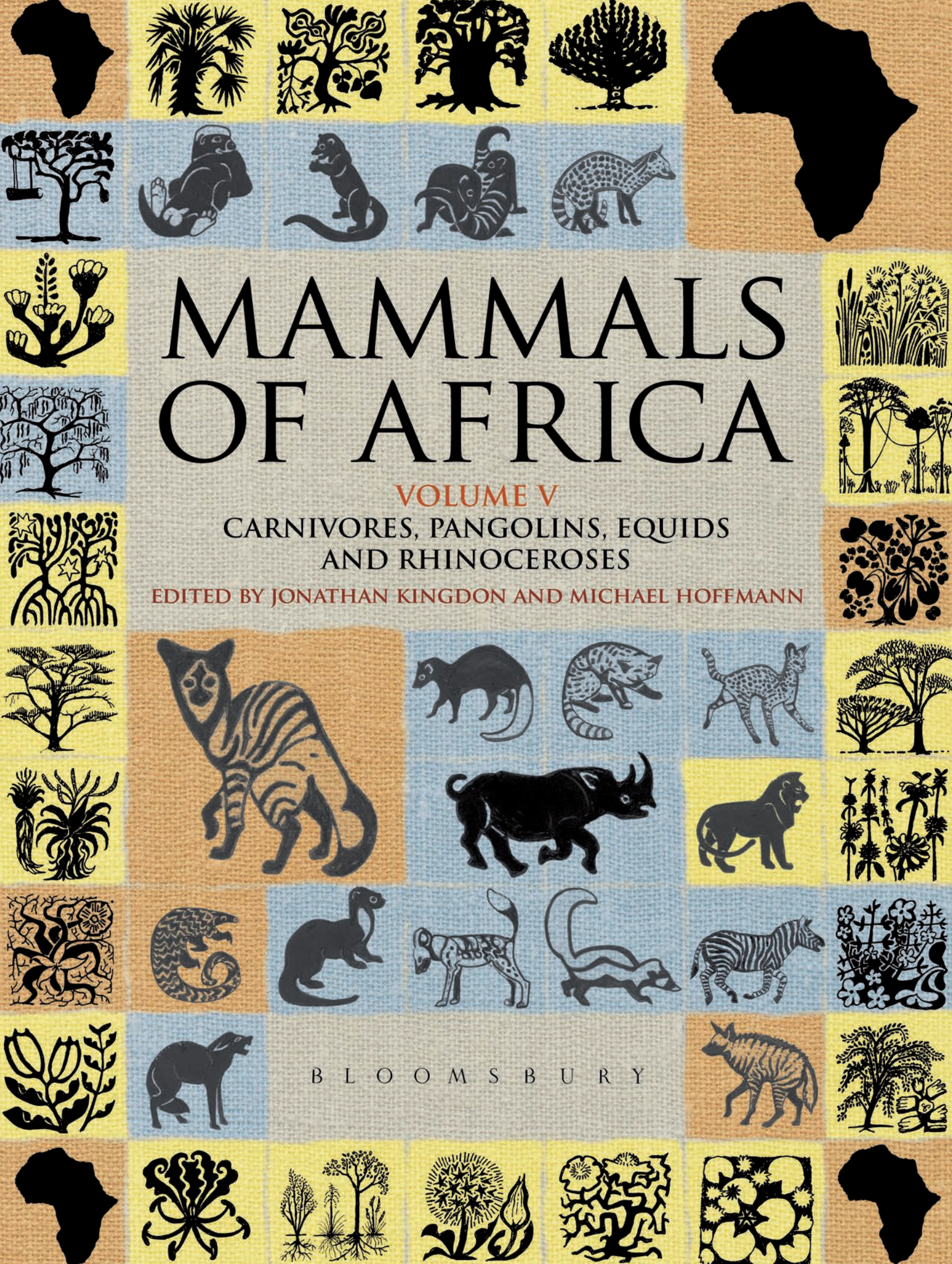


# MAMMALS OF AFRICA

VOLUME V  
CARNIVORES, PANGOLINS, EQUIDS  
AND RHINOCEROSES  
EDITED BY JONATHAN KINGDON AND MICHAEL HOFFMANN



B L O O M S B U R Y

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ILLUSTRATED BY JONATHAN KINGDON

B L O O M S B U R Y

LONDON • NEW DELHI • NEW YORK • SYDNEY

First published in 2013

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Bloomsbury Publishing Plc, 50 Bedford Square, London WC1B 3DP  
Bloomsbury USA, 175 Fifth Avenue, New York, NY 10010

[www.bloomsbury.com](http://www.bloomsbury.com)  
[www.bloomsburyusa.com](http://www.bloomsburyusa.com)

Bloomsbury Publishing, London, New Delhi, New York and Sydney

A CIP catalogue record for this book is available from the British Library.  
Library of Congress Cataloging-in-Publication Data has been applied for.

Commissioning editor: Nigel Redman  
Design and project management: D & N Publishing, Baydon, Wiltshire

ISBN (print) 978-1-4081-2255-6  
ISBN (epdf) 978-1-4081-8994-8

Printed in China by C&C Offset Printing Co., Ltd

This book is produced using paper that is made from wood grown in managed sustainable forests. It is natural, renewable and recyclable. The logging and manufacturing processes conform to the environmental regulation of the country of origin.

10 9 8 7 6 5 4 3 2 1

**Recommended citations:**

*Series:* Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M. & Kalina, J. (eds) 2013. *Mammals of Africa* (6 vols). Bloomsbury Publishing, London.

*Volume:* Kingdon, J. & Hoffmann, M. (eds) 2013. *Mammals of Africa. Volume V: Carnivores, Pangolins, Equids and Rhinoceroses*. Bloomsbury Publishing, London.

*Chapter/species profile:* e.g. Sillero-Zubiri, C. 2013. *Canis simensis* Ethiopian Wolf; pp 45–49 in Kingdon, J. & Hoffmann, M. (eds) 2013. *Mammals of Africa: Volume V: Carnivores, Pangolins, Equids and Rhinoceroses*. Bloomsbury Publishing, London.

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L. Scott and the Smithsonian UK Charitable Trust

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# Series Acknowledgements

Jonathan Kingdon, David Happold, Thomas Butynski,

Michael Hoffmann, Meredith Happold and Jan Kalina

The editors wish to record their thanks to all the authors who have contributed to *Mammals of Africa* for their expert work and for their patience over the very protracted period that these volumes have taken to materialize. We also thank the numerous reviewers who have read and commented on earlier drafts of this work.

We are also grateful for the generosity of our sponsoring patrons, whose names are recorded on our title pages, who have made the publication of these volumes possible.

Special thanks are due to Andy Richford, the Publishing Editor at Academic Press, who initiated and supported our work on *Mammals of Africa*, from its inception up to the point where Bloomsbury Publishing assumed responsibility, and to Nigel Redman (Head of Natural History at Bloomsbury), David and Namrita Price-Goodfellow at D & N Publishing, and the whole production team who have brought this work to fruition. We also acknowledge, with thanks, Elaine Leek who copy-edited every volume. We are grateful to Chuck Crumly, formerly of Academic Press and now the University of California Press, for being our active advocate during difficult times.

We have benefited from the knowledge and assistance of scholars and staff at numerous museums, universities and other institutions all over the world. More detailed and personal acknowledgements follow from the editors of each volume.

The editors are also grateful to the coordinating team of the Global Mammal Assessment, an initiative of the International Union for Conservation of Nature (IUCN), which organized a series of workshops to review the taxonomy and current distribution maps for many species of African mammals. These workshops were hosted by the Zoological Society of London, Disney's Animal Kingdom, the Owston's Palm Civet Conservation Programme, and the Wildlife Conservation Research Unit at the University of Oxford; additionally, IUCN conducted a review of the maps for the large mammals by the Specialist Groups of the Species Survival Commission. We owe a particular word of thanks to all the staff and personnel who made these workshops possible, and to the participants who attended and provided their time and expertise to this important initiative. We also thank IUCN for permission to use data from the *IUCN Red List of Threatened Species*.



photograph by Jan Kalina

ABOVE LEFT: Jan Kalina.

ABOVE: From left to right: Jonathan Kingdon, Thomas Butynski, Meredith Happold, David Happold and Andrew Richford.  
LEFT: Jonathan Kingdon (left) and Michael Hoffmann.

# Acknowledgements for Volume V

It was more than a decade ago (mid-2000) that the first authors were contacted to write profiles for Volume V. As readers of earlier volumes will know (and certainly those intimately involved in this project), *Mammals of Africa* suffered a rather tumultuous period in its latter stages, but tenacity wins out, and we are immensely grateful to all those who have so faithfully supported this project over the years.

We reserve our greatest thanks to the 86 authors who contributed their valuable time and deep experience with Africa's mammals to write the many profiles contained within these pages. Authors not only endured the countless edits and rewrites of profiles, but also responded favourably to requests to help keep their profiles updated during the long gestation period. Of course, as noted elsewhere, circumstances have meant that we have not been entirely successful at ensuring that the content of *Mammals of Africa* is absolutely current, but we likewise feel encouraged that we have managed to keep the text reasonably up-to-date.

We would be remiss not to extend a few words of thanks to several authors who played a key role in advising on their taxonomic groups (including systematics), suggesting authors, and writing and reviewing profiles, in particular: Claudio Sillero-Zubiri and David Macdonald (Canidae); Mark Taylor (Herpestidae); and Philippe Gaubert (Viverridae). Lars Werdelin kindly reviewed the fossil sections of many of the family profiles, and provided valuable taxonomic advice, as did Olaf Bininda-Emonds, João Crawford-Cabral, Philippe Gaubert, Corey Goldman, Colin Groves, the late Peter Grubb, and Mieczysław Wolsan. We fondly remember the late Harry Van Rompaey, who not only authored many small carnivore profiles (with Marc Colyn), but reviewed all of the viverrid and herpestid profiles, and provided critical and valuable taxonomic advice throughout the project on small carnivore systematics. Volume V would be much the poorer were it not for Harry's knowledge and insightful commentaries. Sadly, Harry passed away in February 2007. It is an honour that these pages include his final contributions, some of them never before published. Besides Harry, *Mammals of Africa* also saw the passing of Huw Griffiths, early in the life of the project in 2002; the profile on *Mustela putorius* (written with Fabrice Cuzin) represents Huw's final published work. We hope that this volume serves as a fitting tribute to both Harry and to Huw.

We would like to express our thanks and gratitude to the following people who kindly offered their time and expertise to help review species or higher-level profiles (or parts thereof), or who made available published or unpublished information to authors or editors (apologizing in advance to anyone whose name is inadvertently omitted or misspelled). The contributions, insights, advice and critiques of those listed below contributed immensely to improving the content and accuracy of individual profiles: Menahem Abadi, Alexei V. Abramov, Karl Ammann, Edward Andama, Jeremy Anderson,

Mark Anderson, Francesco Angelici, John Arnould, Anagaw Atickem, Robert Atkinson, Nico Avenant, Ted Bailey, Carolyn Baker, Guy Balme, Zoe Balmforth, Amanda Barrett, Paul Bates, Hans Bauer, Karen L. Bauman, Colleen Begg, Nigel Bennett, Marthán Bester, Olaf Bininda-Emonds, Johnny Birks, Allard Blom, J. du P. Bothma, Tony Bowland, Justin Brashares, Peter Brotherton, David Brugière, Owen Burnham, Tom Butynski, Paolo Cavallini, Colin Chapman, Pierre Charles-Dominique, Judith Chupasko, Cornelius G. Coetzee, Carla Conradie, Nobby Cordeiro, João Crawford-Cabral, Scott Creel, Graham Cumming, Fabrice Cuzin, Danielle D'Amour, Tim Davenport, Tamar Dayan, Daniela De Luca, Koenraad De Smet, Ilaria Di Silvestre, Carlos Driscoll, Johan Du Toit, Will Duckworth, Patrick Duncan, Amy Dunham, Nicole Duplaix, Husain El-Alqamy, Steve Elkan, Richard Emslie, Thomas Engel, Richard Estes, Amina Fellous, Frauke Fischer, Laurence Frank, Karl Fredga, Todd Fuller, Paul Funston, Norman Galli, Philippe Gaubert, Timothy Gaudin, the late Annie Gautier-Hion, Aadje Geertsema, Eli Geffen, Anthea Gentry, Denis Geraads, Michael Ghiglieri, Joshua Ginsberg, Corey Goldman, Helle Goldman, Mike Griffin, the late Huw Griffiths, Jon Grinnell, Colin Groves, the late Peter Grubb, Len Gunter, Johannes Handwerk, John Hart, Martha Heath, Philipp Henschel, Marna Herbst, Lex Hes, Russell Hill, Kes Hillman Smith, Richard Hoath, Sarah Hodge, Kay Holekamp, Bernd Hoppe-Dominik, Ivan Horak, Kim Howell, Robert M. Hunt Jr, Jen Hunter, Luke Hunter, Anya Hurlbert, Peter Jackson, Hélène Jacques, Nicola Jenner, David Jenny, Jan Kamler, Julian Kerbis, Carolyn M. King, Andrew Kitchener, Hans Klingel, Ordino Kok, Hans Kruuk, Sally Lahm, Serge Larivière, Alain Laurent, Lysa Leland, Kevin Leo-Smith, Walter Leuthold, Bruce MacFadden, James Malcolm, Jorgelina Marino, Kim McCreery, Robbie McDonald, Sue McLaren, Anagaw Meshesha, Gus Mills, Patricia Moehlman, David Morgan, François Moutou, David Moyer, Hans Peter Müller, Linda Munson, Jan Nel, John Newby, Owen Newman, Gea Olbricht, Annette Olson, John Ososky, Stephane Ostrowski, Francisco Palomares, Banie Penzhorn, Mike Perrin, Gustav Peters, Netty Purchase, Anne Pusey, Janet Rachlow, Gregory Rasmussen, Galen Rathbun, Justina C. Ray, Matt Ridley, Alan Root, Mary Rowen, Dave Rowe-Rowe, Daniel I. Rubenstein, Mostafa Saleh, Esteban Sarmiento, Dietrich Schaaf, Monica Scheiss, Adrian Shrader, Susanne Shultz, the late John Skinner, Alexander Sliwa, Rebecca Smith, Michael Somers, Naas Steenkamp, Villiers Steyn, Mary Stiner, Gerhard Storch, Thomas Struhsaker, Chris Stuart, Tilde Stuart, Ron Swaisgood, Steve Takata, Mark Taylor, Peter J. Taylor, the late Simon Thirgood, Jo Thompson, Chris Thouless, Caroline Tutin, Carolina Valdespino, the late Harry van Rompaey, Blaire Van Valkenburgh, Géraldine Veron, Petri Viljoen, Tim Wachter, Aaron Wagner, Matt Walpole, Peter Waser, Johan Watson, Robert Wayne, Lars Werdelin, Stuart Williams, Mieczysław Wolsan, Harry Wright, Derek Yalden and Yoram Yom-Tov.

# Mammals of Africa: *An Introduction and Guide*

David Happold, Michael Hoffmann, Thomas Butynski and Jonathan Kingdon

*Mammals of Africa* is a series of six volumes that describes, in detail, every extant species of African land mammal that was recognized at the time the profiles were written (Table 1). This is the first time that such an extensive coverage has been attempted; all previous books and field guides have either been regional in coverage, or have described a selection of mammal species – usually the larger species. These volumes demonstrate the diversity of Africa’s mammals, summarize what is known about the distribution, ecology, behaviour and conservation status of each species, and serve as a guide to identification.

Africa has changed greatly in recent decades because of increases in human populations, exploitation of natural resources, agricultural development and urban expansion. Throughout the continent, extensive areas of forest have been destroyed and much of the forest that remains is degraded and fragmented. Savanna habitats have been altered by felling of trees and development for agriculture. Many of the drier areas are threatened with desertification. As a result, the abundance and geographic ranges of many species of mammals have declined – some marginally, some catastrophically, some to extinction. Hence, it seems appropriate that our knowledge of each

species is recorded now, on a pan-African basis, because the next few decades will see even more human-induced changes. How such changes will affect each mammalian species is uncertain, but this series of volumes will act as a baseline for assessing future change.

The study of African mammals has taken several stages. During the era of European exploration and colonization, the scientific study of African mammals was largely descriptive. Specimens that were sent to museums were described and named. As more specimens became available, and from different parts of the Continent, there was increasing interest in distribution and abundance, and in the ecological and behavioural attributes of species and communities. At first, it was the largest and most easily observed species that were the focus of most studies, but as new methodologies and equipment became available, the smaller and more cryptic and secretive species became better known. Many species were studied because of their suspected role in diseases of humans and livestock, and because they were proven or potential ‘pests’ in agricultural systems. During the past decade or so, there has been greater emphasis on the genetic and molecular characteristics of species. All these studies have produced a wealth of information, especially during the past 40 years or so. These volumes are not only a distillation of the huge literature that now exists on African mammals, but also of much unpublished information.

Readers will notice that there is a huge discrepancy among species in the amount of information available. Some species have been studied extensively for many years, especially the so-called ‘game species’, some species of primates and a few species that are widespread and/or easily observed. In contrast, other species are known only by one or a few specimens, and almost nothing is known about them. Likewise, some areas and countries have been well studied, while other areas and countries have been neglected. During the preparation of these volumes, the editors have often been surprised by the wealth of information about some species when little was anticipated, and by the paucity of information about others, some of which were assumed to be ‘well known’. In addition to presenting information that is based on sound scientific evidence, the aims of these volumes are to point out where there are gaps in knowledge and to correct inaccurate information that has become embedded in the literature. For most taxa, the detail provided in the species profiles allows accurate identification.

*Mammals of Africa* comprises six volumes (Table 2). The volumes consist mainly of species profiles – each profile being a detailed

**Table 1. The mammals of Africa.**

Order	Number of families	Number of genera	Number of species
Hyracoidea	1	3	5
Proboscidea	1	1	2
Sirenia	2	2	2
Afrosoricida	2	11	24
Macroscelidea	1	4	15
Tubulidentata	1	1	1
Primates	4	25	93
Rodentia	15	98	395 <sup>a</sup>
Lagomorpha	1	5	13
Erinaceomorpha	1	3	6
Soricomorpha	1	9	150
Chiroptera	9	49	224
Carnivora	9	38	83
Pholidota	1	3	4
Perissodactyla	2	3	6
Cetartiodactyla	6	41	93
<b>16</b>	<b>57</b>	<b>296</b>	<b>1116<sup>b</sup></b>

<sup>a</sup>Including five introduced species. <sup>b</sup>Species profiles in *Mammals of Africa*.

