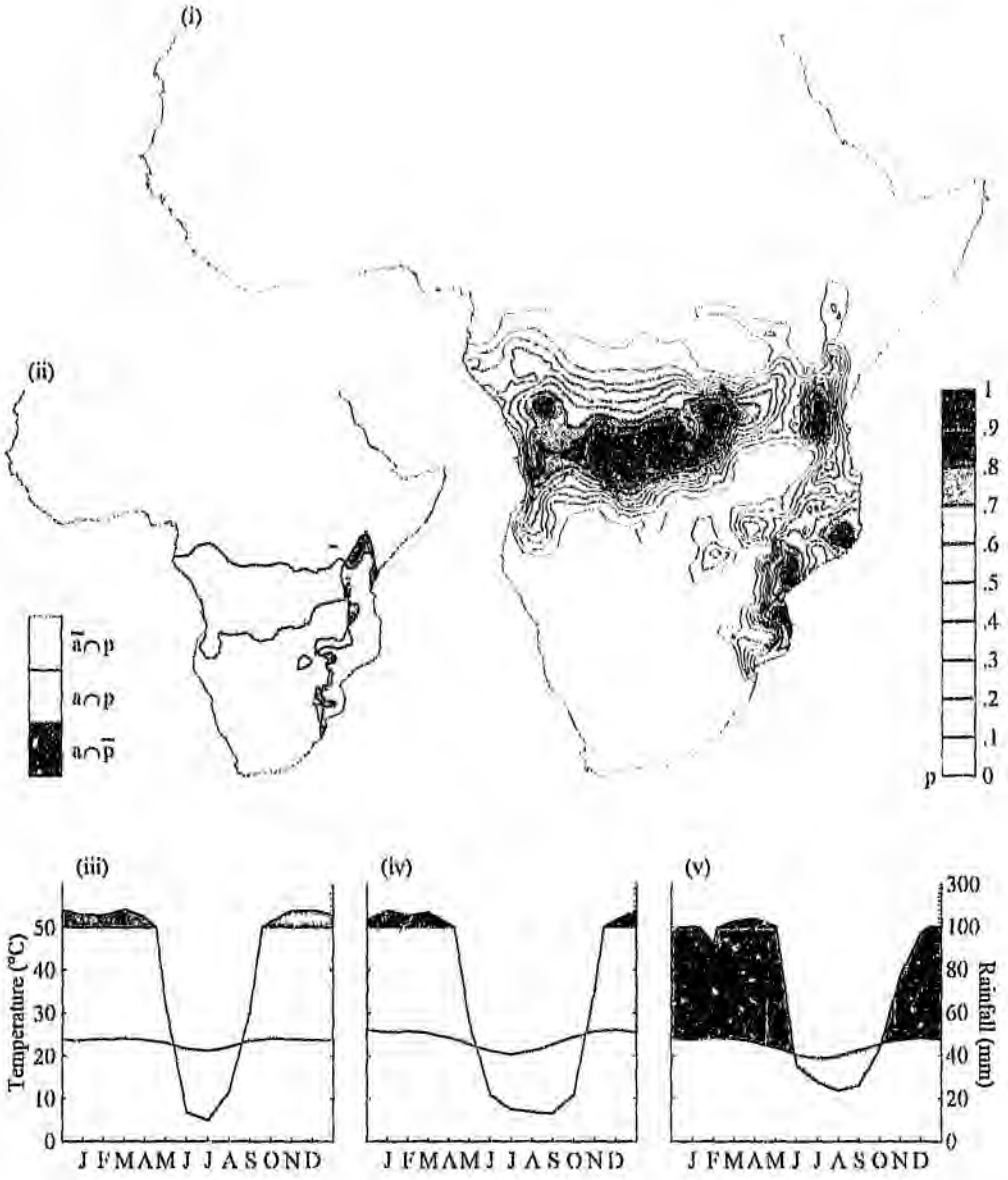


Figure 3.25. *Neotragus moschatus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[18/05/2007 13:32:48.15] #24 Neotragus batesi (Bates' pygmy antelope)

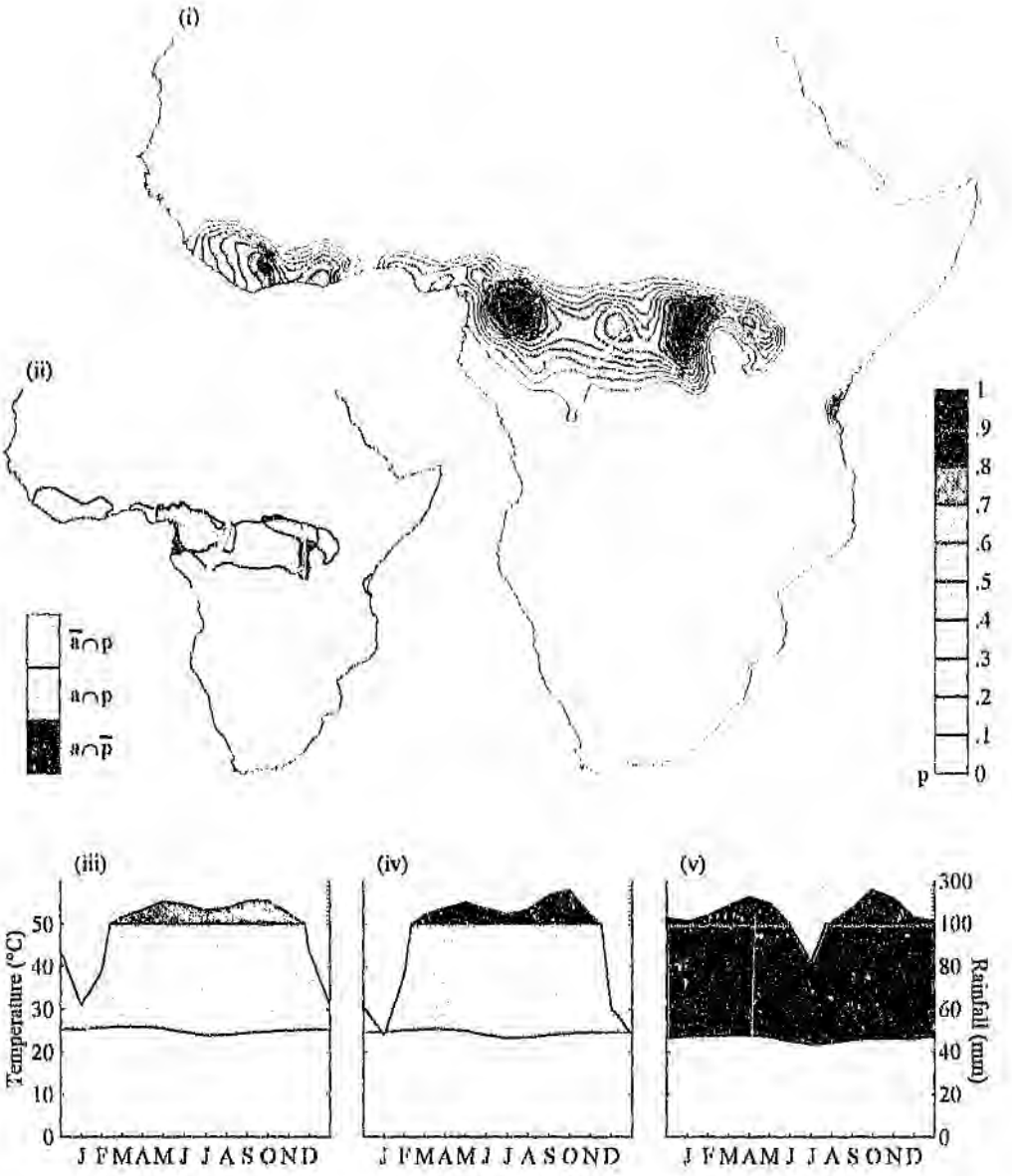


Figure 3.24. *Neotragus batesi*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/07 13:23:20.25) #23 Madoqua saltiana (Salt's / Phillips'dik-dik)

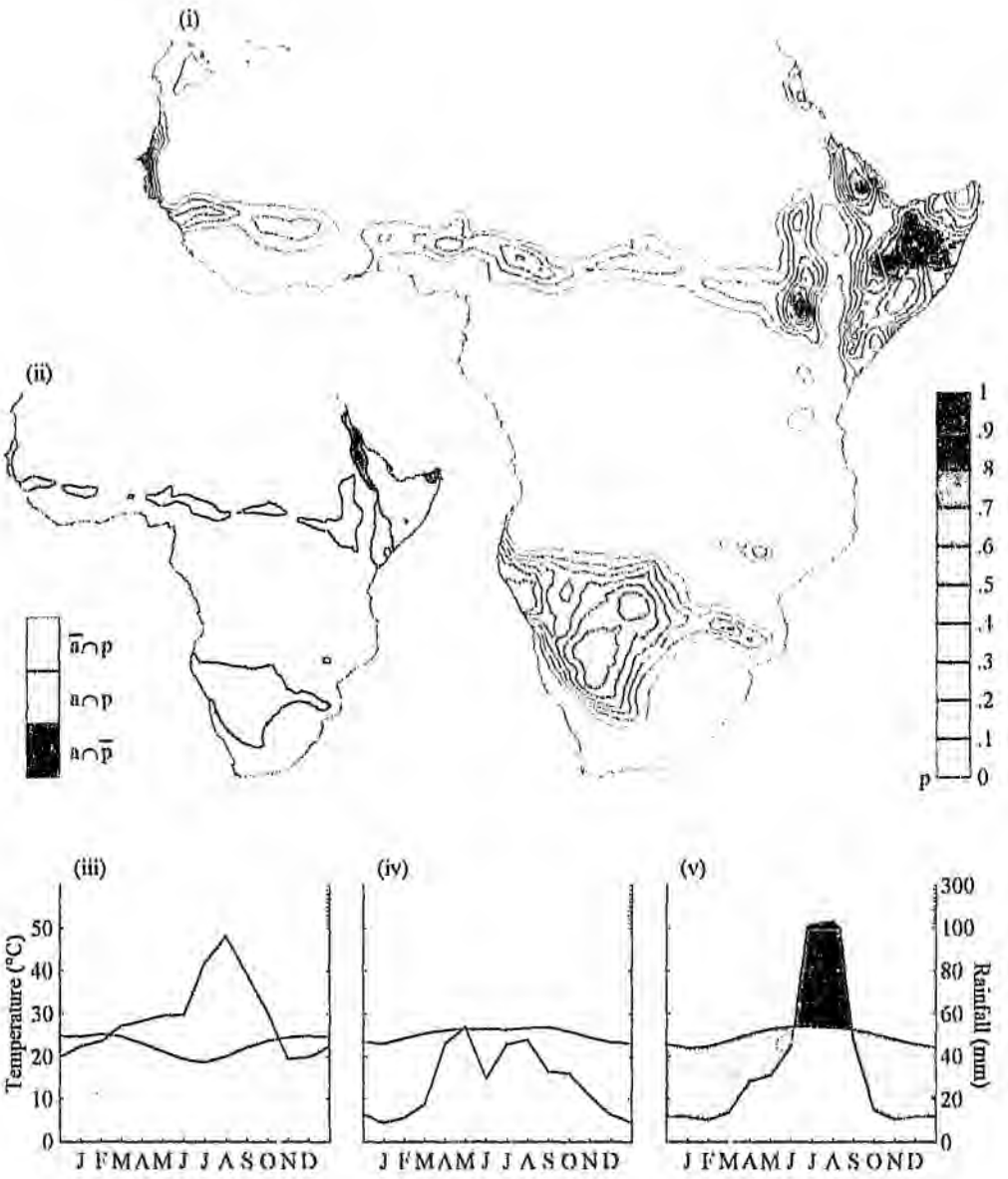


Figure 3.23. *Madoqua saltiana*, (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/07 13:10:45.72) #22 Madoqua kirki (dik-dik)

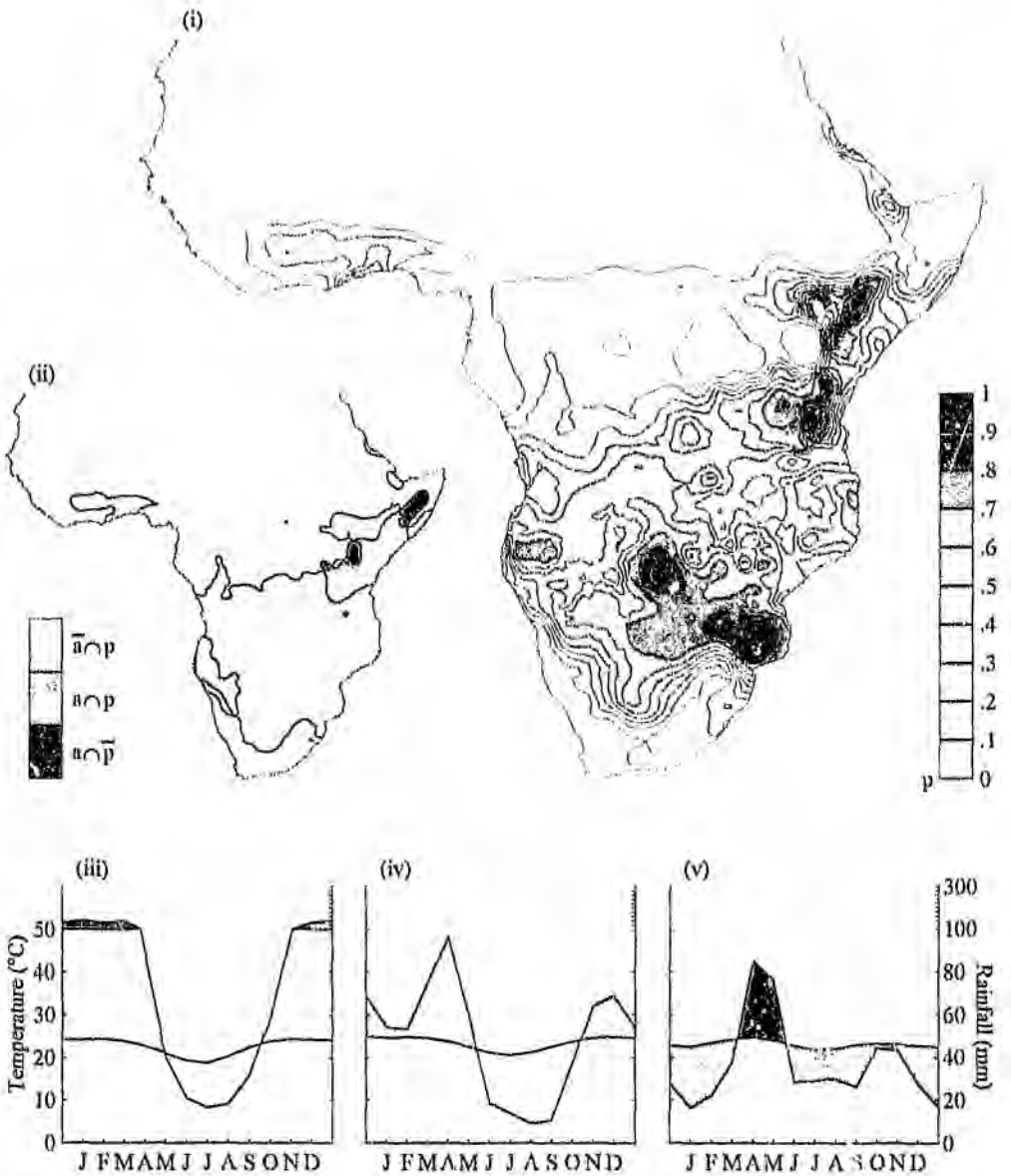


Figure 3.22. *Madoqua kirki*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19960308 13:52:21 59) #53 Cephalophus callipygus (Peters' duiker)

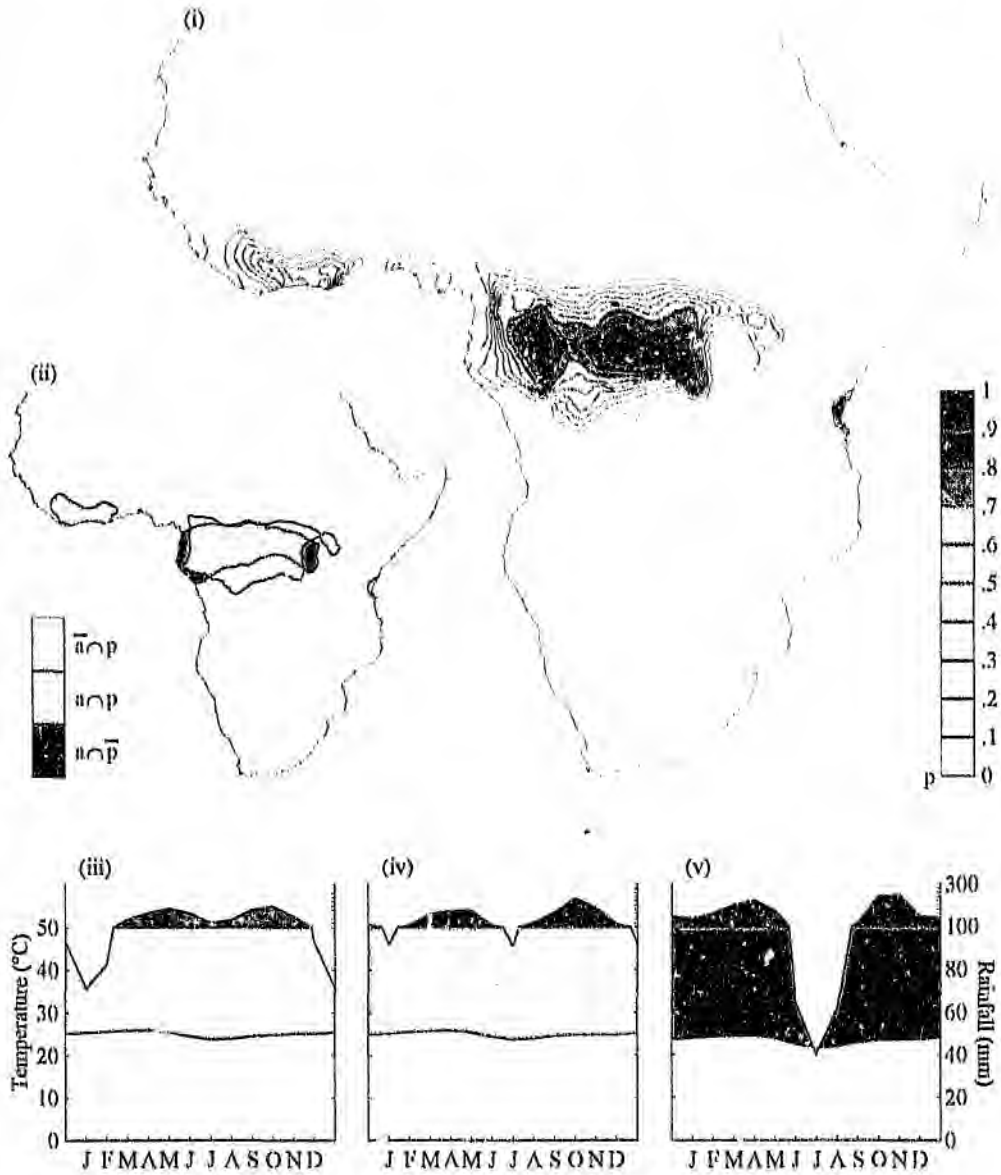


Figure 3.43. *Cephalophus callipygus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

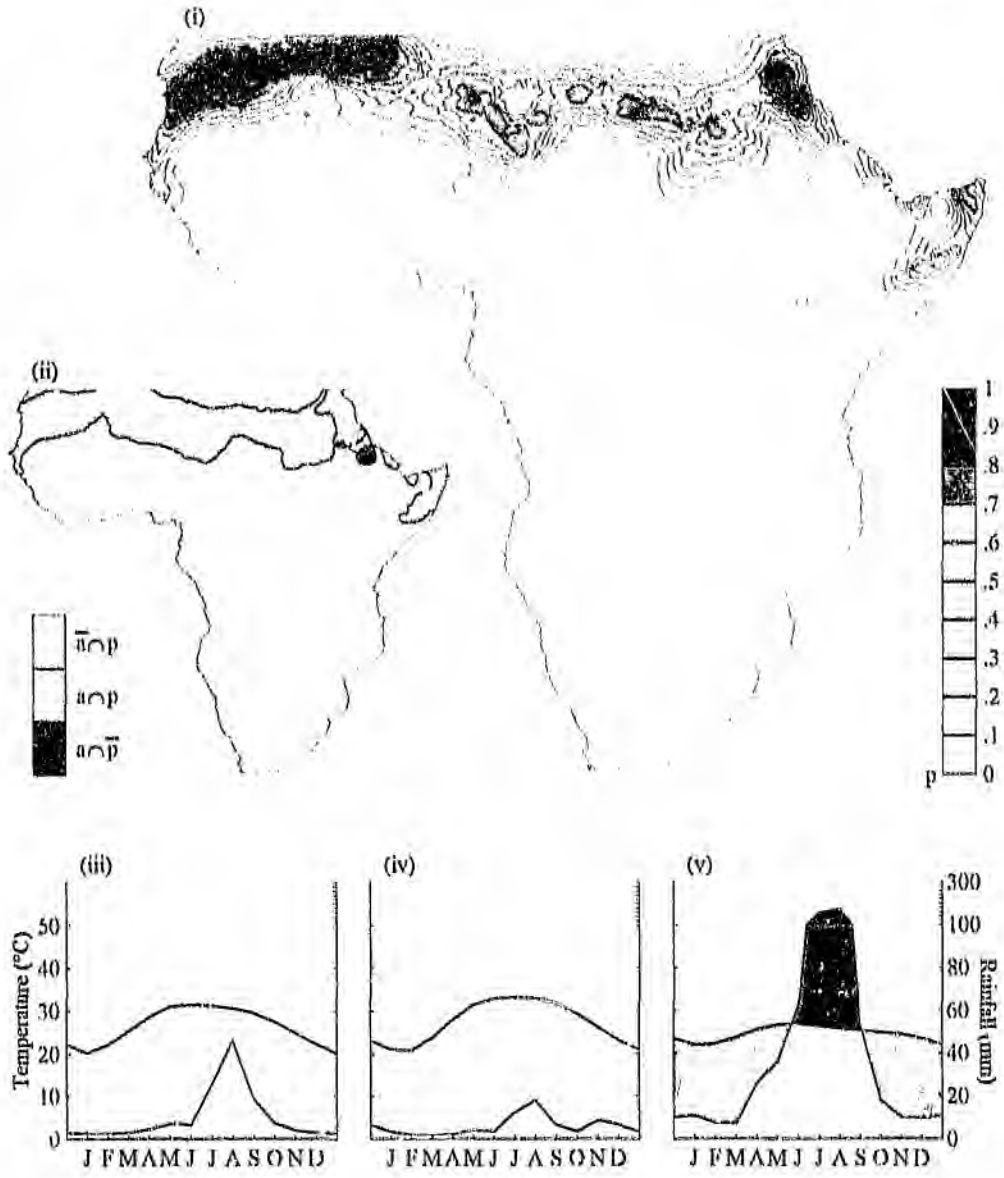


Figure 3.42. *Capra ibex*; (i) probability contours of the habitat model; (ii) intersection of the given dist ibution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19950508 13:36:33 15) #41 Ammotragus lervia (Barbary sheep)

