Human Dispersal and Species Movement

From Prehistory to the Present

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CHAPTER 5

RECONCEPTUALISING THE PALAEOZOOGEOGRAPHY OF THE SAHARA AND THE DISPERSAL OF EARLY MODERN HUMANS

Nick A. Drake and Roger Blench

Abstract

Genetic and archaeological lines of evidence both suggest that *Homo sapiens* dispersed out of Africa sometime between 130 and 50 ka, and that a likely route was across the 'green Sahara'. However, there is an absence of definitive evidence for trans-Sahara dispersal even though some animal species appear to have done so. To further our understanding of this dispersal, we present a model that considers the different ways humans can affect animal distributions and vice versa. We define three different mechanisms: facilitation, co-distribution and translocation. We then use North Africa during the last two interglacial humid phases as a testbed to evaluate each mechanism by analysing animal, fossil and rock art distributions, molecular phylogeny, archaeology and linguistics. We demonstrate strong evidence for facilitation with some evidence for co-distribution and translocation. Facilitation during the penultimate interglacial can be associated with the dispersal of *H. sapiens* out of Africa.

Keywords: Dispersal, facilitation, co-distribution, translocation, Sahara

INTRODUCTION

Saharan palaeozoogeography has traditionally been pursued through phenotypic and distributional analyses of modern and fossil animal species. A revolution in our understanding in this area has been brought about by a significant increase in genetic analyses of desert species, new models of the palaeohydrology of the Sahara and a better knowledge of the role of hominins in the dispersal of a wide variety of species. Ancillary disciplines, such as rock art studies, continue to provide new insights into the presence of larger species and human interactions with them. Synchronic ethnography also brings models of human/animal interactions to bear on the modelling of past relationships. This chapter is intended to bring together these new findings and put forward a preliminary analysis of the relationship between human and animal dispersal in the early Sahara.

Genetic and archaeological studies suggest that *Homo sapiens* dispersed out of Africa sometime between 130 and 50 ka (Macaulay et al. 2005; Gunz et al. 2009; Boivin et al. 2013). This is likely to have been preceded by at least three waves of hominin dispersals out of Africa between 1.9 and 0.7 Ma (Bar-Yosef and Belfer-Cohen 2001), with the possibility of an earlier wave around 2.5 Ma (Dennell 2009), and with additional suggestions of further migrations around 780–700 ka (Martínez-Navarro and Rabinovich 2011) and 600 ka (e.g., Lahr and Foley 1998) and. These dispersals are poorly delimited in both space and time, with little agreement in the literature about the nature of the routes involved or the timing of human movement. This is partly due to a lack of archaeological evidence, but is compounded by our limited understanding of episodes of past climate change that would have facilitated dispersal by specific routes at certain times and precluded it at others.

One important likely dispersal route within Africa, key to human exiting of the continent, is across the Sahara, either via the Nile (Vermeersch 2001) or following the 'green Sahara' during more humid periods (Drake et al. 2011). Population movements via these routes could have led to subsequent dispersal out of Africa via the Sinai. There is evidence in the Late Pleistocene for *H. sapiens* occupation of North Africa, including the North African littoral, the Sahara and the Nile, in the form of the Nubian and Aterian lithic industries (Clarke 1980; Van Peer 1998; Barton et al. 2009; Scerri 2013). These archaic populations could have left Africa around 120 ka (Dennell and Petraglia 2012) given archaeological remains in the Levant (Grün et al. 2005) and the presence of Nubian technology in Arabia (Rose et al. 2011). Archaeological evidence for trans-Saharan dispersals earlier than this is sparse, and it is not clear how, if or when the Sahara provided viable routes to facilitate 'out of Africa' hominin migrations.

One way to evaluate the possibility of a Saharan route 'out of Africa' is to evaluate ancillary information such as contemporary animal distributions and their past dispersals as shown by biogeography, molecular phylogeny and fossil distributions. If a wide spectrum of animals could follow the Nile or cross a 'green Sahara', hominins could do likewise. Furthermore, if animal dispersals were restricted to a few key events, then is likely that hominin dispersals would have been similarly limited. If it was possible for animals to cross the Sahara at different times, then it makes multiple hominin dispersals more likely.

North African biogeography, rock art and Holocene fossils have been studied to further our understanding of the relationship between animal dispersals and the peopling of the Sahara during the last Saharan humid phase in the early to middle Holocene (Drake et al. 2011). This research showed that a number of sub-Saharan savanna animals exhibit trans-Saharan distributions and thus appear to have crossed the desert during the Holocene humid phase (e.g., elephant, giraffe, Nile crocodile). However, some animals (e.g., hippopotamus, Nile perch) are only found in the south-central Sahara, as far as the northern flanks of the Ennedi, Tibesti, Tasilli and Ahoggar Mountains. These species all have more specialised aquatic requirements, such as deep water or long-term water connections. Drake et al. (2011) found that this difference in species distribution between the north and south Sahara can explain the differences in the spatial distribution of the archaeology of the desert and thus the dispersal of people into it, as outlined in more detail later in this chapter.

Fossil studies also allow the analysis of dispersals further back in time across the Sahara (Geraads 2010) and out of Africa (Tchernov 1992; O'Regan et al. 2005). Geraads (2010) found many movements of animals from sub-Saharan Africa to the Maghreb during the Early Pleistocene, indicating relatively easy transit across the Sahara. However, few species actually left the continent, as there was only a limited exchange with the Middle East at this time. Faunal similarities between North-West Africa and East Africa reached their peak during the Middle Pleistocene. Only in the latter part of the Pleistocene does the extinction of many sub-Saharan species and immigration of animals into Africa from Europe and Asia put a Palaearctic stamp on the fauna of the Maghreb. O'Regan et al. (2005) studied large mammal exchange between Africa and the Levant between 1 and 0.5 Ma in order to evaluate faunal connections during a period when a number of hominin dispersals have been postulated. Like Geraads (2010), they found no similarities between mammal species in these areas. The nature of the barrier in the exchange of animals from North-West Africa and the Levant at this time remains unresolved.

Further evidence for animal dispersals is provided by the molecular phylogeny of species likely to have been associated with hominin dispersals (e.g., Gaubert et al. 2009). Though much research has been conducted on many relevant species for other reasons (e.g., Gaubert et al. 2009; Charruau et al. 2011), no comprehensive study that specifically examines the molecular phylogeny of species thought to have dispersed across the Sahara has yet been conducted. Here we rectify this imbalance.

This chapter evaluates the use of animal, fossil and rock art distributions in combination with molecular phylogeny and synchronic ethnography to better understand the ability of particular animals to disperse across the 'green Sahara'. We first evaluate animal distributions to determine what species can be used in such studies (Table 5.1). We then focus on some examples of anthropic species that dispersed across savannas, as hominins appear to have done, presenting a model that deconstructs the notion of 'anthropic', exploring different categories of human/animal interaction. We then interrogate the data, both in isolation and in combination, to see what they say about dispersal across the Sahara. Finally, we link this information to archaeological and linguistic information in order to demonstrate links between specific categories of animal dispersal and that of *H. sapiens*.