**Table 2. The six volumes of *Mammals of Africa*.**

Volume	Contents	Number of species	Editors
I	Introductory chapters. Afrotheria (Hyraxes, Elephants, Dugong, Manatee, Otter-shrews, Golden-moles, Sengis and Aardvark)	49	Jonathan Kingdon, David C. D. Happold, Michael Hoffmann, Thomas M. Butynski, Meredith Happold and Jan Kalina
II	Primates	93	Thomas M. Butynski, Jonathan Kingdon and Jan Kalina
III	Rodents, Hares and Rabbits	408	David C. D. Happold
IV	Hedgehogs, Shrews and Bats	380	Meredith Happold and David C. D. Happold
V	Carnivores, Pangolins, Equids and Rhinoceroses	93	Jonathan Kingdon and Michael Hoffmann
VI	Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids	93	Jonathan Kingdon and Michael Hoffmann

account of the species. They have been edited by six editors who distributed their work according to the orders with which they were most familiar. Each editor chose authors who had extensive knowledge of the species (or higher taxon) and, preferably, had experience with the species in the field. Each volume follows the same general format with respect to arrangement, subheadings and contents. Because *Mammals of Africa* has contributions from 356 authors (each with a different background and speciality), and each volume was edited by one or more editors (each with a different perspective), it has not been possible or even desirable to ensure exact consistency throughout. Species profiles are not intended to be exhaustive literature reviews, partly for reasons of space. None the less, they are written and edited to be as comprehensive as possible, and to lead the reader to the most important literature for each species. Inevitably, not all information available could be accommodated for the better-known species, and so such profiles are a précis of available knowledge. Extensive references in the text alert the reader to more detailed information.

In addition to the species profiles, there are profiles for the higher taxa (genera, families, orders and above). At the very least, there is a profile for each order, for each family within the order, for each genus within the family, and for each species within the genus. For some orders there are additional taxonomic levels, for example, subfamilies (e.g. Mustelinae). The taxonomy used in these volumes mostly follows that presented in the third edition of *Mammal Species of the World: A Geographic and Taxonomic Reference* (Wilson & Reeder 2005), although authors have employed alternative taxonomies when there were good reasons for doing so. Species are often presented alphabetically within genera. Volume I differs from the other volumes in that it contains a number of introductory chapters about Africa and its environment, and about African mammals in general.

## The continent of Africa

For the purposes of this work, 'Africa' is defined as the continent of Africa (bounded by the Mediterranean Sea, the Atlantic Ocean, the Indian Ocean, the Red Sea and the Suez Canal) and the islands on the continental shelf, which, at some time in their history, have been joined to the African continent. The largest of the 'continental islands' are Zanzibar (Unguja), Mafia and Bioko (Fernando Po). All 'oceanic islands', e.g. São Tomé, Príncipe, Annobón (Pagulu), Madagascar, Comoros, Seychelles, Mauritius, Socotra, Canaries, Madeira and Cape Verde are excluded, with the exception of Pemba, which is included because of its close proximity (ca. 50 km) to the mainland.

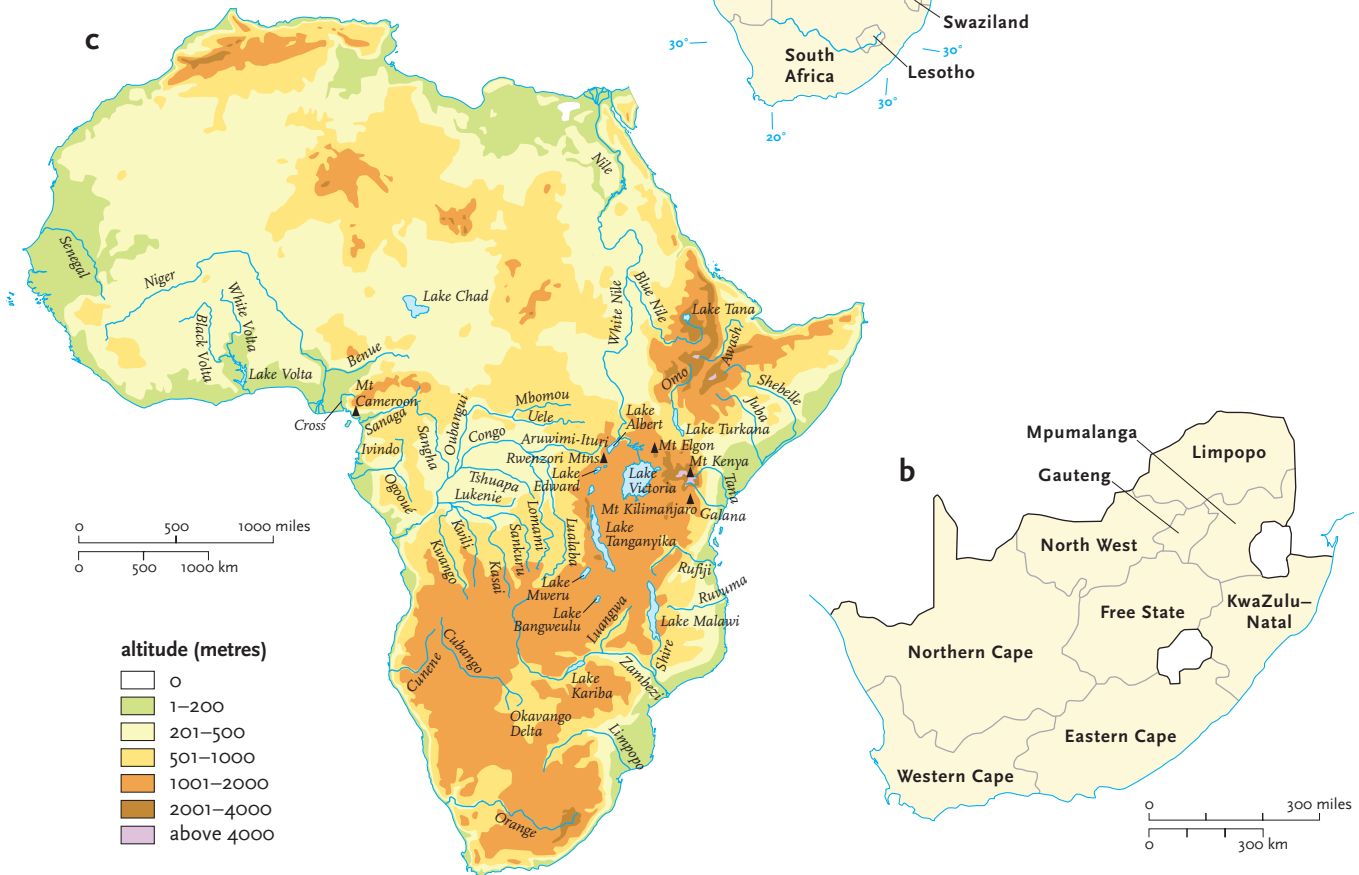
The names of the countries of Africa are taken from the *Times Atlas* (2005). The Republic of Congo is referred to as 'Congo' and the Democratic Republic of Congo (former Zaire) as 'DR Congo'. Smaller geographical or administrative areas within countries are rarely referred to except for Provinces in South Africa, which are used extensively in the literature. A political map of Africa, and of the Provinces of South Africa, is given (Fig. 1), as well as a list of the 47 countries together with their previous names that are used in the older literature on African mammals (Table 3).

Africa is the second largest continent in the world (after Asia), but it differs from other continents (except Australia and Antarctica) in being essentially an island. At various times in the past, Africa has been joined to other continents – a situation that has had a strong influence on the fauna and flora of the continent. Africa is a vast continent (29,000,000 km<sup>2</sup>, 11,200,000 mi<sup>2</sup>) that straddles the Equator, with about two-thirds of its area in the northern hemisphere and one-third in the southern hemisphere. As a result, Africa has many varied climates (with seasons in each hemisphere being six months out of phase), many habitats (including deserts, savannas, woodlands, swamps, rivers, lakes, moist forests, monsoon forests, mountains and glaciers), and altitudes ranging from 155 m (509 ft) below sea level at L. Assal, Djibouti, in the Danakil (Afar) Depression, to 5895 m (19,341 ft) on Mt Kilimanjaro, Tanzania. Africa is comprised of 47 countries, some of which are very large (e.g. Sudan [2,506,000 km<sup>2</sup>; 967,000 mi<sup>2</sup>], Algeria [2,382,000 km<sup>2</sup>, 920,000 mi<sup>2</sup>], and Democratic Republic of Congo [2,345,000 km<sup>2</sup>, 905,000 mi<sup>2</sup>]), and others that are relatively small (e.g. Djibouti [23,200 km<sup>2</sup>, 9,000 sq miles], Swaziland [17,400 km<sup>2</sup>, 6,700 mi<sup>2</sup>] and The Gambia [11,300 km<sup>2</sup>, 4,400 mi<sup>2</sup>]). The human population of each country also varies greatly, from about 346/km<sup>2</sup> in Rwanda to only about 2.5/km<sup>2</sup> in Namibia. With its great size and varied habitats, Africa supports a high biodiversity, including a large number of species of mammals. Likewise, most countries have a high diversity of mammals (especially when compared with temperate countries).

Africa may also be categorized into Biotic Zones (Fig 2.). A biotic zone is defined as an area within which there is a similar environment (primarily rainfall and temperature) and vegetation, and which differs in these respects from other Biotic Zones. Africa can be divided into 13 Biotic Zones, two of which may be divided into smaller categories. The Biotic Zones concept provides a general assessment of the environmental conditions in which a species lives, as well as providing an assessment of the geographic distribution of the species. The Rainforest Biotic Zone and the South-West Arid Biotic Zone may be divided into regions and sub-regions that reflect the different biogeographical distributions of species, each region/



Figure 1. (a) Political map of Africa; (b) provinces of South Africa; (c) altitudes and major rivers of Africa. South Sudan and Somaliland are not identified as separate countries in the text.



**Table 3. The countries of Africa: names, areas and human population density.**

Country name	Area (km <sup>2</sup> ) '000	Area (miles <sup>2</sup> ) '000	Human population '000 (2006)	People per km <sup>2</sup>
Algeria	2,382	920.0	33,500	14.1
Angola (includes Cabinda)	1,247	481.0	15,800	12.7
Benin * [Dahomey]	113	43.0	8,700	77.0
Botswana [Bechuanaland]	582	225.0	1,800	3.1
Burkina Faso * [Upper Volta; Burkina]	274	106.0	13,600	49.6
Burundi [part of Ruanda-Urundi (= part of Belgian Congo)]	27.8	10.7	7,800	280.5
Cameroon [includes former French Cameroon, German Cameroon and part of Eastern Nigeria]	475	184.0	17,300	36.2
Central African Republic #	623	241.0	4,300	6.9
Chad [Tchad]	1,284	496.0	10,000	5.8
Congo [Republic of Congo]	342	132.0	3,700	10.8
Côte d'Ivoire * [Ivory Coast]	322	125.0	19,700	61.2
Democratic Republic of Congo [Belgian Congo; Congo (Kinshasha); Zaire]	2,345	905.0	62,700	26.7
Djibouti [French Somaliland]	23.2	9.0	800	34.5
Egypt	1,001	387.0	75,400	75.3
Equatorial Guinea # (includes Rio Muni [Spanish Guinea] and Bioko I. [Fernando Po])	28.1	10.8	500	17.8
Eritrea (formerly part of Ethiopia)	94	36.0	4,600	48.9
Ethiopia [Abyssinia]	1,128	436.0	74,800	66.3
Gabon #	268	103.0	1,400	5.2
The Gambia	11.3	4.4	1,500	132.7
Ghana [Gold Coast]	239	92.0	22,600	94.6
Guinea *	246	95.0	9,800	39.8
Guinea-Bissau [Portuguese Guinea]	36	13.9	1,400	38.9
Kenya	580	224.0	34,700	59.8
Lesotho [Basutoland]	30.4	11.7	1,800	59.2
Liberia	111	43.0	3,400	30.6
Libya	1,760	679.0	5,900	3.6
Malawi [Nyasaland]	118	46.0	12,800	108.5
Mali *	1,240	479.0	13,900	11.2
Mauritania *	1,030	412.0	3,200	3.1
Morocco [includes former Spanish Morocco and French Morocco]; (now also includes Western Sahara = former Spanish Sahara)	447	172.0	32,100	71.8
Mozambique [Portuguese East Africa]	802	309.0	19,900	24.8
Namibia [South-west Africa]	825	318.0	2,100	2.5
Niger *	1,267	489.0	14,400	11.3
Nigeria	924	357.0	134,500	145.6
Rwanda [part of Ruanda-Urundi (= part of Belgian Congo)]	26.3	10.2	9,100	346.0
Senegal *	197	76.0	11,900	60.4
Sierra Leone	71.7	27.7	5,700	79.5
Somalia § [British Somaliland and Italian Somaliland; Somali Republic]	638	246.0	8,900	13.9
South Africa	1,220	471.0	47,300	38.7
Sudan § [Anglo-Egyptian Sudan]	2,506	967.0	41,200	16.4
Swaziland	17.4	6.7	1,100	63.2
Tanzania [German East Africa; Tanganyika] (now includes Zanzibar I., Mafia I. and Pemba I.)	945	365.0	37,900	40.1
Togo [Togoland]	56.8	21.9	6,300	110.9
Tunisia	164	63.0	10,100	61.6
Uganda	236	91.0	27,700	117.4
Zambia [Northern Rhodesia]	753	291.0	11,900	15.8
Zimbabwe [Southern Rhodesia]	391	151.0	13,100	33.5
<b>Totals/mean density</b>	<b>29,448</b>	<b>11,383</b>	<b>902,600</b>	<b>56.8</b>

Former names are listed in chronological order in square brackets, with the oldest name listed first. Obsolete names are listed because much of the older literature refers to past colonial entities. \* = formerly part of French West Africa. # = formerly part of French Equatorial Africa. § At the time of going to press, the country of Sudan had been divided into two: the Republic of Sudan in the north, and the Republic of South Sudan in the south. § The former British Somaliland is now a self-declared state under the name of the Republic of Somaliland, but remains internationally unrecognized.





Figure 2. The biotic zones of Africa. The numbers refer to the biotic zones as described in the text (from Happold & Lock, Volume I, *Mammals of Africa*).

sub-region having a community of mammals and other animals that is different to any other. Details of the Biotic Zones of Africa, and the regions and sub-regions of the Rainforest Biotic Zone and the South-West Arid Biotic Zone, are given in Volume I of *Mammals of Africa*.

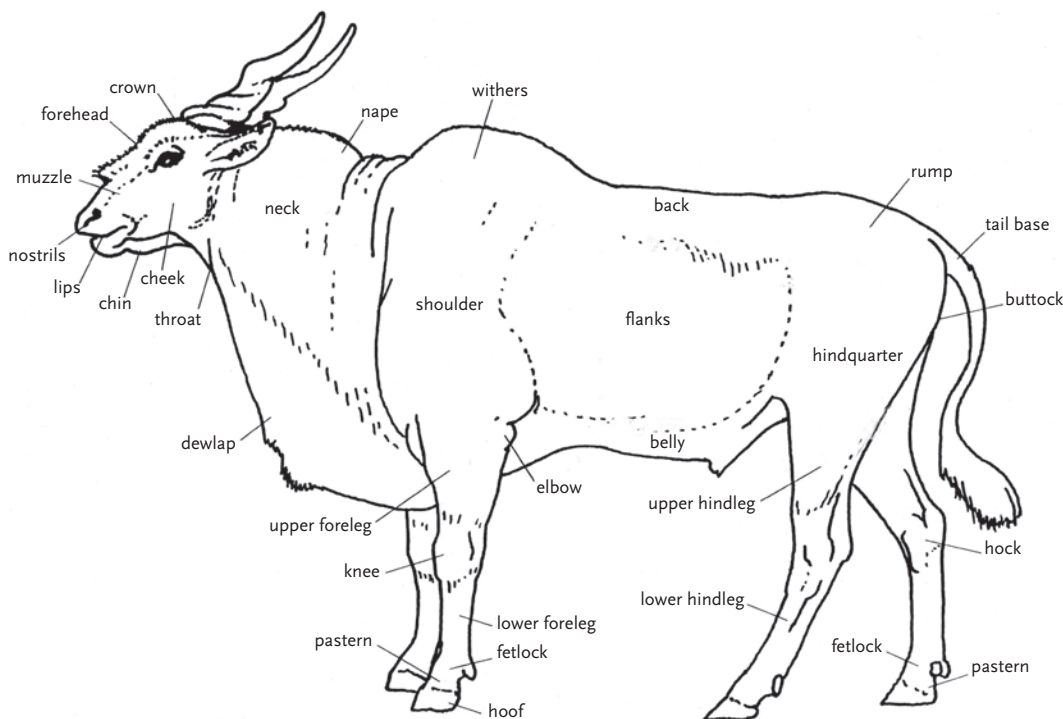


Figure 3. External features of a mammal: Common Eland *Tragelaphus oryx*.

## The carnivores, pangolins, equids and rhinoceroses of Africa

This volume is devoted to the orders Carnivora (carnivores), Pholidota (pangolins) and Perissodactyla (equids and rhinoceroses). The most diverse is the carnivores (83 native species), ranging from iconic charismatic species like the Lion *Panthera leo* and African Wild Dog *Lycaon pictus* to the remarkable diversity of mongooses and genets. Carnivores show a close relationship with the pangolins (4 species) and, in turn, the carnivores and pangolins are allied with a clade that unites the perissodactyls with the cetartiodactyls (pigs, hippopotamuses, chevrotain, giraffes, deer and bovids; the subject of Volume VI). Note that introduced species are mentioned in the higher-level profiles (where relevant), but are not otherwise profiled.

