TABLE OF CONTENTS

List of illustrations	
List of tables	viii
Acknowledgements	ix
Preface	xi

Chapter 1. Introduction	
Early hominin geographic ranges	1
Theory in studies of early human evolution	2
The research project	3
Theoretical summary	3
Research methodology	4
Overview	5
Chapter 2. Species geographic ranges	
Introduction	7
Patterns in species geographic range size	7
Frequency distribution	7
The latitudinal gradient	7
Species richness	9
Variation in geographic range size above the species level	9
The role of species' characteristics	9
Environmental variability and niche breadth	9
Abundance, body size and range size	11
Dispersal ability	12
Environmental limitations	13
Physical and biological boundaries	13
Historical processes	13
Introduction	13
Environmental history	14
Lineage evolution	14
Geography and evolution	14
Conclusion	15
Chapter 3. Models of hominin evolution and range expansion	
Abstract	16
Hominin range expansion	16
Models of hominin range expansion	21
Discussion	21
Niche breadth, behavioural flexibility and environmental change	21
Social learning and transmission and range expansion	24
Trends in the fossil record	26
Life history and dietary breadth	29
Dietary niche	31
Conclusion	33
Chapter 4. Primate biogeography analysis	
Abstract	34

Introduction	34
Predictions for primate distribution	34
Definition of variables	35
Method and analysis	38
Overview	38
Data sources	38
GIS database	40
Dataset composition	40
Analysis of comparative data in evolutionary biology	41
Statistical considerations	43
Results and discussion	44
Alternative measures of behavioural plasticity	44
Range size and behavioural plasticity	44
Opportunism and environmental variability	55
Life history and range size	66
Discussion	70
Conclusion	74
Chapter 5. Dietary adaptation and distribution in African mammals	
Abstract	76
Introduction	76
Carnivore ecology	76
Hominin diet	77
Method	80
Discussion	80
Data sources	81
Calculating biomass	81
GIS	82
Analysis	82
African physical geography	82
Distribution and diversity	83
Range boundaries	87
Body mass	90
Biomass	93
Home range	100
Conclusion	102
Chapter 6. Hominin distribution in the Plio-Pleistocene	
Introduction	103
Context	103
Fossil context	103
Environmental context	104
Analysis	105
Distribution and diversity	105
Body mass	112
Biomass	113
Home range size	117
Discussion	119
$C_{0nclusion}$	120

Chapter 7. Discussion	
Introduction	121
Models of hominin range expansion	121
Primate analysis	122
African mammal analysis	124
Hominin distribution 1.8-0.6 my ago in Africa	126
Conclusions	127
Appendices	
Primate data and results of regression analysis	133
Digital data	150
Primate species geographic range databases	150
Climatic variability maps	152
African mammals maps	154
List of references	157