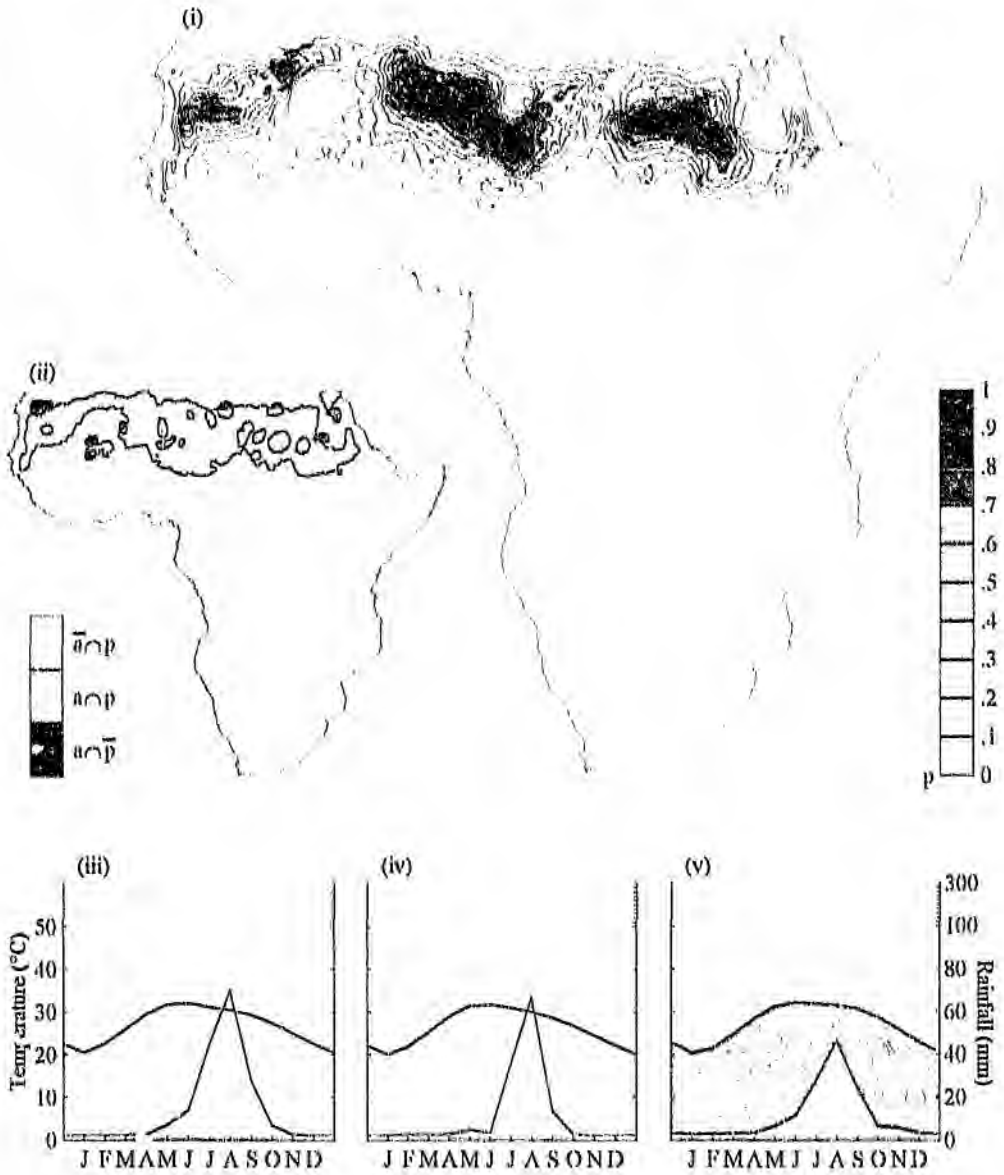


Figure 3.41. *Ammotragus lervia*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

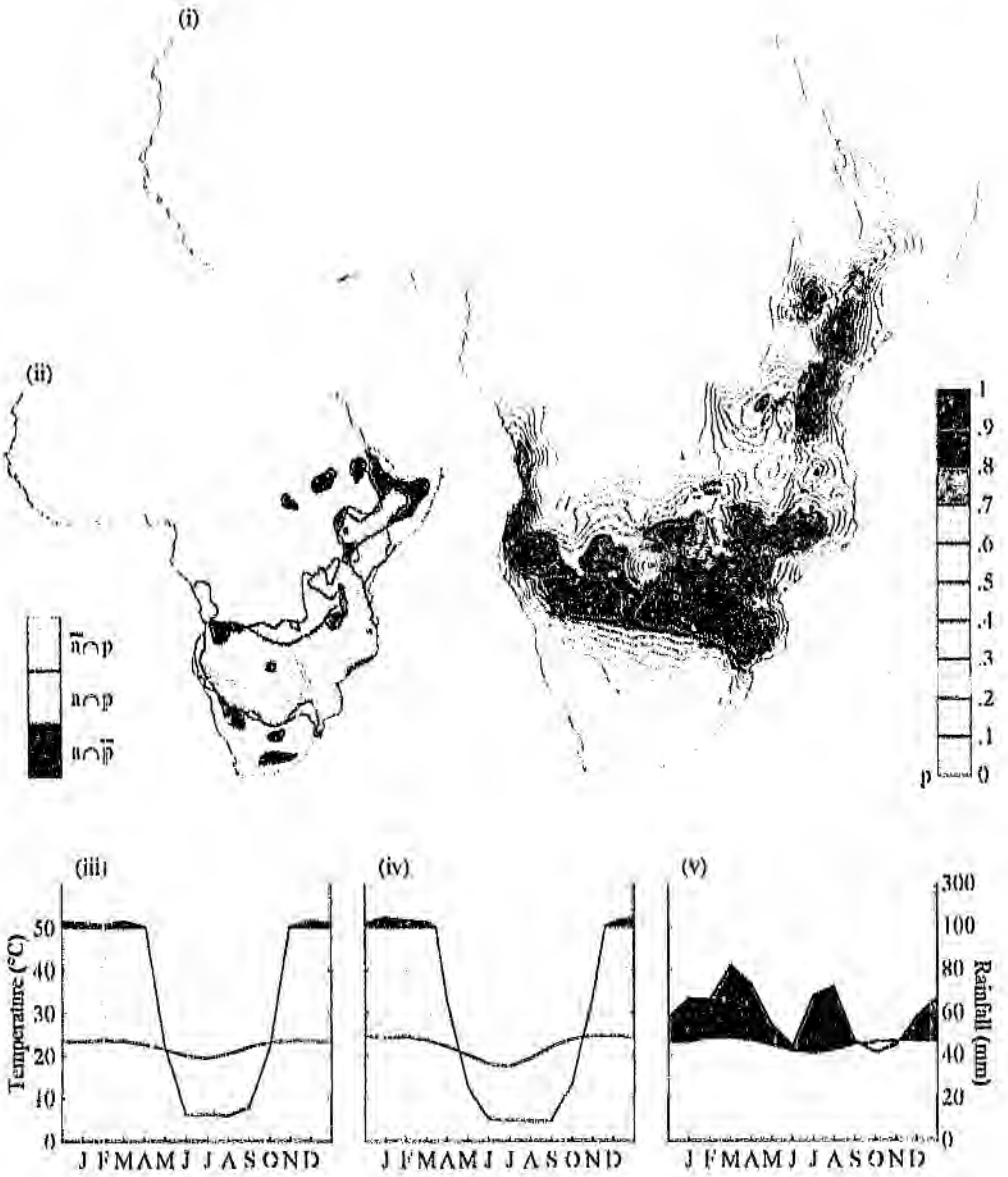


Figure 3.40. *Tragelaphus strepsiceros*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

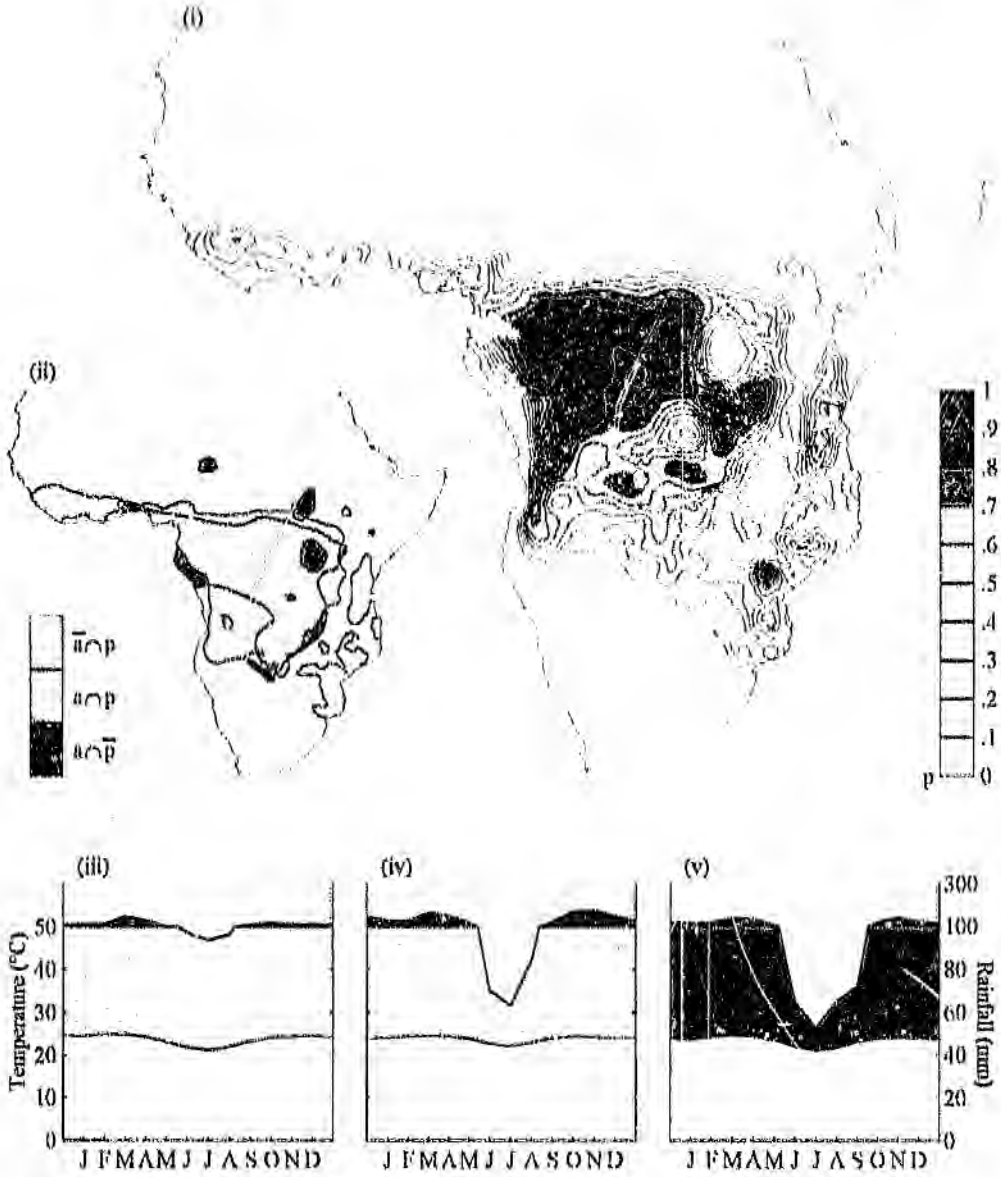


Figure 3.39. *Tragelaphus spekei*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

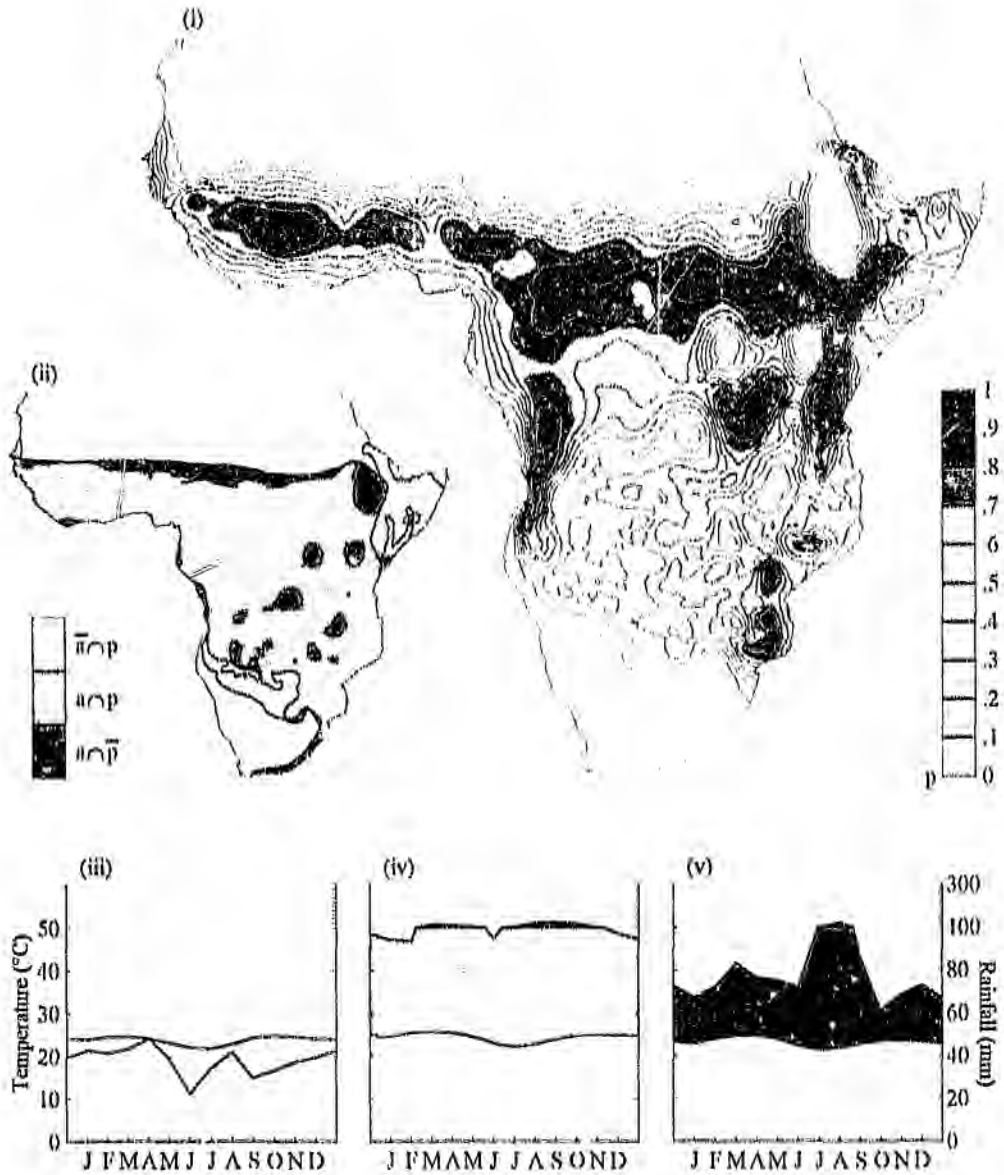


Figure 3.38. *Tragelaphus scriptus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red)

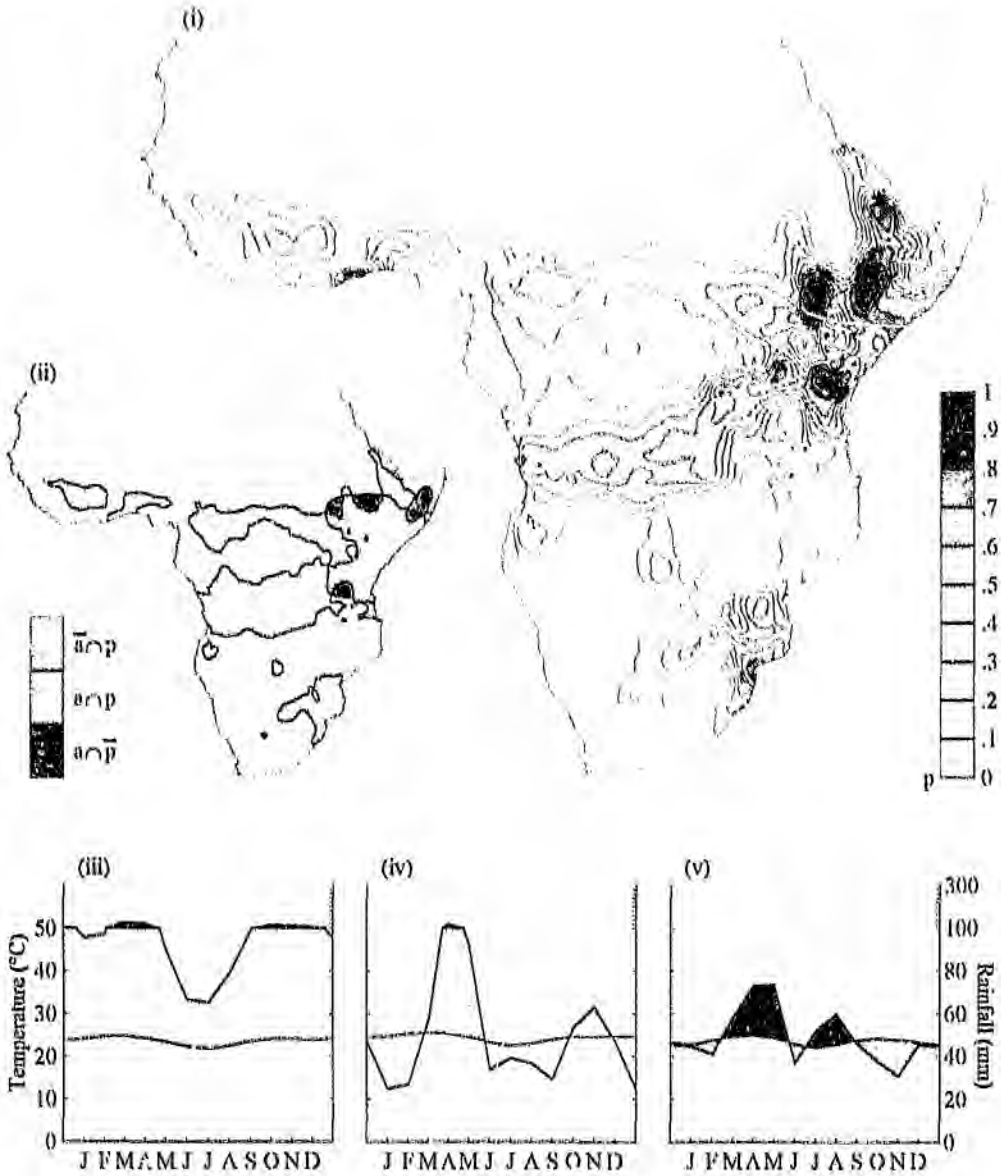


Figure 3.37. *Tragelaphus imberbis*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

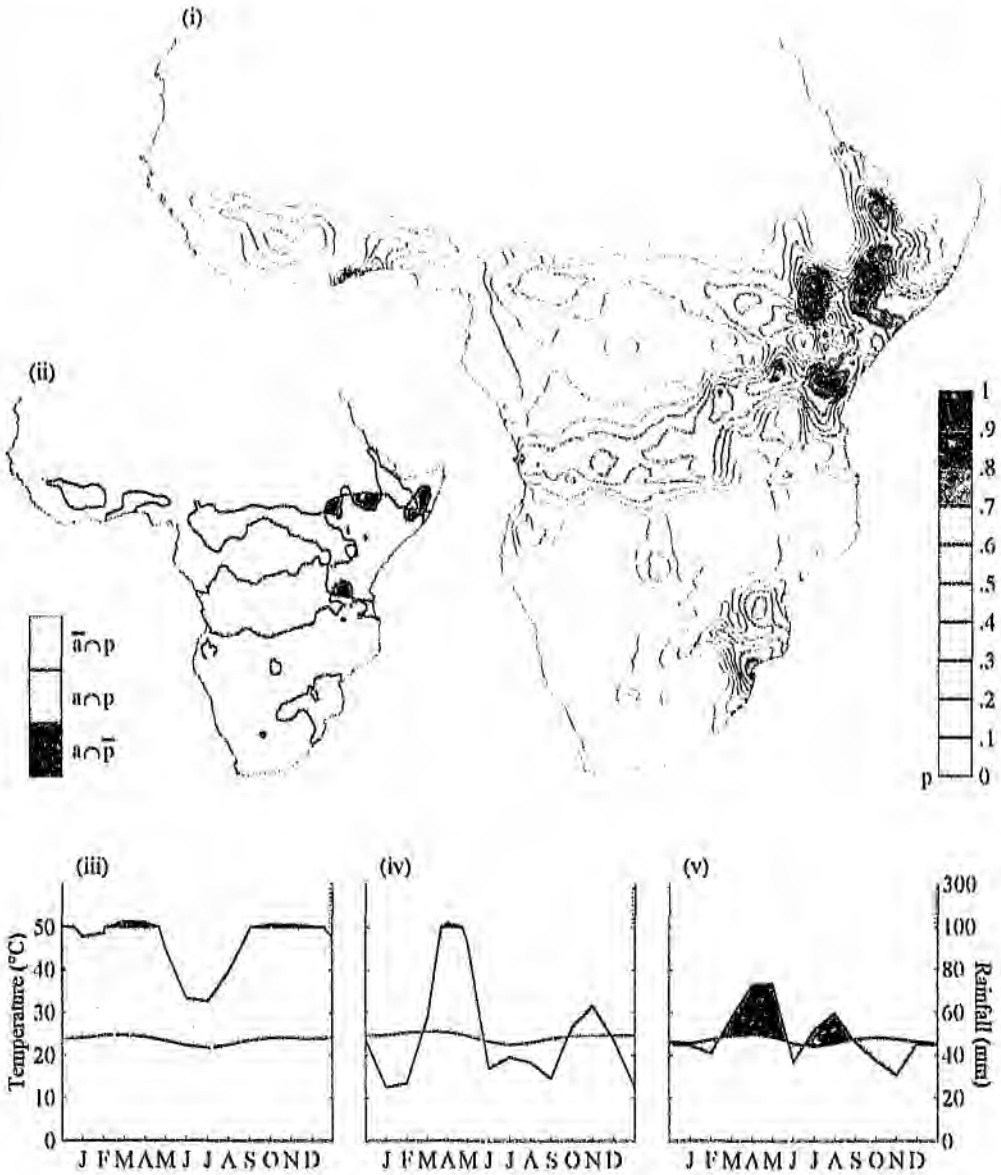


Figure 3.37. *Tragelaphus imberbis*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/05/07 16:04:47.78) #55 Tragelaphus eurycerus (Bongo)

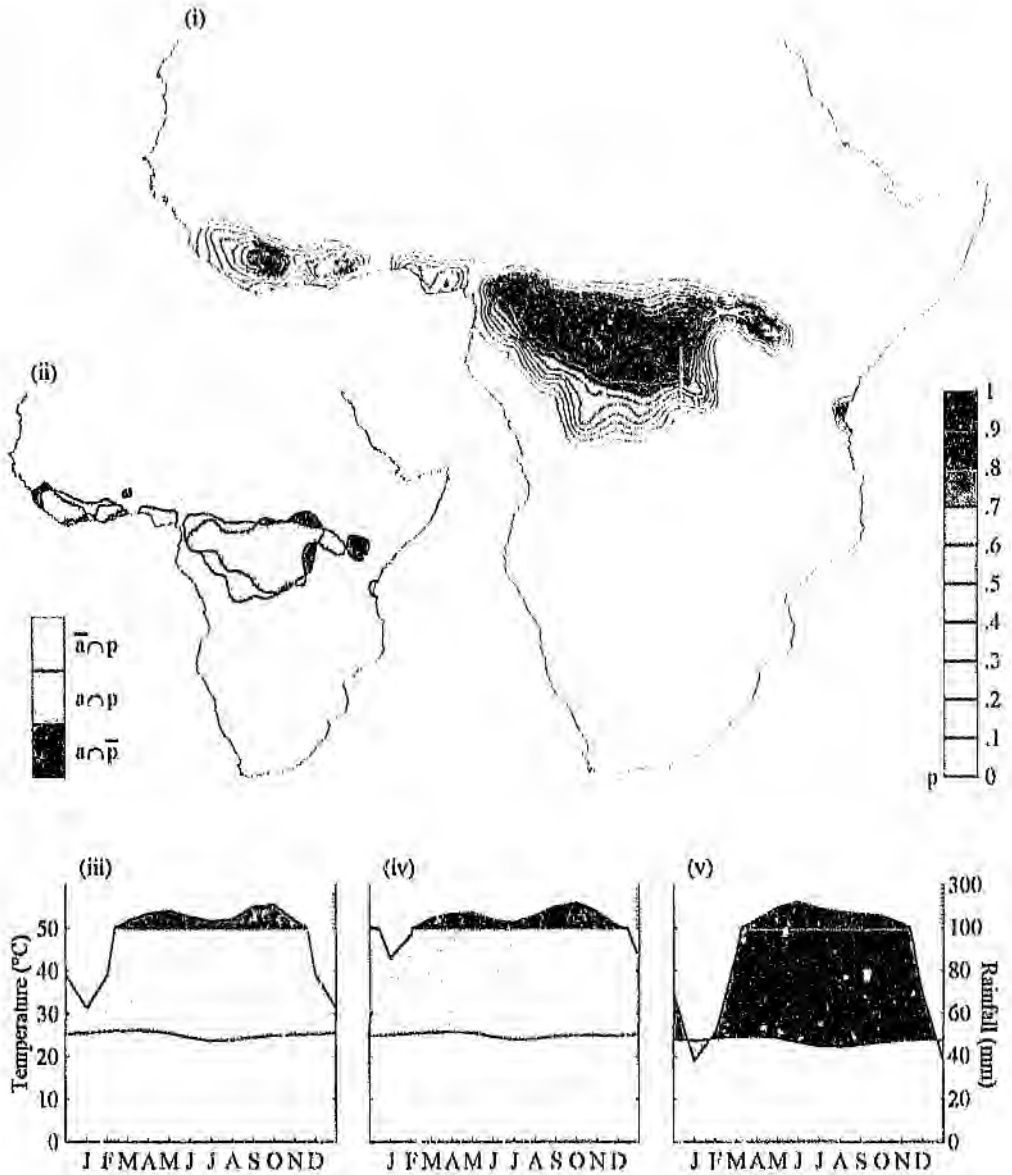


Figure 3.36. *Tragelaphus eurycerus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/06/07 15:56:50 76) #35 Tragelaphus buxtoni (Mountain nyala)