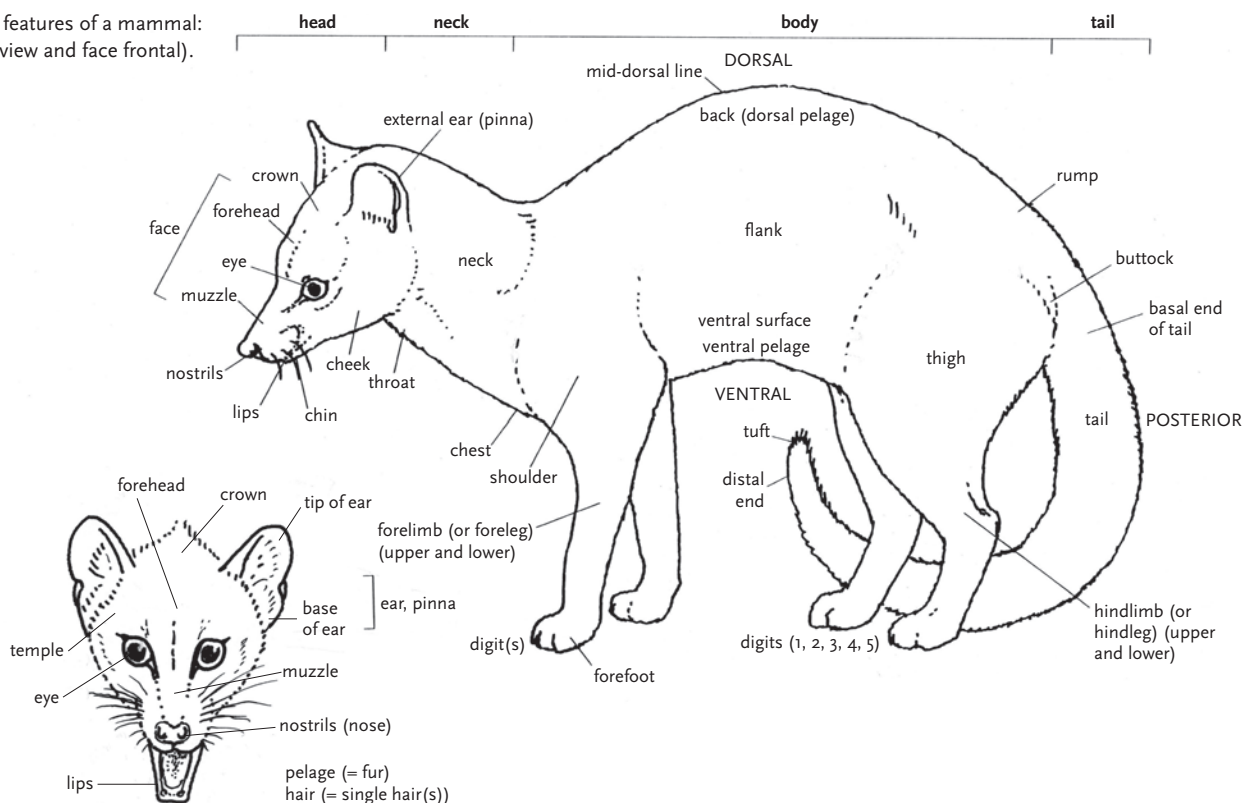
At the time of going to press, genetic research has suggested that a fifth species of the genus *Canis* occurs in Africa, namely the Grey Wolf *C. lupus* (Rueness *et al.* 2011; and see Gaubert *et al.* 2012). Further brief discussion is provided under the genus profile and species profile for the Golden Jackal *Canis aureus*, but the species is otherwise not separately profiled.

As *Mammals of Africa* was being finalized, a new work by Colin Groves and the late Peter Grubb, *Ungulate Taxonomy*, was published but it has not been possible to fully consider and evaluate the conclusions and classification presented in that work.

## Species profiles

Information about each species is given under a series of subheadings. The amount of information under each of these subheadings varies greatly between species; where no information is available, this is recorded as ‘No information available’ or words to this effect. The sequence of subheadings is as follows:

Figure 4. External features of a mammal: *Genetta* sp. (side-view and face frontal).



**Scientific name** (genus and species) The currently accepted name of the species.

**Common names** English, French and German names are given, as available. The first given English name is the preferred common name for the species; alternative names are given in parentheses for some species. Wilson & Cole (2000) list proposed common names for all the world's mammals; most of these names were also given in the third edition of *Mammal Species of the World* (Wilson & Reeder 2005). Although these works have been consulted, the names used have not always been adopted in *Mammals of Africa*. French and German names were usually provided by authors.

**Scientific Citation** This provides the full scientific name of the species, i.e. genus name, species name, authority name, and date of authority. Parentheses around the authority's name and date indicate that the species was originally named in a different genus to its present generic allocation. The scientific name is followed by the publication where the species was described, and the location where the type specimen (or type series) was obtained. Most of this information is taken from Wilson & Reeder (2005).

**Taxonomy** This section contains information on taxonomic problems, if any, associated with the species, and its relationship with other species in the genus. For some species, there is considerable information about these topics; for others, there may be nothing. A list of synonyms (without the taxonomic authority for each) and the number of subspecies (if any) is presented, mostly taken from Wilson & Reeder (2005). The chromosome number is given if available, and in some cases this is followed by other information relevant to the chromosomes.

**Description** This section, together with the illustrations, provides the reader with adequate information to identify the species. The section begins with a brief overall description of the species, including an indication of size. This is followed by a detailed description of the external features of the species' head (and parts of the head), dorsal pelage, legs, feet, ventral pelage, and tail (in this order), as well as any special characteristics unique to the species. For some species, diagnostic characteristics of the skull and dentition are given. The characters described in this section are common to all subspecies of this species (unless otherwise noted). The mammary formula, i.e. the number and arrangement of nipples in adult females, is noted wherever this feature varies between the taxa being discussed.

**Geographic Variation** Variation within the species may be of two sorts: (a) clinal variation without subspecies, or (b) subspecific variation. If (a), there is a description of the character(s) that alter clinally across the geographic range of the species. If (b), each of the subspecies is listed with its geographic range and, where available, the characters that distinguish it from other subspecies of the species. For some species, subspecies have been described that are no longer considered to be valid; in some cases, such names may be listed but without further comment.

**Similar Species** Species that are sympatric or parapatric with the species under consideration, and with which it may be confused, are listed along with diagnostic characteristics (additionally, readers may refer to profiles of the similar species in question). In some instances, species that are allopatric in distribution are also included.

**Distribution** The first sentence 'Endemic to Africa' informs the reader that this is an African species and does not occur on any

other continent; if a species also occurs outside Africa, this is noted at the end of this section with a very brief synopsis of the extralimital range. For widespread species that generally remain so today (e.g. *Herpestes sanguineus*), the text provides a general idea of the range, highlighting only places or countries where the species may have been extirpated, recently newly recorded, or providing clarity on previously incorrectly attributed country records and range limits. In the case of widespread species that have undergone significant range contractions and declines (e.g. *Lycaon pictus*), the text generally differentiates between former and current ranges in an attempt to elucidate a clearer picture of where species do, or no longer, occur. Finally, for more range-restricted species (e.g. *Canis simensis*), the information provided may be quite precise, detailing even localized distribution within the confines of its small range. A distribution map (see below) augments the information given here.

**Habitat** This section provides a description of the range of habitats where the species lives. Details of plant communities, plant species, vegetation structure, soil type and/or structure and water availability, etc. (if available) are also recorded. Other information may include average annual rainfall, altitudinal limits and seasonal variation in habitat characteristics.

**Abundance** A general indication of abundance in the habitat. This may be unquantified, such as abundant, common, uncommon, rare, or phrases such as ‘rarely seen but frequently heard’, etc. For better-known species, abundance may be expressed as estimates of density (e.g. number/ha or number/km<sup>2</sup>), or relative abundance within the community (e.g. ‘comprised x% of carnivores captured’, ‘the second most numerous species’); for the better-known, rare species, actual numbers of individuals for the species may be given. Other information may include seasonal changes in density, frequency of observations, or the relative abundance of specimens in collections.

**Adaptations** This section describes morphological, physiological and behavioural characteristics that show how the species uniquely interacts with its environment, conspecifics and other animals. This section may also describe species-specific adaptations for feeding, locomotion, burrowing, mechanisms for orientation, production of sound, sensory mechanisms and activity patterns. In some instances comparison with related or convergent species allows the unique adaptations of the species under discussion to be detailed or highlighted.

**Foraging and Food** This section provides information on the diet and foraging habits of the species. The diet is described either by a list of the taxa of animals or plants consumed, or as a quantitative measure of the contents of the stomach or the faeces. This section can also include any of the following: location of food, foraging behaviour, times when foraging occurs and daily distance moved; hoarding; seasonal changes in diet and food availability; individual or co-operative behaviour used in foraging and hunting; sex and age differences in foraging and diet; and nomadic or migratory movements in relation to food availability.

**Social and Reproductive Behaviour** Topics in this section may include group structure (whether solitary, social, or colonial),

group size and composition; agonistic and amicable behaviour, comfort behaviour, etc.; home-range (including quantitative data), territorial behaviour, courtship and mating behaviour, behaviour of young, parental–young interactions; presence of helpers, vocalizations, and interactions with other species (mammals, birds, etc.).

**Reproduction and Population Structure** This section begins with an assessment of reproductive strategy (if known) and the times/seasons of the year when individuals are reproductively active (pregnancy and lactation in females, active spermatogenesis in males). Other information may include length of gestation, times/seasons of births, including peaks of births, litter-size, birth-weight and size, spacing of litters, growth and time to weaning, maturity, longevity, and mortality rates. Reproductive strategies, if known, are described with respect to locality, food availability, and population density. Population structure (sex ratio, adult/young ratio, abundance of different cohorts in the population at different times of the year) may be described, and related to seasonal variations in reproduction and environmental variables.

**Predators, Parasites and Diseases** The known predators, parasites and diseases are listed. Information on parasites and diseases is not intended to be exhaustive, but simply to provide an entry point into the literature on the topic. In some cases, information on diseases from captive animals is presented. Additional information is given if the species is a host to diseases that affect humans and domestic stock.

**Remarks** This subheading subsumes five of the above subheadings (Adaptations, Foraging and Food, Social and Reproductive Behaviour, Reproduction and Population Structure, and Predators, Parasites and Diseases) in those instances where there is little or no information available.

**Conservation** The conservation status of the species is stated, as given by the *IUCN Red List of Threatened Species* (version 2011.2). The IUCN Red List categories follow the definitions and criteria given in the *IUCN Red List Categories and Criteria Version 3.1* (Table 4). For those species classified as threatened (i.e. ‘Vulnerable’, ‘Endangered’, ‘Critically Endangered’), the criteria met are also indicated. Some species have changed status due to improved knowledge, taxonomic revision, or the impact of threatening processes or conservation actions. Readers can obtain detailed reasons for the past and present status of a species by going to the IUCN Red List website ([www.iucnredlist.org](http://www.iucnredlist.org)). If a species was listed on Appendix I, II or III under CITES (Convention on International Trade in Endangered Species; [www.cites.org](http://www.cites.org); as of 22 December 2011) or Appendix I or II of CMS (Convention on Migratory Species; [www.cms.int](http://www.cms.int); as of 5 March 2009) this is also indicated. For some species, additional information is provided, such as presence in protected areas, major threats, and current or recommended conservation measures.

**Measurements** A series of morphological measurements is provided. For each species there is a standard set of measurements. The abbreviations for each measurement are given in the Glossary.

**Table 4. Definitions for the IUCN Red List categories (from IUCN – Red List Categories, Version 3.1).**

Category	Description
<b>Extinct (EX)</b>	A taxon is <b>Extinct</b> when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time-frame appropriate to the taxon's life-cycles and life-form.
<b>Extinct in the Wild (EW)</b>	A taxon is <b>Extinct in the Wild</b> when it is known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time-frame appropriate to the taxon's life-cycle and life-form.
<b>Critically Endangered (CR)</b>	A taxon is <b>Critically Endangered</b> when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered, and it is therefore considered to be facing an extremely high risk of extinction in the wild.
<b>Endangered (EN)</b>	A taxon is <b>Endangered</b> when the best available evidence indicates that it meets any of the criteria A to E for Endangered, and it is therefore considered to be facing a very high risk of extinction in the wild.
<b>Vulnerable (VU)</b>	A taxon is <b>Vulnerable</b> when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable, and it is therefore considered to be facing a high risk of extinction in the wild.
<b>Near Threatened (NT)</b>	A taxon is <b>Near Threatened</b> when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for (or is likely to qualify for) a threatened category in the near future.
<b>Least Concern (LC)</b>	A taxon is <b>Least Concern</b> when it has been evaluated against the criteria and does not qualify for the Critically Endangered, Endangered, Vulnerable or Near Threatened categories. Widespread and abundant taxa are included in this category.
<b>Data Deficient (DD)</b>	A taxon is <b>Data Deficient</b> when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. Data Deficient is not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that a threatened classification is appropriate.
<b>Not Evaluated (NE)</b>	A taxon is <b>Not Evaluated</b> when it has not yet been evaluated against the criteria.

A measurement is cited as the mean value (with minimum value to maximum value in parentheses) and sample size. For some, the standard deviation (mean  $\pm$  1 S.D.) is given instead of the range. For most species, data for males and females are presented separately. In some cases, more than a single set of measurements is given; this is particularly the case for widespread species where geographic variation in size may be evident, and also for species with several well differentiated subspecies (in which case, we have endeavoured to present a set of measurements for each). Some

species have additional stand-alone measurements presented beneath the primary series. Skull measurements are generally not provided, with the exception of the small carnivores (Herpestidae, Mustelidae, Nandiniidae and Viverridae). The majority of measurements also contain the location(s) where the specimens were obtained, and the source of the data. Sources are either cited publications, or specimens in museums, or unpublished information from authors or others. The acronyms for museums where specimens were examined and measured are given in Table 5.

**Table 5. Museum acronyms and abbreviations.**

Acronym	Museum name	Acronym	Museum name
AMNH	American Museum of Natural History, New York, USA	MZUF	Museo Zoologico de 'la Specola', Firenze, Italy
BMNH	Natural History Museum, London, UK [formerly British Museum (Natural History)]	NHMB	Naturhistorisches Museum, Berlin, Germany
CMNH	Cleveland Museum of Natural History, Ohio, USA	NMNH	Smithsonian National Museum of Natural History, Washington DC, USA
DM	Durban Natural Science Museum, Durban, South Africa	PCM	Powell-Cotton Museum, Birchington, UK
FMNH	Field Museum of Natural History, Chicago, USA	RMNH	Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (formerly Rijksmuseum Natuurlijke Historie)
IRSN	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium	SBP	Station Biologique de Paimpont, Université Rennes 1, France
JFBM	James Ford Bell Museum of Natural History, Minnesota, USA	SMF	Senckenberg Museum, Frankfurt, Germany
LACM	Los Angeles County Museum of Natural History, Los Angeles, USA	SMNK	Staatliches für Naturkunde, Karlsruhe, Germany
MCZ	Museum of Comparative Zoology, Harvard University, USA	SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
MHNC	Musée d'Histoire Naturelle, La Chaux-de-Fonds, Switzerland	ZFMK	Zoologisches Forschungsmuseum, Alexander Koenig, Bonn, Germany
MNHN	Muséum National d'Histoire Naturelle, Paris, France	ZMA	Zoologisch Museum, Amsterdam, The Netherlands
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium	ZMB	Zoologisches Museum der Alexander von Humboldt Universität, Berlin, Germany
MSUM	Michigan State University Museum, Michigan, USA	ZMMU	Zoological Museum, Moscow University, Moscow, Russia
		ZSM	Zoologische Staatssammlungen München, Munich, Germany

**Key References** A select list of references, which provides more general information on the species, or a work that is generally considered to be a key reference work on the species. Each reference is given in full in the Bibliography. Citations given in the text (but not cited in ‘Key References’) are also given in full in the Bibliography. In general, profiles account for all literature published up until the end of 2007. Authors and editors have endeavoured to keep the species profiles fully up-to-date throughout the long production schedule, and references published from 2008 onwards have been incorporated where possible. None the less, certain key recent papers will have been missed or omitted.

**Author** The name of the author, or authors, is given at the end of each profile. All profiles should be cited using the author name(s).

**Tables** With a few exceptions, the use of tables to present data has been avoided in Volume V of *Mammals of Africa*.

## Higher taxon profiles

The profiles for orders, families and genera are much less structured than for the species profiles. Each profile usually begins with a listing of the taxa in the next lower taxon; for example, each family profile lists the genera in that family. An exception to this arrangement is where a taxon has only one lower taxon. Higher taxa profiles provide the characteristics common to all members of that taxon. Some of these characteristics (for example, number of nipples or dental formula) may not be repeated in lower taxon profiles (unless essential for identification), so readers are encouraged to consult also the higher-taxon profiles, e.g. the species profile for *Canis simensis* should be consulted in association with the genus *Canis* profile. Likewise, a generic profile, such as *Canis*, should be read in association with the family Canidae profile.

## Distribution maps

Each species profile contains a pan-African map showing the geographic range of the species. The purpose of the maps is to show current known limits of distribution of the species within historical range, recognizing that within this mapped range a particular species’ distribution will not be homogeneous. Reintroductions within the former range of a species are included and mapped, but

introductions outside of the former known range are not. Note that due to the sensitivity around the location of rhinoceros populations in Africa, the maps for these species are degraded to the country level. Subspecies are only indicated in cases where the boundaries can be reasonably delineated.

Each map shows the boundaries of the 47 countries of Africa, some of the major rivers (Nile, Niger–Benue, Congo [with the tributaries Ubangi, Lualaba and Lomani], Zambezi and Orange), and Lakes Chad, Tana, Turkana (formerly Rudolf), Albert, Edward, Victoria, Kyoga, Kivu, Tanganyika, Malawi, Mweru, Bangwuela and Kariba. The map projection is Transverse Mercator, with the following parameters: False Easting: 0; False Northing: 0; Central Meridian: 20; Linear Unit: metre; Datum: Clarke 1866.

The geographic distribution of a species is indicated as:

- red shading = current range. Different colour shading denotes subspecies, where appropriate.
- × = isolated locations considered to be separate from the main geographic range(s); some locations indicated by × may include two or more closely spaced locations.
- ? = uncertain, but possible, presence.
- red arrow = recorded from the island indicated by the arrow.

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# Cohort FEREUUNGULATA

Fereuungulata Waddell, Okada & Hasegawa, 1999. *Syst. Biol.* 48: 3.

Fereuungulata is a mammalian cohort that unites the carnivores and pangolins with what were traditionally and popularly dubbed 'Ungulates', a category that sometimes, but not always, has been thought to have a relationship with whales. Use of the taxon name Fereuungulata, instead of Ferungulata (*sensu* Simpson 1945, who included also paenungulates, but not pholidotes or cetaceans) follows Asher & Helgen (2010).

The orders Artiodactyla and Perissodactyla, or more commonly the even-toed and odd-toed 'ungulates', respectively, both made their first appearance in the fossil record in the earliest Eocene, around 55 mya. Members of both orders are known across the northern hemisphere at this time, but their origin is commonly assumed to be in Asia (Beard 1998). This time period coincides with a major fall in sea level and with dispersal events among many mammalian groups.

It has been commonly assumed that artiodactyls and perissodactyls had a common evolutionary origin, in part based on their dental and post-cranial similarities, and yet many of these features can be shown to have evolved convergently, including hooves (Prothero *et al.* 1988, Prothero & Shoch 2002). Recent molecular studies have further complicated traditional efforts to fathom the evolutionary history of 'Ungulates'.

Of major significance has been the excision of 'subungulates' or 'paenungulates' (elephants, hyraxes and sirenians, plus some related extinct groups) from any possibility of close relationship. Several molecular phylogenetic studies have shown that these African groups must be removed from the same clade as the northern ungulates. As a result of these studies, Paenungulata is now a cohort in its own

right within the new supercohort Afrotheria (see Springer *et al.* 2005; and Supercohort Afrotheria in *Mammals of Africa*, Volume 1).

Another complication has been the creation of a clade to embrace both whales and artiodactyls (see Springer *et al.* 2005 for a review of the molecular evidence for higher order mammalian clade relationships). For several decades cetaceans (whales and dolphins) were presumed to have a relationship to artiodactyls, but molecular studies now place them as a suborder *within* what used to be called the Artiodactyla (the two former orders now combined in order Cetartiodactyla). However, there is still much dissension between molecular biologists and morphologists as to exactly how whales are related to other artiodactyls.