TABLE 5.1 *Species with trans-Saharan distributions. Spatial information derived from sources outlined in Table 5.2. Rock art and fossil information obtained from Mauny (1955); Uerpmann (1987); Van Neer (1989); Tchernov (1992); Le Quellec (1993); Petit-Maire (1993); Vernet (1995); Pieters and von den Driesch (2003); Jousse (2006) Sereno et al. (2008); O'Regan et al. (2005); and Geraads (2010)*

Species found North and South of the Sahara

Species	*Latin Name*	*Common Name*
Reptiles		
Lizards	*Acanthodactylus boskianus*	Bosc's fringe-toed lizard
	Acanthodactylus scutellatus audouinii	Walleye, Acanthodactyle, Nidua fringe-fingered lizard
	Chalcides ocellatus	Ocellated skink, Eyed skink, Gongilo
	Messalina gutullata	Small-spotted lizard, Desert lacerta
	Scincopus fasciatus	Peters' banded skink
	Tarentola hoggarensis	African wall gecko
	Tropiocolotes tripolitanus	Algerian northern sand gecko
	Uromastyx dispar maliensis	Sudanese spiny-tail lizard, South Saharan mastigure
	Varanus griseus	Desert monitor
Snakes	*Malpolon moilensis*	False cobra
	Telescopus obtusus	Egyptian catsnake
	Lamprophis fuliginosus	African house snakes
Chelonians	*Mauremys leprosa*	Spanish pond turtle or Mediterranean turtle
Molluscs		
	Pisidium casertanum	Pea cockle, pea clam
	Unio elongatulus	Freshwater mussel
Mammals		
Rodents	*Crocidura Lusitania*	Mauritanian shrew
	Suncus etruscus	Etruscan shrew
Bats	*Nycticeius schlieffeni*	Schlieffen's twilight bat
	Rhinopoma microphyllum	Greater mouse-tailed bat
	Rhinolophus blasii	Blasius's horseshoe bat
Hedgehog	*Paraechinus aethiopicus*	Desert hedgehog
Felids	*Genetta genetta*	Common genet
Mustelid	*Mellivora capensis*	Honey badger
Birds		
	Numida meleagris	Guinea fowl

Green Sahara

Species	*Latin Name*	*Common Name*
Reptiles		
Lizards	*Acanthodactylus boskianus*	Bosc's fringe-toed lizard
	Acanthodactylus dumerili	Duméril's fringe-fingered lizard
	Acanthodactylus longipes	Long fringe-fingered lizard
	Acanthodactylus scutellatus (group)	Walleye, Acanthodactyle, Nidua fringe-fingered lizard
Snakes	*Bitis arietans*	Puff adder
	Echis leucogaster	White-bellied carpet viper, Roman's saw-scaled viper

(*continued*)

TABLE 5.1 (*continued*)

Species found North and South of the Sahara		
Species	***Latin Name***	***Common Name***
	Spalerosophis diadema	Diadem snake
Skinks	*Mesalina olivieri*	Olivier's sand lizard
	Mesalina guttulata	Small-spotted lizard, Desert lacerta
	Scincopus fasciatus	Peters' banded skink
	Scincus scincus	Sandfish
	Scincus albifasciatus	White-banded sandfish
Geckos	*Tarentola ephippiata*	African wall gecko
	Trapelus mutabilis	Desert agama, Hobny
	Tropiocolotes steudneri	Dwarf gecko
	Tropiocolotes tripolitanus	Algerian northern sand gecko
	Stenodactylus petriei	Dune gecko
Varanid	*Varanus griseus*	Desert monitor, Nile monitor
Fish		
	*Tilapia zillii**	Redbelly tilapia
	*Clarias gariepinus**	North African catfish
	Hemichromis letourneauxi (or letourneuxi)*	Jewel fish
	*Raiamas senegalensis**	Silver fish
Mollusc		
	*Melanoides tuberculata**	Red-rimmed melania
	Ancylus fluviatilis	River limpet
	Afrogyrus coretus	None
	*Bulinus truncates**	None
Mammal		
Felids	*Felis sylvestris*	Wild cat
	Felis caracal	Caracal
Hyraxes	*Procavia capensis*	Rock hyrax
Bats	*Hipposideros caffer tephrus*	Sundevall's roundleaf bat, Sundevall's leaf-nosed bat
	Hystrix cristata	Crested porcupine
	Nycteris thebaica	Egyptian slit-faced bat
	Pipistrellus kuhli	Kuhl's pipistrelle
	Rhinolophus clivosus	Geoffroy's horseshoe bat
	Tadarida aegyptiaca	Egyptian free-tailed bat
	Taphozous nudiventris	Naked-rumped tomb bat

North South and Nile

Species	***Latin Name***	***Common Name***
Reptile		
Snake	*Naja haje*	Egyptian cobra
Varanid	*Varanus niloticus*	Nile monitor, Water leguaan, River leguaan
Skink	*Trachylepis quinquetaeniata*	Five-lined mabuya, Rainbow mabuya, Rainbow skink
Chelonian	*Trionyx triunguis*	African softshell turtle

(*continued*)

TABLE 5.1 *(continued)*

Species found North and South of the Sahara		
Species	***Latin Name***	***Common Name***
Molluscs		
	Lymnaea natalensis	None
Mammals		
Fruit bat	*Rousettus aegyptiacus*	Egyptian fruit bat
Evidence for Green Sahara and/or Nile but now Extinct		
Species	***Latin Name***	***Common Name***
Mammals		
Equids	*Equus quagga quagga*	Common zebra
Hippos	*Hippopotamus amphibius*	Hippopotamus
Suids	*Phacochoerus africanus*	Common warthog
Giraffidae	*Giraffa camelopardalis*	Giraffe
Bovids	*Syncerus caffer*	African buffalo
Proboscids	*Loxodonta africana*	African elephant
Rhinocerotidae	? sp.	
Felids	*Panthera pardus*	Leopard
	Panthera leo	Lion
	Acinonyx jubatus	Cheetah
	Crocuta crocuta	Spotted hyaena
Antelopes	*Alcelaphus buselaphus*	Hartebeest
	Connochaetes gnou	Black wildebeest, White-tailed gnu
	Connochaetes taurinus	Blue wildebeest, Brindled gnu
	Hippotragus equinus	Roan antelope
	Redunca redunca	Bohor reedbuck
	Taurotragus oryx	Common eland
	Kobus kob	Kob
	Tragelaphus spekii	Sitatunga
Birds		
	Struthio camelus	Ostrich
Reptiles		
Crocodilians	*Crocodylus niloticus*	Nile crocodile

A MULTIDISCIPLINARY APPROACH TO SAHARAN PALAEZOOGEOGRAPHY

A review of the biogeography of animals in North Africa has been conducted in order to identify animals that exhibit biogeographical distributions that suggest they could have crossed the Sahara during past humid periods. Three different distributions were identified, as outlined below:

1. Species found both north and south of the Sahara, but not in central regions. Although these species must have dispersed across the Sahara,

TABLE 5.2 *Sources for animal distribution maps*

Reference	Covers
Borkin (1999)	amphibians of North Africa, Europe, Western Asia
Borrow & Demey (2001)	birds of West-Central Africa
De Smet (1998)	crocodile of the Sahara Desert
Kingdon (1997)	mammals of Africa
Granjon & Duplantier (2009)	rodents of Sahelian Africa
LeBerre (1989 a and b)	mammals, fish, amphibians and reptiles,
Lévêque (1990)	fish fauna in the central Sahara
Sindaco et al. (2008)	reptiles of the Western Palearctic
Trape et al. (2012)	lizards, crocodiles and tortoises of the western Sahara
Van Damme (1984)	freshwater mollusca of Northern Africa

the question of whether this was by the Nile or Green Sahara route cannot be determined without additional fossil evidence. Figure 5.1a illustrates this distribution using the case of the common genet.