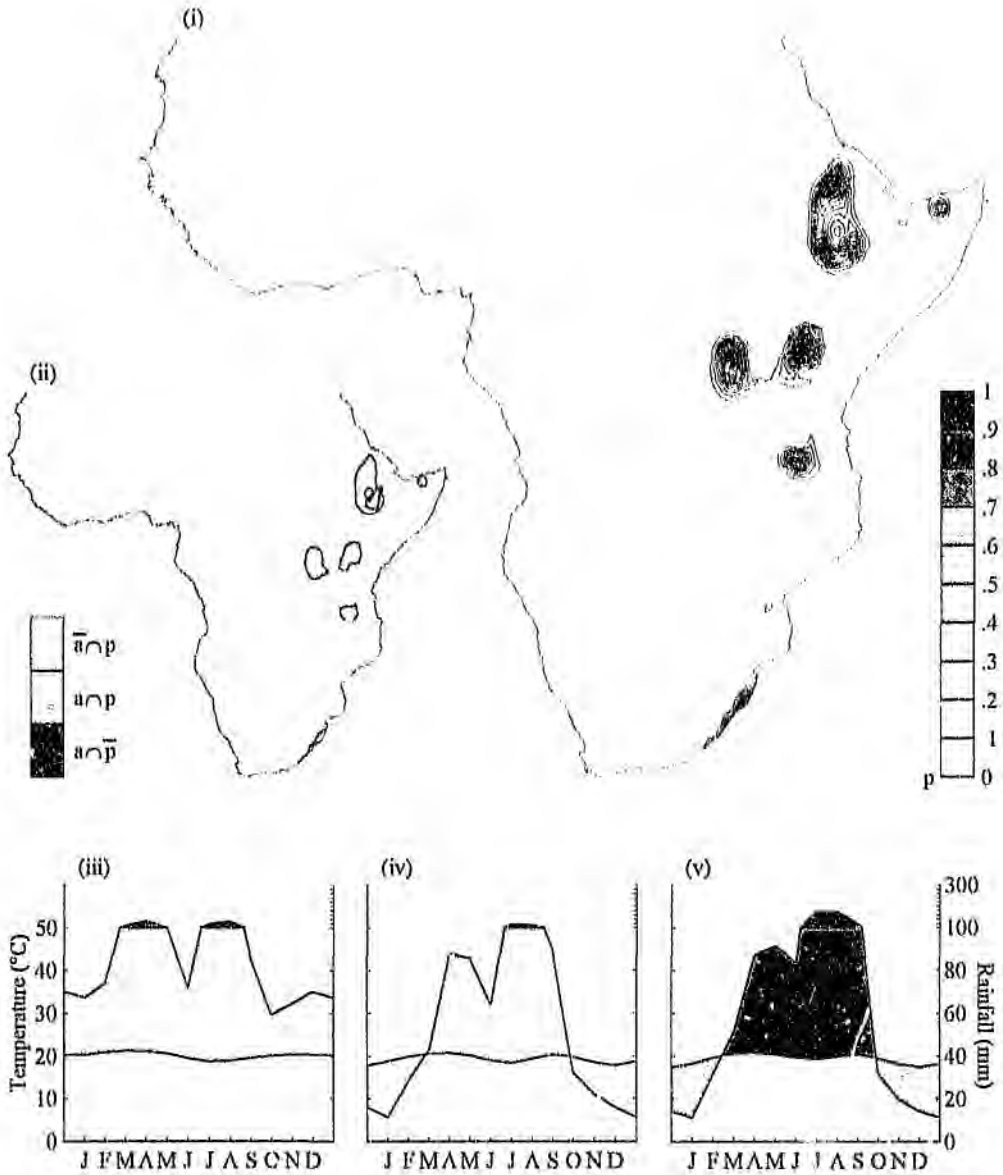


Figure 3.35. *Tragelaphus buxtoni*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1956)0107 15:38:14:68)

#34 Tragelaphus angasi (Nyala)

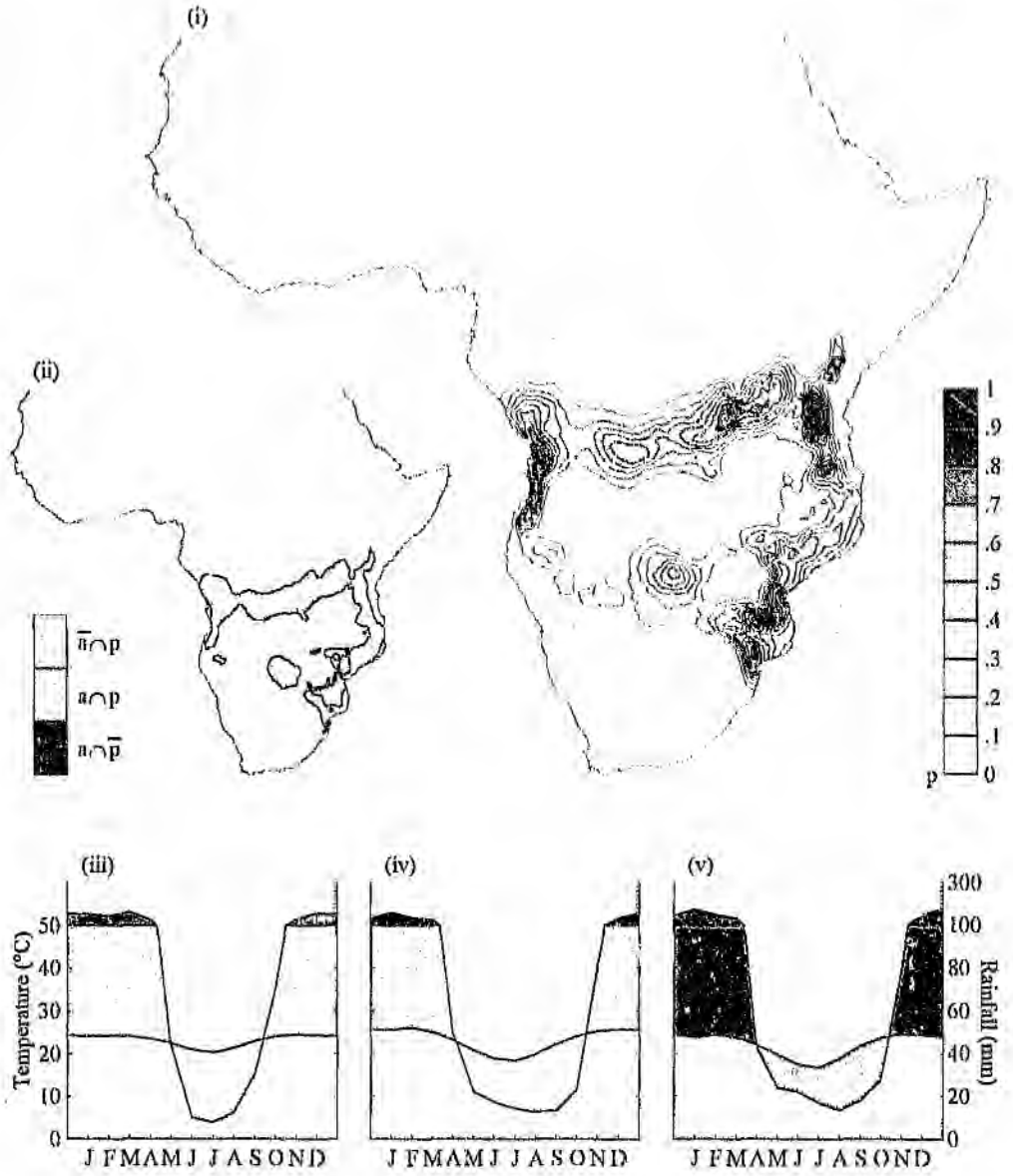


Figure 3.34. *Tragelaphus angasi*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/07 15:43:14.68)
#34 Tragelaphus angasi (Nyala)

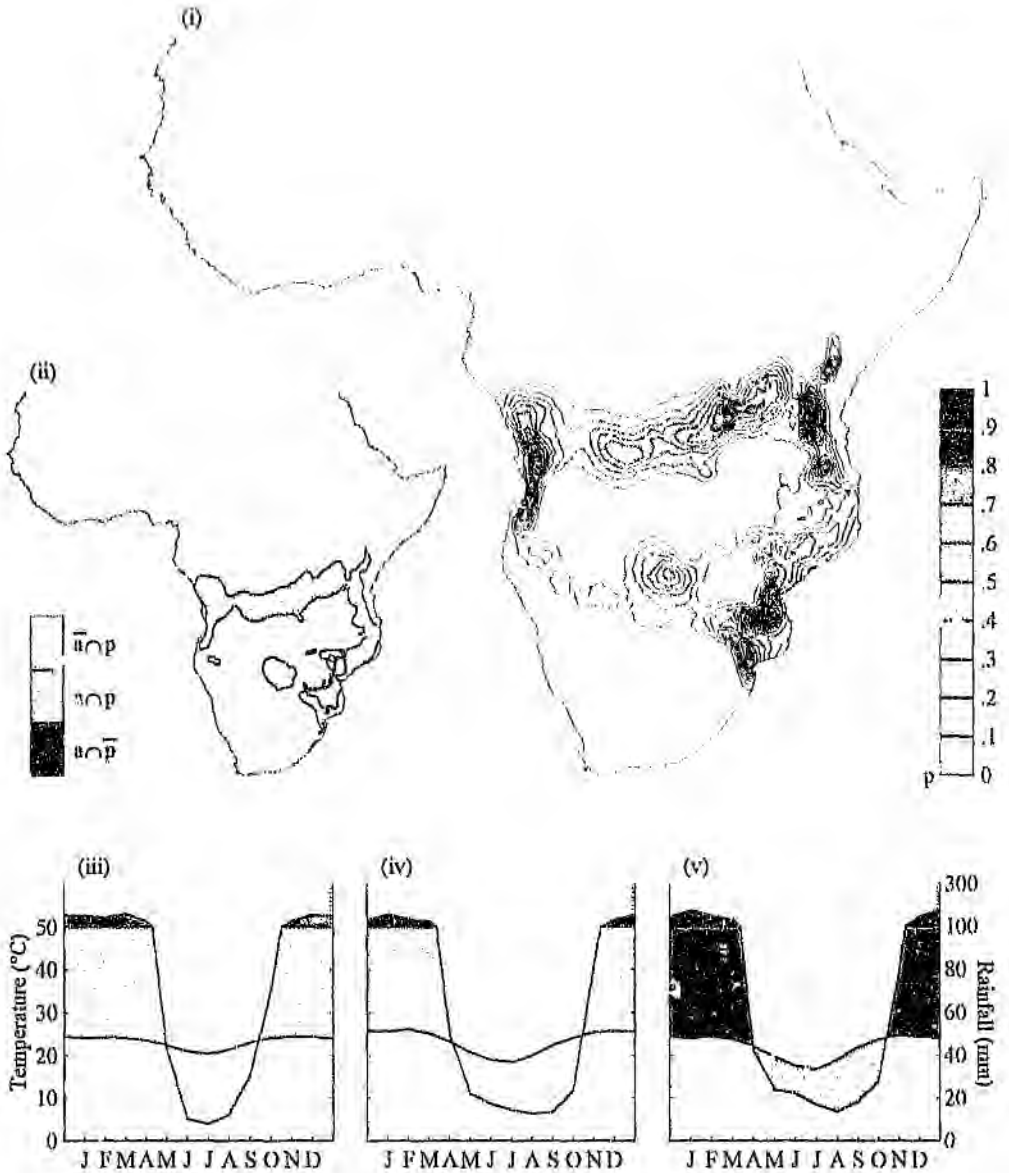


Figure 3.34. *Tragelaphus angasi*; (i) probability contours of the habitat model; (ii) intersection of the giv'' listribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[19/6/2008 15:59:55.24] #55 Sylvicapra grimmia (Common grey or common duiker)

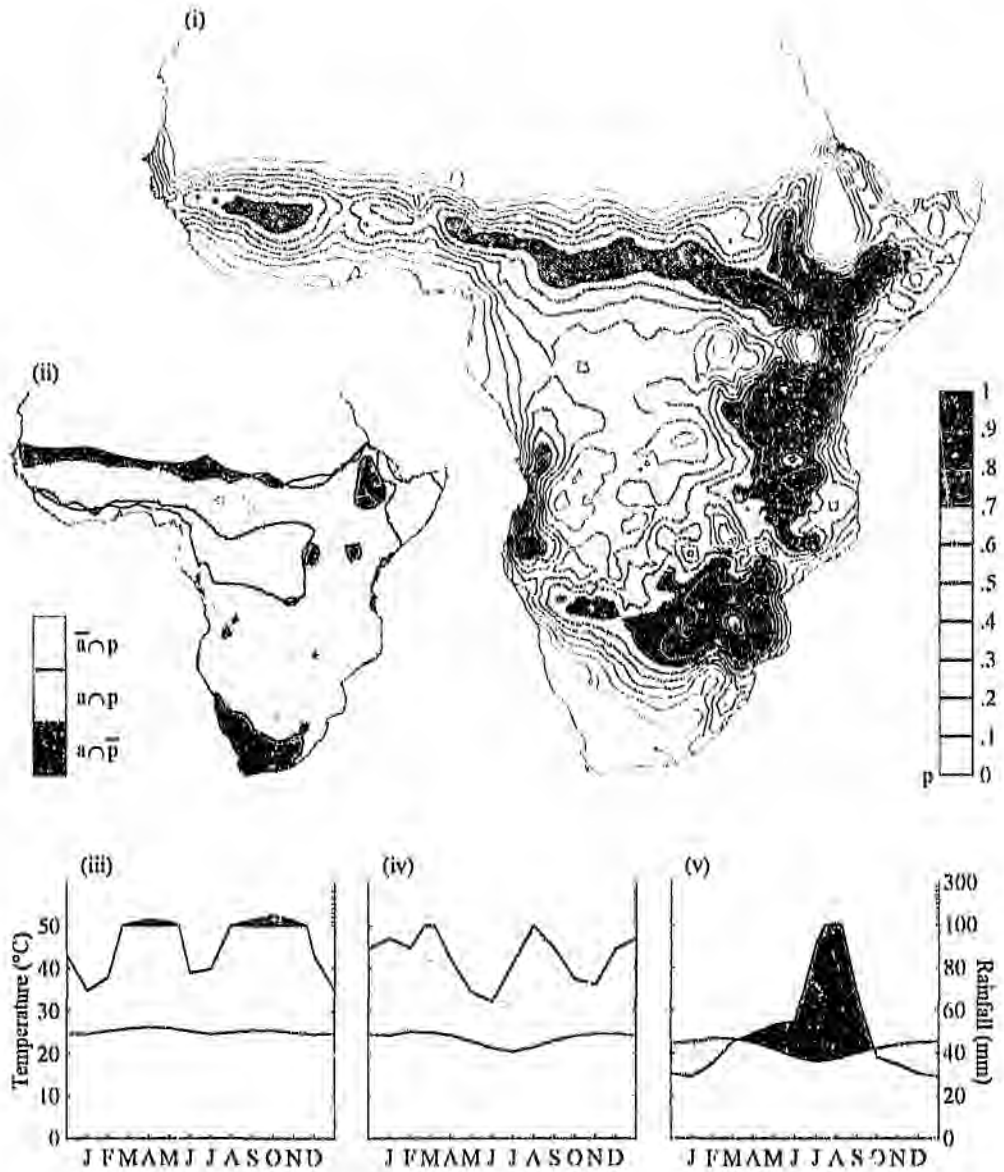


Figure 3.56. *Sylvicapra grimmia*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[19950908 15:38 8 41]

#54 Cephalophus zebra (banded duiker)

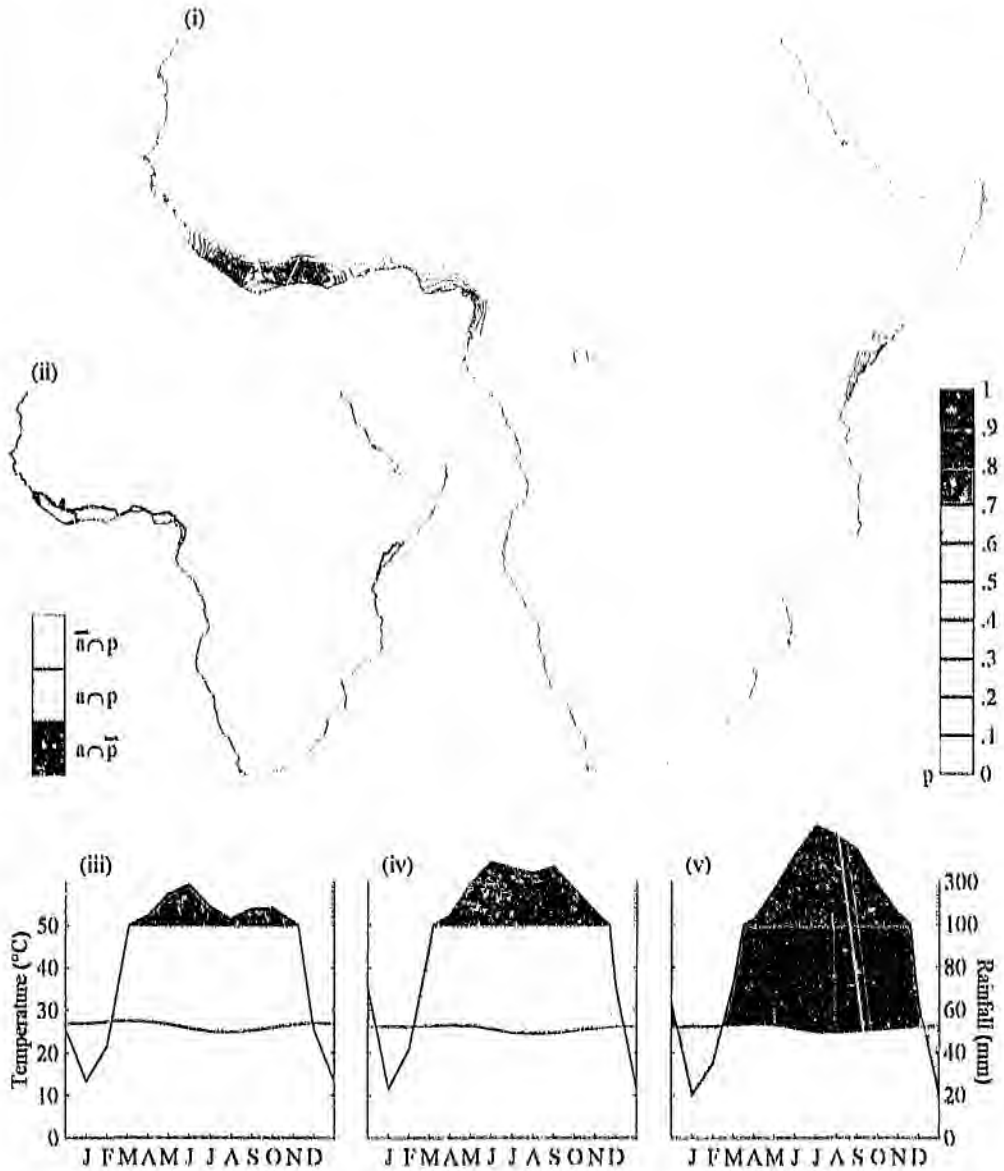


Figure 3.54. *Cephalophus zebra*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19920908 15:27:16)

#53 Cephalophus sylvicultor (Yellow-backed duiker)

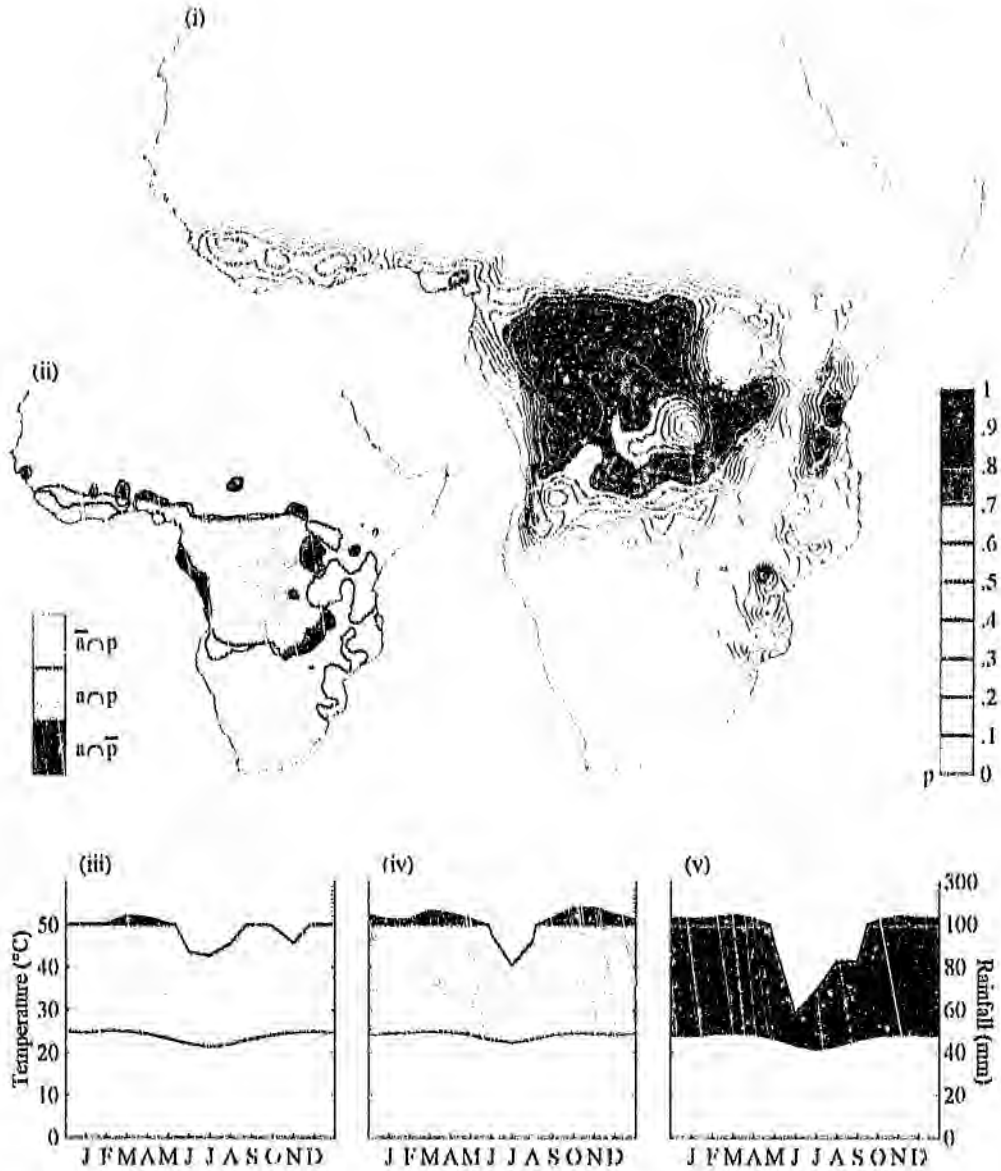


Figure 3.53. *Cephalophus sylvicultor*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[1995?] 15:52:?? #50 Cephalophus spadix (Abbott's duiker)

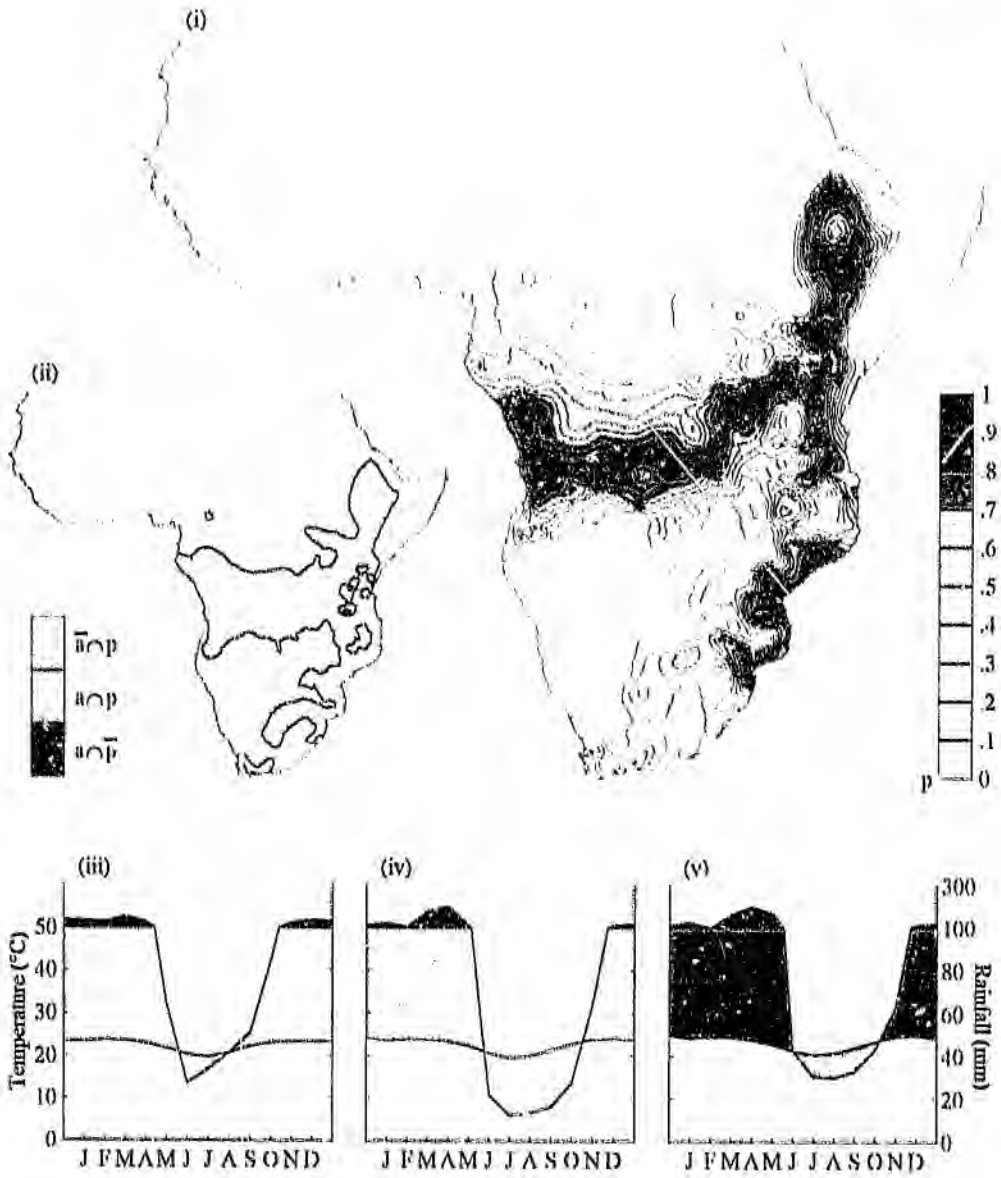


Figure 3.52. *Cephalophus spadix*: (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