It is also not clear whether artiodactyls (= cetartiodactyls) and perissodactyls form a monophyletic group. Molecular studies (e.g. Liu *et al.* 2001, Meredith *et al.* 2011) unite a clade of Carnivora plus Pholidota (pangolins) as the Ferae (see below), and in turn show a close relationship to these ungulates. But while some studies place the Ferae clade outside of the grouping of the two ungulate orders (thus making the ungulate grouping monophyletic), others group the Ferae as the sister taxon to Perissodactyla (e.g. Waddell *et al.* 1999), although the morphological support for this grouping is slender. Some molecular studies also place bats within this clustering of carnivores



Golden Jackal *Canis aureus*.

and ungulates (as related to perissodactyls), while others have bats as the sister taxon to ungulates plus carnivores (see Meredith *et al.* 2011). In spite of such uncertainties, this work has provisionally adopted a molecular taxonomy that aligns a monophyletic clade comprising the orders Cetartiodactyla and Perissodactyla (Euungulata, after Waddell *et al.* 2001) with a monophyletic Ferae (Carnivora + Pholidota) under the cohort 'Fereuungulata' (and see Zhou *et al.* 2012).

Modern Carnivora have, in general, modified their cranial anatomy less radically than have Cetartiodactyla (the most extreme, of course, being the whales). The diversification of carnivores is sketched out in the Carnivora profile. Modern Pholidotes (pangolins), totally toothless, have made their affinities particularly difficult to fathom so the discovery by geneticists of a molecular link with carnivores has, at last, provided some sort of a lead, however distant, into the remotest origins of this most enigmatic of mammal orders. None the less, by adopting such a specialized ant and termite diet, and evolving the equivalent of mediaeval armour, the pangolins are almost as different from their nearest affines as whales are from pigs and hippos.

Many phylogenies have positioned artiodactyls and perissodactyls as 'closely related'. Today, we may well see living artiodactyls and perissodactyls as being rather similar types of mammals: horses are not so dissimilar from cows (i.e. both are largish, long-legged grazing mammals) and rhinos are not superficially remote from hippos (but note there has never been a perissodactyl equivalent for the huge radiation of omnivorous pigs among the artiodactyls). It is, thus, important to remember that during the Eocene, when most of the northern hemisphere was covered by tropical-like forests and the earliest artiodactyls and perissodactyls had begun their radiation, each lineage represented emphatically different types of mammals (see Janis 2008).

Artiodactyls were mainly small forms, rather like present-day mouse deer (Tragulidae) in both size and ecology. Their dental morphology indicated omnivorous (or, at best, soft browsing diets that included berries, buds and non-fibrous leaves). The perissodactyl equivalent of these early artiodactyls would have been the early equids ('horses'). Perissodactyls also branched out into a number of different, and larger, ecological types, most with more specialized browsing diets. These included ceratomorphs (rhinos and true tapirs) and a diversity of extinct lineages: a diversity of small 'tapiroids', the rhino-like brontotheres, and the rather horse-like chalicotheres that substituted claws for hooves.

By the late middle Eocene, around 45 mya, the northern hemisphere climate commenced cooling and drying, a trend that characterized the rest of the Cenozoic (see Morley & Kingdon, *Mammals of Africa*, Volume 1, pp. 43–56). Tropical forests started to retreat, replaced by more temperate woodlands, and this period heralded a time of great evolutionary turnover among the ungulates, among which artiodactyls apparently pulled ahead of the perissodactyls in terms of 'evolutionary success'. The first fossil ruminants (still small, tragulid-like forms) are known from this time in Asia and North America.

This change in fossil diversity has long been interpreted as reflecting some evolutionary superiority of artiodactyls, presumed to relate to the rumen-based foregut method of fermentation of fibrous vegetation in at least some clades, in contrast to the less derived mode of hindgut fermentation in perissodactyls (see Hofmann & Kingdon, *Mammals of Africa*, Volume 6, p. 84). However, the fossil record does not support the notion of a blanket competitive replacement. Moreover, it is certainly not the case that rumen-based fermentation is inevitably superior to hindgut fermentation under *all*

ecological circumstances. The rise of the more folivorous clades of artiodactyls (Ruminantia and Tylopoda) during the late Eocene, and the decline of the perissodactyls, is best explained by changes that would have taken place in vegetational quantity, quality and seasonal availability that would favor these animals' mode of feeding selection (small amounts of high-quality food: see discussion in Janis 2008).

Among the later Eocene artiodactyls a clear division emerged. As presented in these volumes, this has taken the form of four modern suborders: Suiformes (pigs and peccaries), Tylopoda (camelids), Whippomorpha (hippos and whales) and Ruminantia (modern ruminant groups, including tragulids). There is considerable debate as to how the artiodactyl suborders are interrelated, and as to where extinct groups would fit in. Hippos, long supposed to have some sort of affinity with suids, have been declared as close whale relatives by molecular biologists (with Whippomorpha as a sister group of the Ruminantia by Price *et al.* 2005). Craniodental morphologies have linked tylopods and ruminants as sister taxa in the 'Neoselenodontia', but molecular biology has broken this grouping up, and placed camelids as basal to other artiodactyls (including whales) (see Price *et al.* 2005). In any event, the modern lineages of artiodactyls gained their first evolutionary foothold during the late Eocene (about 40–35 mya). At this time some clear divisions emerged and the contemporary descendants of these early radiations are provisionally presented in these volumes in the form of the aforementioned modern suborders.

The late early Miocene, around 20–18 mya, marks another critical point in the patterns of ungulate evolution. Out of the initial diversification of perissodactyls, only four families remained: rhinocerotids, tapirs, chalicotheres (which survived into the Pleistocene) and horses. At this time, the first of the more derived equids (subfamily Equinae) appeared in North America (first appearing in the Old World around 10.5 mya). These equids were of a larger body size (pony-sized) and larger than previous forms, with high crowned (hypsodont) cheekteeth indicative of a diet that included at least a good proportion of grass, and with limbs more adapted for locomotion in open habitats.

The radiation of equids in North America has long been a well-known example of evolution (although they subsequently became extinct on that continent). In the Old World there is today only a single genus of grazing equid (*Equus*, comprising some seven, mostly allopatric, species) in contrast with the broad diversity of antelopes (although only a minority of antelope species are specialized grazers). However, horses in the middle to late Miocene of North America, including both grazing and browsing forms, were equal in their taxonomic diversity to the present day African bovids. Their decline in the latest Miocene predated the entry of bovids to North America, and was likely related to climatic changes. The genus *Equus* only reached Africa in the Pleistocene (although there was a moderate African late Miocene/Pliocene radiation of immigrant equids of the three-toed genus *Hipparion*). When zebras today, in substantial numbers, share their African pastures with grazing bovids, their present-day ecological success echoes the success that horses achieved in North America, albeit now expressed outside of their continent of origin.

In spite of possessing different digestive systems, bovids and equids represent the evolution of specialized grazers on different continental land masses, rather than two competing adaptive types with clear 'winners' and 'losers'.

## Superorder FERAЕ

Ferae Linnaeus, 1758. Syst. Nat., 10th edn, 1: 37.

The superorder Ferae describes the recognition of a very unexpected affiliation between Carnivora and the pangolins, Pholidota, a clade that is well supported in molecular studies (Liu *et al.* 2001, Murphy *et al.* 2001a, b, Springer *et al.* 2005, Meredith *et al.* 2011, Zhou *et al.* 2012). Use of the name Ferae follows Asher & Helgen (2010); alternatively, the name Ostentoria has been applied to this clade of pangolins plus carnivorans (e.g. Amrine-Madsen *et al.* 2003).

The later radiations of Carnivora are becoming better known, and these are outlined in the appropriate profiles, but what still earlier divergence could have led to pangolins? The multiplicity of extant carnivores includes many forms that are relatively conservative and some of these, such as the Two-spotted Palm Civet *Nandinia binotata*, are omnivorous (including insects), well-clawed and also arboreal. It is very likely that the earliest proto-pangolin was also a small, sharp-clawed, tropical Asiatic tree-climber with omnivorous or insectivorous tastes, and, given the crucial role of the tail in all pangolin species, that its long tail was prehensile and scaly. The beginnings of scales, which are cornified extrusions of outer skin, can be seen on the tails of various mammals such as rats, some insectivores and some afrotherians, while the most explicitly counter-abrasive tail-scales are found among anomalurid rodents. Carnivore-like proto-pangolins could, therefore, have been well-entrenched arboreal omnivores or insect-eaters with strongly prehensile and abrasion-resistant tails. Strong tails can also serve to mitigate accidents and predation in that it is harder for their owners to be dislodged. As a fifth limb, such tails also make it easier

for animals to engage in vigorous action while climbing, foraging or fighting.

Ants and termites have probably been a major component in the canopy of tropical rainforests for about as long as there have been rainforests and many species of arboreal ants and termites build nests in or on branches, or live in symbiosis with ‘ant-plants’, *Myrmecodia* and *Hylocophytum*, that have evolved chambers to accommodate the ants (Huxley 1978). Whereas many canopy resources are ephemeral, seasonal or unreliable, ants tend to be more predictably perennial inhabitants of the tropical canopy. Even in the Palaeocene, any arboreal predator that could penetrate the ants’ physical defences and also digest their chitinous, formic acid-protected bodies would have been assured of a reliable food supply. Once embarked on such a specific diet, the earliest pangolins, probably very small animals, must have progressively modified their teeth, tongues and digestions, and lost most of their fur as scales spread from the tail to body and limbs. Eventually some forms came to the ground and some became much larger (possible affinities between pangolins are discussed in the Manidae profile).

Modern pangolins no more resemble carnivores than whales do giraffes, yet fossils, genes and biological logic continue to reveal that such affinities, even when separated by many millions of years, can become comprehensible. As evidence accumulates we can expect that the intervening adaptive steps that have taken highly derived taxa ever further from their less-specialized origins can eventually be reconstructed with some confidence.

Jonathan Kingdon

## Order CARNIVORA – Carnivores

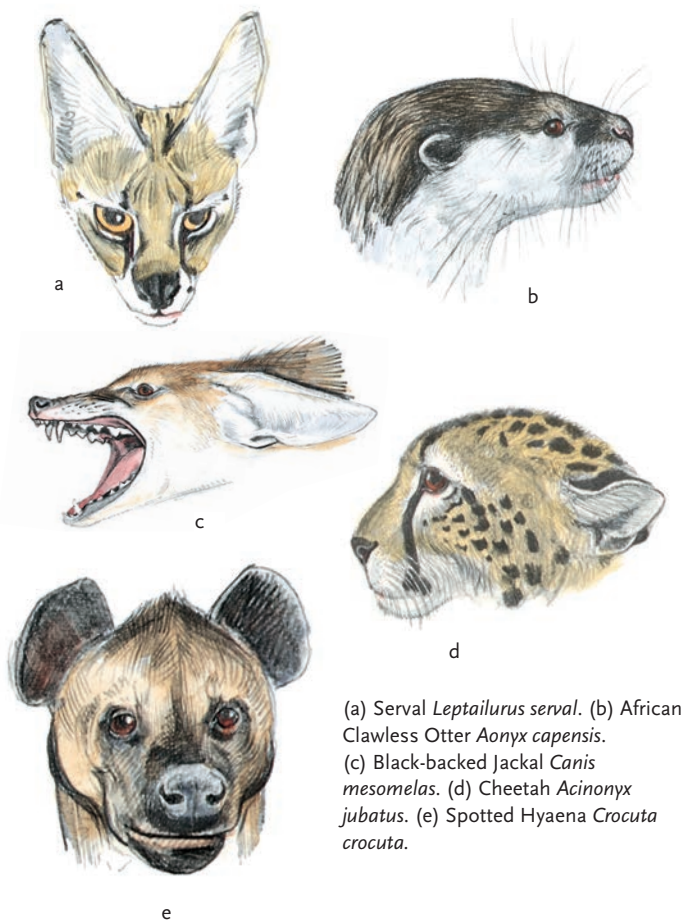
Carnivora Bowdich, 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. Paris, J. Smith, 115 + [31] pp., 16 plates.

<b>Caniformia</b>		
Canidae (4 genera, 12 species)	Foxes, Wolves, Jackals, Dogs	p. 28
Mustelidae (8 genera, 11 species)	Weasels, Polecats, Otters, Ratel and allies	p. 82
Otariidae (1 genus, 1 species)	Fur Seals	p. 126
Phocidae (1 genus, 1 species)	True Seals	p. 132
<b>Feliformia</b>		
Nandiniidae (1 genus, 1 species)	Two-spotted Palm Civet	p. 138
Felidae (6 genera, 10 species)	Cats	p. 144
Viverridae (3 genera, 17 species)	Genets, Linsangs, Civets	p. 211
Hyaenidae (3 genera, 4 species)	Hyaenas, Aardwolf	p. 260
Herpestidae (14 genera, 26 species)	Mongoose	p. 293

Carnivora are highly diverse in Africa. From Lions *Panthera leo*, Cheetahs *Acinonyx jubatus*, hyaenas and mongooses to clawless otters, polecats, Cape Fur Seals *Arctocephalus pusillus* and African Wild Dogs *Lycaon pictus*, this varied array of predators, scavengers, piscivores and omnivores play keystone roles in many African habitats, from the Serengeti Plains to the Congo rainforest. Yet, it is noteworthy that the key anatomical feature usually associated with Carnivora, elaborated and restricted carnassial shear in the dentition, predates its appearance in modern forms. The carnivory indicated by this primary dental adaptation has been substantially modified in the dietary specialization of many living carnivorans, with varying degrees of hypocarnivory to hypercarnivory, reflecting a wide range of specialized diets.

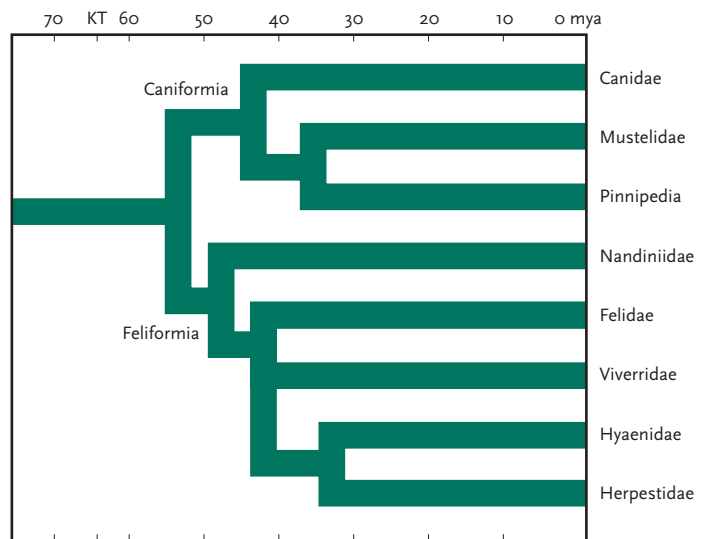
Even though many carnivorans retain a relatively generalized anatomy, diversity also marks virtually every aspect of their biology.





Carnivora are remarkably diverse taxonomically, being the fourth most speciose of modern mammalian orders with >280 species (see Wozencraft 2005 for a recent classification of the order). Species diversity varies markedly among the major extant clades, from the monospecific Nandiniidae, Ailuridae and Odobenidae to the dozens of mustelid species, and with terrestrial–freshwater taxa outnumbering the marine Pinnipedia by roughly 7 to 1. Carnivoran ecological diversity embraces diurnal, crepuscular and nocturnal forms; cursors, climbers, diggers, swimmers (freshwater and marine); and flesh eaters, herbivorous forms, insect eaters, piscivores and omnivores. The breadth of their geographic and environmental range spans land to water, all continents, from pole to pole, from deserts to high mountains to rainforests. An outstanding fossil record also makes Carnivora one of the most important and widely studied groups of mammals.

While ambling plantigrade forms are common, both speed and hunting range can be remarkable in cursorial carnivorans, with the Cheetah noteworthy as the fastest mammalian short-distance sprinter. Body size (correlated with many life history and physiological attributes) among living Carnivora ranges over more than four orders of magnitude, exceeding that observed in any other mammalian ‘order’, from the tiny Least Weasel *Mustela nivalis* at just 100 g to the gargantuan Southern Elephant Seal *Mirounga leonina* at up to 4000 kg. Delayed implantation of embryos is widespread among mammals, but is particularly common in mustelids and mephitids, representing almost half of the documented mammalian cases (Thom *et al.* 2004). Although it appears to be correlated with longevity, maximum latitude of geographic range and maternal investment (after correcting for phylogeny; Thom *et al.* 2004), the

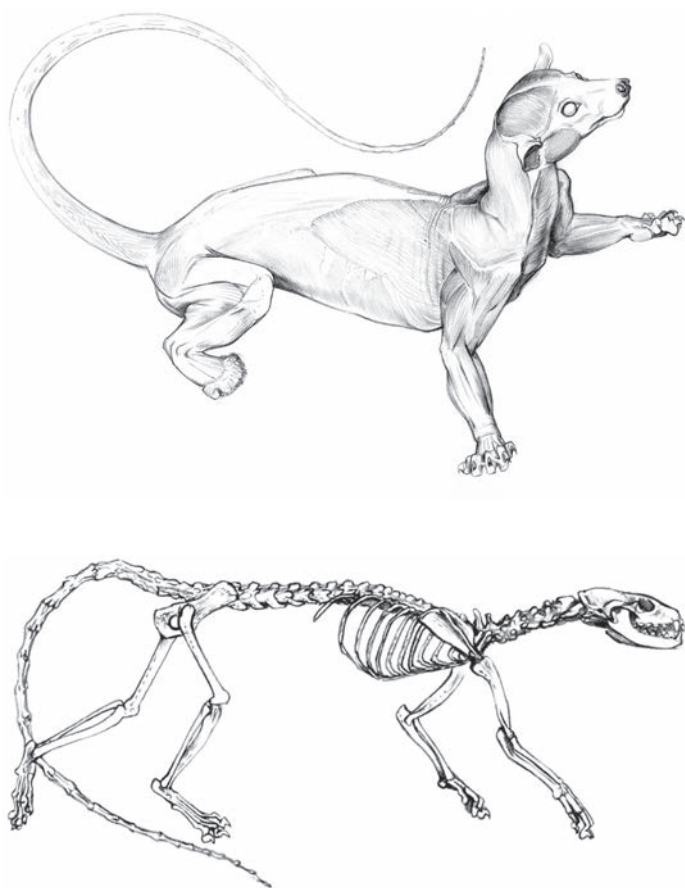


Tentative phylogenetic tree for extant African carnivora (after Flynn *et al.* 2005, Eizerik & Murphy 2009).

observation of delayed implantation in marine carnivorans (e.g. Ross Seals *Ommatophoca rossii*) and inference that it may occur in all pinnipeds, indicate that much remains to be learned about this important reproductive trait. Of course, the marine pinnipeds differ from their terrestrial relatives in many key features related to their specialized aquatic habitus, such as locomotor, metabolic and respiratory adaptations (e.g. the Weddell Seal *Leptonychotes weddellii* can remain submerged for 80 minutes during foraging dives to 700 m, while the champion diver is the Southern Elephant Seal, spending some 90% of its time submerged at depths up to 2150 m and for up to 120 minutes). Social systems also vary widely, from the many solitary species, to pair or small-group forming taxa, to the diverse array of social forms (e.g. Lion prides, colonial herpestids, or pack-hunting canids), all of which are found in Africa today.