2. 'Nilotic' species, i.e., those that occupy the Nile corridor today, but are also found both north and south of the Sahara and could have used the Nile Valley as a corridor. The Egyptian cobra is an example of a species with this distribution (Figure 5.1b).
3. 'Green Sahara' species with population centres both north and south of the Sahara, and (sometimes) small relict populations in the central regions. This suggests a trans-Saharan distribution in the past, with subsequent local isolation of central Saharan populations during the more recent arid phase. Figure 5.1c shows an example of this distribution, in this case for the skink *Mesalina olivieri.*

Lists of animal species that satisfy these criteria were compiled from maps of Saharan animal distributions (Table 5.1), drawing on a range of sources (Table 5.2). These lists were then expanded with animals that showed one of these three distributional patterns but which were extirpated in North Africa, following hunting and other human pressures during or before the twentieth century (i.e., leopard, lion, cheetah, hartebeest, striped hyena and ostrich). Finally, anthropic species not picked up in the literature review were reviewed to see if they had relevant distributions. This led to the identification and addition of the guinea fowl. A total of eighty-five species with trans-Saharan distributions were identified.

No single source covers all species so these lists have been combined from all references. Sometimes these show marked disagreement in distributions. For example, Le Berre (1989b) shows the greater mouse-tailed bat (*Rhinopoma microphyllum*) only north and south of the Sahara, while

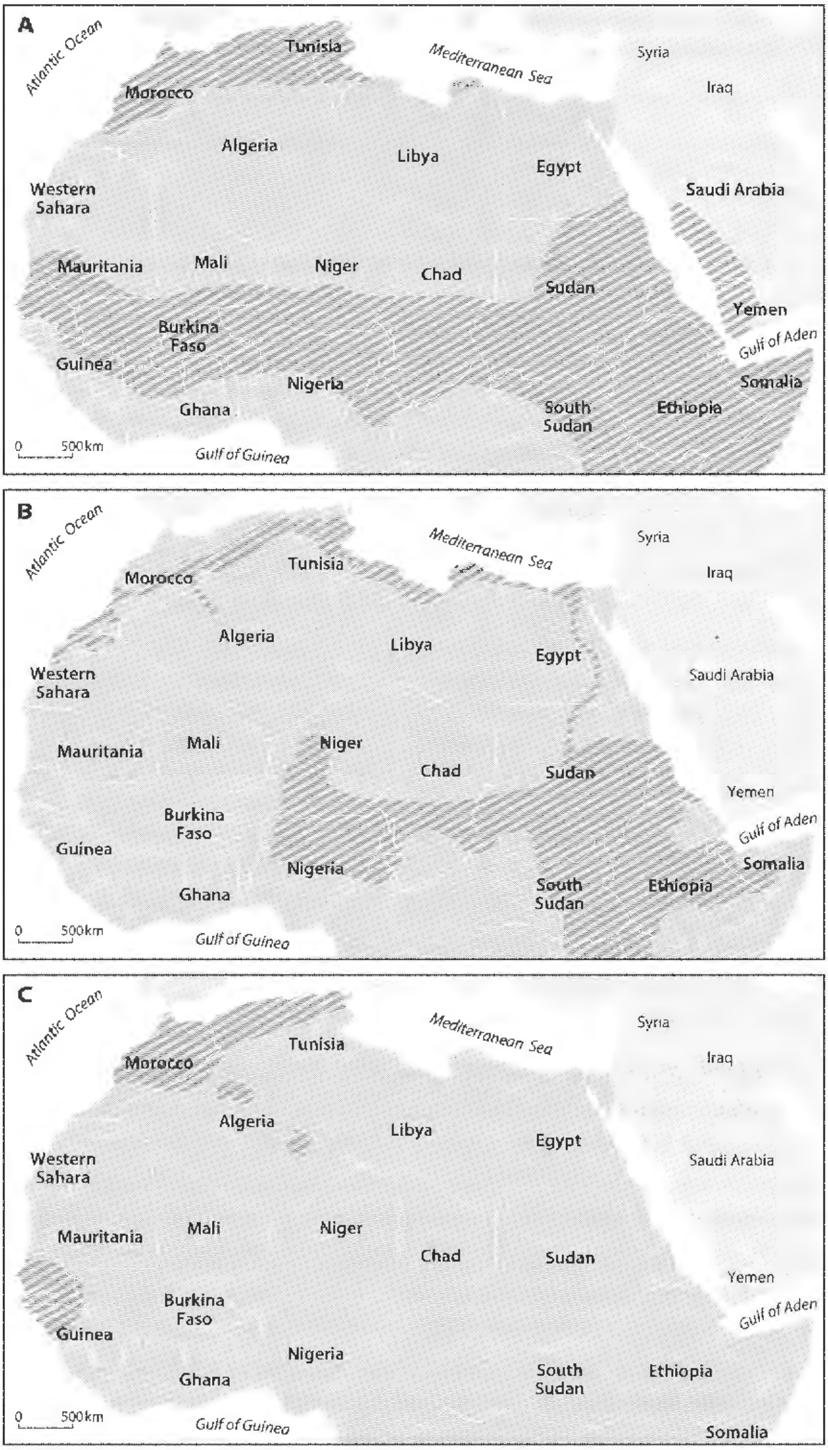

Figure 5.1 Maps that illustrate examples of the different animal biogeographical distributions that are considered in this study. (a) The common genet, (b) the Egyptian cobra and (c) Olivier's sand lizard. Source: Le Berre, M. 1989a and b.

Hulva et al. (2007) show it in the central regions as well. When such discrepancies were found, the most recent maps were consulted with the assumption that they were based on more up-to-date information. Re-studies of taxonomy can sometimes lead to elimination of species from distributional categories. For example, the lizard *Trapelus mutabilis* was mapped by Le Berre (1989a) as having a 'green Sahara' distribution, but it has recently been identified as a species complex and thus an artificial grouping of unrelated taxa (Wagner et al. 2011). Molecular phylogeny has identified a few such complexes mapped by Le Berre (1989a, b) as a single species, and no doubt more will be found in the future.

We have also conducted a review of the genetics literature to determine if there are molecular phylogenetic studies for the selected animals in the relevant North African ranges. Genetic information has been reviewed to determine what evidence it can provide on trans-Saharan dispersals and their timing. To augment the information on animal distributions in the Holocene, review papers on Saharan rock art have been consulted and incorporated into this chapter (Vernet 1995; Le Quellec 1993; Mauny 1955). Information on the location of Holocene fossils has also been employed, relying largely on the work of Van Neer (1989), Petit-Maire (1993), Pieters and von den Driesch (2003), Jousse (2006) and Sereno et al. (2008). Information on pre-Holocene fossils is from Uerpmann (1987), Tchernov (1992), O'Regan et al. (2005) and Geraads (2010).