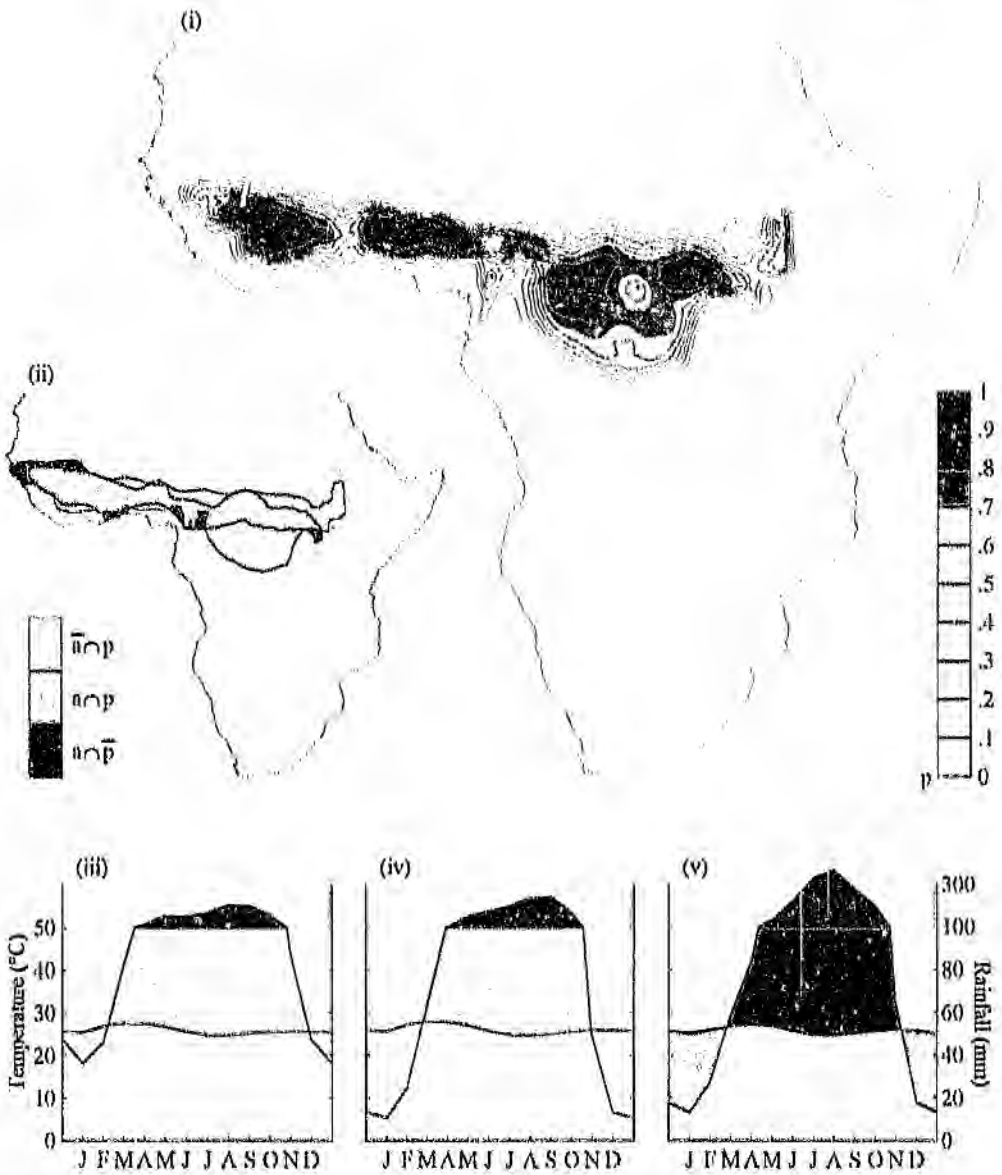


Figure 3.51. *Cephalophus rufilatus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

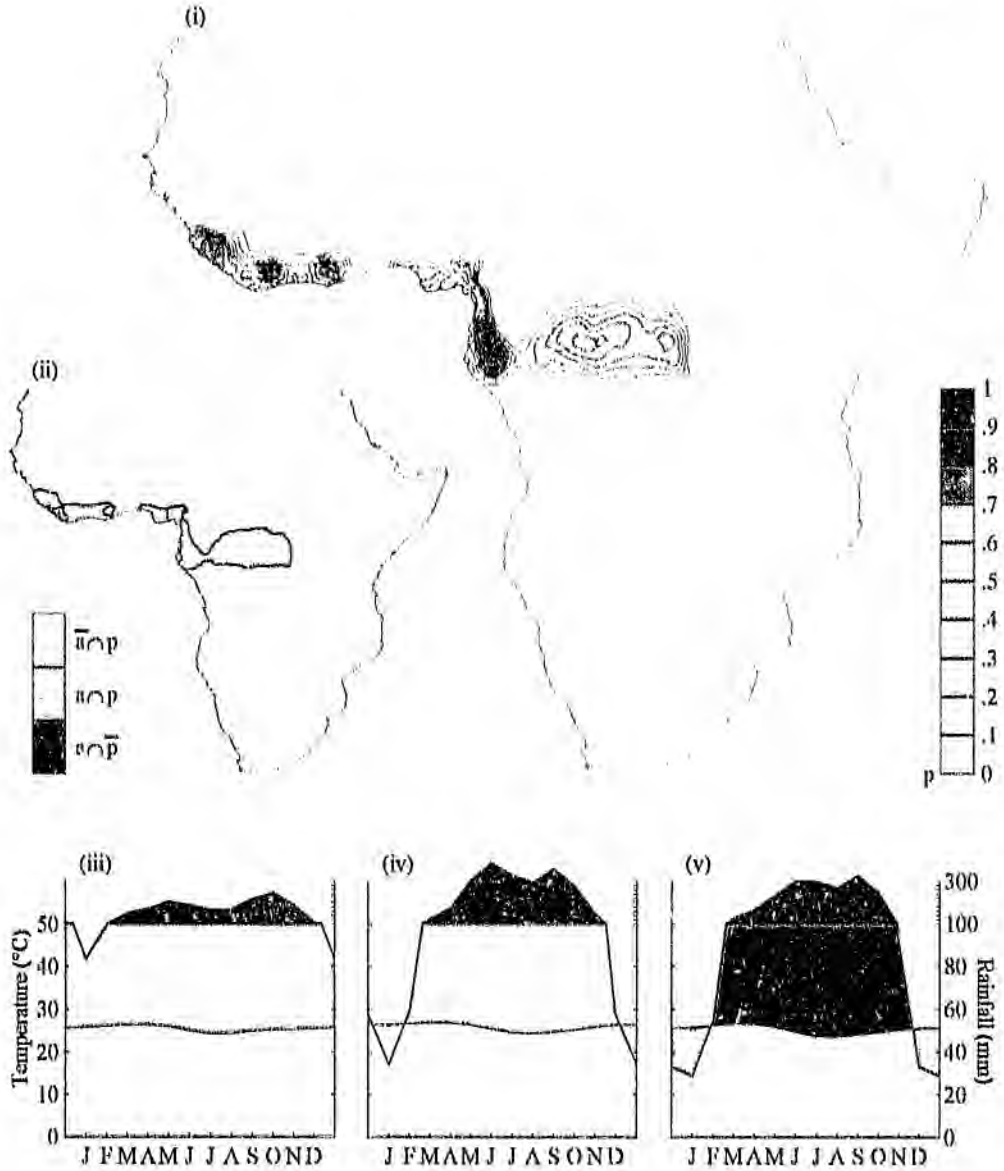


Figure 3.50. *Cephalophus ogilbyi*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

19955/9408 14:43:0.50) #13 Cephalophus nigrifrons (Black-fronted duiker)

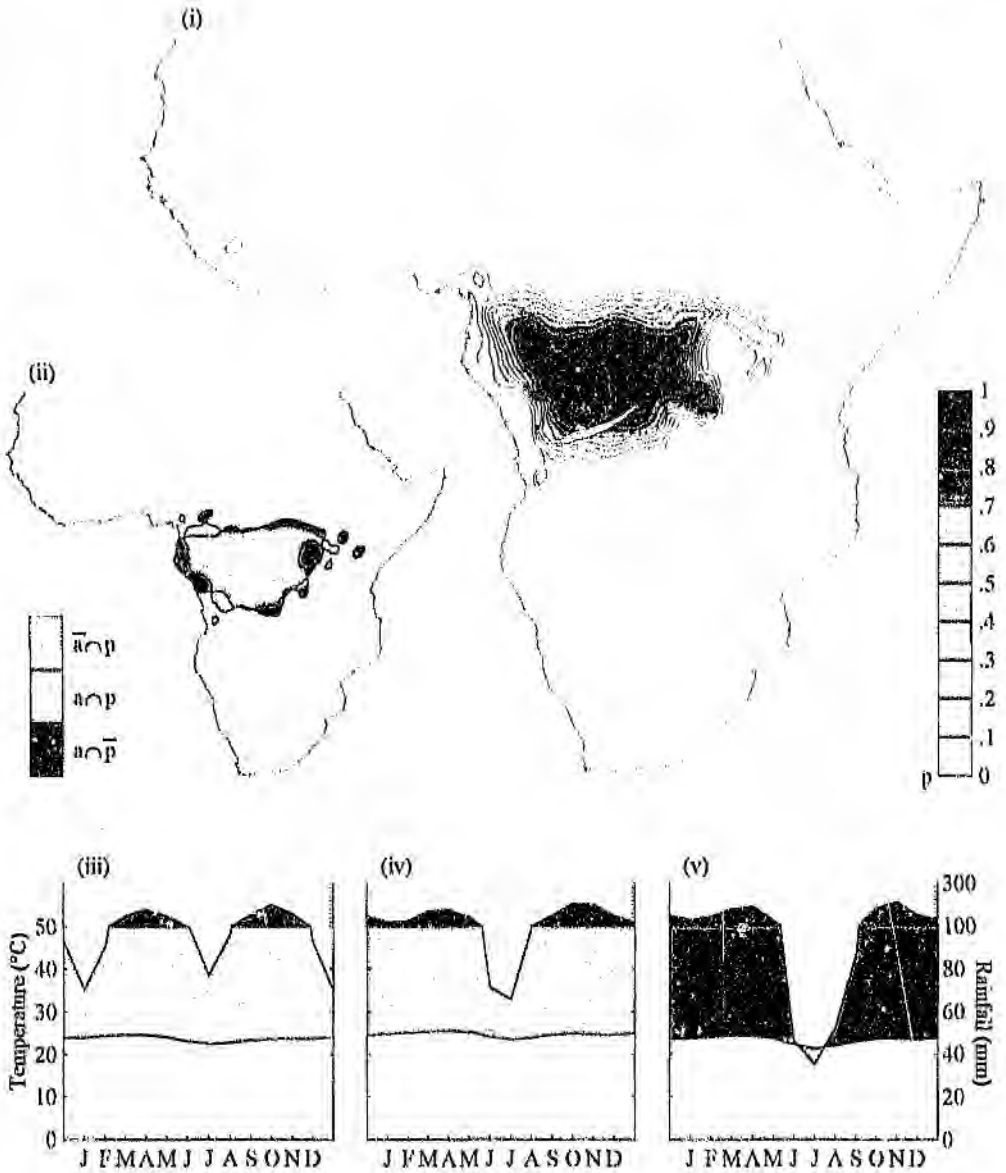


Figure 3.49. (*'ephalophus nigrifons*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[19950908 14:40:28.32] #43 Cephalophus niger (black duiker)

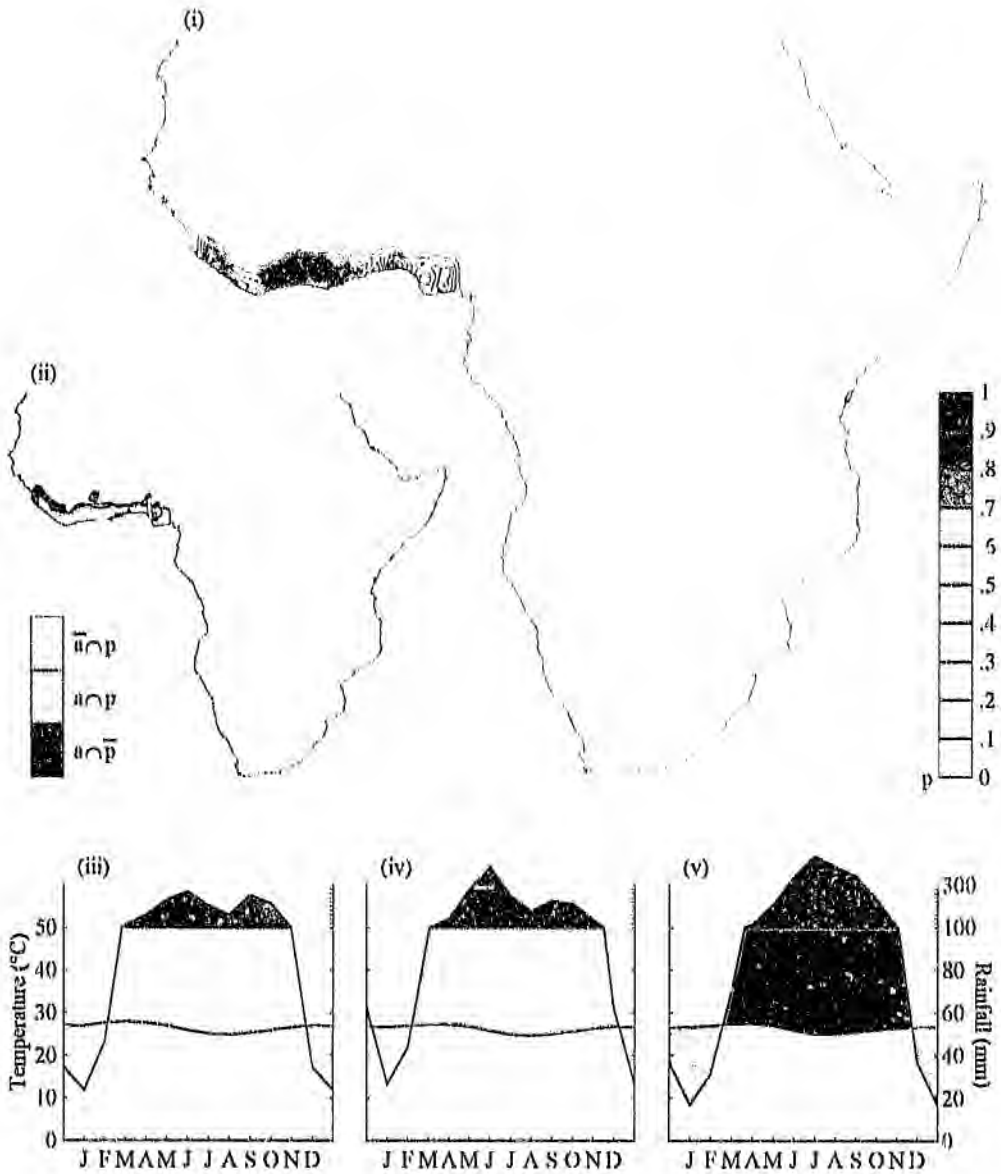


Figure 3.48. *Cephalophus niger*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, $\mathbf{a}$ (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/08 14:29:8.51) #47 Cephalophus natalensis (Red forest duiker)

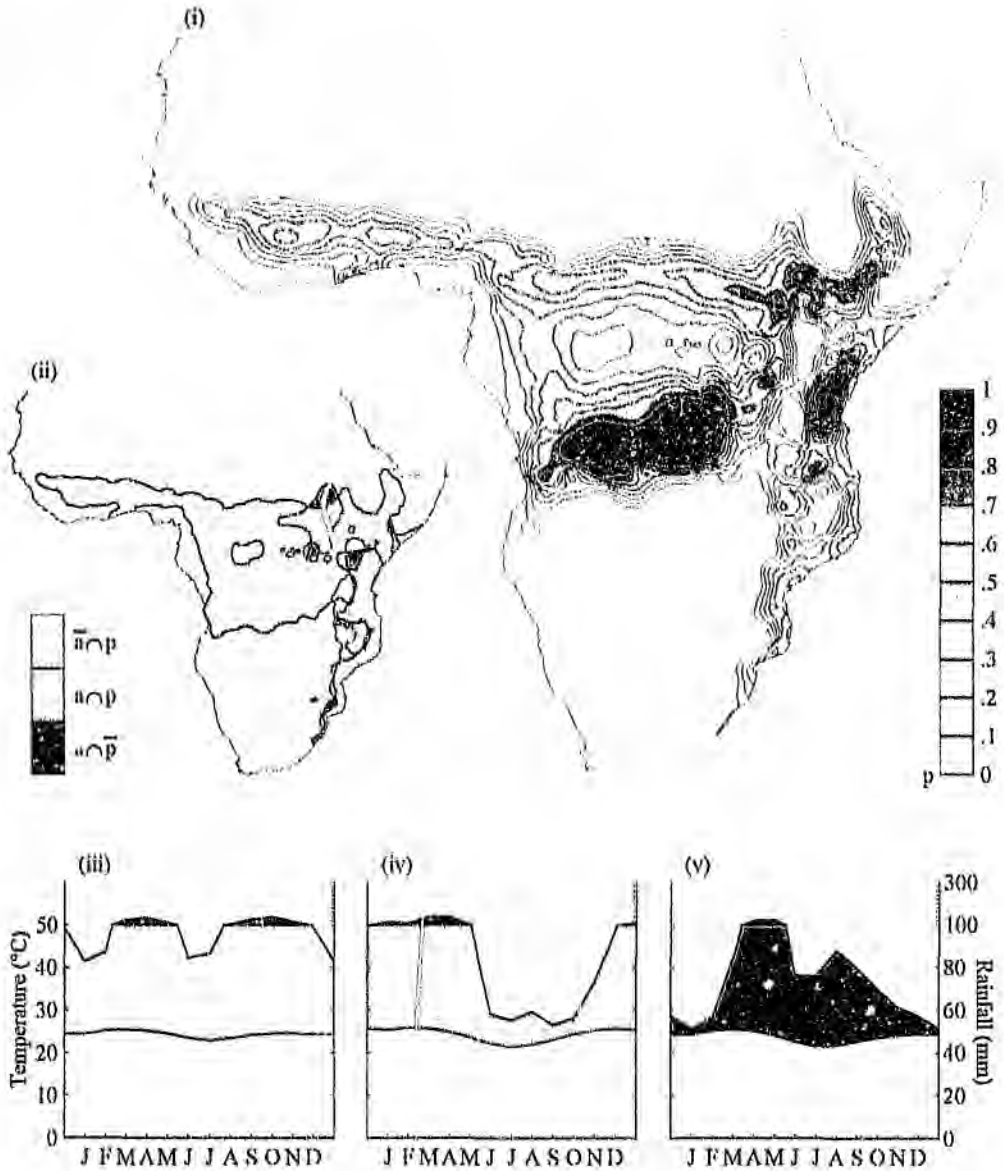


Figure 3.47. *Cephalophus natalensis*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19950908 141934 SZ)

#46 Cephalophus leucogaster (Gabon or white-bellied duiker)

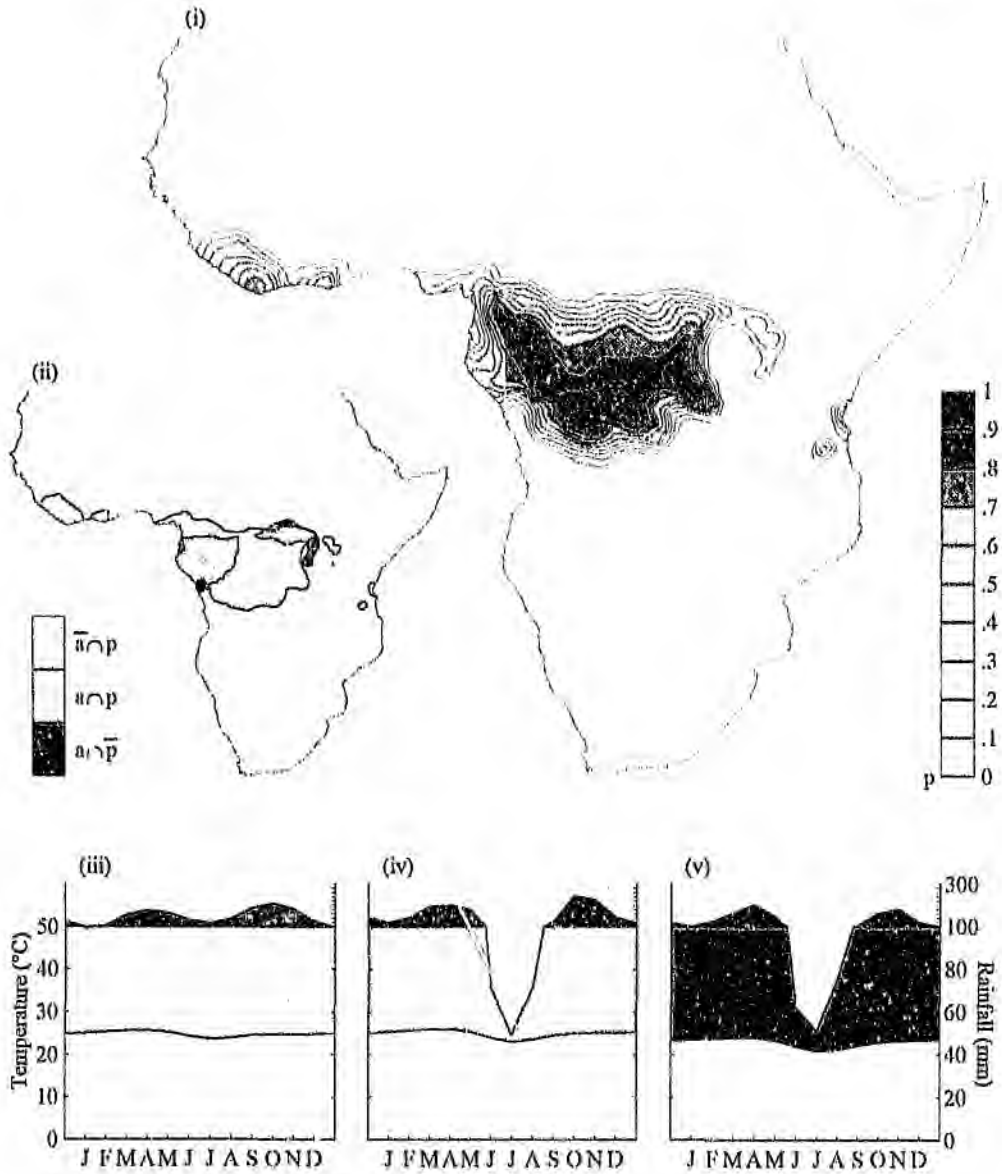


Figure 3.46. *Cephalophus leucogaster*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/08 14:12:12.11) #45 Cephalophus jentinki (Jentink's duiker)