LIST OF ILLUSTRATIONS

Figure 2.1.	Frequency distribution of primate geographic range size in km ² (data from Wolfheim 1983).	8
Figure 2.2.	The general theoretical relationship between latitude, niche breadth and geographic range size.	10
Figure 2.3.	The general theoretical relationship between species range size and abundance and body mass,	
	combined with the general positive correlation between range size and niche breadth, to identify	
	some expected species characteristics in relation to range size (after Eeley and Lawes, 1999).	12
Figure 3.1.	Earliest fossil hominin sites.	16
Figure 3.2.	Distribution of the australopithecines A.afarensis, A.anamensis and A.bahrelghazali (4.2-3.8 my ago).	17
Figure 3.3.	Distribution of A.aethiopicus and A.africanus (2.7-2.3 my ago).	18
Figure 3.4.	Distribution of Paranthropus species.	18
Figure 3.5.	Distribution of early <i>Homo</i> , <i>A.garhi</i> and the earliest stone tools (>2my).	19
Figure 3.6.	Dates of fossils attributed to <i>H.ergaster/erectus</i> .	20
Figure 4.1.	Branch of phylogenetic tree. From Harvey (1991).	41
Figure 4.2.	Scatterplot of habitat niche breadth against corrected innovation frequency. Frequencies are	
	corrected for research effort by taking the residuals from a ln-ln plot through the origin of innovation	
	frequency against research effort. The raw data, with each point representing one species.	45
Figure 4.3.	Scatterplot of habitat niche breadth against corrected innovation frequency. The independent	
	contrast data. Outliers circled.	45
Figure 4.4.	Scatterplots of geographic range size in m ² (natural log transformed) against corrected innovation	
_	frequency. Frequencies are corrected for research effort by taking the residuals from a ln-ln plot	
	through the origin of innovation frequency against research effort. The raw data, with each point	
	representing one species.	46
Figure 4.5.	Scatterplot of contrasts in geographic range size in m ² (natural log transformed) against corrected	
C	innovation frequency. Outliers circled.	46
Figure 4.6.	Geographic range size in m ² (natural log transformed) and corrected tool use frequency. The raw	
C	data, with each point representing one species.	47
Figure 4.7.	Geographic range size in m ² (natural log transformed) and corrected tool use frequency. The	
C	independent contrast data. Outlier circled.	48
Figure 4.8.	Geographic range size in m ² (natural log transformed) and corrected social learning frequency.	
C	The raw data, with each point representing one species.	48
Figure 4.9.	Geographic range size in m ² (natural log transformed) and corrected social learning frequency.	
C	The independent contrast data. Outliers circled.	49
Figure 4.10.	Geographic range size in km ² and corrected innovation frequency for South American primates.	
J	The raw data, with each point representing one species. Cebus apella circled.	50
Figure 4.11.	Geographic range size (m²) and absolute brain weight (g) (both variables natural log transformed).	
-8	The raw data, with each point representing one species.	51
Figure 4.12.	Geographic range size (m²) and absolute brain weight (g) (both variables natural log trasnformed).	
-8	The independent contrast data. Outliers circled.	51
Figure 4.13.	Geographic range size in m ² (natural log transformed) against relative brain weight. Relative brain	
	weights are calculated by taking the residuals of a log-log plot of brain weight (g) and female body	
	mass (kg). The raw data, with each point representing one species.	52
Figure 4.14.	Geographic range size in m ² (natural log transformed) against relative brain weight. Relative	
	brain weights are calculated as the residuals of a plot of the independent contrasts of absolute brain	
	weight (g) and female body mass (kg), both variables natural log transformed. The independent	
	contrast data.	52
Figure 4.15.	Geographic range size (m²) and neocortex ratio, both variables natural log transformed. Neocortex	
116010 11131	ratio is calculated as the ratio of neocortex volume to the volume of the rest of the brain. The raw	
	data, with each point representing one species.	53
Figure 4 16	Geographic range size (m²) and neocortex ratio, both variables natural log transformed. The	_
1 15 at 0 -1.10.	independent contrast data. Outlier circled.	53
Figure 4.17.		-
1 15ut 0 7.1 /.	The raw data, with each point representing one species.	54