The clade Carnivora is actually a relative latecomer to the African continent and the fossil record documents similar predator niches being first occupied by the now-extinct creodont clade Hyaenodontidae (first arriving in Africa during the late Eocene). Creodonts went extinct in Africa about 13 mya. The late arrival of Carnivora partially explains the uneven modern distribution of subclades in Africa. For example, many predominantly herbivorous forms that occur on other continents (e.g. Giant Panda *Ailuropoda melanoleuca*, Red Panda *Ailurus fulgens*) do not occur in Africa. In addition, members of the families Ailuridae, Procyonidae, Mephitidae, Eupleridae, Odobenidae and Ursidae do not occur in mainland Africa today. However, fossil bear (Ursidae) remains have been retrieved from north, north-east and southern Africa. Others, like Phocidae (one species) or Viverridae (two subfamilies), are much more diverse elsewhere. Several other entirely extinct higher-level clades also occurred in the past in Africa, such as various sabretooths and ‘false sabretooths’, Machairodontinae (Felidae) and Nimravidae, respectively, which flourished and diversified within Africa between the Miocene and about 1.5 mya, and the ‘bear-dogs’ of the family Amphicyonidae as well as the aforementioned creodonts.

Of living families, only one is found solely on mainland Africa: the monospecific Nandiniidae (recently raised to this rank based on strong genetic support for the Two-spotted Palm Civet *Nandinia binotata*



Two-spotted Palm Civet *Nandinia binotata* myology (above) and skeleton (below).

forming the outgroup to all other living feliform Carnivora, well outside of its traditional placement as a member of the Viverridae). In addition, the Eupleridae are now recognized to be a monophyletic array embracing all the carnivorans that are endemic to Madagascar (although they appear to have originated in Africa during the middle Cenozoic prior to their dispersal to the island; Yoder *et al.* 2003). Tectonic, environmental and biogeographic events and processes have profoundly influenced the global distributions of Carnivora (reviewed in Deméré *et al.* 2003, Hunt & Tedford 1993, Flynn & Wesley-Hunt 2005; for novel divergence times and biogeographic hypotheses in the Felidae, see Johnson *et al.* 2006).

Flynn & Wesley-Hunt (2005), Flynn *et al.* (2010) and Spaulding & Flynn (in press) have provided detailed overviews of higher-level phylogeny and taxonomy, temporal distributions and biogeography of modern Carnivora and their extinct relatives. Similarly, the higher-level phylogeny of living Carnivora has been investigated comprehensively by Flynn *et al.* (2005; using primary molecular data), while Bininda-Emonds *et al.* (1999) adopted a 'supertree' approach that derives from phylogenetic tree topologies from earlier studies. Several recent studies have begun expanding taxon or character sampling for living and fossil forms, such as the morphological studies of early fossil Carnivoramorpha (Spaulding *et al.* 2010, Spaulding & Flynn in press) and the molecular analyses of Eizirik *et al.* (2010; 14 nuclear loci for representatives of all extant families), Agnarsson *et al.* (2010; mitochondrial cyt b for about 80% of extant species), Yu *et al.* (2011; 22 new nuclear introns for 16

extant caniforms) and Meredith *et al.* (2011; 164 mammals, 26 loci, >35kb/11k amino acid sequences). Other authors in this volume provide in-depth treatments of current thinking about the phylogeny and evolution of the African Carnivora.

Recent analyses of, and controversies about, the higher-level phylogeny of Carnivora have centred on three hierarchical levels: (1) their closest relatives among the Eutheria (both living and fossil); (2) whether early Cenozoic fossils commonly assigned to the Miacidae and Viverravidae ('Miacoidae') are members of the crown-clade Carnivora or nearest outgroups to the living carnivorans (which together would be considered the Carnivoramorpha); and (3) the composition and positions of various subclades within Carnivora (especially the pinnipeds, Ailuridae, 'Mustelidae' and interrelationships among the modern feliform families).

Some of these problems now appear to have been resolved with significant molecular and palaeontological support, whereas others remain uncertain in spite of intense study and thus are the focus of continuing analysis. Carnivora have been among those living mammal orders that have remained difficult to ally to any others via morphological analyses (see Novacek 1992). These difficulties were often tied to the idea that the orders diversified extremely rapidly following the K/T boundary event (extinction of the dinosaurs). Among extinct forms, anatomical features that might associate Carnivora most closely with creodonts were noted by Wyss & Flynn (1993). Modifying an original conception of Linnaeus (1758), Simpson (1945) classed both as Ferae, a usage of the name accepted by the current author contra the broader definition used in the prior section of this volume. Among living forms, Wyss & Flynn (1993) also noted anatomical features shared by Carnivora and lipotyphlans, while initial molecular studies linked carnivorans to many other distinct lineages, from ungulates to bats, but the most comprehensive molecular samplings to date (e.g. Murphy *et al.* 2001) have suggested a surprising sister-group relationship between Carnivora and Pholidota (pangolins). Morphological support for this would come from an ossified tentorium in the braincase, which is shared by carnivorans, pangolins and creodonts (Wyss & Flynn 1993).

Monophyly of Carnivora is very strongly supported by both molecular and anatomical evidence. Likewise, a major split within the order of Caniformia ('dog-like') and Feliformia ('cat-like') is well supported. Within Caniformia, canids are outgroup to all the remaining forms (Arctoidea). Among arctoids there is sequential branching of ursids, pinnipeds and Musteloidea. Within musteloids there is a tritomy of Mephitidae (now removed from Mustelidae), Ailuridae and the clade of Mustelidae + Procyonidae. *Nandinia* has now been shown to be the outgroup to all other living feliforms. The monophyletic Malagasy Eupleridae is most closely related to Herpestidae, which together form a sister-group to Hyaenidae. Remaining ambiguity centres on the pattern of interrelationships among the Felidae, Viverridae and the HHE (or Hyaenidae–Herpestidae–Eupleridae) clades. In addition, recent documentation of the monophyly of all of Madagascar's Carnivora has resulted in a grouping of anatomically diverse forms that formerly had been placed in at least three separate families: Herpestidae, Viverridae, Felidae (Yoder *et al.* 2003). Furthermore, it has been proposed that prionodontine linsangs, formerly placed in Viverridae, might actually be allied with cats (Gaubert & Véron 2003, Gaubert *et al.*

2005a). These taxonomic upheavals suggest a much more complex pattern of behavioural and morphological transformations within the Feliformia than had previously been indicated.

The pre-Holocene fossil record for modern families is patchy (e.g. none for Eupleridae, extensive for Canidae), which partly reflects dominant habitats, geographic distributions and uneven palaeontological sampling. Entirely extinct clades have provided novel information about carnivoran history and the sabre-toothed nimravids, 'bear-dog' amphicyonids and the early fossil 'miacoids' are well represented. Anatomical data noted a century ago by Matthew (1909) suggested possible placement of the Miacidae and Viverravidae within a crown-clade Carnivora as basal caniforms and feliforms, respectively (Flynn & Galiano 1982). The most recent molecular and palaeontological studies now provide strong evidence for virtually all of these 'miacoids' being stem Carnivoramorpha lying outside the Carnivora (e.g. Wesley-Hunt & Flynn 2005, Spaulding & Flynn in press). It now appears that 'miacids' form a paraphyletic array of sequential outgroups to the Carnivora, with a monophyletic grouping of Viverravidae situated at the base of the Carnivoramorpha. This topology of fossil and living forms is highly significant for evolutionary and ecosystem studies because earlier results suggested that the origin of Carnivora and the split between caniforms and feliforms could have been as old as 65–60 mya, whereas the latest results suggest much younger ages for these events (minimum divergence estimate of 43 mya).

The 'order' Creodonta, named more than 125 years ago by Cope (1875), comprised an entirely extinct radiation of early to middle Cenozoic forms that resembled Carnivora in meat-eating specializations and in some locomotor features. In body form, creodonts were generally large-bodied, terrestrial predators or scavengers, with relatively large heads and plantigrade locomotion (Savage 1977). However, their relationship to the Carnivora has long been questioned and creodonts are of debatable monophyly themselves (see Flynn & Wesley-Hunt 2005).

A variety of craniodental and post-cranial features have been used to characterize living Carnivora, including reduction or loss of the clavicle, loss of the stapedial artery in the basicranium, fully ossified auditory bulla (except in *Nandinia*), thin lamina between the head and neck of the malleus, fusion of the scaphoid and lunar bones of the wrist (into a single scapholunar) and the specifically carnivoran P<sup>4</sup>/M<sub>1</sub> carnassial pair. However, given that modern carnivorans are reasonably easy to identify, it is noteworthy that it has been difficult to rigorously diagnose the clade based on unique derived characters. There are a variety of potential reasons for this, notably their rapid divergence from other eutherians. Inferences of broader patterns of evolution across the entire Carnivora have been hindered by poor resolution of their higher-level interrelationships. Also, as mentioned above, the classical synapomorphy of Carnivora (P<sup>4</sup>/M<sub>1</sub> carnassial shear) now appears to have much deeper roots in evolutionary ancestry, appearing first in early Cenozoic stem-Carnivoramorpha fossils (Palaeocene Viverravidae, ~63 mya) (for these and features cited below, see Wesley-Hunt & Flynn 2005). Similarly, a completely ossified bulla fused to the basicranium is not a synapomorphy of Carnivora, but rather evolved independently several times within the group, while the retractile claws found only in a few living clades

now appear to be a deep synapomorphy, with subsequent loss or reduction independently several times.

Carnivoramorpha are distinguished from all other Mammalia, including creodonts, by dental features such as P<sup>4</sup>/M<sub>1</sub> carnassial shear (P<sup>4</sup> with anteriorly situated paracone), and a broad M<sub>1</sub> parastyle that is equal to or larger than the metastyle. Numerous advanced features of the crown-clade Carnivora were acquired sequentially, with Carnivora now uniquely diagnosed by a flange on the basioccipital (attachment for the entotympanic of the bulla), loss of M<sup>3</sup>, fusion of the scaphoid and lunar, and an expanded braincase (Wesley-Hunt & Flynn 2005).

Various features have been used to diagnose major subclades within the Carnivora ever since Turner's (1848) and Flower's (1869a) pioneering use of auditory bulla shape and bony internal partitions (see Ivanoff 2001, Wesley-Hunt & Flynn 2005). Those features that distinguish family and lower-level groups are summarized elsewhere in this volume but it should be remembered that many fossil Carnivora (and the living *Nandinia*) lack a fully ossified auditory bulla. 'The fully ossified entotympanic (wholly or partially fused to the basicranium) evolved independently within the Caniformia and Feliformia, although an increasingly strong attachment and incorporation of the bulla to the basicranium can be inferred along the phylogeny' (Wesley-Hunt & Flynn 2005: 14). Among interesting examples of anatomical specializations in these groups are the marked expansion of the maxilloturbinals in the Caniformia and a long and stylized baculum in Canoidea.

There have been many recent interesting studies of the comparative biology, ecology and evolution of carnivorans, including synthesis of evolutionary patterns through time (Van Valkenburgh 1999); palaeoecology, especially of large carnivorans (Turner 1990, Van Valkenburgh 1996); locomotion (Heinrich & Rose 1997); body size evolution or life history strategies (Gittleman 1993, 1994a, Meiri *et al.* 2004a, b, 2009); brain size (Gittleman 1991, 1994b, Gittleman & Van Valkenburgh 1997); social structure (Creel & Macdonald 1995, Geffen *et al.* 1996); and physiology, energetics or diet (Lee *et al.* 1991, McNab 1995, Carbone *et al.* 1999). Furthermore, the growing resolution and strength of support for the phylogeny of most major groups has brought greater precision to evolutionary analyses, adding genes and fossils to the study of living taxa and this synthesis from different disciplines will surely yield many more exciting results in the near future. Among selected relevant studies are: palaeoecology and ecomorphology (Werdelin 1996a, Van Valkenburgh *et al.* 2003, Werdelin & Lewis 2005, Wesley-Hunt 2005), locomotion (MacLeod & Rose 1993, Wang 1993, MacLeod 2001), body or brain size or correlated life history traits (Lindenfors *et al.* 2003, Webster *et al.* 2004, Finarelli & Flynn 2006, 2009, Flynn *et al.* 2010), biogeography (Hunt & Tedford 1993, Deméré *et al.* 2003) and novel approaches in genetics (Fondon & Garner 2004), modelling and comparative anatomy (Polly 2008) and developmental biology and morphological integration (e.g. relative influences of diet, brain size and phylogeny on cranial anatomy; Goswami 2006). In this thriving discipline are volumes that sample many other approaches and results, notably Gittleman (1989, 1996), Mazin & de Buffrénil (2001), Perrin *et al.* (2002) and Flynn (2003).

John J. Flynn

**Table 6. Carnivore niches.**

Habitat	Fruits	Sessile or cryptic invertebrates and eggs	Active invertebrates	Aquatic or semi-aquatic fauna	Reptiles and amphibia	Small mammals and birds	Medium-sized mammals	Large mammals	Carrion
Forest		← Nandinia →	← Crossarchus →		← Nandinia →				Nandinia
		← Bdeogale nigripes →			← Atilax* →				
		← Genetta servalina →			← Bdeogale nigripes →				
		← Genetta victoriae →			← Genetta spp. →				
Secondary growth		← Dologale →				← Profelis aurata →			
		← Ichneumia* →			← Ichneumia →				
		← Genetta tigrina* →			← Genetta tigrina →				
		← Civettictis* →			← Civettictis* →				Civettictis
		← Rhynchogale →			← Poecilogale* →				
Moist savannas and woodlands		← Bdeogale crassicauda →			← B. crassicauda →	← Panthera pardus →			
		← Mellivora* →			← Mellivora →				
		← Canis adustus* →			← Canis adustus →				C. adustus
		← Herpestes sanguineus* →			← Herpestes sanguineus →				
					← Leptailurus serval →				
Marshes and aquatic				← Atilax* →	← Atilax →				
				← Aonyx congicus (forest swamps and rivers) →					
				← Aonyx capensis (swamps and rivers) →					
				← Hydrictis (rivers and lakes) →					
Thickets, dry savannas and woodlands		← Helogale* →			← Helogale →				
		← Hyaena →			← Felis silvestris* →				Hyaena
		← Otocyon →			← Otocyon →				
		← Genetta genetta →			← G. genetta →				
		← Canis mesomelas →			← Canis mesomelas →				C. mesomelas
					← Caracal caracal →				
(interzones)		← Ictonyx* →			← Ictonyx →				
		← Proteles* →					← Lycaon* →		
Grasslands		← Mungos* →			← Mungos →		← Crocuta →		
		← H. ichneumon* →			← Herpestes ichneumon* →				
		← Canis aureus →			← Canis aureus →				C. aureus
					← P. leo →		← Acinonyx* →		
							← Panthera leo →		

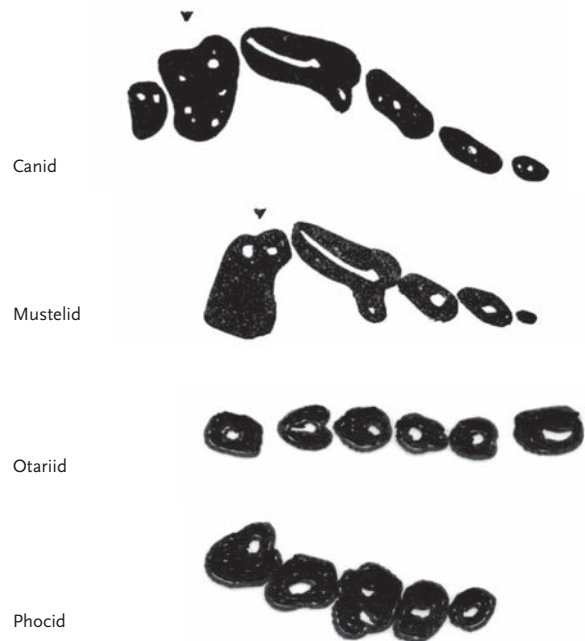
\* Species thus marked occupy a wider range of habitats than can be suggested in a simplified table.

## Suborder CANIFORMIA – Canids, Mustelids, Pinnipeds

Caniformia Kretzoi, 1943. Földtani Közlöny 73: 194.

Suborder Caniformia is traditionally subdivided into the Cynoidea, containing the family Canidae, and Arctoidea, represented by Ursidae (bears) (the most basal clade), Phocidae (true seals), Odobenidae (Walrus *Odobenus rosmarus*), Otariidae (fur seals and sea lions), Ailuridae (Red Panda *Ailurus fulgens*), Procyonidae (raccoons), Mustelidae (weasels, polecats, otters, ratel and allies) and Mephitidae (skunks). This taxonomic arrangement is consistently well supported both by morphological and molecular data (e.g. Flower 1869a, Flynn & Wesley-Hunt 2005, Eizirik *et al.* 2010, Meredith *et al.* 2011; but see Agnarsson *et al.* [2010] who suggest the possible placement of the Red Panda as sister to canids). In Africa, the suborder is represented by the Canidae (four genera and 12, and probably 13, species), Phocidae (one genus, one species), Otariidae (one genus, one species) and Mustelidae (eight genera and 11 species).

Michael Hoffmann



Carnivore molar teeth.

## Family CANIDAE

### FOXES, WOLVES, JACKALS, DOGS

Canidae Fischer, 1817. Mém. Soc. Imp. Nat. Moscow 5: 372.