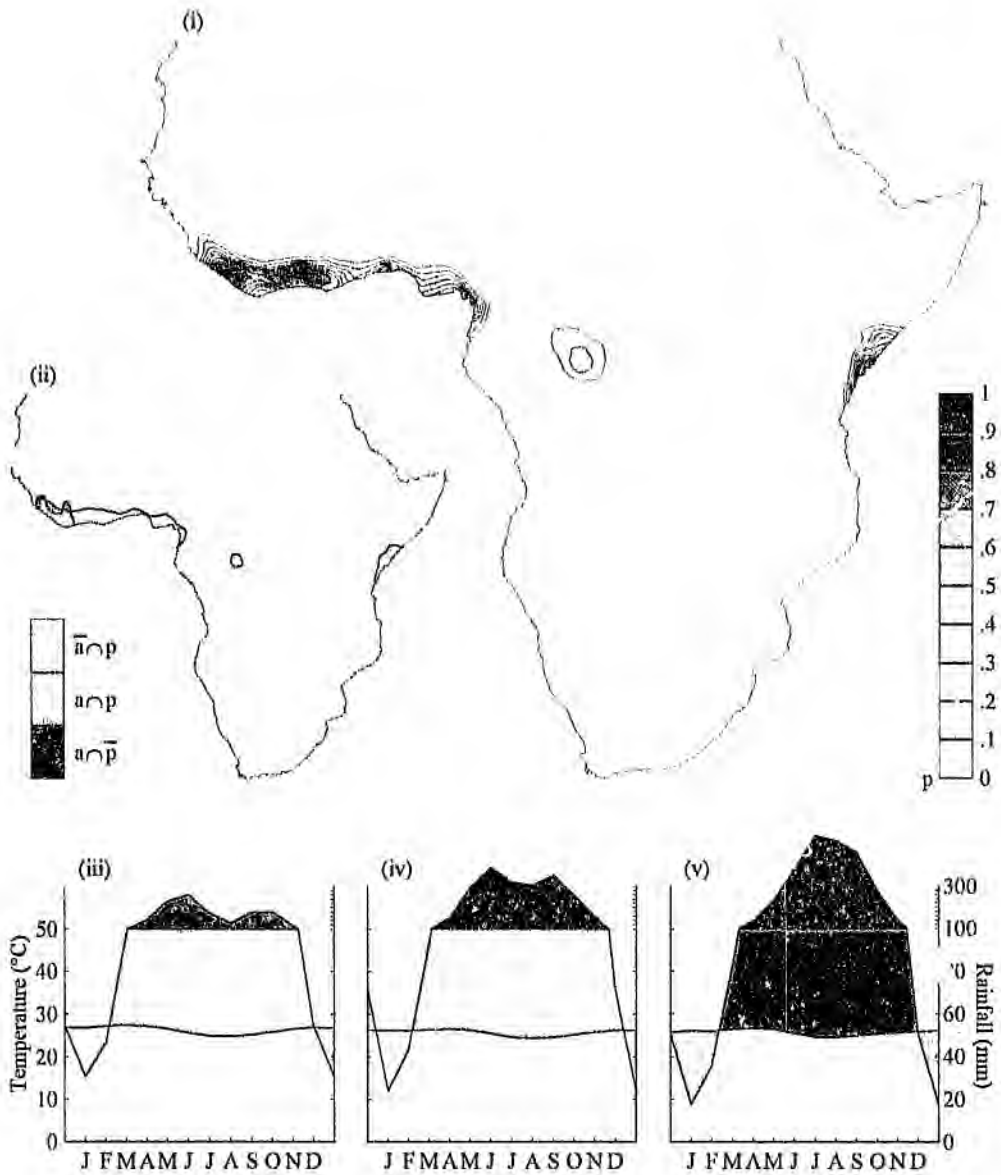


Figure 3.45. *Cephalophus jentinki*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/09/08 14:03:55.64)

#44 Cephalophus dorsalis (Bay duiker)

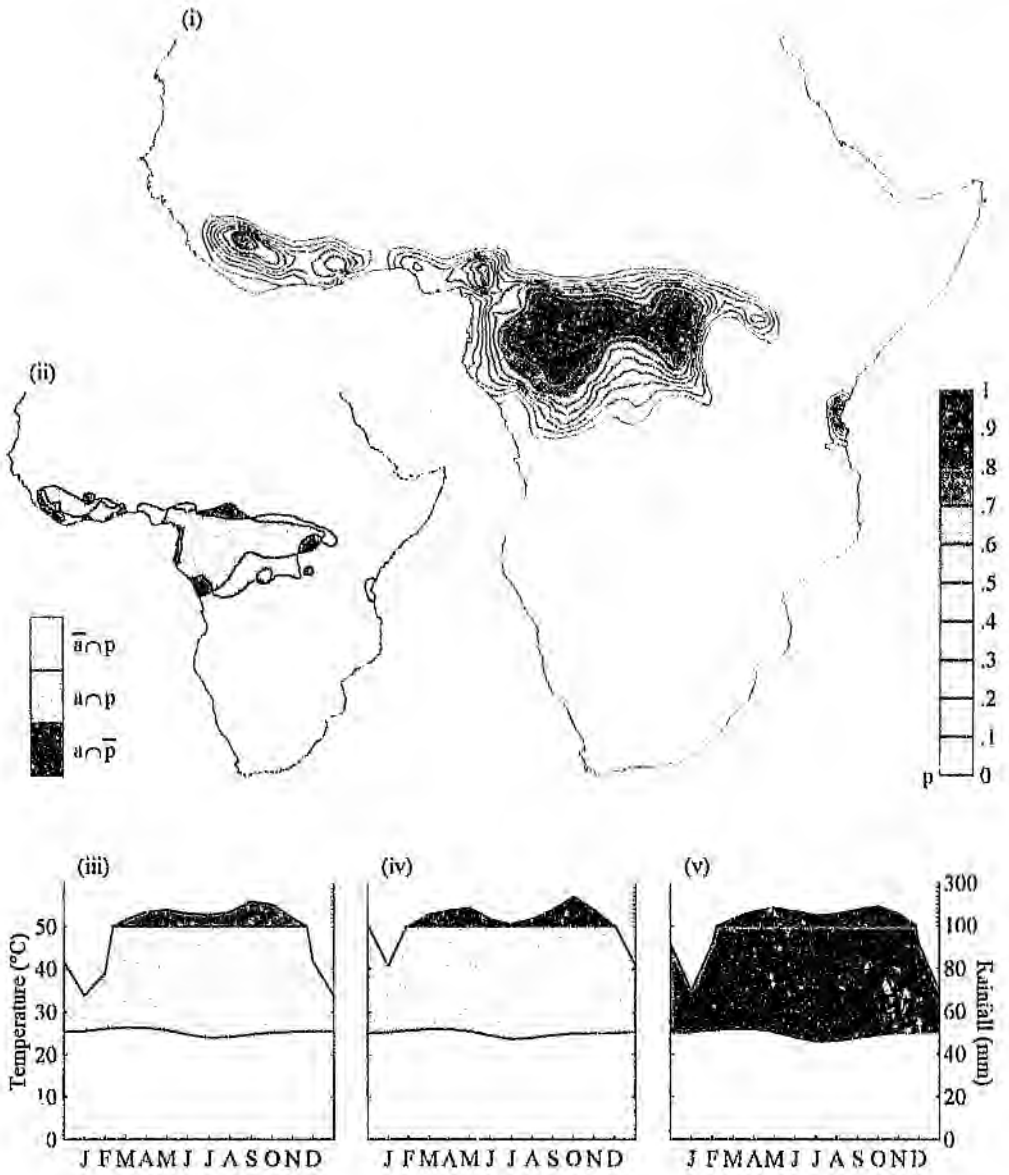


Figure 3.44. *Cephalophus dorsalis*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19960909 17:32:55.74) #98 Kobus vardoni (Trau)

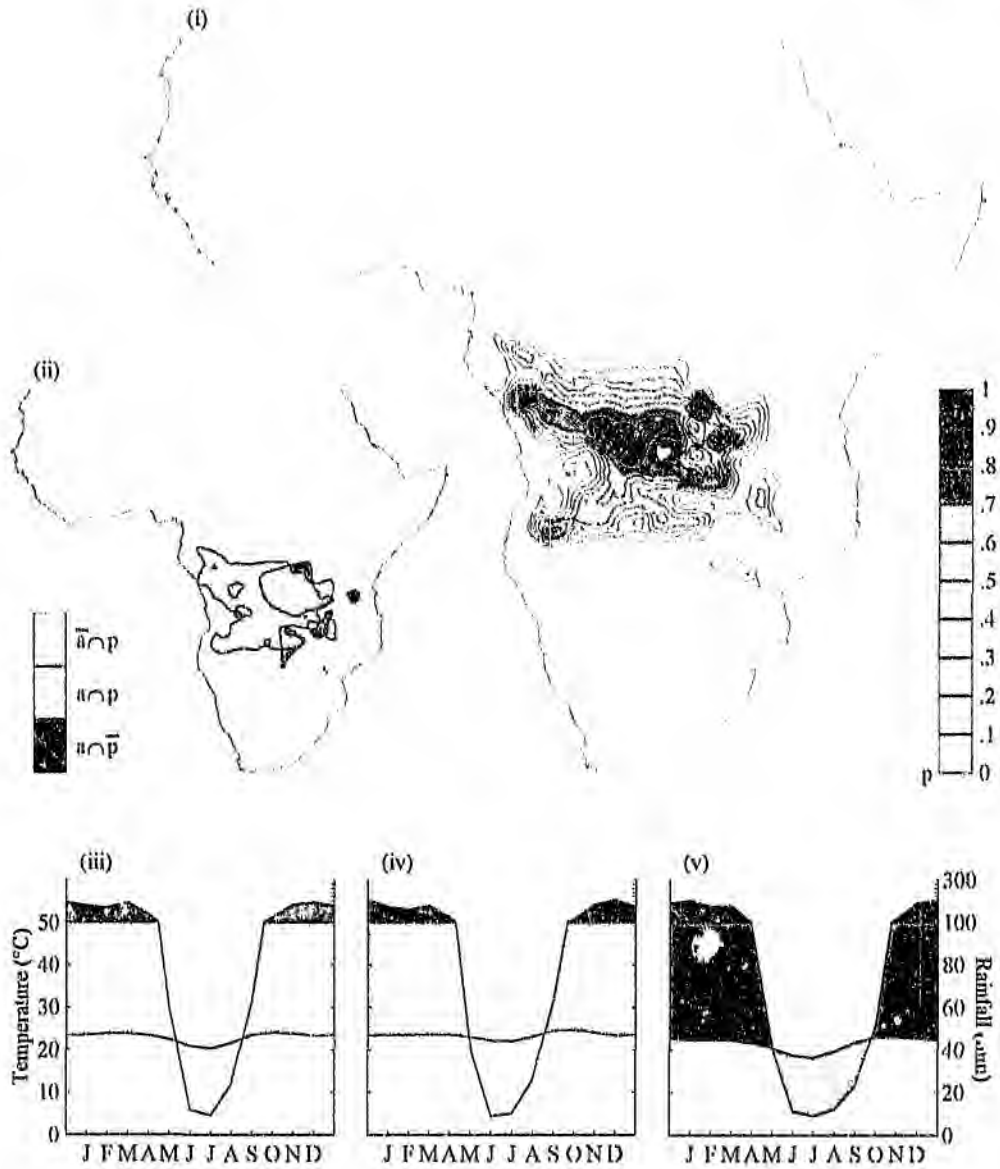


Figure 3.68. *Kobus vardoni*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[19950109 17:24:43:7] #57 Kobus megaceros (N.'e lechwe)

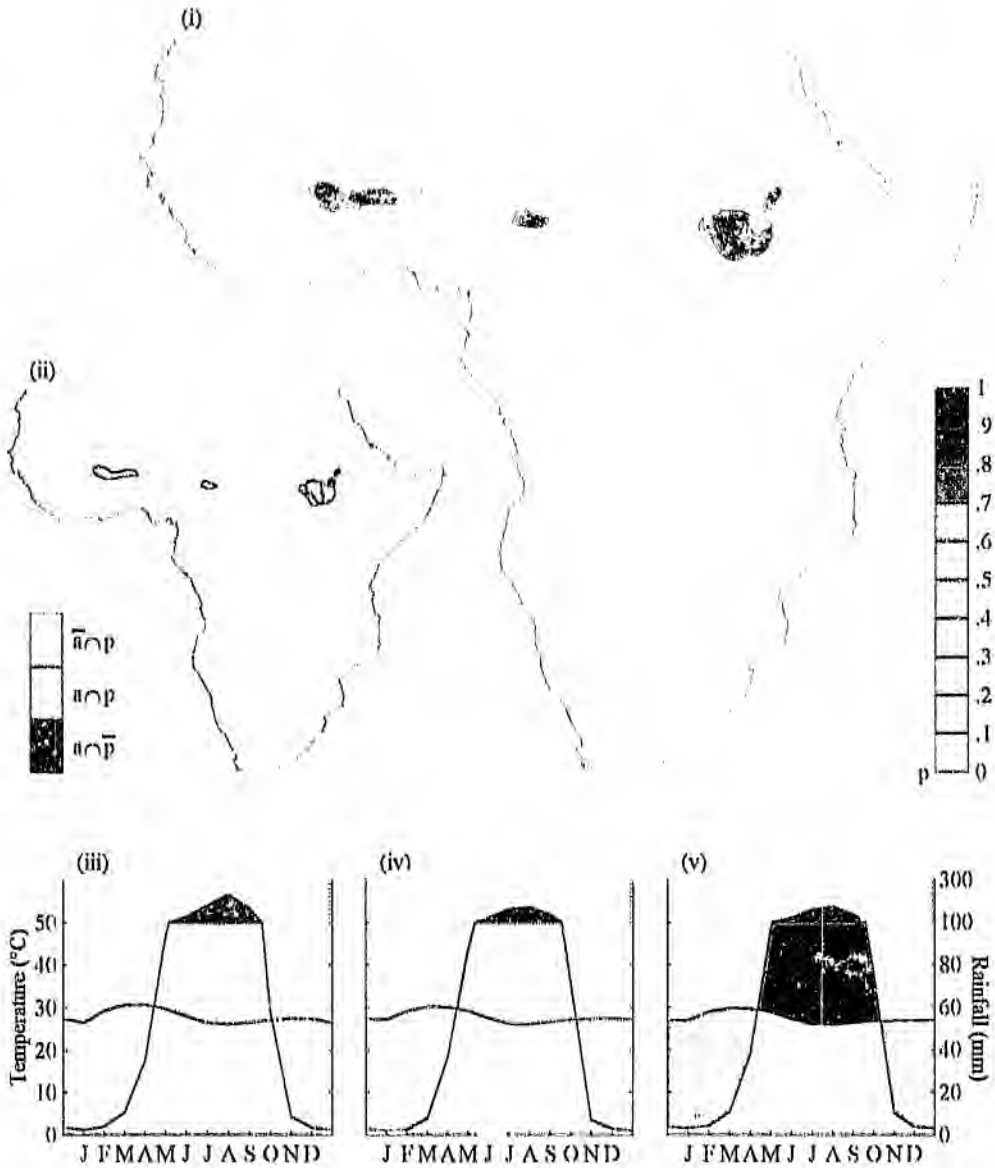


Figure 3.67. *Kobus megaceros*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

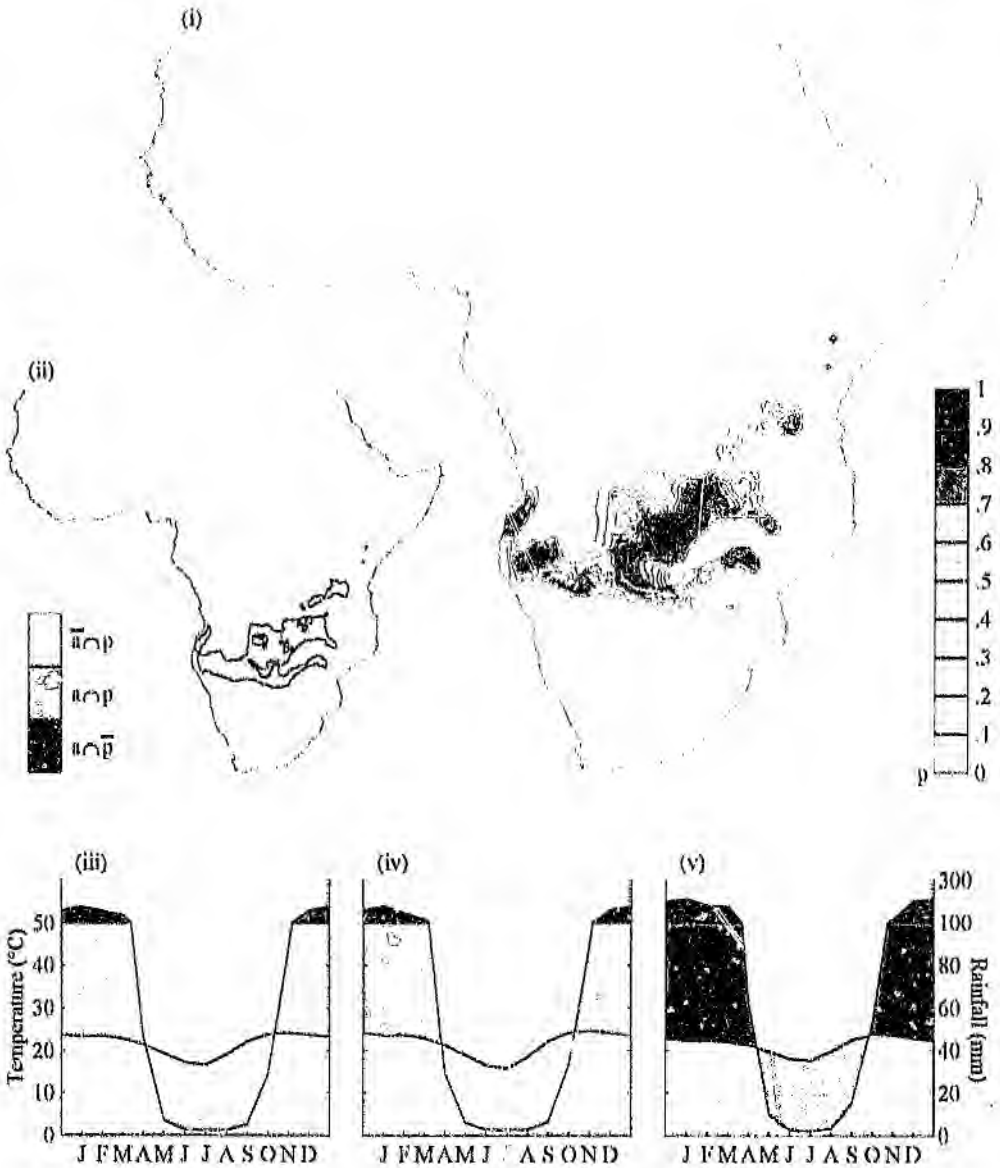


Figure 3.66. *Kobus leche*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

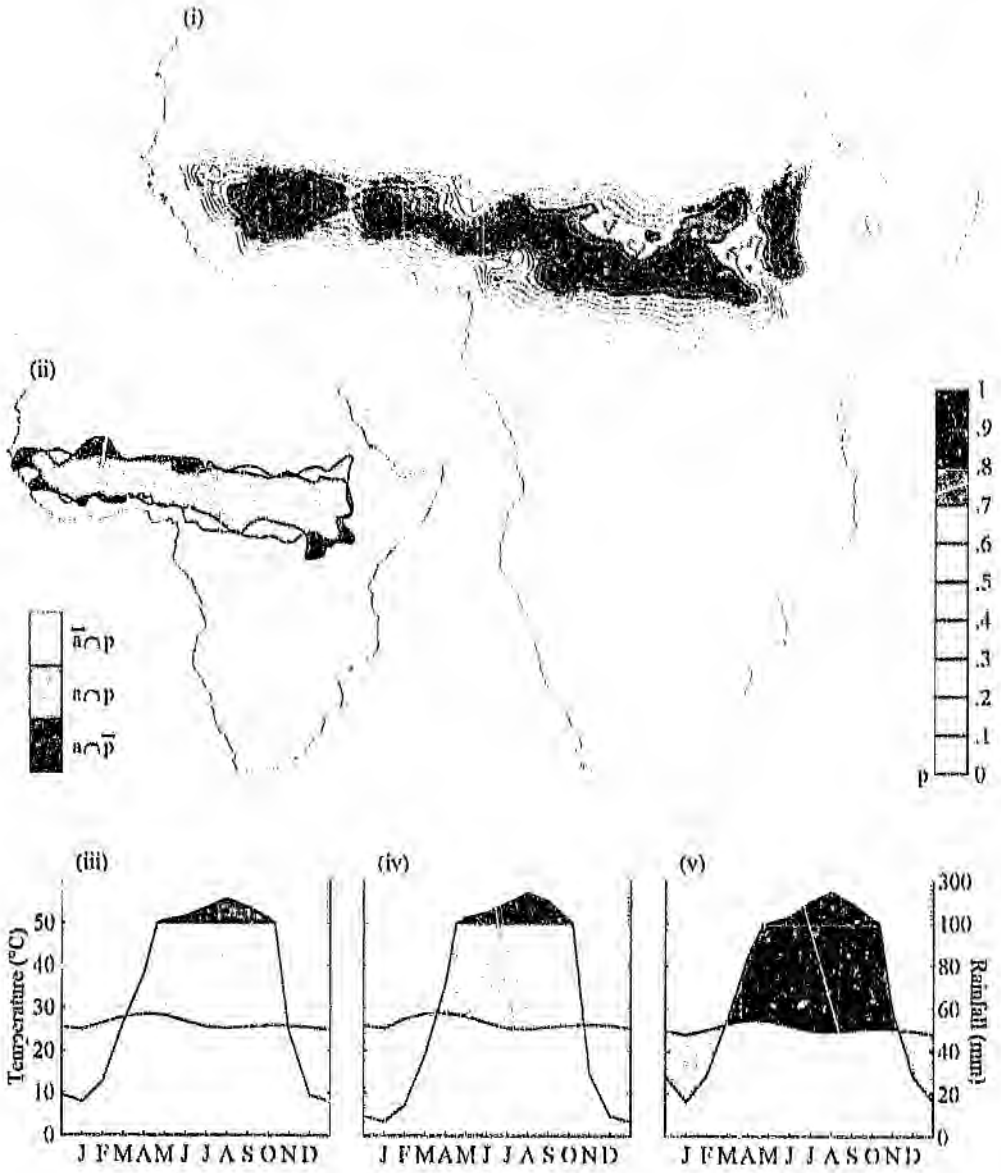


Figure 3.65. *Kobus kob*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

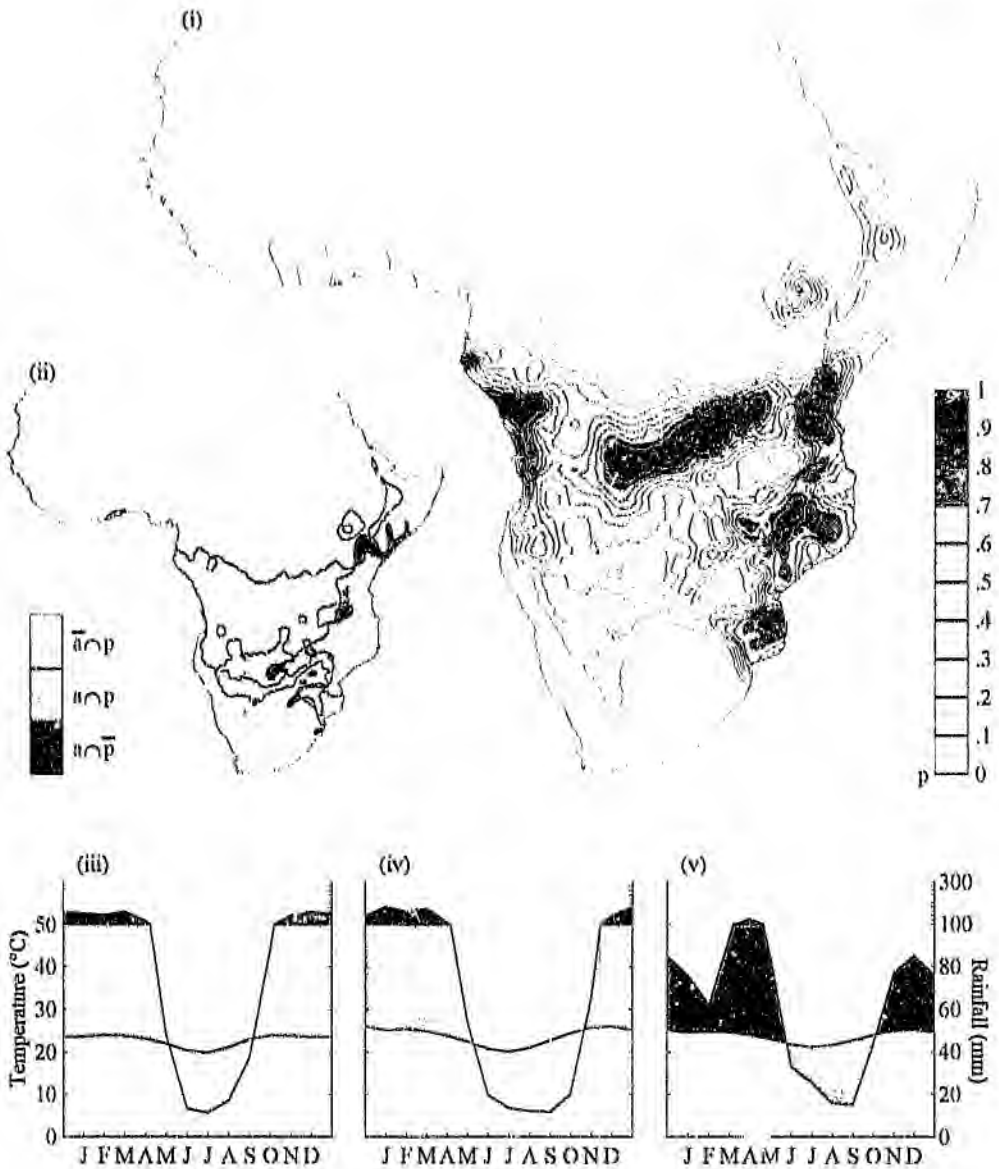


Figure 3.64. *Kobus ellipsiprymnus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(18/5/2009 8:47:52) 353 Pelea capreolus (Least grey rhebok)