DISTINGUISHING PATTERNS OF ANTHROPIC ANIMAL DISPERSAL

Though some animal dispersals must occur that are not related to hominin dispersal, others reflect complex layers correlated with various degrees of human involvement. We can assume that animals that dispersed prior to the appearance of hominins did so purely in accordance with resource imperatives, ecology and availability of food. However, once hominin hunters appear on the scene, creating hunting pressures quite unlike those in previous epochs, anthropic effects on species distributions must always be a consideration. Furthermore, as hunting strategies and technology have increased in complexity and effectiveness over time, the influence on animal distributions can only have increased. At some point hominin activities start to affect other aspects of their surrounding habitat – for example, through the use of fire – and these indirect effects will also have an impact on animal species distributions. We have developed a theory that suggests that there are three possible ways that these direct and indirect effects can manifest themselves:

a. **Facilitation:** The activities of hominins or animals facilitate the dispersal of each other. This occurred in three different ways.
   1. Unintentional human facilitation, whereby animal dispersals can be an unintended consequence of human action, for example, when

humans set fires to hunt, thereby creating savanna corridors that facilitated movement.

2. Intentional human facilitation is a deliberate action that promotes dispersal – for example, when rivers are cleared of silt in order to increase yields of aquatic resources, or ponds created to provide additional hydrological space.
3. Animal facilitation operates in the other direction, and occurs when the dispersal of animals attracts human hunters and resource gatherers. For example, when climate change caused large parts of the Sahara Desert to transform into a savanna at the start of the Holocene, animals subsequently dispersed into it and hunter-gatherers followed (Drake et al. 2011).

b. **Co-distribution:** Human activities, perhaps unintentionally, create a resource for an individual species which then disperses to exploit that resource. This has three subsets:
   1. Oppositional co-distribution occurs when the dispersing species is an active nuisance but cannot be excluded by humans. Examples include the west African house snake, rats, shrews and mice (cf. Granjon and Duplantier 2009 for European rats and mice).
   2. Commensalism occurs when the dispersing species is managed by humans to the advantage of both, often as a prelude to domestication. Examples include the early phases of domestication of the camel, dog and donkey.
   3. Mutualism arises when one species benefits while another experiences no negative consequences from the relationship. A typical example is carrion-eaters, which benefit from the expansion of resources for animals which die, leave carcasses and thus provide for an expanded population. Thus, if human activities provide increased food and water resources and therefore benefit antelopes, this indirectly benefits hyenas.

c. **Translocation:** Humans intentionally transport individual species across ecological barriers, in order to hunt or otherwise exploit them. This in turn has two subsets:
   1. The translocated animal is confined to a known space, such as a pond or well in the case of fish or turtles.
   2. The translocated animal is released into the wild, but with the intention of capturing it when required. Examples from mainland Africa include the tilapia and the catfish. The feral bushpig, *Potamochoerus larvatus*, on Madagascar and the Comoro islands, is a human-mediated maritime translocation (Garbutt 1999).

DEMONSTRATING ANTHROPIC ANIMAL DISPERSAL

To conclusively demonstrate human influenced animal dispersal (or vice versa) it is necessary to show that one or more of these mechanisms has operated – no easy task when examining the Sahara of thousands of years ago. However, we show in this chapter that it can be achieved to a certain extent by demonstrating relationships between artefacts and specific animals. For example, when excavating archaeological sites, if a specific type of tool is consistently found in association with the remains of a particular species it suggests the tool was for hunting that animal or processing products from it. The identity of these hunters can then, in some cases, be identified by showing an association between the animal in question and language distributions. Here we assess the evidence for the different types of dispersal outlined above across the Sahara, and evaluate the significance of this data for the dispersal of *H. sapiens* as well as the later Holocene dispersal of hunter-gatherers.

A remarkably large number of species exhibit distributions that suggest they have dispersed across the Sahara (Table 5.1). Of the species studied, thirty-three have a 'green Sahara' distribution. Twelve are found both north and south of the Sahara and along the River Nile, but five of these also have a 'Green Sahara' distribution, suggesting that the Nile has been a less effective dispersal route than the green Sahara. Twenty-four species are found north and south of the Sahara but not in the desert itself, and twenty-one species appear to have a past trans-Saharan distribution but are now extirpated from large parts of their previous range. Thus, in total, eighty-five animal species appear to exhibit a trans-Saharan distribution, or did so in the past. Many of these are savanna animals and thus can be considered as facilitated species movements. However, there are also examples of the other classes of anthropic dispersals such as co-distribution and translocation. Below we consider eight of the eighty-five animals identified in Table 5.1, selecting animals that we consider illustrate different anthropic dispersal mechanisms. The other animals will be considered in a follow-on paper. This chapter accordingly provides a starting point for a more comprehensive study.

Facilitation

Numerous large savanna mammals appear to have dispersed across the Sahara from south to north during past humid periods. The hartebeest (*Alcelaphus buselaphus*) provides a strong case for animals facilitating the dispersals of *H. sapiens*. It is a bovid that lives in open savanna and grasslands, and the archaeological record suggests that it is an animal whose movement strongly facilitated human dispersal. The hartebeest is one of the most common fossils found in Aterian period archaeological deposits (~30–160 ka), thus it may have been an important food source for *H. sapiens* (Drake and Breeze 2016; Table 5.3) and was again a species commonly hunted in the Holocene Sahara

TABLE 5.3 *The fauna found at the Aterian sites that contain faunal remains and their frequency of occurrence. A total of twenty-six sites contain both faunal remains and Aterian artefacts (Source: Drake and Breeze 2016)*

Common Name	Species	Number of Sites
Zebra (extinct)	*Equus mauritanicus*	18
Hartebeest	*Alcelaphus buselaphus*	17
Wild boar	*Sus scrofa*	12
Aurochs (extinct)	*Bos primigenius*	13
Rhinoceros	*Rhinocerotidae*	11
Warthog	*Phacochoerus aethiopicus*	9
Blue Wildebeest	*Connochaetes taurinus*	9
Golden Jackal	*Canis aureus*	8
Gazelle	*Gazella* sp.	8
Red Fox	*Vulpes vulpes*	8
Crested Porcupine	*Hystrix cristata*	8
Barbary Sheep	*Ammotragus lervia*	7
Gazelle (extinct)	*Gazella atlantica*	6
Spotted Hyena	*Crocuta crocuta*	6
Striped Hyena	*Hyaena hyaena*	5
Deer	*Cerus* sp.	5
Dorcas Gazelle	*Gazella dorcas*	5
Hippo	*Hippopotamus amphibious*	5
Leopard	*Felis Pardus*	5
Spur-thighed Tortoise	*Testudo graeca*	5
Giant Buffalo (extinct)	*Pelorovis antiquus*	4
Lion	*Panthera leo*	4
Elephant	Elephantidae	4
Bovid	*Bovidae* sp.	4
Equid	*Equus* sp.	4
Cuvier's Gazelle	*Gazella cuvieri*	4
Ostrich	*Struthio camelus*	4
Hare	*Lepus* sp.	4
European Rabbit	*Oryctolagus* sp.	3
Hedgehog	*Erinaceus* sp.	3
Camel	Camelidae	3
Oryx	*Oryx* sp.	2
Reedbuck	*Redunca* sp.	2