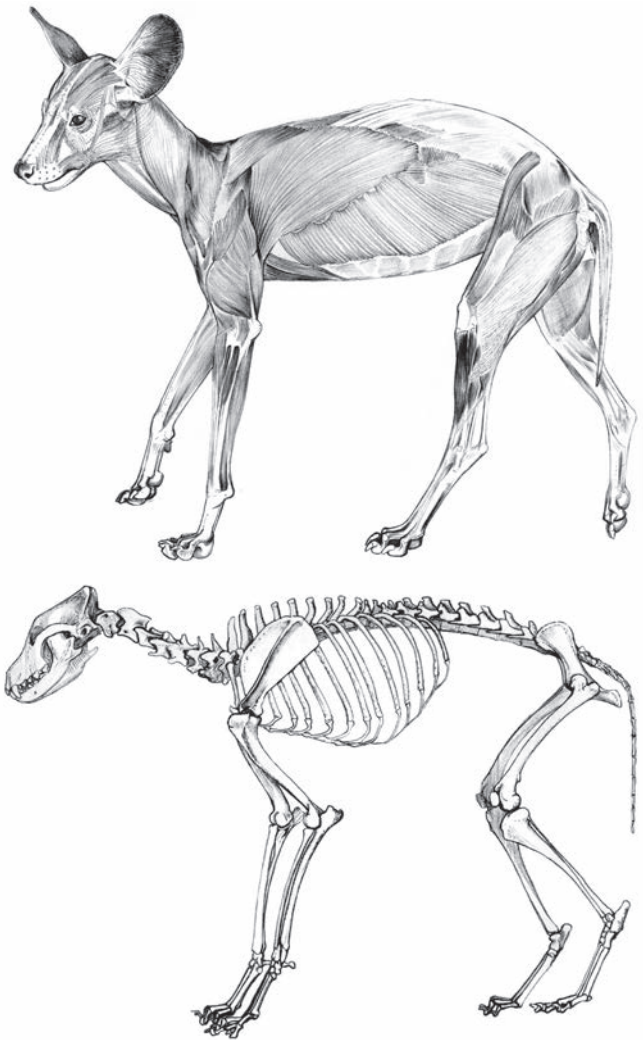
<i>Canis</i> (4, probably 5, species)	Jackals, Wolves	p. 30
<i>Lycaon</i> (1 species)	African Wild Dog	p. 50
<i>Vulpes</i> (6 species)	Foxes	p. 59
<i>Otocyon</i> (1 species)	Bat-eared Fox	p. 77

Canidae – the dog family – is morphologically a relatively homogeneous, polygeneric taxon, distributed widely in all continents with the exception of Antarctica (Macdonald & Sillero-Zubiri 2004). Although much of canid evolution was in open grasslands, their great adaptability has enabled them to flourish in arid habitats, the Arctic, mountains, woodlands and rainforests (and, indeed, cities). Their anatomy is adapted for the cursorial pursuit of prey in relatively open environments, with tall, lithe bodies, a bushy tail, long limbs and digitigrade, four-toed feet. They have triangular heads with long, pointed muzzles, well-developed jaws and prominent, roughly triangular pointed ears (which, in some desert species, are very large).

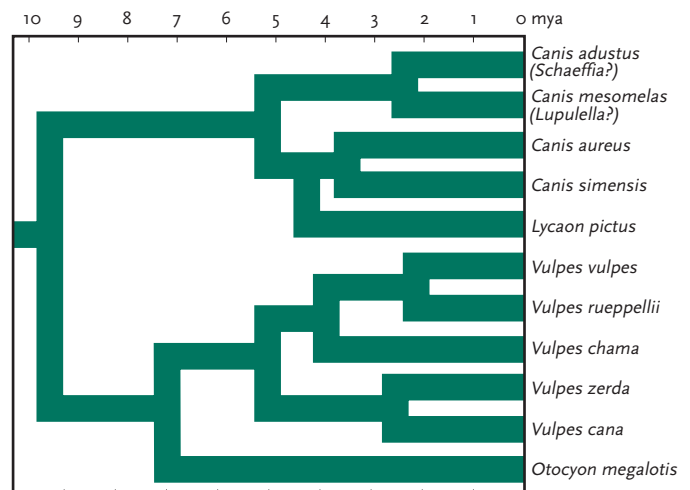
There are three major groups (subfamilies) in the family Canidae: Hesperocyoninae, Borophaginae and Caninae, the first two represented by fossil forms only. The Hesperocyoninae is the most ancient group of all canids, and its basal member, *Hesperocyon*, gave rise to the two more advanced subfamilies, Borophaginae and Caninae (Wang 1994). Canids originated in North America in the Eocene 56–34 mya and underwent extensive radiations from there before reaching the Old World towards the end of the Miocene (ca. 7 mya) (Wang 1994, Wang *et al.* 1999). The oldest records of canids in Africa are those of a small fox from Chad (de Bonis *et al.* 2007) at 7–6 mya, and Kenya, where remains of the genus *Eucyon* date to 6.1–5.6 mya (Morales *et al.* 2005). Prior to these discoveries, the oldest canid in Africa was known from the very earliest Pliocene of Langebaanweg, South Africa, probably referable to *Eucyon* and dated ca. 5.3–5 mya (Rook 1993, Tedford & Qiu 1996).

The genus *Canis* is first known in Africa from South Turkwel, Kenya at 3.5 mya (Werdelin & Lewis 2000), although material from Laetoli (if demonstrated as belonging to *Canis*) may be older (Werdelin & Dehghani 2011). Until the identification of *Canis ferox* from North America as the oldest member of the genus (Tedford *et al.* 2009), the record from South Turkwel – at the time, more than half a million years older than the oldest record of *Canis* elsewhere – suggested a possible African origin for the genus. Various fossils referred to different species of jackal have been recovered from Plio-Pleistocene deposits, but their relationship to modern jackals is uncertain (Werdelin & Lewis 2005). Interestingly, a primitive member of the racoon-dog lineage (no longer extant in Africa) is known from Laetoli in Tanzania at more than 3.8 mya (Barry 1987, Werdelin & Lewis 2005, Werdelin & Dehghani 2011) and younger members of the genus *Nyctereutes* are known from Morocco (Geraads 1997), South Africa (Ficcarelli *et al.* 1984) and Ethiopia (Geraads *et al.* 2010).

The Canidae can broadly be divided into two distinct lineages, the ‘wolf-like’ and ‘fox-like’ forms (e.g. Tedford *et al.* 1995), which diverged between 9 and 5 mya. Fox-like canids are generally small in size, have a low diploid chromosome number ( $2n = 36–66$ ) and



African Wild Dog *Lycaon pictus* myology (top) and skeleton (bottom).



Tentative phylogenetic tree for African Canidae (after Lindblad-Toh *et al.* 2005, Wayne & Ostrander 2007).

are typically rodent hunters (Geffen *et al.* 1992d). Wolf-like canids (wolves, coyotes, jackals, dogs) are medium-sized to large and typically have a diploid chromosome number of  $2n = 74-78$  (Wayne *et al.* 2004). The family blossomed in the Oligocene (19 genera) and exploded in the Miocene (42 genera), declining to the 13 genera recognized today. Bininda-Emonds *et al.* (1999) present a species-level phylogeny for the family, which indicates that some uncertainty remains, particularly among the monotypic canine genera (e.g. *Cuon*, *Speothos*, *Chrysocyon*).

For the most part, the taxonomy of wild canids is largely uncontroversial, although there is some disagreement regarding, for example, the use of the genus name *Pseudalopex* or *Lycalopex* for the South American genera, the validity of the Red Wolf *Canis rufus* as a distinct species, and the status of the Dingo and Guinean Singing Dog (Wang *et al.* 2004, Wozencraft 2005). Of the 13 extant genera and 35 species of Canidae, four genera and 12 species occur in Africa today: *Canis* (four, and probably five, species); *Lycaon* (one species); *Otocyon* (one species); and *Vulpes* (six species).

The Canidae range in size from the Fennec Fox *Vulpes zerda*, weighing less than 1 kg, to the Grey Wolf *Canis lupus*, which can weigh up to 62 kg (Mech & Boitani 2004). Most fox species weigh 1.5–9.0 kg, most other species 5–27 kg. Sexual dimorphism, when present at all, is minimal, with males slightly larger than females but similar in colour. Pelage is relatively short, with dense underfur mixed with longer guard hairs (colour is generally tawny brown or grey, but black, white and shades of ochre also occur). The underparts are usually paler than the rest of the body. The tail is generally bushy, often with a white tip and a darker, bristly patch covering the dorsal supracaudal scent gland near the root.

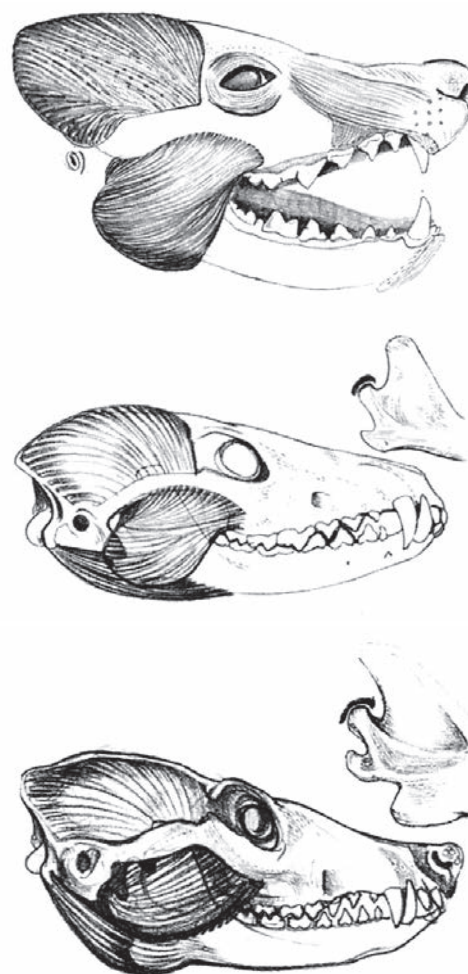
The facial region of the typical canid skull is elongated (although relatively shorter in *Canis* than in *Vulpes* and the South American *Pseudalopex*), with wide zygomatic arches and bony orbits that do not form a complete ring (Clutton-Brock *et al.* 1976). The temporal ridges are sometimes united in a sagittal crest. The auditory bullae are relatively large. Powerful jaw-closing muscles are adaptations for seizing, biting and holding prey. A complex cerebral cortex indicates that these carnivores are intelligent. The characteristic dental formula for the family is  $I^{3/3}, C^{1/1}, P^{4/4}, M^{2/3} = 42$ , although the Bat-eared Fox *Otocyon megalotis* departs from this pattern with 46–50 teeth. The shearing carnassial teeth ( $P^4/M_1$ ) and crushing molars are well developed and the largest teeth in all species, except *Otocyon* (where they are molariform and no larger than the rest). The canine teeth are long and sharply pointed in all species. All canids have excellent senses of smell and hearing, with sight being less acute, although good.

The Canidae are cursorial, running on their toes or the small palmar pad (i.e. digitigrade), with long, slender limbs, compact feet with four functional toes and blunt, non-retractible, claws. A vestigial fifth toe (pollex or dew-claw) on the front feet occurs on all except the African Wild Dog *Lycaon pictus*. Other adaptations to running include fusion of scaphoid and lunar bones in the wrist, and locking of radius and ulna in the front leg to restrict rotation. Caecum always present, coiled into an S-shape.

Male canids have a well-developed grooved penis bone (baculum) and there is a copulatory tie during mating that can last up to an hour or more. This mechanism involves the pair facing away from each other, with the consequence that the blood trapped in the engorged

penis prevents withdrawal. Wild canids usually reach sexual maturity at one year old, and reproduce once annually (gestation lasts approximately nine weeks). However, social suppression of reproduction is common, so reproduction is often delayed and in larger species first reproduction is often after two years. Females have 6–16 nipples and have their young in underground dens. Litter-sizes typically range from 2 to 13; African Wild Dogs, for example, have very large litter-sizes, averaging 10–11, and occasionally as large as 21.

Although canids evolved in relatively open spaces, today they occur in all major African habitats, spanning tropical forests, woodland, savanna, deserts, mountains and afroalpine heathlands. The family is characterized by a great flexibility of diet, opportunistic and adaptable behaviour, and complex social organization with much within- and between-species variation. Most of the smaller species are opportunistic omnivores, eating anything from mammals to birds, reptiles, insects, fruit and carrion. Larger, group-living species may be more strictly carnivorous, preying on medium to large-sized mammals. All canids will feed on some carrion and vegetable matter. Several species – most notably in Africa, jackals and African Wild Dogs (although attitudes to the latter are changing) – are considered pests due to predation on livestock and game species.



Myology showing masticatory muscles and teeth in: African Wild Dog *Lycaon pictus* (wounding bite) (top); Side-striped Jackal *Canis adustus* (firm, puncturing grip) (centre); Bat-eared Fox *Otocyon megalotis* (rapid champing) (bottom).

From solitary to very social, most smaller canids live as territorial pairs (a relatively rare system amongst mammals as a whole) or small family groups, while the larger species are typically, but not invariably, pack hunters (Macdonald & Sillero-Zubiri 2004). Many of the smaller canids are nocturnal, whereas most of the social species are diurnal. Some species hunt in packs, whereas the Ethiopian Wolf *Canis simensis* hunts solitarily but also lives in groups. Benefits of living in groups besides pack hunting include cooperative defence of territories, monopoly of large carcasses and communal care and protection of offspring.

There is a tendency across the family for social system to vary with body size, such that where smaller species form groups these tend to include a dominant pair and female helpers and for dispersal to be male-biased, whereas amongst larger species the tendency is for dispersal to be female-biased and for groups to contain a preponderance of male helpers. In intermediate-sized canids, such as jackals, there is an approximately equal sex ratio of helpers. Scent-marking with both urine and faeces, often aloft visually conspicuous objects (such as tussocks of vegetation) and at trail junctions, is ubiquitous amongst canids – in the case of Ethiopian Wolves territorial border patrols are associated with intensive scent-marking.



African Wild Dog *Lycaon pictus* facial features.

**Claudio Sillero-Zubiri & David W. Macdonald**

## GENUS *Canis* Jackals, Wolves

*Canis* Linnaeus, 1758. Syst. Nat., 10th edn, 1: 38.

*Canis* is a polytypic genus, comprising six or seven wild species depending on whether the Red Wolf *Canis rufus*, from North America, is considered a valid distinct species or not (Wozencraft 1993, 2005). Coyotes, jackals and wolves are distributed throughout North America, Europe, Asia and Africa, with the dingo (*Canis lupus dingo*) taken to Australasia by man during prehistoric times. Although canids typically favour open biotopes they occur in a wide range of habitats, adapting readily to forests, arid regions, high-altitude mountainous habitats and human-dominated environments.

The genus has generally been considered to include four species in Africa: Golden Jackal *Canis aureus*, Side-striped Jackal *C. adustus*, Black-backed Jackal *C. mesomelas* and Ethiopian Wolf *C. simensis*. The three species of jackals have wide distributions, utilizing most habitat types although absent from dense tropical forests. In contrast, the Ethiopian Wolf is confined to afroalpine grasslands and heathlands in the Ethiopian Highlands. The Grey Wolf is present in the Sinai Desert, Egypt, but has not typically been considered as a species occurring on the African continent. However, several authors have proposed that the taxon *C. aureus lupaster*, present in arid areas of Egypt and Libya (Osborn & Helmy 1980), may actually represent a small Grey Wolf rather than a large jackal (Ferguson 1981; and see Qumsiyeh 1996, Ferguson 2002). Recent genetic data also indicate that *C. a. lupaster* represents an ancient wolf lineage, which most likely colonized Africa prior to the northern hemisphere radiation (Rueness *et al.* 2011). The latter authors detected individuals at two localities in the Ethiopian Highlands, some 2500 km south of

the known distribution, an indication that the taxon may be more widely distributed. An observation in Eritrea may also represent a Grey Wolf (Tiwari & Sillero-Zubiri 2004). The current treatment is cognisant of these recent findings, but as this research became available at the time of going to press, only four species in the genus are profiled here.

Members of the genus *Canis* are medium-sized carnivores (HB varies from 65–140 cm, body mass 8–62 kg), well adapted to a cursorial way of life, with a relatively tall body and long limbs, and feet compact, with four functional toes. Members look alike, their heads being characteristically triangular with a conical muzzle and triangular ears. The pelage of all species is relatively short, with dense underfur mixed with longer guard hairs. The tail is bushy, broadest at its middle, and shorter than half of body length; a darker, bristly patch covers the supracaudal gland, of which the odour is, to the human nose, generally faint and somewhat sweet. They have interdigital glands whose function is unknown, as is that of the well-developed anal sacs, and all use urine and faeces for communication, including in the context of territoriality. Females have 8–10 nipples.

The dental formula is typically canid (although the lower third molar is sometimes absent in the Ethiopian Wolf), with short and heavy canines and upper carnassials highly developed; the upper incisors are predominantly lobed. The skull is heavy set with an elevated frontal region, large frontal sinuses and temporal ridges that are close together, united in a sagittal crest. The facial region of the

skull is relatively shorter than in *Vulpes* and *Pseudalopex*, except in the Ethiopian Wolf (Clutton-Brock *et al.* 1976). The latter had initially been placed in a separate genus or subgenus *Simenia* (Allen 1939), but morphological and genetic analysis places it unambiguously within *Canis* (Clutton-Brock *et al.* 1976, Gottelli *et al.* 1994). Hybridization has been recorded in the wild between Ethiopian Wolves and domestic dogs (Gottelli *et al.* 1994), suggesting a recent common ancestor for this group.

Reproduction in *Canis* is generally monopolized by dominant ♀♀, and non-breeding individuals of both sexes may act as helpers (although evidence that their contribution increases survival of the pups is surprisingly equivocal for the Ethiopian Wolf, although compelling for Black-backed and Golden Jackals). There is evidence of infanticide by dominant ♀♀, of allosuckling and of spontaneous lactation (associated with pseudopregnancy). The sociality in *Canis* species is conspicuously intricate, and variable between species, populations and individuals. The fundamental social unit is the

monogamous pair, but delayed dispersal of young (sometimes indefinitely) leads to the development of groups that, in some cases, become both large and structured. The most ubiquitous element of cooperation in these societies is in care of the young, but cooperative hunting and defence of resources are well documented, as is cooperative territorial defence.

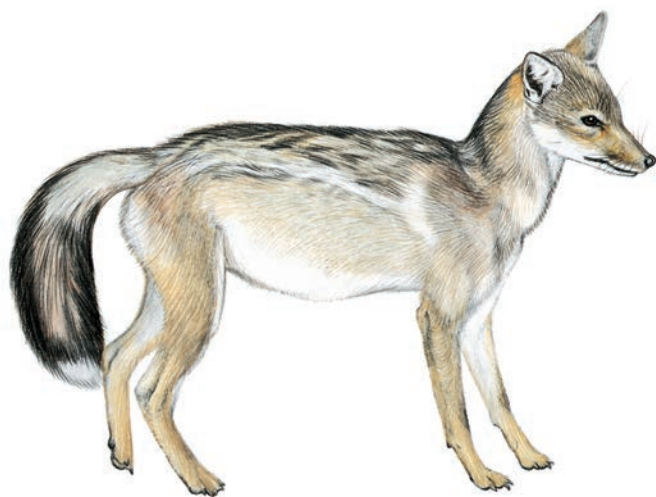
While jackals have a generalist diet of medium and small-size mammals, invertebrates and fruits, Ethiopian Wolves have evolved into afroalpine specialists, existing almost exclusively on a diet of small mammals. The considerable similarity between all *Canis* species may underlie the intensity of intra-guild aggression between them: larger species tend to harass smaller ones throughout the family (and indeed throughout the order Carnivora), with the interesting exception that Black-backed Jackals have been reported as dominating the slightly larger sympatric Side-striped Jackal.