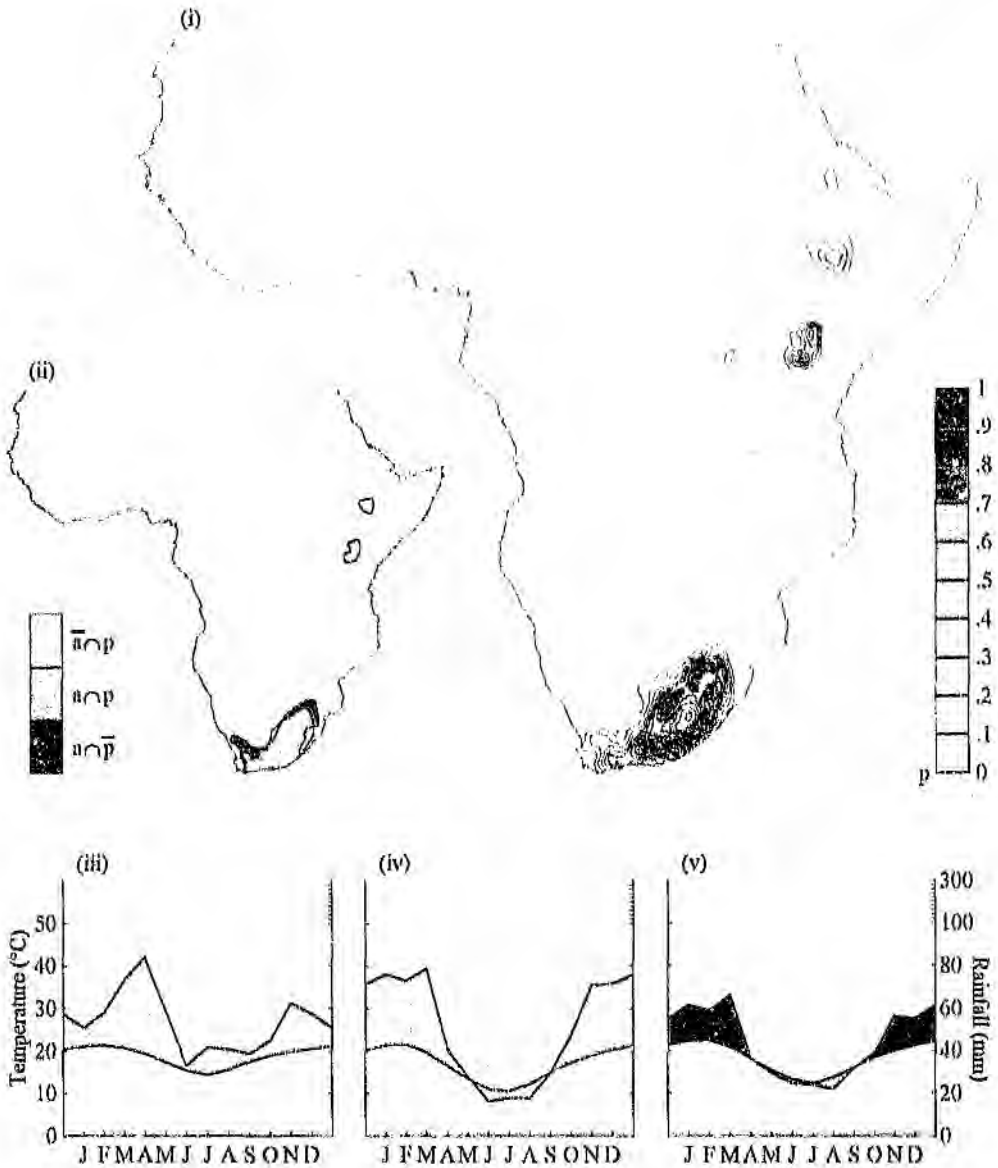


Figure 3.63. *Pelea capreolus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

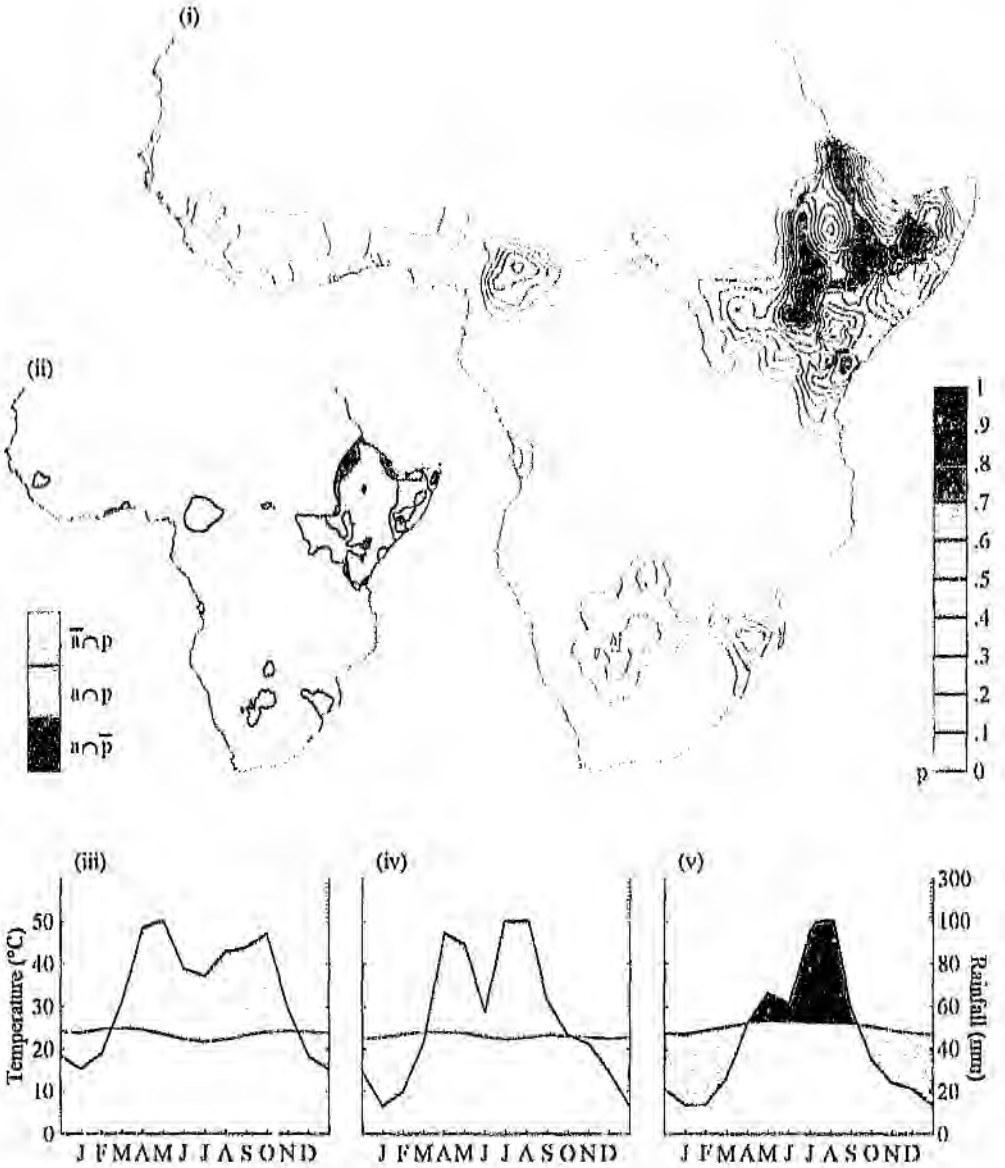


Figure 3.62. *Oryx leucoryx*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

[1998/09/03 16:23:22.45] #61 Oryx gazella (Gemsbok)

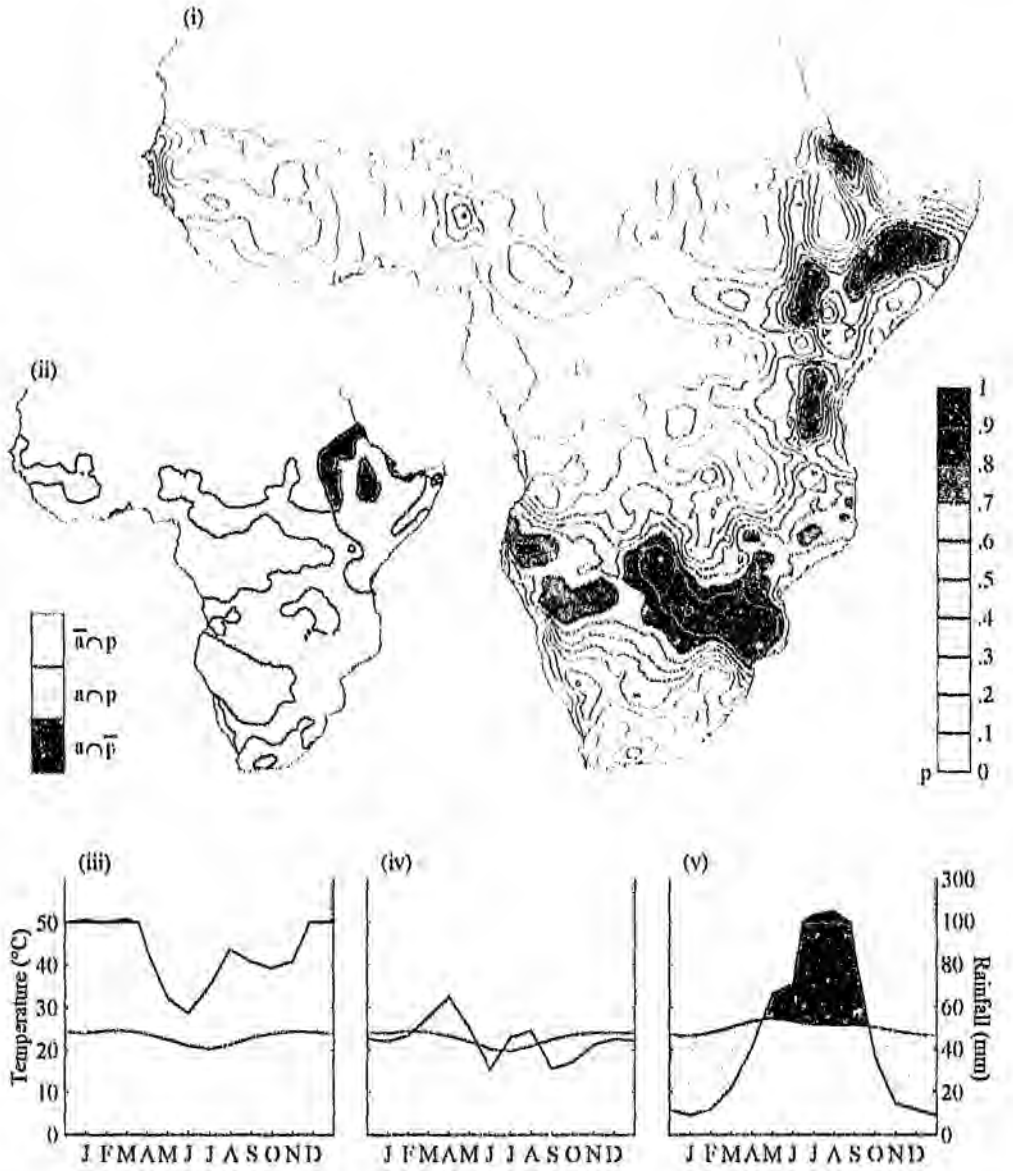


Figure 3.61. *Oryx gazella*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/08/09 16:12:48 CS) #60 Oryx dammah (Scimitar-horned or Beisa oryx)

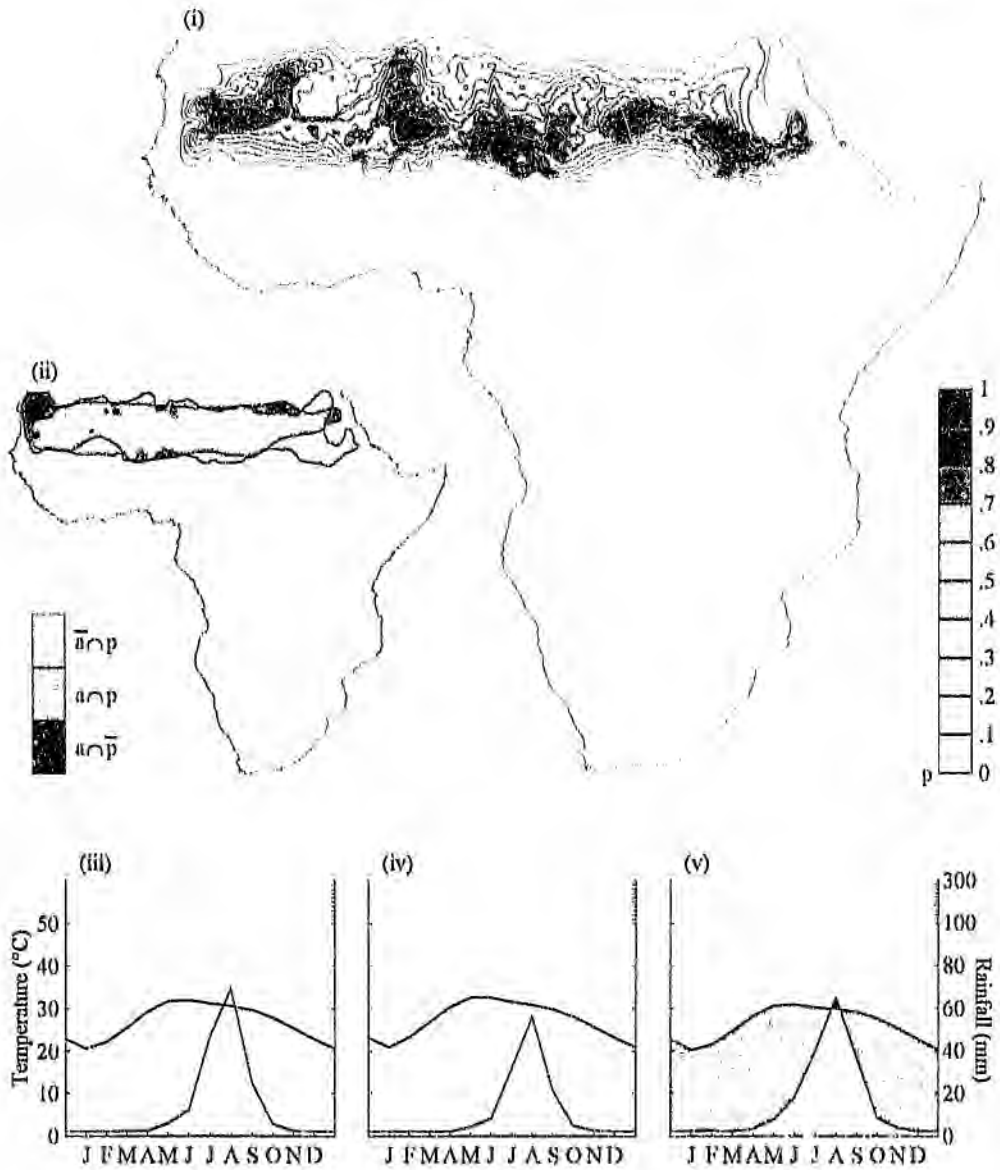


Figure 3.60. *Oryx dammah*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(19950908 17:00:12.7)
#59 Hippotragus niger (Sable antelope)

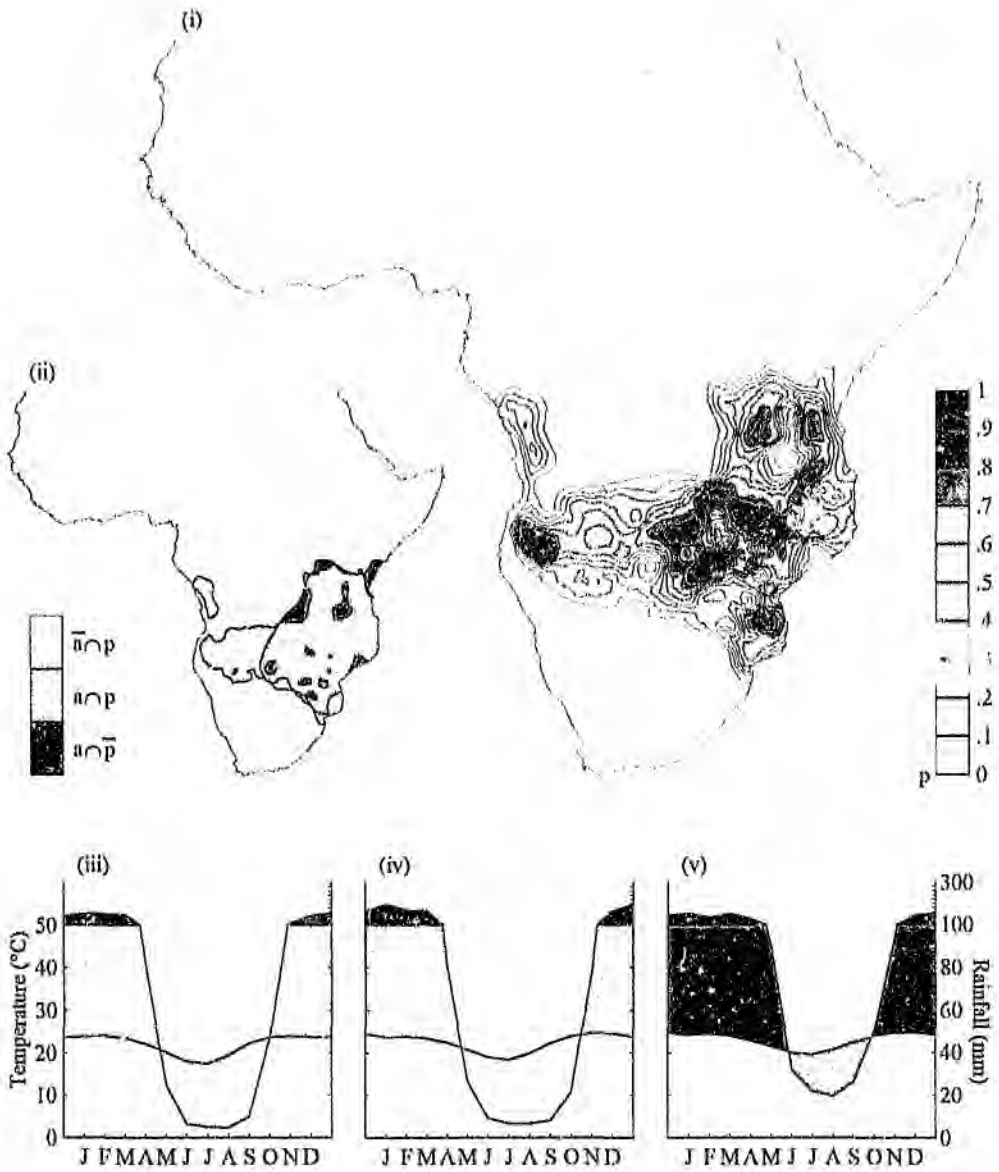


Figure 3.59. *Hippotragus niger*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1992/05/08 16:36:39 64) #58 Hippotragus equinus (Roan antelope)

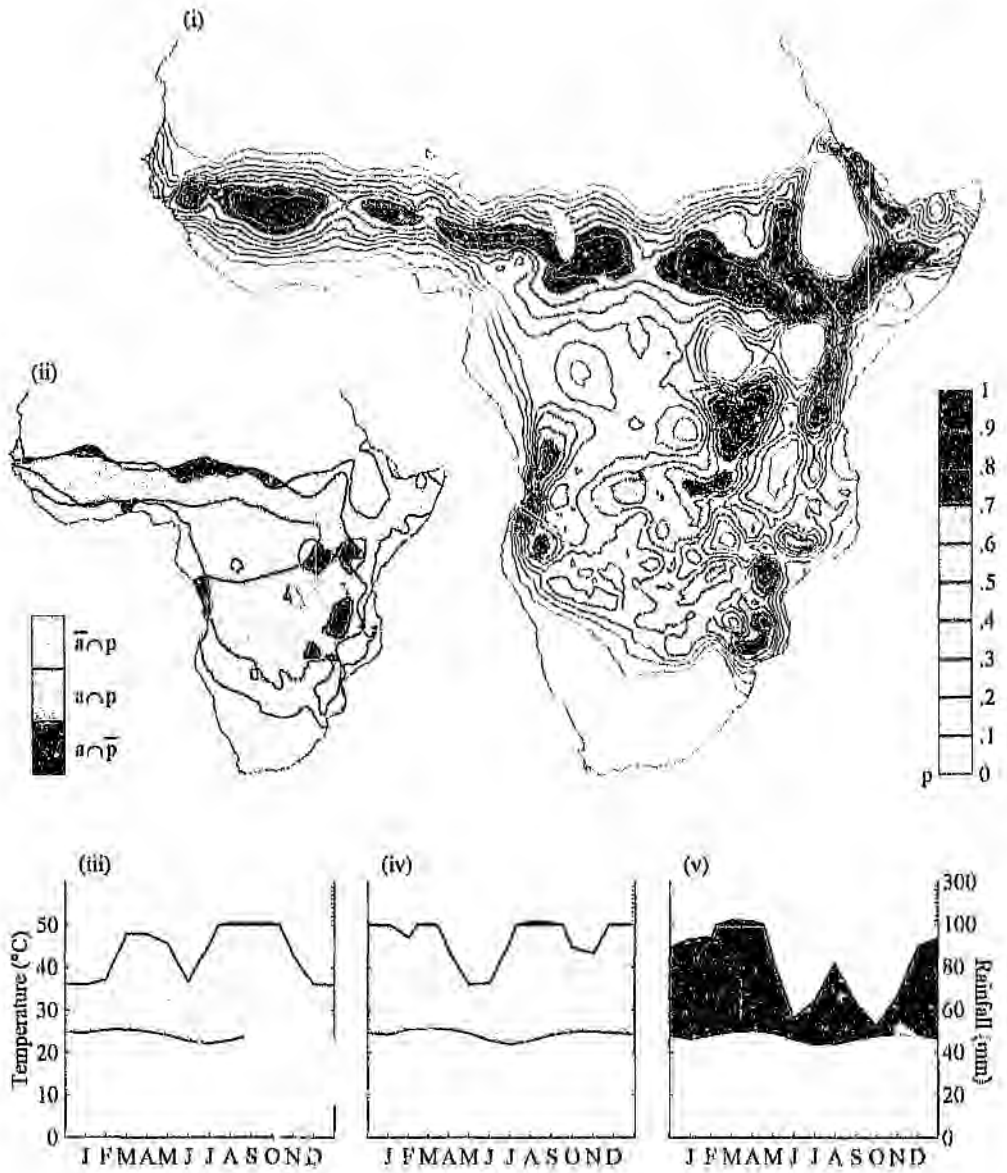


Figure 3.58. *Hippotragus equinus*: (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1995/08/28 16:25:44.7) #57 Addax nasomaculatus (Addax)