(Jousse 2006). The hartebeest provides interesting preliminary phylogenetic information on trans-Saharan dispersals that can be strengthened from fossil evidence. Phylogeographic analysis of the hartebeest was conducted using two mtDNA markers (Flagstad et al. 2001; Figure 5.2). Results show that it originated in east Africa and dispersed from there, splitting into southern and northern African lineages about 495 ± 85 ka. The northern lineage then split into east and west African clades at around 398 ± 41 ka. There is evidence that

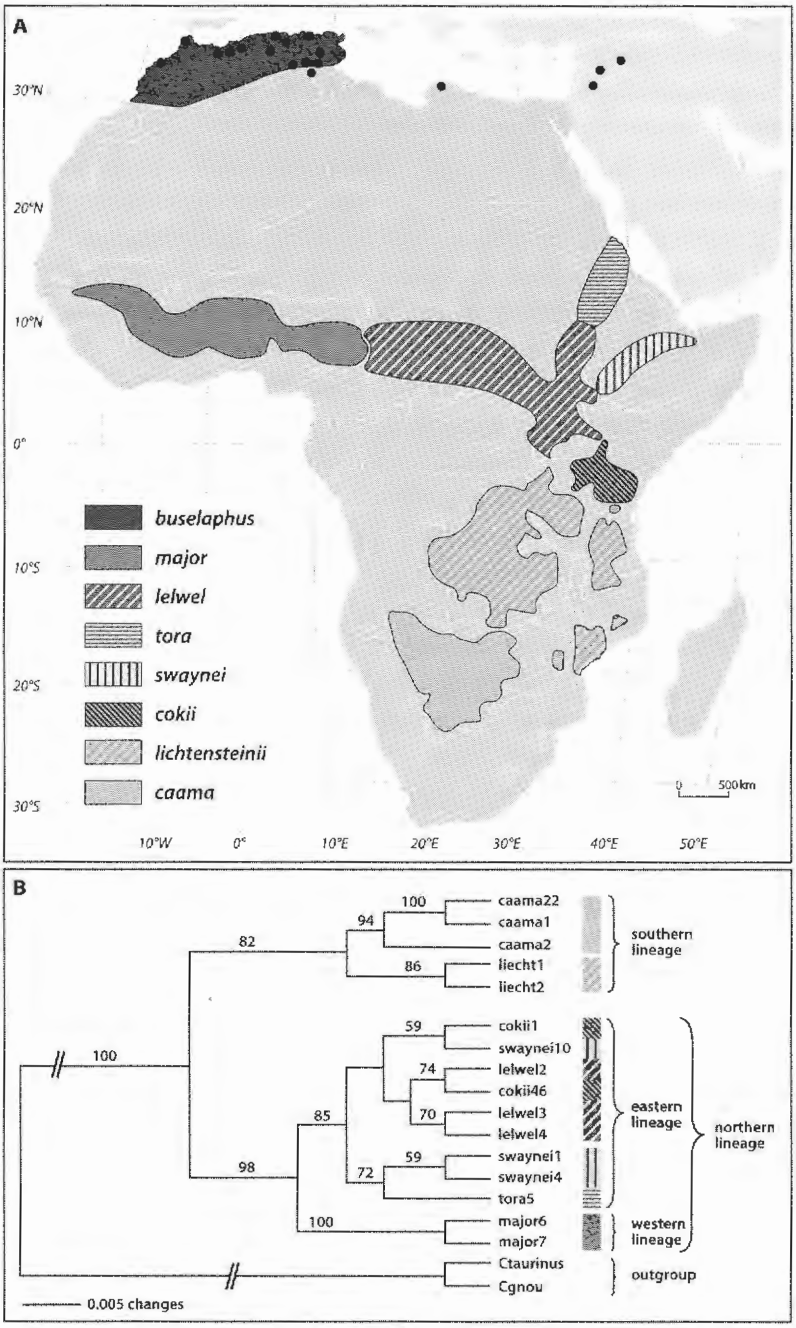

Figure 5.2 Hartebeest distribution phylogenetics and fossil sites north of the Sahara. A) Spatial distribution of the different hartebeest subspecies and location of fossil sites north of the Sahara containing Aterian lithics in North Africa and Middle Palaeolithic in the Levant. B) Phylogenetic relationships within the hartebeest complex as estimated from the cytochrome *b* mitochondrial DNA marker. Source: Flagstad et al. (2001).

the western clade underwent a population expansion at about 140 ka, and this clade crossed the Sahara, giving rise to the now extinct northern African clade. However, the lack of northern African specimens means we cannot yet give a genetic divergence age estimate for this event. Fossil evidence north of the Sahara indicates that the hartebeest crossed the Sahara during the last interglacial humid period, 130 to 70 ka (Geraads 2010). Furthermore, fossils from the Maghreb (Drake and Breeze 2016), Cyrenaica (Klein and Scott 1986) and the Levant (Uerpmann 1987) suggest that the hartebeest dispersed throughout Africa north of the Sahara and out of Africa into the Levant at this time. Thus, it is possible that hunting of animals such as hartebeest may have facilitated human dispersal into the newly opened savannas of the Sahara, followed by the Mediterranean shrublands north of the Sahara and into the Levant.

Genetic studies suggest that many felids dispersed across the Sahara at a similar time, a good example being the cheetah. Though the cheetah is usually thought of as savanna-adapted, it can survive in semi-arid and even some arid regions. Indeed, it still survives in some of the mountains of the central Sahara today, and thus it is no surprise that it managed to cross the Sahara during past humid phases. Charruau et al. (2011) investigated the molecular phylogeny of the cheetah nsing several different methods to estimate divergence times. They found that the Northern-East African cheetah subspecies (*Acinonyx jubatus soemmeringii*) population split from southern African cheetahs (*Acinonyx jubatus jubatus*) sometime between 16 and 72 ka. As the Sahara was humid from about 130 to 70 ka, and this was followed by a largely dry period until the early Holocene (Drake and Breeze 2013), the cheetah probably dispersed across the Sahara at the end of this humid phase (~70 ka).

Lions (*Panthera leo*) are less tolerant of aridity, yet still crossed the Sahara. Based on phylogenetic analysis of multiple maternal (mtDNA), paternal (Y-chromosome) and biparental nuclear (nDNA) markers and subtype variation of the lion feline immunodeficiency virus genetic markers, Antunes et al. (2008) found that that lion populations derive from Pleistocene refugia in eastern and southern Africa sometime between 324 and 169 ka and expanded into central and northern Africa and into Asia around 100 ka. Thus, they appear to have crossed the Sahara at a similar time to cheetahs, perhaps during the same humid phase. Large carnivores such as cheetah and lion can be considered good indirect indicators of animal facilitation, whereby as the climate improves, animals move into the new available habitats, and *H. sapiens* follow. Being at the top of the food chain meant that there were many herbivores for these carnivores to hunt, and they are therefore a sign of a productive environment, presumably just the sort of environment hunter-gatherers would find optimal. Thus, though not direct indicators of facilitation of the dispersal of *H. sapiens*, they are suggestive of this.