Figure 4.18.	Individual home range size in km ² (natural log transformed) and corrected innovation frequency. The independent contrast data. Outliers circled.	55
Figure 4.19.	Corrected innovation frequency and threat status. The raw data, with each point representing	55
1 iguic 4.17.	one species.	56
Figure 4.20.	Corrected innovation frequency and threat status. The independent contrast data. Outliers circled.	56
Figure 4.21.	Mean annual rainfall in Africa and South America (mm/day*10).	57
Figure 4.22.	Annual temperature range in Africa and South America (°C*10).	57
Figure 4.23.	Coefficient of interannual variation in rainfall in Africa and South America (%).	58
Figure 4.24.	Spatial variation in rainfall and corrected innovation frequency. The spatial variation within a	50
1 iguic 4.24.	species' range is calculated as the coefficient of variation in mean daily rainfall in mm/day*10	
	between 0.5° cells. The raw data, with each point representing one species.	59
Figure 4.25.	Spatial variation in rainfall and corrected innovation frequency. The independent contrast data.	"
1 iguic 4.25.	Outliers circled.	59
Figure 4.26	Spatial variation in rainfall and corrected social learning frequency. The raw data, with each point	3)
11gure 4,20.	representing one species.	60
Figure 4.27.	Spatial variation in rainfall and corrected social learning frequency. The independent contrast data.	00
riguie 4.27.	Outlier circled.	60
Figure 4.28.	Spatial variation in mean rainfall and relative brain weight. Relative brain weights are calculated	
	as the residuals of a log-log plot of absolute brain weight (g) against female body weight (kg).	
	The raw data, with each point representing one species.	62
Figure 4.29.	Spatial variation in mean rainfall and brain weight corrected for body weight. Relative brain	
	weights are calculated by taking the residuals of a plot of the independent contrasts of absolute	
	brain weight (g) and female body mass (kg), both variables natural log transformed. The	
	independent contrast data.	62
Figure 4.30.	Temperature range in °C (natural log transformed) against corrected innovation frequency.	
	Temperature range for each species is calculated as the mean across the range. The raw data,	
	with each point representing one species.	63
Figure 4.31.	Temperature range in °C (natural log transformed) against corrected innovation frequency. The	
	independent contrast data. Outliers circled.	63
Figure 4.32.	Temperature range in °C (natural log transformed) against corrected social learning frequency. The	
	raw data, with each point representing one species.	64
Figure 4.33.	Temperature range in °C (natural log transformed) against corrected social learning frequency. The	
	independent contrast data. Outliers circled.	64
Figure 4.34.	Temperature range in °C (natural log transformed) and relative brain weight. Relative brain weights	
	are calculated by taking the residuals of a log-log plot of brain weight (g) and female body mass (kg).	
	The raw data, with each point representing one species.	65
Figure 4.35.	Temperature range in °C (natural log transformed) and relative brain weight. Relative brain weights	
	are calculated as the residuals of a plot of the independent contrasts of absolute brain weight (g) and	
	female body mass (kg), both variables natural log transformed. The independent contrast data.	65
Figure 4.36.	Interannual variation in rainfall in % (natural log transformed) and corrected innovation frequency.	
	Interannual variation is calculated as the coefficient of variation in annual rainfall. The value for	
	each species is the mean for the geographic range. The raw data, with each point representing one	
	species.	67
Figure 4.37.	Interannual variation in rainfall in % (natural log transformed) and corrected innovation frequency.	
	The independent contrast data. Outliers circled.	67
Figure 4.38.	Interannual variation in rainfall in % (natural log transformed) and corrected social learning	
	frequency. The raw data, with each point representing one species.	68
Figure 4.39.	Interannual variation in rainfall in % (natural log transformed) and corrected social learning	
	frequency. The independent contrast data. Outlier circled.	68
Figure 4.40.	Interannual variation in rainfall in % (natural log transformed) and relative brain weight. Relative	
	brain weights are calculated by taking the residuals of a log-log plot of brain weight (g) and female	
	body mass (kg). The raw data, with each point representing one species.	69
Figure 4.41.	Interannual variation in rainfall (natural log transformed) and relative brain weight. Relative brain	
	weights are calculated as the residuals of a plot of the independent contrasts of absolute brain	