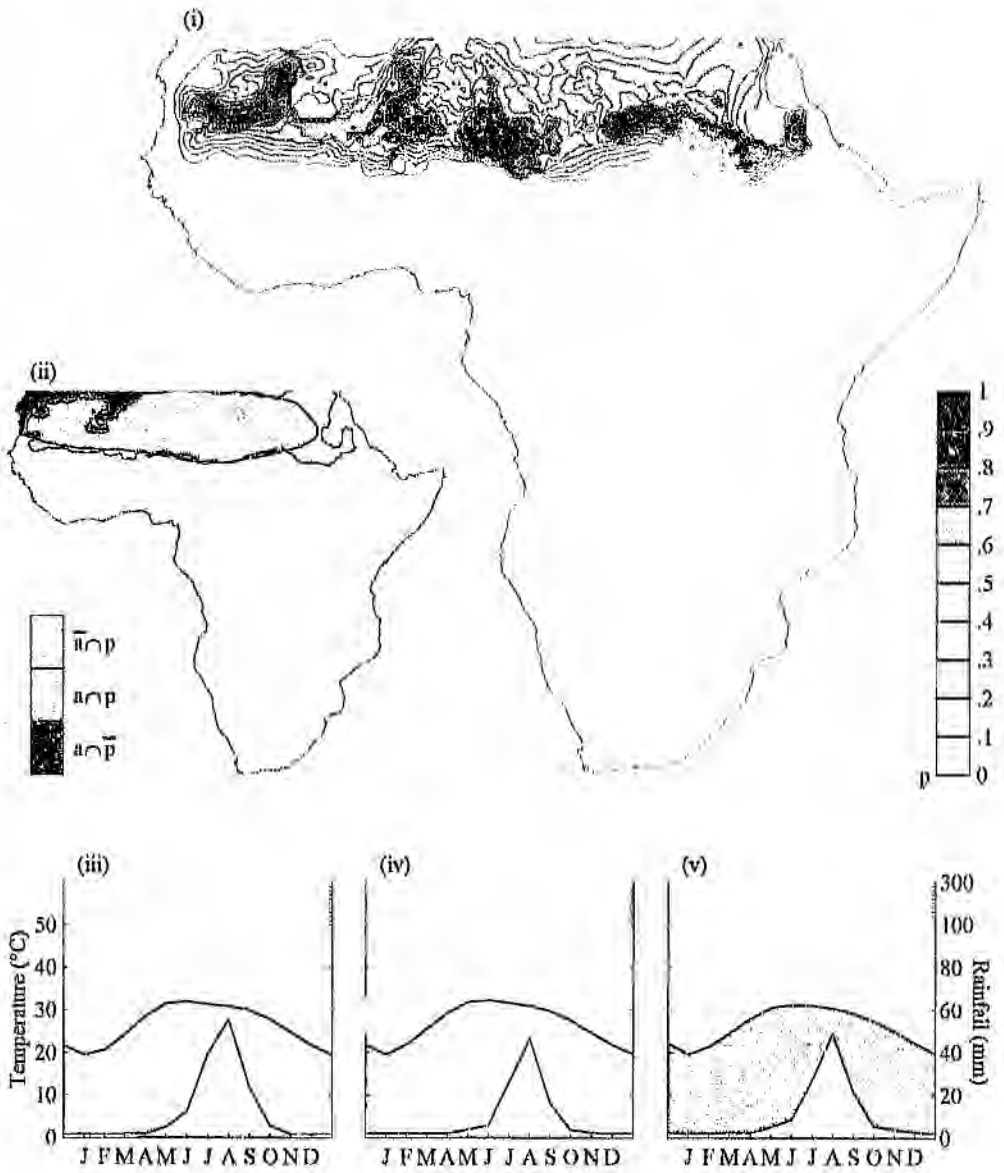


Figure 3.57. *Addax nasomaculatus*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

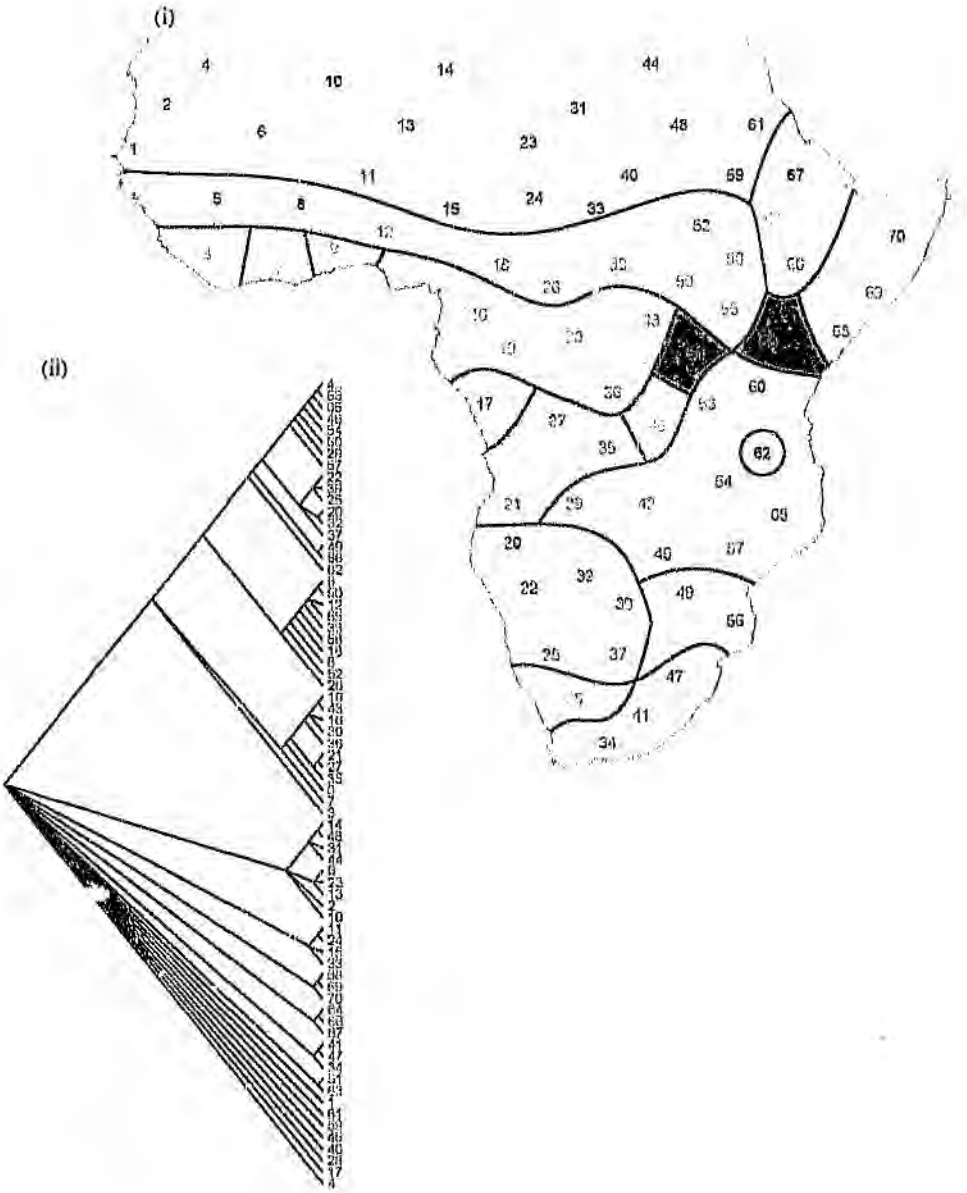


Figure 8. Areas of endemism and their historical relationships. (i) Regions are grouped by colour (except yellow) to show the major resolved clades on the area cladogram. (ii) Replicate of the cladogram in Figure 7(i). Numbers refer to 70 point localities chosen to cover the major features shown in Figure 6.

(1995/0928 00:02:48.73) The real thing

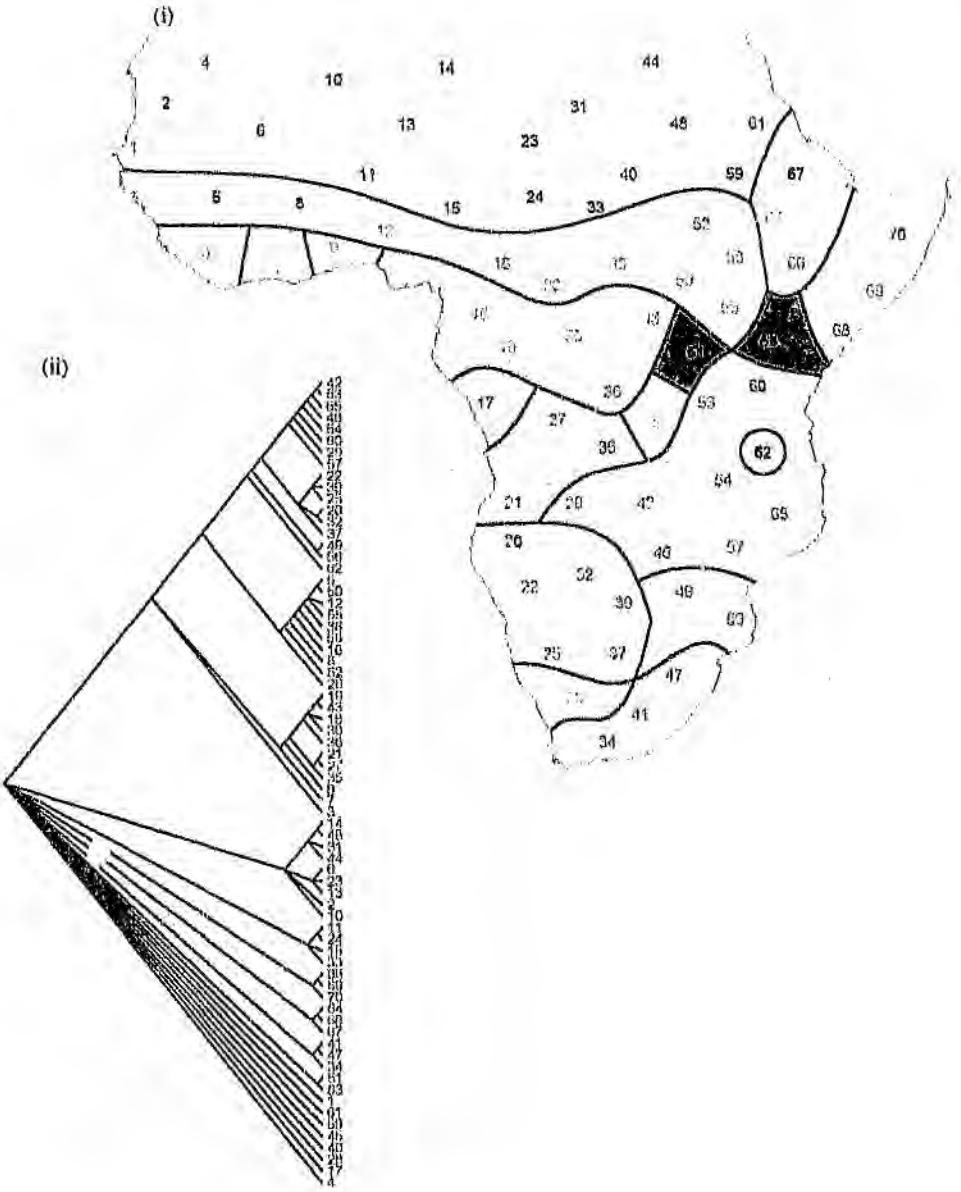


Figure 8. Areas of endemism and their historical relationships. (i) Regions are grouped by colour (except yellow) to show the major resolved clades on the area cladogram. (ii) Replicate of the cladogram in Figure 7(i). Numbers refer to 70 point localities chosen to cover the major features shown in Figure 6.

[1998/10/04 01:52:20.17] Weighted - Unweighted

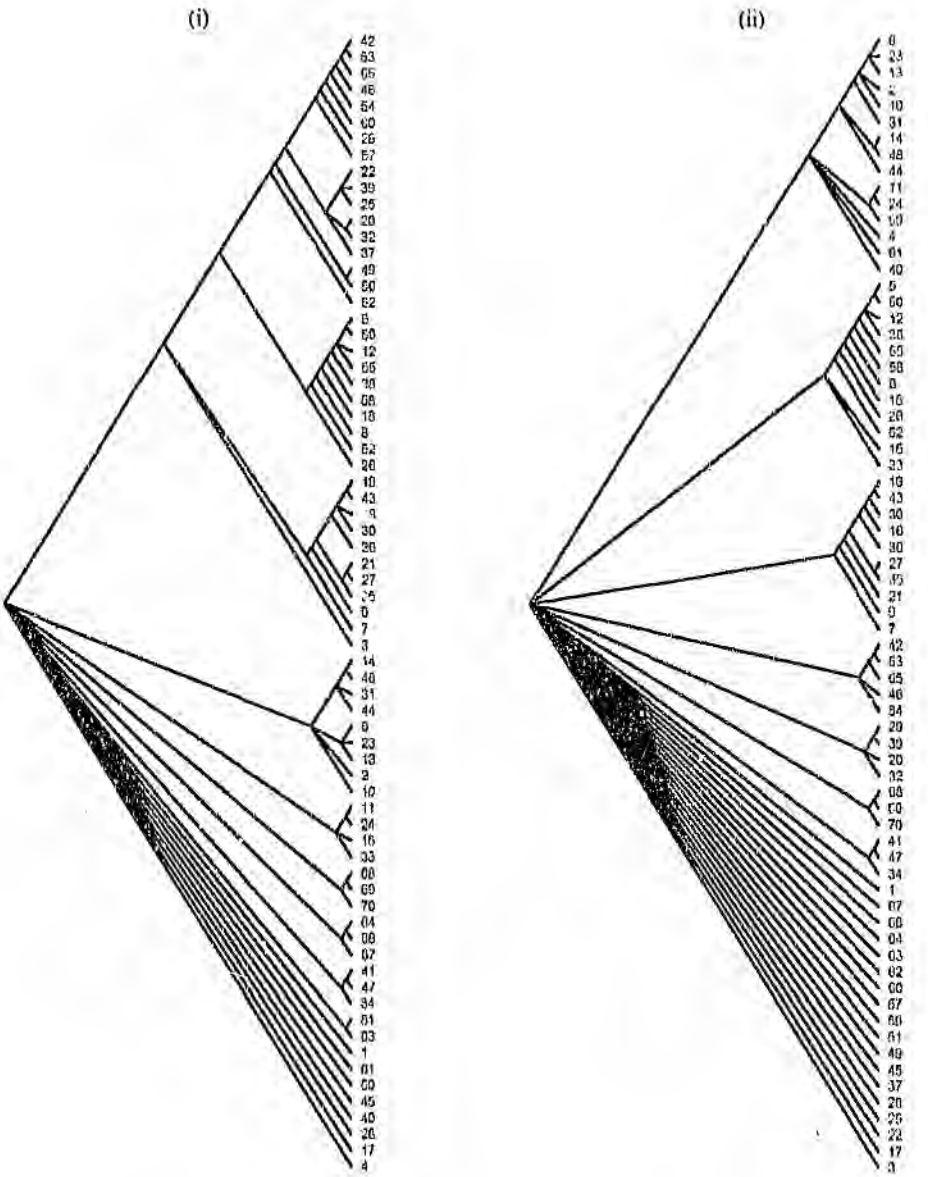


Figure 7. Area cladograms for the numbered localities shown in Figure 8.
(i) Cladogram derived by the method of ecological induction for widespread taxa. See Table 3 for details of the weighting scheme. (ii) Cladogram based on unweighted species distributions.

(1995/09/24 15:29:20.65) UPGMA cluster map

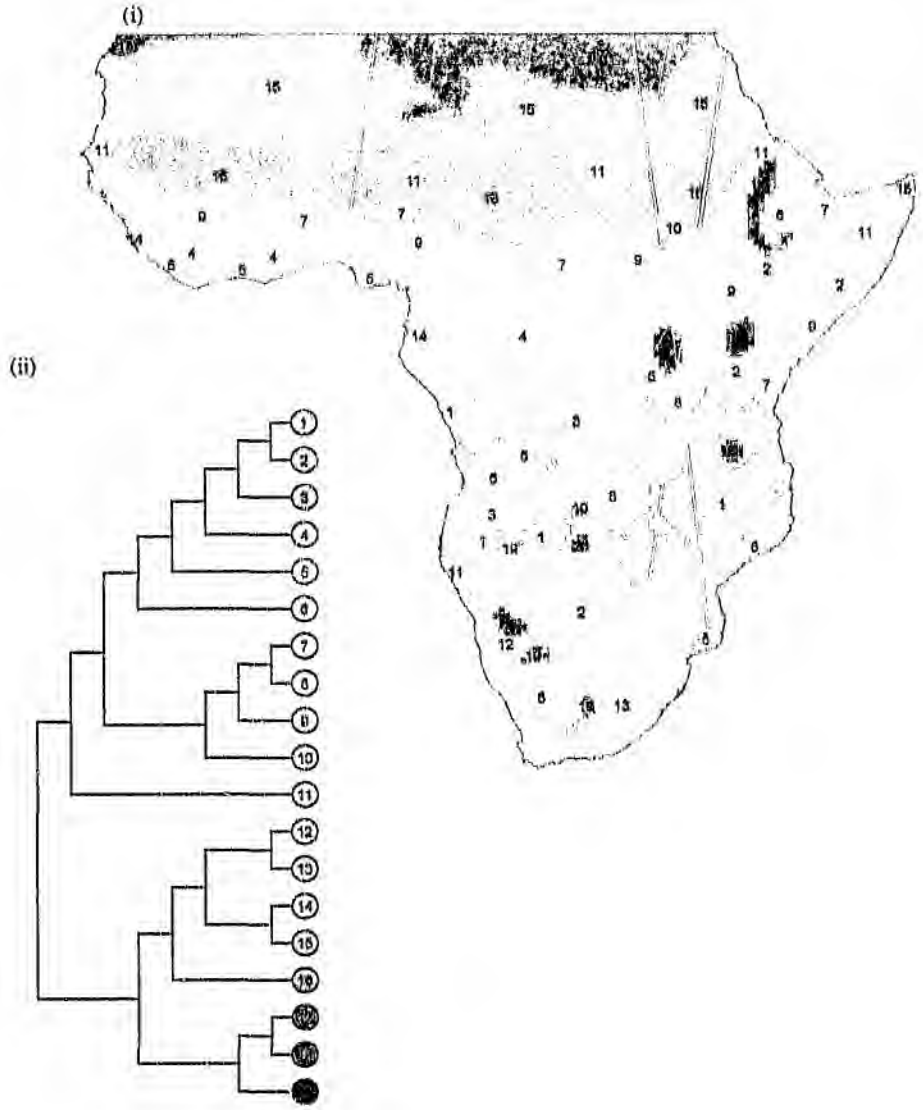


Figure 6. Ecological regions derived from the UPGMA cluster tree shown in Figure 5. (i) Mean values of the habitat models for the group of species in each cluster are mapped and colour coded according to the cluster having the maximum value at any locality (edges have been enhanced); (ii) Cluster tree topology.

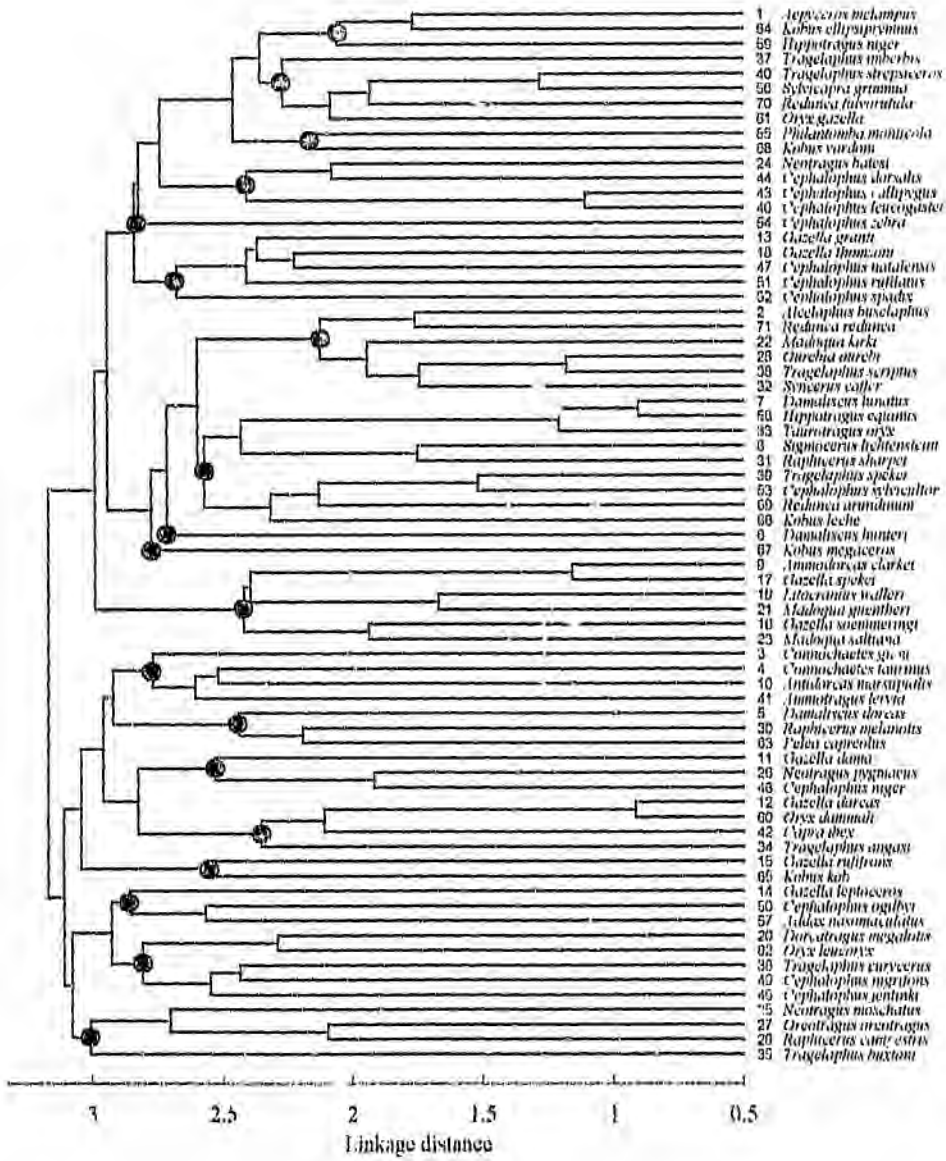


Figure 5. UPGMA cluster tree derived from the habitat model parameters (eigenvectors of the first five principal components). Species are numbered as in Table 1. Red circles mark the 19 clusters used in the ecological region analysis presented in the text and summarised in Figure 6.

(1995/05/05 18:36:11.86) GREEN+BLUE

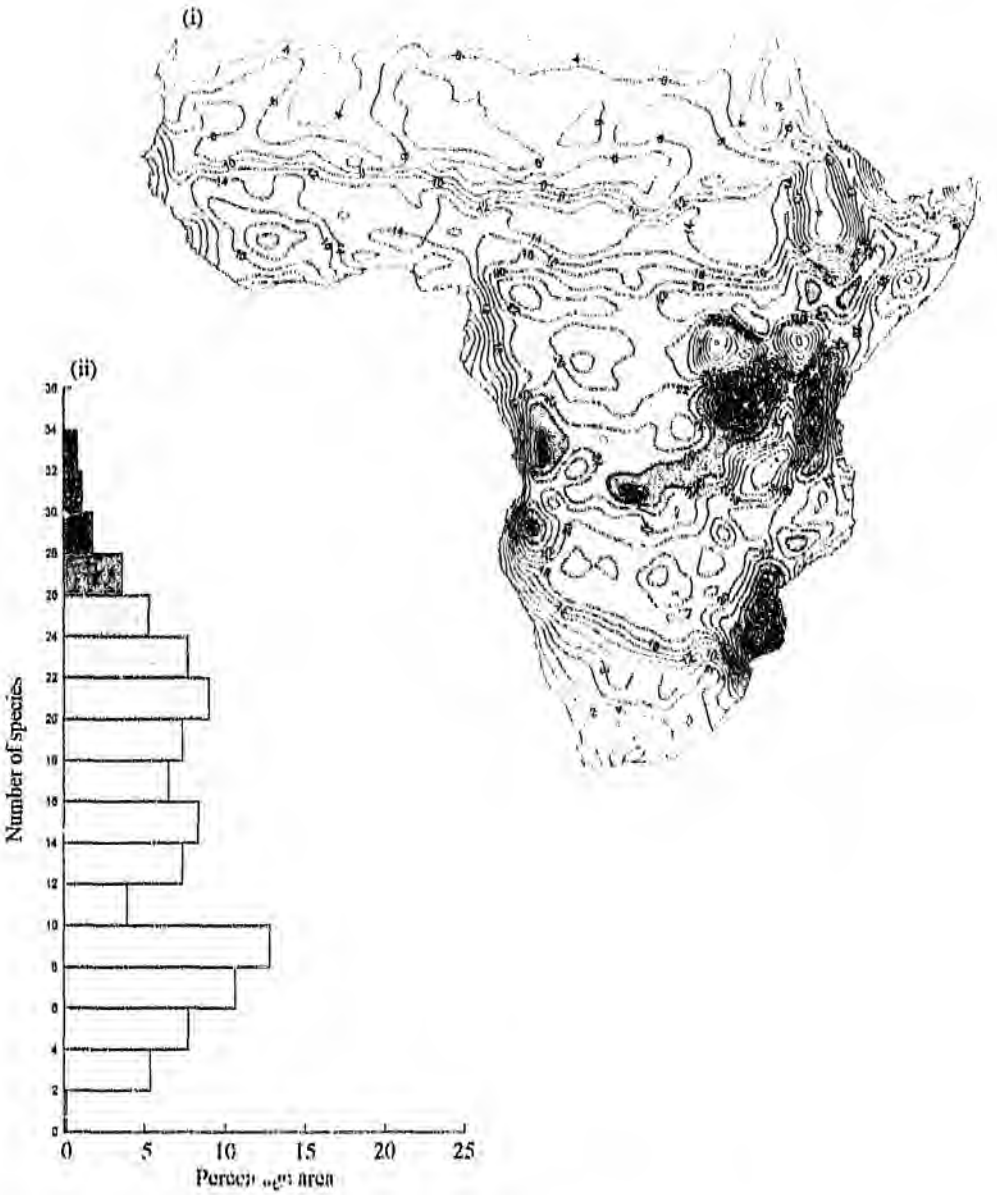


Figure 4.5. (i) Total species diversity calculated for the regions **p** (blue + green) in Figures 3.1-3.71; (ii) histogram of number of species by percentage area.