All the animals discussed so far appear to have crossed the Sahara during the last interglacial, a likely time for the dispersal of *H. sapiens* through the region. However, many other savanna species, such as the rhinoceros, appear to have done so during the following Holocene humid period, at the start of the current interglacial. Although there are no relevant phylogenetic studies to draw upon, an abundance of rock art and fossil evidence show a trans-Saharan distribution for the rhinoceros during the Holocene. This is also the case for the giraffe, elephant and crocodile (Drake et al. 2011). Taken together, these various patterns suggest significant savanna animal dispersals across the desert during humid episodes within the last two interglacials, both of which are likely times for the dispersal of hnmans through the region.

Drake et al. (2011) show that during the Holocene dispersal in the Sahara, hunter-gatherers moved into the environment of the animals they were hunting, and the distribution of animals thus largely maps against the human dispersal pattern. The best example of this is the expansion of the hippopotamus into the south-central Sahara during the Holocene, as testified by fossils and rock art (Figure 5.3). Figure 5.3a suggests that when the Saharan climate became more humid, the rivers became reactivated, thereby feeding numerous lakes. Consequently, the hippopotamus and other deep water aquatic fauna could reach these regions from areas to the south. The spatial distribution of barbed bone points (harpoons) is remarkably similar to the fossil and rock art evidence for the hippopotamus, as is the distribution of Nilo-Saharan language phylum (Figure 5.3b). Drake et al. (2011) provide summary evidence for the reconstruction of lexemes for 'hippo' and 'crocodile' in Nilo-Saharan languages, indicating their salience for speakers. Taken together, the data suggests that Nilo-Saharan-speaking hunter-gatherers followed aquatic fauna into the newly reactivated hydrological systems of the south-central Sahara in order to hunt them. Thus, the combination of evidence from fossils, rock art, barbed bone points and Nilo-Saharan languages provides strong evidence for animal facilitation of human dispersals.

Unintentional human facilitation operates when humans inadvertently promote animal dispersals. As mentioned above, this can be caused by humans changing the surrounding habitat and promoting the dispersal of animals adapted to this habitat. However, there are many other possible causes. It can be promoted by hunting pressure, by eliminating populations near settlements, thereby causing animals to seek more remote food resources. Similarly, the elimination of carnivores or predators allows expansions of populations that would otherwise be constrained. Disease can also be a factor. Livestock disease such as rinderpest spreads where high concentrations of cattle are associated with humans, but can also spread to wild species such as buffalo, driving bovids away from human settlement. Similarly, distemper in the domestic dog can be lethal even to species that are not closely related, such as the African hunting dog. Though it is possible to come up with many examples of how human

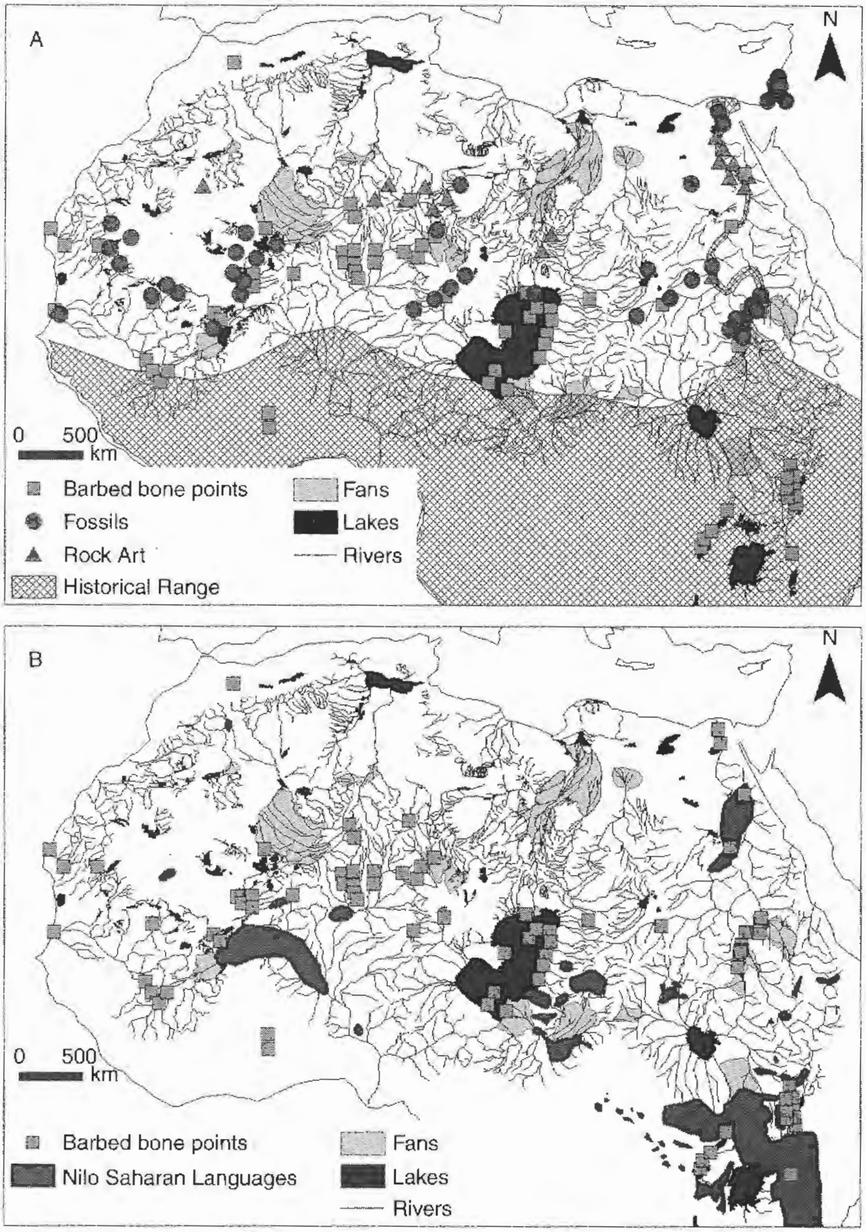

Figure 5.3 Map showing the palaeohydrology of North Africa with the distribution of: (a) hippopotamus fossils, rock art and barbed bone points, (b) Nilo-Saharan languages and barbed bone points. Adapted from Drake et al. (2011).

facilitation might happen, demonstrating it in the Sahara over the timescale of the evolution of *H. sapiens* is not currently possible as there are not long-term paleoenvironmental records that conclusively demonstrate that *H. sapiens* influenced the ecology of a region (though see Petraglia (this volume) which demonstrates the likelihood of such influences).

Co-distribution

The common genet (*Genetta genetta*) is a good example of a species that exhibits co-distribution. The common genet is often found around human settlements in sub-Saharan Africa, probably because it preys upon other anthropic species associated with human occupation, such as rodents and lizards. Genets are tolerated or even encouraged because they suppress household vermin and animal pests on crops. The English term 'genet' actually derives from the Berber language of the Maghreb (Corriente 2008). It originally came into Arabic as *zanāti*, meaning 'member of the Berber tribe of Zenata, known for horse-breeding', hence 'light horseman' > 'bandit' > 'genet' (for its depredations).