Claudio Sillero-Zubiri & David W. Macdonald

### *Canis adustus* SIDE-STRIPED JACKAL

Fr. Chacal à flancs rayés; Ger. Streifenschakal

*Canis adustus* Sundevall, 1847. Ofv. K. Svenska Vet.-Akad. Forhandl. Stockholm 1846, 3: 121 [1847].  
'Caffraria Interiore'; fixed by Sclater (1900) as 'Magaliesberg' [South Africa].



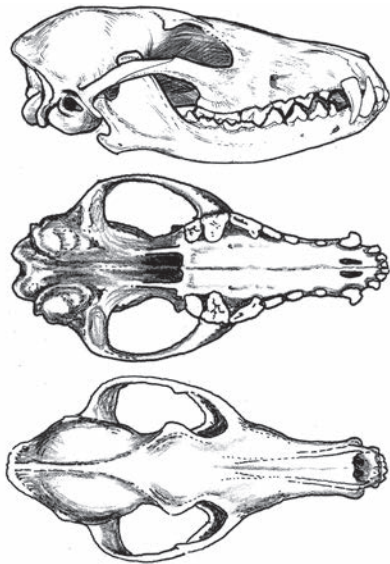
Side-striped Jackal *Canis adustus*.

**Taxonomy** Allen (1939) listed seven subspecies from the continent, Coetzee (1977) reduced this to five, while Kingdon (1997) recognizes only three (*C. a. adustus* from southern Africa, *C. a. lateralis* from Equatorial Africa and *C. a. kaffensis* from Ethiopia and Somalia) but without comment. Many authorities have pointed out that, as with Black-backed Jackal *C. mesomelas*, subspecies are hard to distinguish (e.g. Schouteden 1945), and the differences may be a consequence of individual variation (Ansell 1960a, Rosevear 1974, Kingdon 1997). None is recognized here, pending a revision of subspecies classification. Synonyms: *bweha*, *centralis*, *holubi*, *kaffensis*, *lateralis*, *notatus*, *studerii*, *wunderlichi*. Chromosome number:  $2n = 78$  (Wayne 1993).

**Description** Medium-sized canid, grizzled, brown-grey to buff-grey, with white side-stripe half-way up the flanks, and distinctive white tip to tail (sometimes absent). Coat thick, long on back and neck and fluffy on chest, throat and underside. Underfur dark, overlaid by light beige or buff guard hairs. Head grizzled buff-grey; muzzle dark grey with black nose. Ears blackish-grey behind; considerably smaller in proportion to the head than those of other jackals. Back darker in colour (almost black in some animals) than underside and chest, while flanks are marked by white stripes running from elbow to hip with black lower margins. The boldness of markings, particularly flank-stripes, varies between individuals; those of juveniles less well defined than those of adults. Legs are tinged rufous-brown. Tail bushy and may be fluffed out when the animal is threatened or during intra-specific agonistic encounters; it is predominantly black and almost always bears the distinctive white tip (occasionally absent; see Rosevear 1974). Five digits on forefeet; four on hind. First digits on the front feet carry the dew-claw, and is situated far back on the plantar pad, not marking in the spoor. Claws between 15 and 20 mm long and dog-like (Skinner & Chimimba 2005). Two pairs of nipples.

Skull is similar to the Black-backed Jackal, but longer and less robust, with a noticeably narrower and longer rostrum. Elongation of rostrum is evident when the breadth at P<sup>3</sup> is considered relative to the distance from the back of this tooth to the incisors and is compared in the two species: in the Black-backed Jackal the ratio is about 31/42 or 74%, as opposed to about 28/55 or 51% in the Side-striped Jackal (Skinner & Chimimba 2005). Sagittal crest much better defined, and zygomatic arches of lighter build. Interparietal crest only slightly developed, and the bullae are smaller and flatter (Clutton-Brock *et al.* 1976). Canines are longer and more curved, but outer upper incisors not as large or robust as in the Black-





Lateral, palatal and dorsal views of skull of Side-striped Jackal *Canis adustus*.

backed Jackal. As a result of elongation of the rostrum, third upper premolar lies almost in line with the others and not at an angle as in the Black-backed Jackal (Skinner & Chimimba 2005). Permanent dentition starts erupting at 4–5 months. Relative pulp cavity width of the canine can be used to distinguish young adults from mature adults, but is of no value in determining age after one year (Bingham & Purchase 2003).

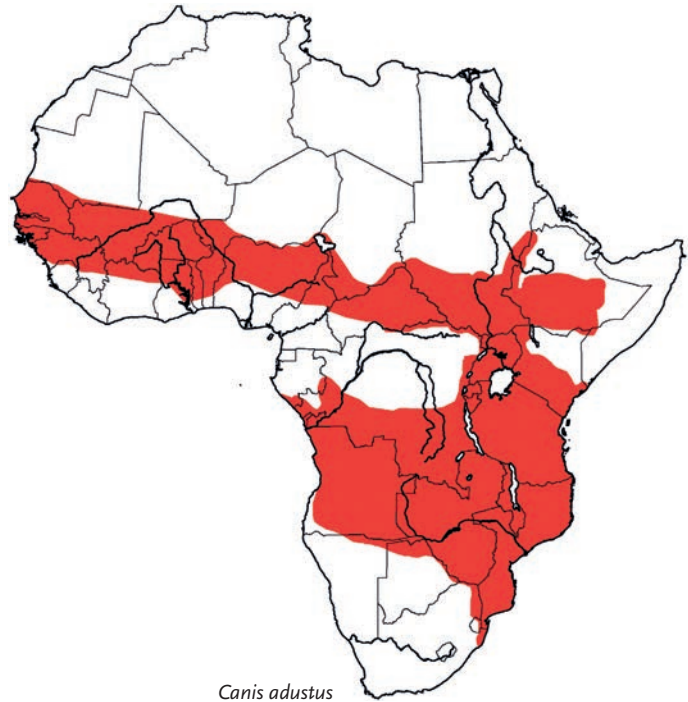
**Geographic Variation** Ansell (1960a) and Rosevear (1974) both commented on the great deal of individual variation in pelage colour within the species, and this has contributed to much confusion in apparent geographic variation; the form *centralis* from Cameroon and Central African Republic was apparently noteworthy for its very light ground colour.

### Similar Species

*Canis mesomelas*. Sympatric in parts of eastern and southern Africa; in SW Angola, they appear to have a parapatric distribution (Crawford-Cabral 1993a). Characterized by a prominent dark 'saddle' and black-tipped tail, as well as reddish flanks and limbs; ears reddish-brown behind; lacks white-tipped tail characteristic of the Side-striped Jackal (and see Description above for notes on skull).

*C. aureus*. Sympatric in parts of East Africa and the Sahelian regions. Golden coat colour, and cream-coloured underparts; ears golden-brown behind; lacks white-tipped tail.

**Distribution** Endemic to Africa; distributed over much of sub-Saharan Africa, from Gambia and Senegal through the Sahelian regions of West Africa to the Central African Republic, Sudan, Ethiopia and Somalia, southwards into southern Africa, being absent or marginally distributed in the more arid westerly regions of southern Africa (Rosevear 1974, Kingdon 1977, Grubb *et al.* 1998, Skinner & Chimimba 2005). Distribution broadly coincides with broadleaved guinea woodland savannas, especially miombo (*Brachystegia*) woodland of central and southern Africa. In southern part of its range occurs marginally in NE KwaZulu–Natal (South Africa), at an altitude below 100 m, this marking its most southern



*Canis adustus*

occurrence on the continent (Rowe-Rowe 1992a). Also occurs occasionally in neighbouring lowveld regions of Swaziland, but is more common in the south (Monadjem 1998).

**Habitat** Found in a wide range of habitats. Distribution tends to coincide with the well-watered woodlands and woodland mosaics of central and West Africa (Coe & Skinner 1993, Skinner & Chimimba 2005). Tends to avoid areas of dry open savanna (areas often favoured by Black-backed Jackals), and is absent from the equatorial forest zone, but may enter in the wake of human cultivation (Kingdon 1997). Other habitats used include areas of abandoned cultivation, marshes and montane habitats up to 2700 m (Kingdon 1977, Estes 1991, Yalden *et al.* 1996). Side-striped Jackals frequently occur near rural dwellings and farm buildings, and penetrate peri-urban and urban areas (Skinner & Chimimba 2005).

Habitat use by the Side-striped Jackal varies considerably between different areas, dependent partly on habitat availability, but often more importantly, on the presence or absence of other jackal species. When allopatric, it occupies a wide range of habitats and appears especially to use grassland (as in Niokolo-Koba N. P., Senegal [C. Sillero-Zubiri pers. comm.], Rwenzori Mountains N. P., Uganda [Kingdon 1977] and NE KwaZulu–Natal [Rowe-Rowe 1992a]), but also savanna woodland on raised plateaux in Niokolo-Koba N. P. (Sillero-Zubiri *et al.* 1997). In Zambia it uses open woodland and grassland, avoiding forest (Ansell 1960a). Similarly, where this species is allopatric in N Zimbabwe, Atkinson (1997) found that grassland was used preferentially over woodland.

However, when it occurs in sympatry with other jackal species habitat is segregated. The Side-striped Jackal uses more thickly vegetated habitats, leaving open grassland and woodland to the other species. In Serengeti N. P., Tanzania it uses dense thicket and riverine habitats (Williams 1967, Wyman 1967, Kingdon 1977, Lamprecht 1978, Moehlman 1983, Estes 1991), with Black-backed Jackals using *Acacia* woodland and Golden Jackals using grassland; a similar

pattern occurred in Laikipia, Kenya (Fuller *et al.* 1989). In southern Africa, when occurring alongside the Black-backed Jackal, the Side-striped Jackal uses the dense vegetation of forest and river valleys and the Black-backed Jackal the open and lightly wooded areas (Pienaar 1969, Loveridge & Macdonald 2002, Skinner & Chimimba 2005). At least in W Zimbabwe, the mechanism for segregation between the two species is aggressive displacement of Side-striped Jackals by Black-backed Jackals (Loveridge & Macdonald 2002).

**Abundance** Generally common within its range in southern Africa. Rhodes *et al.* (1998) found that the resident population of territory-holding adults was 20–30 per 100 km<sup>2</sup> expanding to a breeding season peak of 80–120 jackals per 100 km<sup>2</sup> in N Zimbabwe. In W Zimbabwe (near Hwange N. P.) densities were approximately 54–79 per 100 km<sup>2</sup> expanding to as much as 97 per 100 km<sup>2</sup> in the breeding season (Macdonald *et al.* 2004). Ziegler *et al.* (2002) suggest that Side-striped Jackals are ‘rare in West Africa’, an observation that is borne out by the relatively low densities (7 per 100 km<sup>2</sup>) found in Niokolo-Koba N. P. (Galat *et al.* 1996, Sillero-Zubiri *et al.* 1997). The dietary flexibility of the Side-striped Jackal and its ability to co-exist with humans on the periphery of settlements and towns suggests that populations are only vulnerable in cases of extreme habitat modification, or intense disease epidemics.

**Adaptations** Like the Black-backed Jackal, this species is relatively unspecialized but well adapted anatomically and behaviourally for opportunism. Kingdon (1997) suggests that, in ecological terms, it is the tropical equivalent of the Red Fox *Vulpes vulpes*. The dentition is well suited to an omnivorous diet (Skinner & Chimimba 2005). The canines are long, curved and sharp-pointed, with a sharp ridge on their posterior surfaces. The upper outer incisors are canine-like, the carnassial shear well adapted for slicing, while the first and second upper molars are broad and developed for crushing. In comparison to the Black-backed Jackal, Side-striped Jackals have similar-shaped carnassials, and hence similar adaptation to carnivory; however, Side-striped Jackals have a larger grinding surface on their premolars and molars and are, therefore, better adapted to an omnivorous life-style (Van Valkenburgh 1991, Van Valkenburgh & Wayne 1994).

The Side-striped Jackal has smaller, more rounded ears than other jackals, which is the case with many forest-dwelling canid species,



Side-striped Jackal *Canis adustus* facial details.

such as the Bush Dog *Speothos venaticus* and the Small-eared Dog *Atelocynus microtus* of South America (Stains 1975). This suggests that the Side-striped Jackal is perhaps adapted to more mesic environments and the other jackal species to more arid regions.

The white tail tip of this species is possibly a ‘badge of nocturnal status’ (Kingdon 1977). The Red Fox and the White-tailed Mongoose *Ichneumia albicauda* also have white tail tips and correspondingly nocturnal habits. Macdonald (1987) suggests that a white tail flash may enhance tail signalling in nocturnal species. The white tail flash may also allow members of a foraging group to locate one another in the dark and avoid moving through areas from which food items have already been disturbed and gleaned by other group members (Loveridge 1999).

**Foraging and Food** Omnivorous, feeding on a wide array of items including small mammals, birds, reptiles, insects, carrion and vegetable matter (Smithers & Wilson 1979, Estes 1991, Atkinson *et al.* 2002a, Loveridge & Macdonald 2003). Their diet is very responsive to both seasonal and local variation in food availability. On commercial farmland in the Zimbabwe highveld, they eat mainly wild fruit (30%) and small (<1 kg) to medium-sized (>1 kg) mammals (27% and 23%, respectively), with the remainder of their diet comprising birds, invertebrates, cattle cake, grass and carrion (Atkinson *et al.* 2002a). In wildlife areas of W Zimbabwe, Side-striped Jackals feed largely on invertebrates during the wet season and small mammals up to the size of springhares *Pedetes* spp. during the dry months of the year.

Side-striped Jackals scavenge extensively from safari camp rubbish dumps and occasionally from large carnivore kills (although they are out-competed for this resource by Black-backed Jackals) (Loveridge & Macdonald 2003). In the Ngorongoro Crater, Estes (1991) recorded the species competing with Black-backed Jackals to catch Grant’s Gazelle *Nanger granti* fawns. Certain fruits (e.g. Mobola plum *Parinari curatelifolia*, wild fig *Ficus capensis* and waterberry *Syzgium guineense*) may be taken almost exclusively when in season (Smithers & Wilson 1979, Atkinson *et al.* 2002a).

As with Black-backed Jackals, this species is primarily nocturnal, with peaks in activity after sunset and before dawn (Loveridge & Macdonald 2003). Occasionally, they are seen active during the late afternoon in areas where they are not persecuted (Kingdon 1977). Side-striped Jackals feed solitarily, although in W Zimbabwe family groups have been observed foraging together on abundant invertebrate food resources (Loveridge 1999), and Estes (1991) mentions that as many as 12 have been counted at kills or scavenging offal outside towns. Similarly, groups have been observed scavenging from both Lion *Panthera leo* and Spotted Hyaena *Crocuta crocuta* kills in Liuwa Plains N. P., Zambia, with as many as 5–10 seen at any one time (G. Purchase pers. comm.).

As with other canids, this species exhibits extreme flexibility in its foraging strategies. Kingdon (1977) observed a captive, free-ranging individual bump vegetation with its body to dislodge invertebrates. A similar pattern of behaviour was observed in Hwange, Zimbabwe, where Side-striped Jackals ‘stamped’ the ground to disturb concealed grasshoppers (Loveridge 1999). Atkinson *et al.* (2002b) found that instead of searching for preferred foods, jackals in farmland tended to use the most seasonally abundant resources, moving through the agricultural landscape using an optimal foraging pathway (with fractal characteristics) for opportunistic use of spatially random



Side-striped Jackal *Canis adustus* action drawing.

and temporally variable resources. It is likely that this is a common foraging pattern in omnivorous medium-sized canids.

In all studies on the species, there is very little evidence for extensive predation on domestic stock (Shortridge 1934, Roberts 1951, Ansell 1960a, Smithers 1971, Smithers & Wilson 1979, Rowe-Rowe 1992a), or game larger than a baby antelope (Kingdon 1977, Estes 1991).

**Social and Reproductive Behaviour** Because their tendency to use wooded terrain makes it hard to confirm group sizes, Side-striped Jackals were at one time considered solitary; however, it is now known that they form social groups. As with other jackal species, the basis for the social system is the mated pair, which is known to be stable over several years. They may occasionally occur in family groups, or come together in feeding aggregations (though not as large as in Black-backed Jackals).

In game areas of W Zimbabwe, home-ranges varied from 0.2 km<sup>2</sup> in the hot dry season to 1.2 km<sup>2</sup> in the cold dry season, whereas in highveld farmland, they were seasonally stable and in excess of 4.0 km<sup>2</sup>. In highveld farmland, territories are configured to encompass sufficient patches of grassland, where resources are most available, and the structure of the habitat mosaic appears an important factor. Pairs in N Zimbabwe used their home-range with a high degree of concordance, using the same areas with similar intensity and largely at the same times. The central core of each home-range is used exclusively by its occupants, but the peripheral third of the range may overlap widely with four or more neighbouring pairs; home-ranges overlapped by about 20% in highveld farmland and 33% in game areas (Atkinson 1997). In Hwange, Zimbabwe, at least four of five Side-striped Jackal territories included extra-pair members (up to five in one case, two of which were known to be between one and two years of age), and there is evidence for alloparental care in that young adults have been recorded returning to their natal home-ranges during the breeding season (Loveridge & Macdonald 2001).

Side-striped Jackals are not as vocal as other jackal species. The most obvious call is a series of staccato barks (an explosive 'bwa'), which may be repeated for up to 10 minutes, usually in bouts of 13–17 barks over 30 seconds, with 4–5 seconds between bouts

(Loveridge 1999). These are often used as alarm/mobbing calls in the presence of Leopards *Panthera pardus*, and also during the breeding season where animals from neighbouring territories may answer calls. Side-striped Jackals do not howl, instead they have an 'owl-like hoot' (Kingdon 1977). This call was never heard in Hwange, Zimbabwe (A. Loveridge pers. obs.).

Pups are born in subterranean dens, often abandoned Aardvark *Orycteropus afer* holes or excavated termitaria that the ♀ modifies to her own requirements (Skinner & Chimimba 2005); the breeding chamber often has multiple entrances. Dens are sometimes used by the same pair over consecutive years (Kingdon 1977, A. Loveridge pers. obs.). During the early stages of pup growth, only the ♂ provisions the pups and the ♀, but after weaning both parents assist in rearing the young, returning at intervals of 2–3 hours through the night to feed the pups on food that is probably regurgitated (Moehlman 1979). The pups are aggressive towards each other, as evidenced by the degree of wounding seen.