(19950506 09:51Z) RED+BLUE

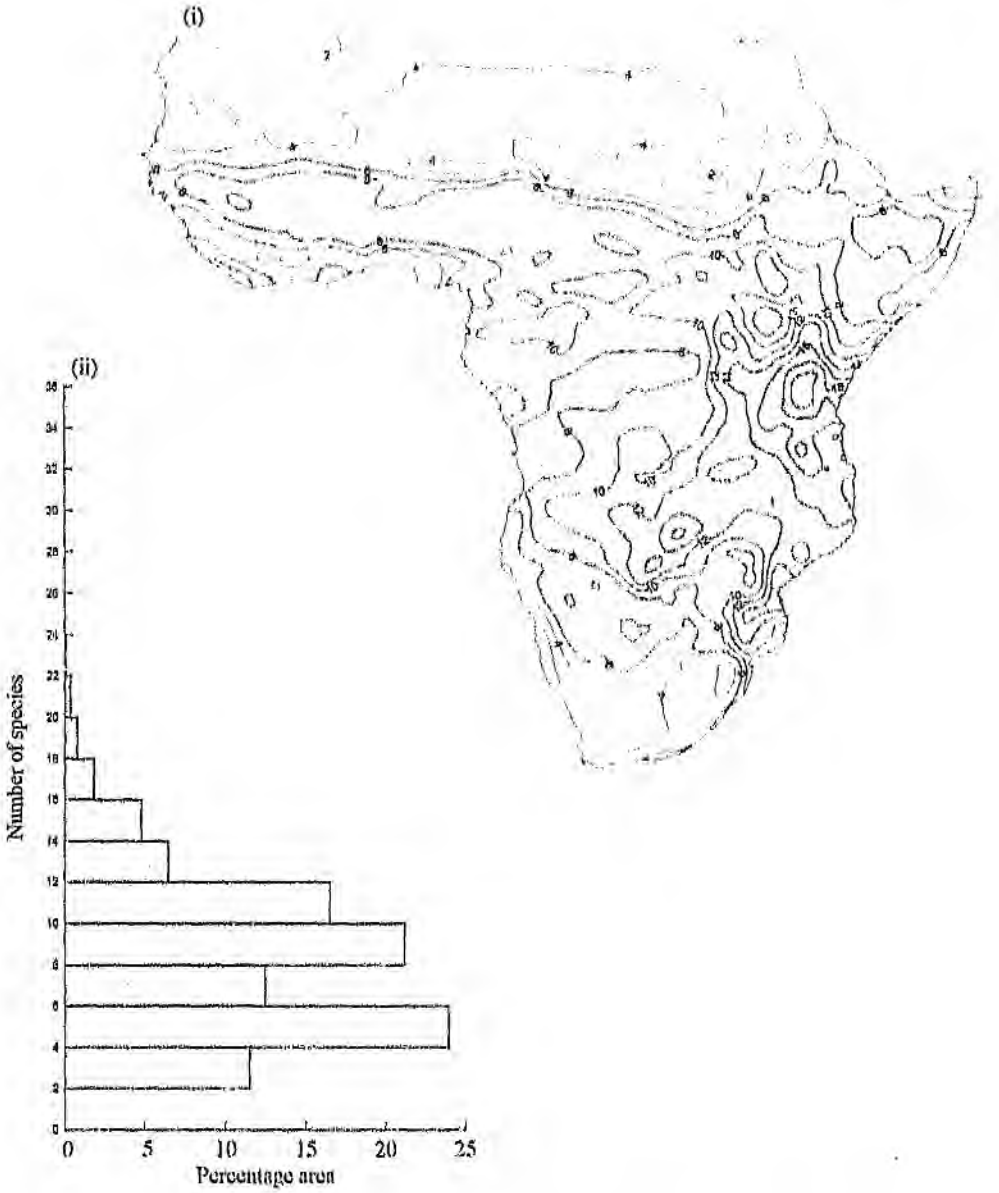


Figure 4.4. (i) Total species diversity calculated for the regions a (blue + red) in Figures 3.1-3.71; (ii) histogram of number of species by percentage area.

1995/09/26 03:58:14 GREEN

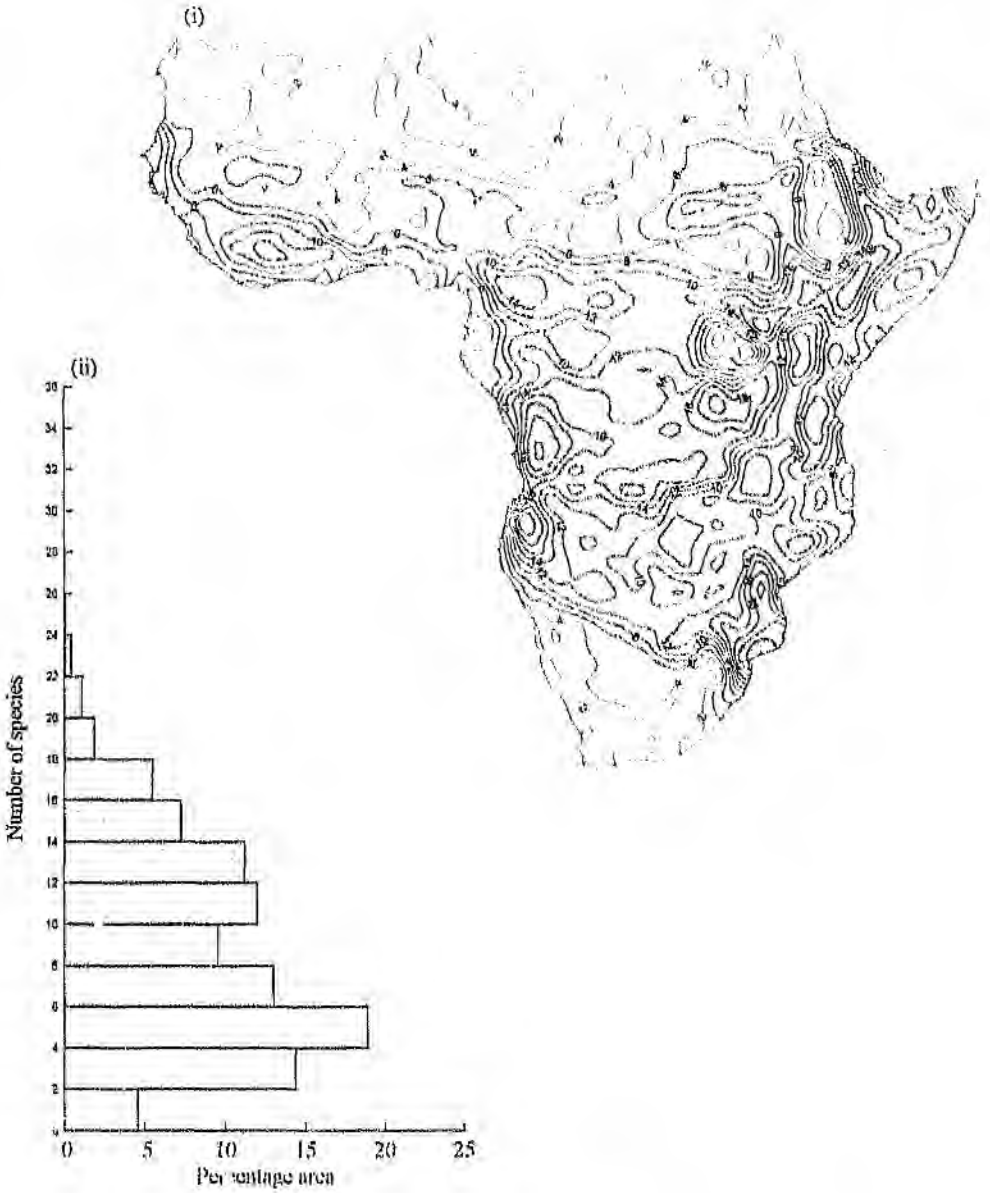


Figure 4.3. (i) Total species diversity calculated for the regions $\bar{\mathbf{n}} \cap \mathbf{p}$ (green) in Figures 3.1-3.71; (ii) histogram of number of species by percentage area.

(1956)0906 09 4934 33) ELLE

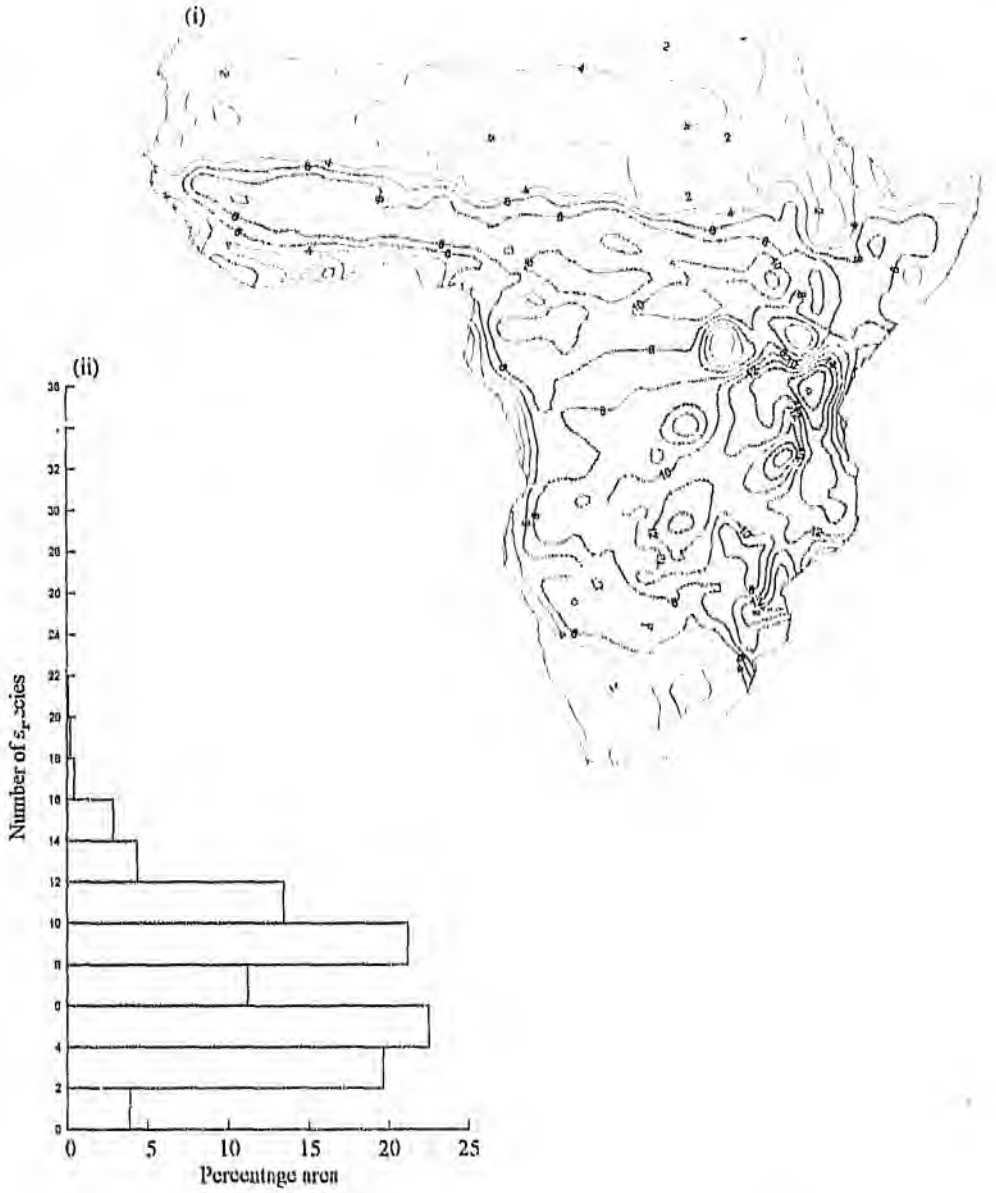


Figure 4.2. (i) Total species diversity calculated for the regions **a** ∩ **p** (blue) in Figures 3.1-3.71; (ii) histogram of number of species by percentage area.

[19950905 03:51:45:37] RED

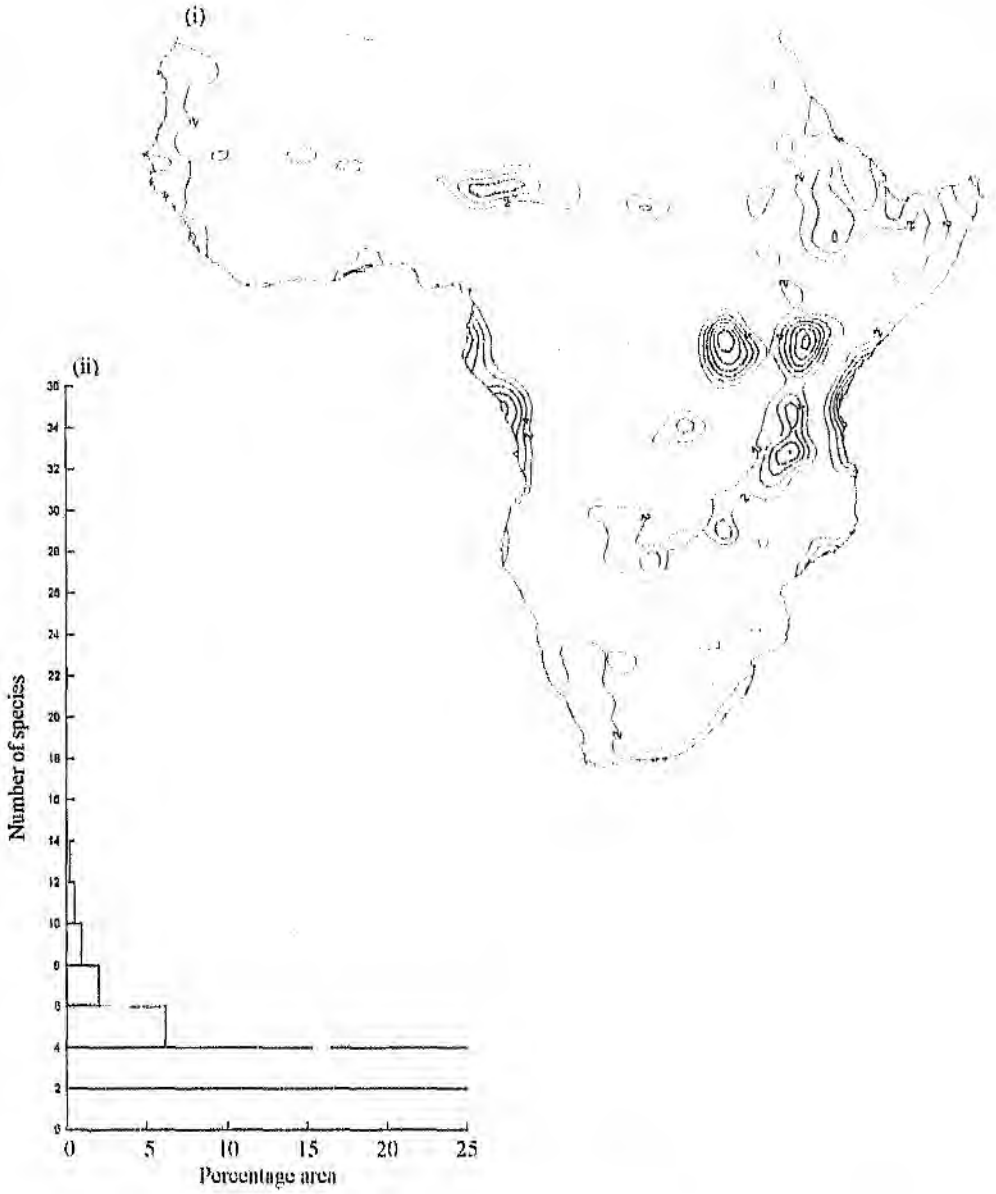


Figure 4.1. (i) Total species diversity calculated for the regions $\mathbf{a} \cap \bar{\mathbf{p}}$ (red) in Figures 3.1-3.71; (ii) histogram of number of species by percentage area.

(1956/09/09 18:03:12.84) #71 Redunca redunca (Bohor reedbuck)

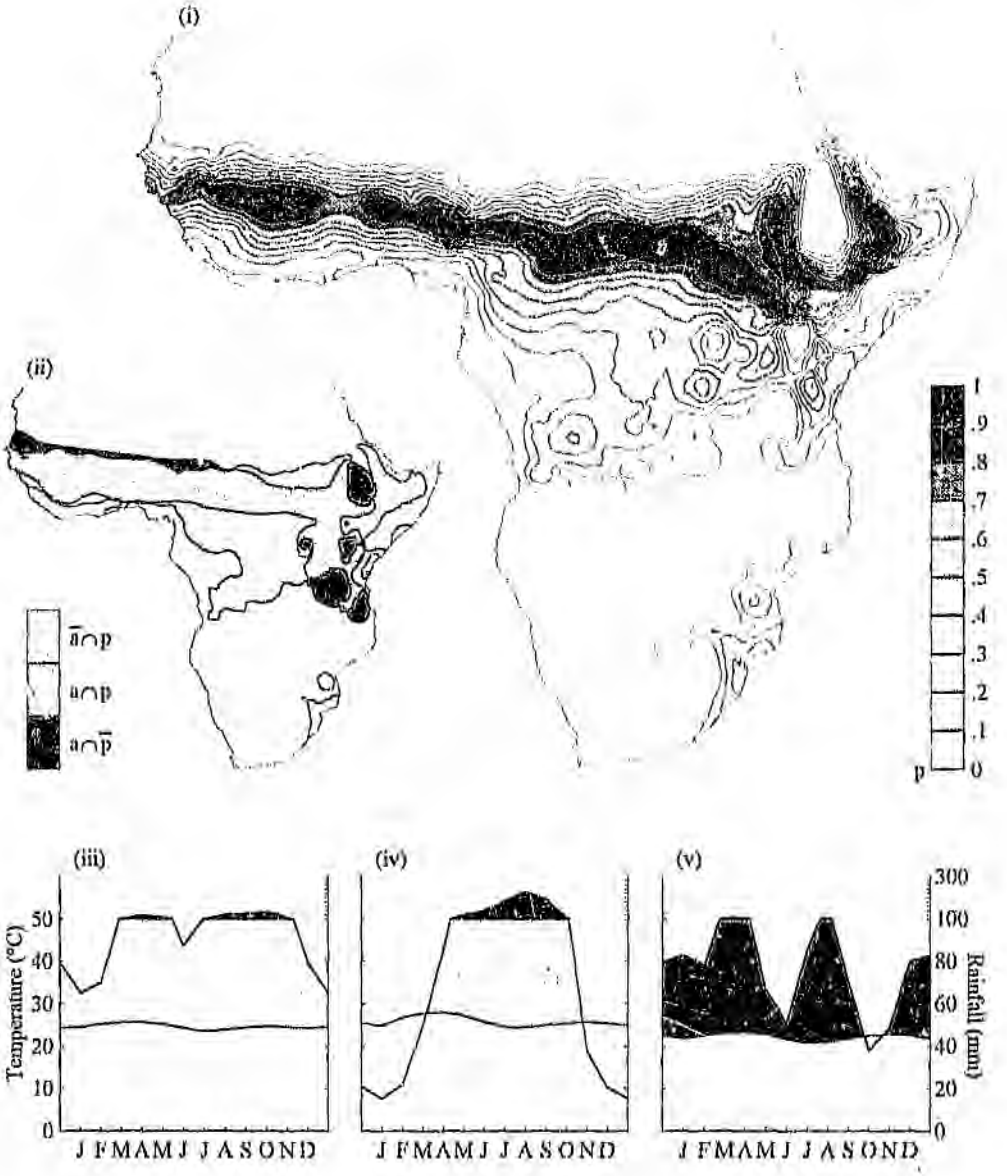


Figure 3.71. *Redunca redunca*, (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p} \geq 0.2$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

(1996/09/09 17:53:26.23) #70 Redunca fulvorufula (Mountain reedbuck)

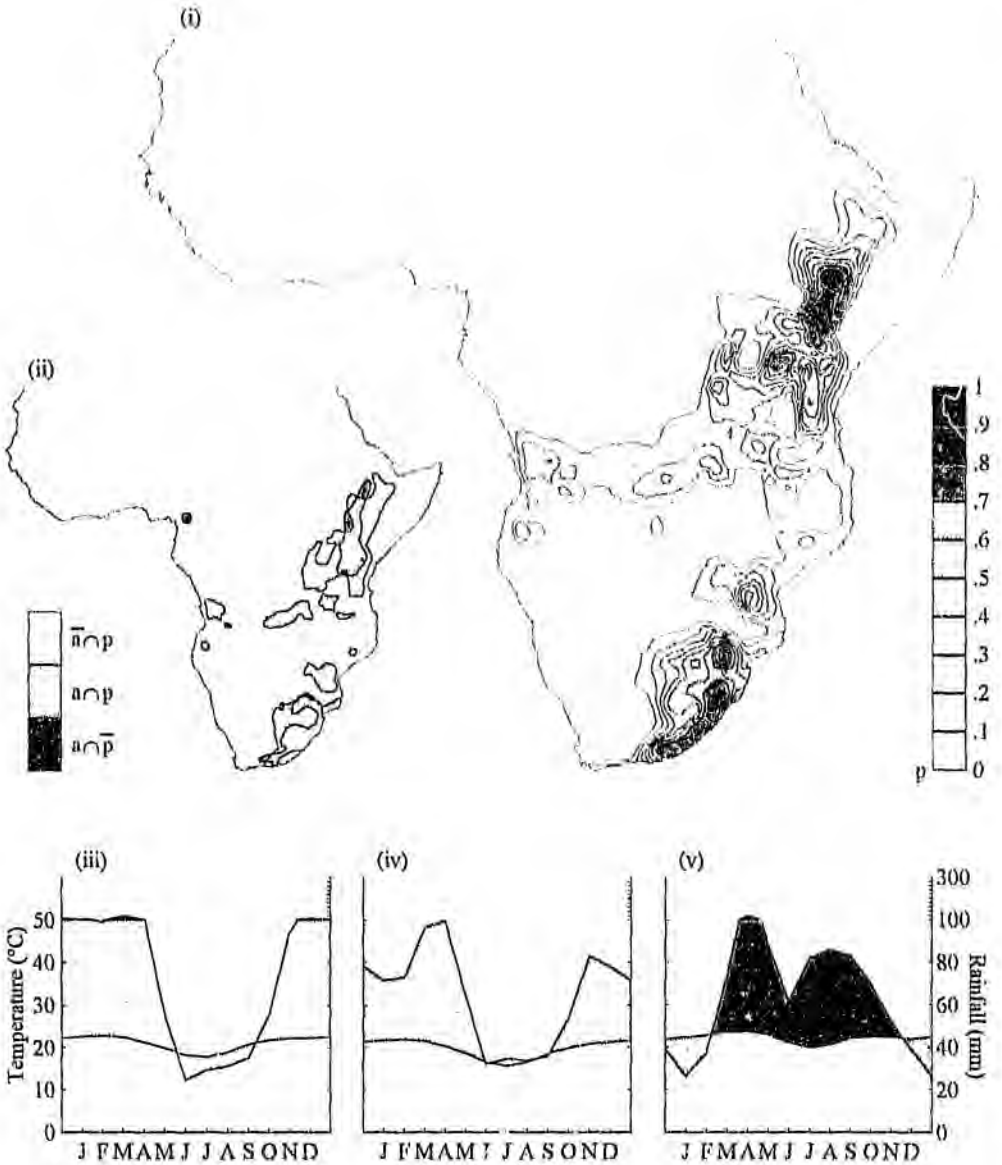


Figure 3.70. *Redunca fulvorufula*; (i) probability contours of the habitat model; (ii) intersection of the given distribution, **a** (blue + red), with probability contour $\mathbf{p \geq 0.2}$ (blue + green); (iii) generalised climate diagram for $\bar{\mathbf{a}} \cap \mathbf{p}$ (green); (iv) $\mathbf{a} \cap \mathbf{p}$ (blue); (v) $\mathbf{a} \cap \bar{\mathbf{p}}$ (red).

Author: Caithness, N.
Name of thesis: Pattern, process and the evolution of the african antelope (Mammalia- Bovidae)

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