Molecular phylogenetic studies show that the genet has a remarkable ability to disperse. Gaubert et al. (2009) identify four lineages within the native species range (Figure 5.4): south-western Europe and northern Algeria (Clade I); Arabian Peninsula (Clade II); southern Africa (Clade III); south and western Africa and the Maghreb, including Algeria (Clade IV). This genetic structuring of populations is ascribed to fluctuations in northern African palaeoclimate during the past 3 to 4 million years (Ma). Gaubert et al. (2009) propose that the common genet originated in northern Algeria. The ancestors of Clade 1 (south-western Europe and northern Algeria) diverged from the other clades at about 3.47 (2.86–4.42) Ma, but recurrent arid phases produced genetic bottlenecks that affected northern Algeria and gave rise to Clade 1 at about 0.43 (0.35–0.55) Ma, as suggested by a significantly lower mitochondrial diversity compared to other lineages. This was followed by dispersal from the Maghreb southwards across the Sahara into southern and west Africa (Clade III) at about 2.67 (2.20–3.40) Ma, and from northern Africa into Arabia (Clade II) at around 1.53 (1.26–1.94) Ma. The western African lineage then dispersed back into the Maghreb at 0.13 (0.11–0.17) Ma, giving rise to Clade IV. Thus, the common genet appears to have crossed the Sahara twice over the past ~3 Ma, and when it dispersed northwards across the Sahara it did so at the same time as the other carnivores outlined above. Clade 1 was later transported to Spain by the Moors, who highly prised its pelt (Gaubert et al. 2009) – an example of translocation following its early dispersal. The genet has since colonised the Iberian Peninsula and southern France, demonstrating that once translocated it could take advantage of an open niche and spread without further human action.

The cane rat (*Thryonomys swinderianus*) is also strongly co-associated with human settlement (Asibey 1974). Although part of the pre-*H. sapiens* African fauna, it proves to be well adapted to consuming human foods, and thus wherever cultivation expands, cane rats typically also increase in numbers. Currently found in the Sudanese and Guinean savannas, to the south of the Sahara, Holocene fossil evidence suggest that during the last humid period it

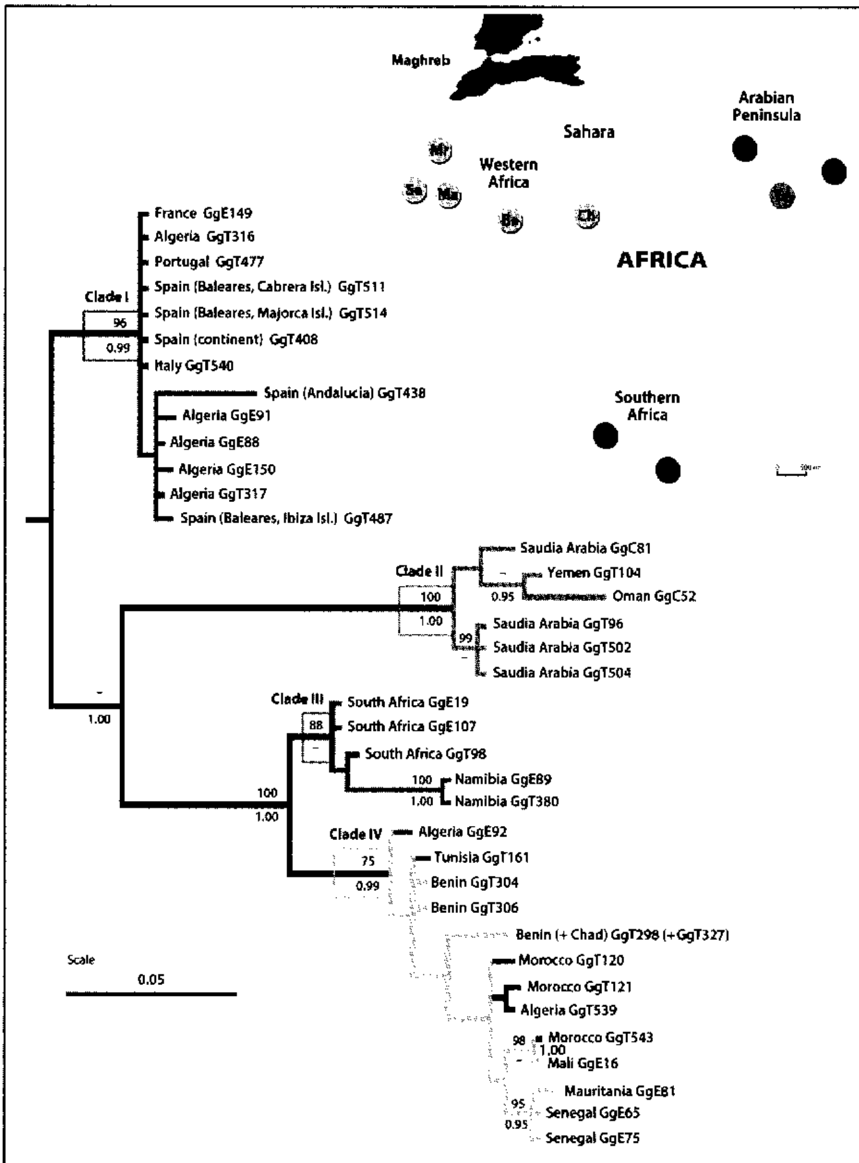

Figure 5.4 Common genet phylogenetic relationships inferred from Bayesian analysis of cytochrome b and the left domain of control region (900 bp + 3 indels). Values above and below nodes indicate bootstrap indices C75% (ML analysis) and Bayesian posterior probabilities C0.95, respectively. Scale bar corresponds to 5% sequence divergence. Source: Gaubert et al. (2009).

was found as far north as the Hoggar Mountains in the central Sahara. Given the close association of this species with humans, this dispersal could have been promoted by them.

The most well-known examples of oppositional co-distribution are rodents, for example, the Polynesian rat (*Rattus exulans*), which dispersed around the

Pacific in the canoes of the Polynesians, and the Asian house shrew (*Suncus murinus*), which is found around the Indian Ocean (Hutterer and Trainier 1990). Examples are easier to discern in maritime zones since animals cannot swim long distances. However, in large land masses, this type of anthropic distribution has to be distinguished from natural dispersals. Evidence from western Africa suggests that species such as the cane rat and the common genet take advantage of open habitats created by humans to raid food stores and seek rodents in the vicinity of settlement.

Translocation

Perhaps the best example of a species that could have been deliberately translocated across the Sahara is the tilapia fish. Today tilapia and catfish provide an important food resource for humans and because of this they are translocated and placed in rivers, ponds and wells as a food source, as has been documented in ethnographic surveys in north-east Nigeria (RIM 1992).