	weight (g) and female body mass (kg), both variables natural log transformed. The independent	
	contrast data.	69
Figure 4.42.	Geographic range size in m ² and gestation length in days, both variables natural log transformed.	
	The raw data, with each point representing one species.	7
Figure 4.43.	Geographic range size in m ² and gestation length in days, both variables natural log transformed.	
	The independent contrast data.	71
Figure 4.44.	Geographic range size in m ² and maximum lifespan in years (both variables natural log transformed).	
	The raw data, with each point representing one species.	72
Figure 4.45.	Geographic range size in m ² and maximum lifespan in years (both variables natural log transformed).	
	The independent contrast data.	72
Figure 4.46.		
	data, with each point representing one species.	73
Figure 4.47.	Geographic range size in m ² and body mass in kg (both variables natural log transformed). The	
	independent contrast data. Outlier circled.	73
Figure 5.1.	Mean annual rainfall in Africa in mm/year (from New et al. 1999).	82
Figure 5.2.	Net primary productivity (Foley, 1996, Kucharik, 2000).	83
Figure 5.3.	Mean daily temperature (°C). From New et al. (1999).	84
Figure 5.4.	African topography (from GTOPO30, provided by the USGS-NASA Distributed Active	
D' 6.6	Archive Centre).	84
Figure 5.5.	Histogram of primate species geographic ranges (km²), based on AMD assessment of suitable	0.6
m: <i>5.6</i>	habitats.	85
Figure 5.6.	Histogram of carnivore species geographic ranges (km²), based on AMD assessment of suitable	0.5
D: 6.5	habitats.	85
Figure 5.7.	Histogram of ungulate species geographic ranges (km²), based on AMD assessment of suitable	0.4
F: 50	habitats.	86
Figure 5.8.	Carnivore (left) and ungulate (right) species richness.	86
Figure 5.9.	Primate species richness.	87
	Distribution of primate species range boundaries.	88
Figure 5.11.	• •	89
Figure 5.12.	Distribution of ungulate species range boundaries.	89
Figure 5.13.	1 3	90
Figure 5.14.	• • • •	91
-	Distribution of maximum (left) and range (right) of body mass in primates (kg).	91 92
_	Distribution of maximum (left) and range (right) of body mass in carnivores (kg). Primate biomass in kg/ha.	92
_	Carnivore biomass in kg/ha.	94
-	Ungulate biomass in kg/ha (from Thackeray 1995).	94
	Frequency distribution of mean annual rainfall (mm) in each contour of primate biomass.	96
•	Frequency distribution of average daily temperature (°C) in each contour of primate biomass.	96
-	Frequency distribution of of mean annual rainfall (mm) in each contour of carnivore biomass.	97
-	Frequency distribution of average daily temperature (°C) in each contour of carnivore biomass.	97
-	Ungulate biomass in relation to mean annual rainfall (mm) and temperature (°C), from	,
1 15010 3.2 1.	(Thackeray 1995).	98
Figure 5.25.	Carnivore biomass in relation to mean annual rainfall (mm) and temperature (°C).	98
-	Ungulate biomass in kg/ha.	99
Figure 5.27.	Frequency distribution of ungulate biomass (kg/ha) in each contour of carnivore biomass.	99
Figure 5.28.	· · ·	100
Figure 5.29.	• • • • • • • • • • • • • • • • • • •	101
Figure 5.30.		101
Figure 5.31.	·	101
Figure 6.1.		107
Figure 6.2.		107
Figure 6.3	·	109

LIST OF TABLES

Table 6.1.	Hominin body mass estimates, from McHenry, 1994.	112
Table 6.2.	Comparison of <i>H. erectus</i> and robust australopithecine distribution in Africa and number of cranial	
	fossils.	114
Table 6.3.	Comparison of numbers of fossils attributed to robust and non-robust lineages at Omo Shungura	
	Formation, based on fossil data from Suwa et al. (1996) and dates from Conroy (1997, p.154).	115
Table 6.4.	Average greatest distance (AGD) for the transfer of lithic raw material at different periods.	
	N = number of sites/members in the sample. Data from (Feblot-Augustins, 1997b). Minimum	
	home range area is estimated as the area of a circle for which AGD is the diameter; maximum area	
	is estimated as the area of a circle for which AGD is the radius. *Estimates from (Gamble and	
	Steele, 1999)	118