Using a combination of rock art and Holocene zooarchaeological evidence, Drake et al. (2011) show that the Redbelly tilapia (*Tilapia zillii*) and the African sharptooth catfish (*Clarias gariepinus*) dispersed across the Sahara during the Holocene. Both these species have specialised mechanisms that could have promoted natural dispersal. For example, Clarid fish (catfish) can employ terrestrial locomotion, whilst *Tilapia zillii* can survive living in fresh, brackish and nearly saline waters. Thus, it is possible that they could have dispersed unaided across the Sahara during past humid periods. However, the translocation of these species from one water body to another by humans would have promoted this. The isolated populations of *Tilapia guineensis* in southern Morocco (Qninba et al. 2009; Qninba et al. 2012), 1000–1400 km further north from anywhere it is found naturally today, may well represent an escaped translocated tilapia population (Figure 5.5), though when this occurred is not clear. Similarly, in Morocco there are two isolated populations of galliforms: the guinea fowl, *Numidia meleagris sabyi*, and the double-spurred francolin, *Francolinus bicalcaratus ayesha*. Both species are strongly co-associated with humans in sub-Saharan Africa, and the guinea fowl in particular has a commensal relation in West Africa (Donkin 1997).

Translocation of animal species is well known from island habitats both in the Pacific (Matisoo-Smith 2007; see also Hunt and Lipo, this volume) and in the Indian Ocean (Blench 2007; see also Boivin, this volume). It has been demonstrated that *H. sapiens* were translocating opossums and rodents in Oceania as early as 30,000 years ago in order to release them and subsequently hunt them as a food resource (Flannery et al. 1988). There is also evidence for inland translocation of fish in antiquity: the Yucatan Maya, for example, were transporting live reef fish from the coast into the remote interior, apparently for their colours rather than as food, as early as 500 A.D. Similarly with birds, we

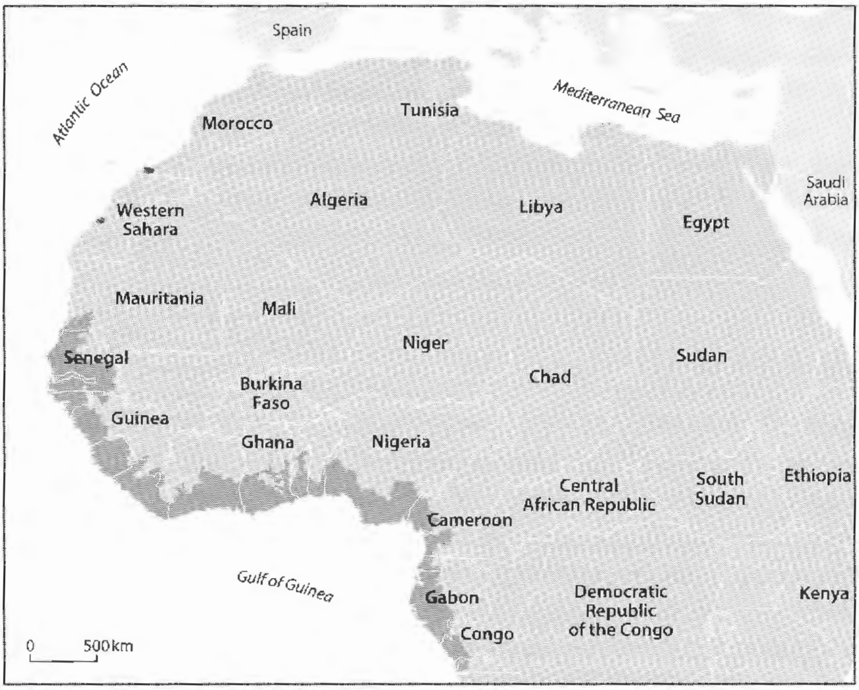

Figure 5.5 *Tilapia guineensis* distribution. Source: ICUN Red List Assessment, Qninba et al. (2009) and Qninba et al. (2012).

know that the painted jay, *Cyanocorax dickeyi*, which has an isolated population in Western Mexico, was translocated from its natural range in Ecuador and Northern Peru, probably for its feathers (Anawalt 1992).

OTHER FACTORS INVOLVED IN SAHARA FAUNAL DISPERSALS

Apart from the processes detailed in this chapter, other elements in the predator/prey relationship between humans and animals are also implicated in dispersals. Climate change of any type affects animal biogeography and thus the humans that hunt these species. There are effectively two types of climate change: ephemeral and long-term. Ephemeral episodes of climate change – for example, a drought that lasts several years but does not impact statistically on the overall climate regime – can nonetheless cause migration of species, especially in the semi-arid regions. Flexible foragers are likely to follow such movements, without backtracking their route when the climate improves. Long-term climate change can play a similar role in promoting dispersal of hunters and their prey. *H. sapiens* dispersed into a humid Sahara, largely through animal facilitation, but when it became more arid they sought wetter environments. Desertification in the Sahara is likely to have started in central regions and spread outwards, due to the southward migration of the rain-bearing monsoon and the northward movement of the north Atlantic

Westerlies (Drake et al. 2013), so those people that came from the south but dispersed more than half way across the Sahara may have been pushed north, being 'pumped' across the Sahara.

Climate and environmental manipulation are not the only possible drivers. The 'easy pickings' when humans encounter naïve fauna is also likely to have encouraged expansion of hunting territories (Dennell, this volume; Hunt and Lipo, this volume). This is most well-exemplified in Australia, where the first migrants to reach northwest Australia ca. 55,000 BP proceeded inland and rapidly began to decimate the native megafauna (e.g., Miller 2005). Megafaunal extinctions are also well attested in Madagascar (Blench 2007) and New Zealand (Worthy and Holdaway 1994), and it is likely the first settlement by foragers began by eliminating the naïve megafauna.

Other, less obvious factors may have driven dispersals. Quite remarkably, it has recently been shown, for example, that elephants can distinguish specific human languages as well as the sex of the speakers, and show appropriate fear responses to those that present a greater threat (McComb et al. 2014). The experiment in question demonstrated that elephants could discriminate between the language of Maasai hunters and that of Kamba agriculturalists. In the Holocene Sahara, when large mammals had to evaluate the threats of bow and arrow hunters, fishing peoples and other groups, this ability might have been an essential factor in survival, and might have led to animals removing themselves from proximity to specialised hunters, thus driving dispersal processes.

CONCLUSIONS

Evaluation of animal, fossil and rock art distributions in combination with molecular phylogeny, synchronic ethnography, archaeology and linguistics provides a powerful tool to examine how animals and *H. sapiens* dispersed across the 'green Sahara'. Numerous animal species made this journey during the last two interglacial humid phases, and hence the characterisation of the region as a barrier to dispersal is clearly inaccurate.

In the absence of definitive archaeological evidence for trans-Saharan movement of *H. sapiens* during the penultimate interglacial period, at a time when particular animal species did disperse through the region, we present a model that links the two. The model considers some of the different ways humans can affect the zoogeography of individual species and the reverse. We define three different mechanisms: facilitation, co-distribution and translocation (each with subsets), and show that animal dispersal can be linked to the Holocene archaeological and linguistic record. We then show how this model can be applied to past human and animal movements across the Sahara, and that there were interrelated animal and human movements during the last two interglacial humid phases. The early dispersal may also be associated with the dispersal of *H. sapiens* out of Africa, as its timing coincides with the establishment of the Aterian technocomplex in the Maghreb and earliest evidence for *H. sapiens* in the Levant.

Of the mechanisms considered in this chapter, there is strong evidence for animal facilitation and some evidence for co-distribution and translocation. We conclude by recognising that there are other processes that can promote dispersal that may interact with the anthropic mechanisms we describe and thus enhance its speed, range and directionality.

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