**Reproduction and Population Structure** Reproduction can occur in the first year, with most mating occurring in July in Zimbabwe (Bingham & Purchase 2002, 2003). However, the breeding season is variable in different parts of Africa. In Zimbabwe pups are usually born in Sep and Oct, after a 57–60 day gestation period (Bingham & Purchase 2002, Skinner & Chimimba 2005); however, pups are born in Jun and Jul in Uganda, and Sep and Oct in S Kenya (Kingdon 1977) and Sep–Nov in Zambia (Ansell 1960a). Skinner & Chimimba (2005) report mean litter-sizes for Side-striped Jackals of 5.4 pups, and Bingham & Purchase (2002) give (from examination of foetuses and placental scars) a mean pre-birth litter-size of 5.8 (range 3–8). Perinatal litter loss is around 20% (Bingham & Purchase 2002) and Rhodes *et al.* (1998) estimate that only two per litter survive past six months. Lactation lasts about 10 weeks. Juveniles are probably independent before they are one year old and have been recorded dispersing up to 15 km (mean = 4.6 ± 3.51 km) (Loveridge & Macdonald 2001). As with Black-backed Jackals, longevity has been given as 10–13 years (Ginsberg & Macdonald 1990, Weigl 2005), but this is probably more representative of longevity in captivity, and Rhodes *et al.* (1998) suggest that the average life-span in the wild is probably closer to 3–4 years.

**Predators, Parasites and Diseases** Leopards are the only regular predator of the Side-striped Jackal, although it seems likely that other predators may take pups and young adults as they do with the other jackal species.

In Zimbabwe, seroprevalence of canine distemper virus, canine parvovirus and canine adenovirus (type 1) were 50%, 12.5% and 37.5%, respectively, in 22 free-ranging Side-striped Jackals sampled between 1990 and 1993 (Spencer *et al.* 1999); however, although jackals act as reservoirs for these diseases, susceptibility is not known. Side-striped Jackals, along with other jackal species, are vulnerable to rabies (Bingham & Foggin 1993, Bingham *et al.* 1999a, b), tick fever and sarcoptic mange (Kingdon 1977), for all of which they are known or suspected reservoirs and vectors for domestic dog infection. Computer simulations (Rhodes *et al.* 1998) suggest rabies can only persist in Side-striped Jackal populations where the density is very high – such as around towns – and that most rabies occurrence in Side-striped Jackals is a result of spillover from domestic dogs living on communally owned land. Side-striped Jackals can contract the disease from domestic dogs, conspecifics and other jackal species, although it appears that transmission of rabies cycles does not appear to occur from areas where Black-backed Jackals are the numerically dominant species to areas where Side-striped Jackals are prevalent (Bingham *et al.* 1999a).

Horak *et al.* (1987) collected the following parasites from a single Side-striped Jackal taken in Kruger N. P. in South Africa: *Amblyomma hebraeum*, *Haemaphysalis leachi* and *Rhipicephalus* spp. Ntiamoa-Baidu *et al.* (2005) recorded *Rhipicephalus sulcatus* and *Amblyomma variegatum* from jackals in Ghana.

**Conservation** IUCN Category: Least Concern. CITES: Not Listed.

Side-striped Jackals are persecuted primarily for their role in rabies transmission and their putative role as stock killers, which although unlikely to affect overall numbers may affect local abundance. In areas of high human population density, snaring may be the commonest cause of death in adults, and may account for as much as a third of adult deaths in such areas (Atkinson 1997, Atkinson & Loveridge 2004). Ziegler *et*

*al.* (2002) did not observe any Side-striped Jackals during a mammal survey in Upper Niger N. P., Guinea (where they have previously been recorded), perhaps because the level of illegal hunting is high. In towns and suburbs they may be run over by vehicles (Kingdon 1977). High reproductive productivity ensures this species is capable of rapid recovery following population crashes (Bingham & Purchase 2002). There may be some limited trade in jackal parts, because of their role in traditional practices and beliefs in parts of East Africa (Kingdon 1977), but this is not thought to be extensive. This species occurs in a number of well-managed protected areas throughout its range, including Niokolo-Koba N. P. (Senegal), Comoé N. P. (Côte d'Ivoire), Queen Elizabeth N. P. (Uganda), Serengeti N. P. (Tanzania), Hwange N. P. (Zimbabwe) and Kruger N. P. (South Africa), and seems well able to exploit semi-urban and urban habitats (Atkinson & Loveridge 2004).

### Measurements

#### *Canis adustus*

TL (♂♂): 1082 (960–1165) mm, n = 50  
 TL (♀♀): 1075 (1000–1170) mm, n = 50  
 T (♂♂): 361 (305–390) mm, n = 50  
 T (♀♀): 354 (310–410) mm, n = 50  
 HF c.u. (♂♂): 172 (160–190) mm, n = 50  
 HF c.u. (♀♀): 168 (153–178) mm, n = 50  
 E (♂♂): 88 (80–97) mm, n = 50  
 E (♀♀): 86 (80–95) mm, n = 50  
 WT (♂♂): 9.4 (7.3–12.0) kg, n = 50  
 WT (♀♀): 8.3 (7.3–10.0) kg, n = 50  
 Zimbabwe (Smithers 1983)

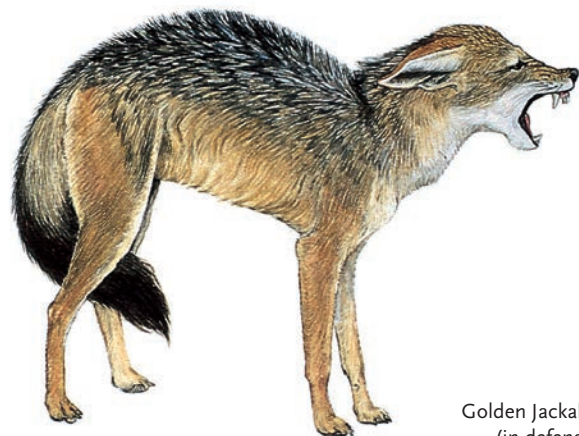
**Key References** Atkinson 1997; Bingham & Foggin 1993; Fuller *et al.* 1989; Kingdon 1977; Loveridge 1999; Loveridge & Macdonald 2001; Skinner & Chimimba 2005.

**Andrew J. Loveridge & David W. Macdonald**

## *Canis aureus* GOLDEN JACKAL (ASIATIC JACKAL, COMMON JACKAL)

Fr. Le Chacal commun; Ger. Goldschakal

*Canis aureus* Linnaeus, 1758. Syst. Nat., 10th edn, 1: 40 'oriente';  
 restricted by Thomas (1911) to 'Benna Mountains, Laristan, Southern Persia' [Iran].

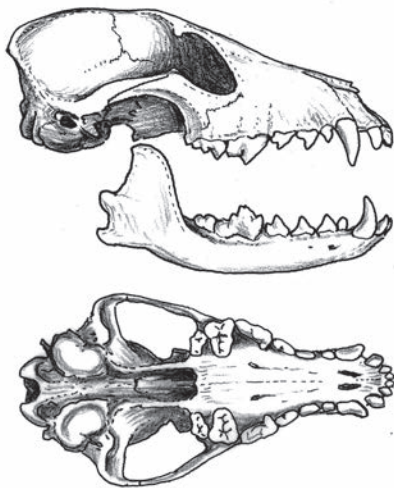


Golden Jackal *Canis aureus*  
 (in defensive posture).

**Taxonomy** Some 12 subspecies have been distinguished across the range (Allen 1939, Ellerman & Morrison-Scott 1951), and Coetzee (1977) listed seven for Africa, including the East African population, *C. aureus bea*, which is almost discrete (and see Heller 1914, Swynnerton & Hayman 1950). Ferguson (1981) has suggested that the taxon *C. aureus lupaster*, present in arid areas of Egypt and Libya (Osborn & Helmy 1980) may actually represent a small Grey Wolf *Canis lupus* rather than a large jackal. It is retained here as a form of the Golden Jackal following Wozencraft (2005) (see also Qumsiyeh 1996, Ferguson 2002). However, recent genetic data suggest that *C. a. lupaster* represents an ancient wolf lineage, which most likely colonized Africa prior to the northern hemisphere radiation (Rueness *et al.* 2011). The latter authors detected individuals at two localities in the Ethiopian Highlands, some 2500 km south of the known distribution, an indication that the taxon

may be more widely distributed than thought. Synonyms: *algirensis*, *anthus*, *bea*, *doederleini*, *grayi*, *hagenbacki*, *lamperti*, *lupaster*, *maroccanus*, *mengesi*, *nubianus*, *riparius*, *sacer*, *senegalensis*, *somalicus*, *soudanicus*, *studer*, *thooides*, *tripolitanus*, *variegatus*. Chromosome number:  $2n = 78$  (Wurster & Benirschke 1968).

**Description** Considered to be the most typical representative of the genus *Canis*, without any outstanding features or specialization (Clutton-Brock *et al.* 1976), the Golden Jackal is medium-sized, with ears upright, legs relatively long and feet slender with small pads. Basic coat colour is golden but varies from pale creamy-yellow to a dark tawny hue on a seasonal basis. Pelage on the back is often a mixture of black, brown and white hairs, such that they can appear to have a dark saddle similar to the Black-backed Jackal *C. mesomelas*. Belly and underparts are a lighter pale ginger to cream. Unique lighter markings on throat and chest (Macdonald 1979a) and facial and body scars (Moehlman 1983) make it possible to differentiate individuals in a population. Tail is bushy with tan to black tip. Approximately 12% difference in body weight between sexes, with mean female body mass of 5.8 kg and mean male body mass 6.6 kg (Moehlman & Hofer 1997). Females have four pairs of nipples.



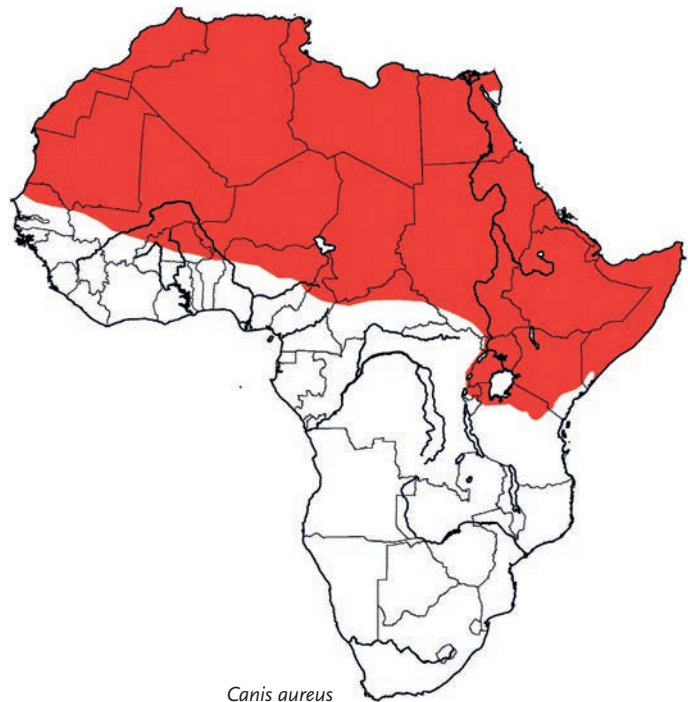
Lateral and palatal views of skull of Golden Jackal *Canis aureus*.

Skull has: well-developed, high-crowned teeth; interparietal crest present; facial region somewhat short; and often a well-marked cingulum on labial side of upper first molar. In these respects, skull is more similar to that of the Coyote *C. latrans* or a small Grey Wolf than that of the Black-backed Jackal, Side-striped Jackal *C. adustus*, or Ethiopian Wolf *C. simensis* (Clutton-Brock *et al.* 1976).

**Geographic Variation** Jackals inhabiting rocky, mountainous terrain may have a greyer coat shade (Sheldon 1992), and melanistic and piebald forms are sometimes reported (Muller-Using 1975, Jerdon 1984, P. Moehlman pers. obs.).

### Similar Species

*Canis mesomelas*. Sympatric in East Africa. Distinguished by the smaller size and shape of its skull and, usually, a prominent dark saddle (the latter sometimes apparent in the Golden Jackal though usually not as prominent), and a distinct rufous tinge to flanks and legs.



*Canis aureus*

- C. adustus*. Sympatric in parts of East Africa and the Sahelian regions. Relatively shorter ears, a pale side stripe and a white-tipped tail; interparietal crest poorly developed; cheekteeth less high-crowned.
- C. simensis*. Ethiopian Highlands only. Larger, with longer legs; distinctive reddish coat, white underparts, throat, chest and tail markings.

**Distribution** Occurs across much of north-east and North Africa, from Senegal (though there is no confirmed record from Gambia; see Grubb *et al.* 1998), Mauritania, Morocco (including Western Sahara), and Algeria in the west through Libya, Niger, N Nigeria and Chad, to Egypt, the Horn of Africa (including Ethiopia, Djibouti, Eritrea and Somalia) and south to Kenya and N Tanzania. A record from Guinea-Bissau (Frade & Silva 1980) is the result of confusion with the Side-striped Jackal (Crawford-Cabral & Esteves 1989).

Extralimital to Africa, ranges from the Arabian Peninsula into western Europe to Austria and Bulgaria, and then continues eastwards into Turkey, Syria, Iraq, Iran, central Asia, the entire Indian sub-continent, then east and south to Sri Lanka, Myanmar, Thailand and parts of Indo-China (Jhala & Moehlman 2004).

**Habitat** Due to tolerance of dry habitats and omnivorous diet, the Golden Jackal can inhabit a wide variety of habitats, from the Sahara Desert (except the most hyper-arid parts) and Sahel to the evergreen forests of Myanmar and Thailand. In Africa, typically prefers semi-desert, short to medium grasslands and savannas, and has been recorded at 3800 m altitude in the Bale Mts of Ethiopia (Sillero-Zubiri 1996, Yalden *et al.* 1996).

**Abundance** Fairly common throughout its range. High densities are observed in areas with abundant food and cover. In Serengeti N. P. densities can be as high as two adults per km<sup>2</sup> (Moehlman 1983, 1986, 1989).

**Adaptations** The medium body size is energetically flexible and allows Golden Jackals to live off small prey items such as invertebrates, rodents, reptiles and even wild berries. They can trot for long distances in search of food, and are reported to have the ability to forego water, obtaining much of their moisture requirements from their food (Kingdon 1977); Golden Jackals have been observed on Pirotan I., in the Gulf of Kutch, India, where there is no fresh water (Y. Jhala pers. comm.).

**Foraging and Food** Golden Jackals are omnivorous and opportunistic foragers, and their diet varies according to season and habitat (Wyman 1967). In Serengeti N. P., although they consume invertebrates and fruit, over 60% of their diet is vertebrates and they will kill rodents (particularly gerbils; see Senzota 1990), lizards, snakes, birds (from quail to flamingos), hares, Thomson's Gazelle *Eudorcas thomsonii* and Grant's Gazelle *Nanger granti* (Wyman 1967, Moehlman 1983, 1986, 1989). They also scavenge the carcasses of larger herbivores, such as Common Wildebeest *Connochaetes taurinus*, Plains Zebra *Equus quagga* and African Buffalo *Syncerus caffer*. In C Niger, an analysis of scat samples (n = 143) showed that vegetable matter (including various species of grasses, *Acacia* seeds and *Cordia sinensis* and *Ziziphus mauritiana* fruit) and invertebrates (ants, dung beetles, grasshoppers and scorpions) constituted the main identifiable items in the diet. Several rodent species, including gerbils, spiny mice and the Striped Ground Squirrel *Xerus erythropus*, were recorded, as were the remains of hares. Bird remains were recorded in 23.7% of scats, and in one sample, eggshell fragments were recovered. The remains of an unidentified snake were also found in one scat (McShane & Grettenberger 1984). Jackals have been recorded feeding on desert snails (*Eremica desertorum*) in Egypt, and digging freshwater snails (*Pila wernerei*) out of cracks in a mud pan in NE Sudan (Osborn & Helmy 1980 and references therein).

Single individuals typically hunt smaller prey such as rodents and birds, using their hearing to locate rodents in the grass and then pouncing on them by leaping through the air, or digging out gerbils from their burrows. However, individual animals will also hunt Thomson's Gazelle fawns. Golden Jackals have been observed to hunt young, old and infirm ungulates that are sometimes 4–5 times their own body weight (Van Lawick & Van Lawick-Goodall 1970, Eisenberg & Lockhart 1972). Admasu *et al.* (2004a) suggest that Golden Jackals in Bale may be more solitary than elsewhere in the range, with animals having been observed foraging alone on 87% of occasions. This is likely because food resources were widely dispersed and rarely concentrated enough for jackals to forage in groups (Admasu *et al.* 2004a). In Serengeti N. P., mated pairs will hunt cooperatively and regularly kill Thomson Gazelle fawns and occasionally adults; pairs have a higher kill rate than individuals (Wyman 1967, Kruuk 1972, Rosevear 1974). Indeed, cooperative hunting permits them to harvest much larger prey in areas where available. In some areas, particularly where food resources are clumped, aggregations of jackals may occur. Van Lawick & Van Lawick-Goodall (1970) reported 14 jackals on a carcass in Ngorongoro, and aggregations of between five and 18 jackals have been sighted scavenging on carcasses of large ungulates in India (Y. Jhala pers. obs.). Golden Jackals will cache excess food.

Golden Jackals are known to predate on domestic livestock. In C Niger, 17 of 37 herders reported losses of livestock to jackals, with an average of 1.7 goats and 0.24 sheep reported lost each year. Most



Golden Jackal *Canis aureus* facial detail.

predation was reported to occur during the day, when animals were unattended and away from camp, though some also occurred at night (McShane & Grettenberger 1984). In Egypt, jackals living near the Nile Valley and Delta are reputed to feed on various cultivated crops and fruit, as well as to prey upon domestic animals (Osborn & Helmy 1980).

**Social and Reproductive Behaviour** Social organization is extremely flexible depending on demography and food resources (Macdonald 1979a, Moehlman 1983, 1986, 1989, Fuller *et al.* 1989, Moehlman & Hofer 1997, Admasu *et al.* 2004a). The basic social unit is the breeding pair. Some offspring from the previous year's litter may remain with the parents and help to raise the current litter of pups (Moehlman 1983, 1986, 1989). In Tanzania, Golden Jackals usually form long-term pair bonds, both members of which mark and defend their territories, hunt together, share food and cooperatively rear the young (Moehlman 1983, 1986, 1989). Moehlman & Hofer (1997) give average group size as 2.5 (Serengeti N. P., Tanzania), similar to average group size (3; n = 7) in Velavadar N. P., India (Y. Jhala pers. obs.).

In Serengeti N. P., Golden Jackals (Moehlman 1983) maintain year-round exclusive territories of 0.5–7.0 km<sup>2</sup> in size (Moehlman 1983) and 2–5 km<sup>2</sup> in Ngorongoro (Van Lawick & Van Lawick-Goodall 1970), but will make excursions beyond these territorial boundaries to gain access to fresh carcasses. In Algeria, Khidas (1990) recorded seasonal territories as small as 0.39 km<sup>2</sup>. Home-range size may depend on the age of individuals, demography and the distribution of food resources. For example, home-range size for an adult pair in *Acacia* woodland in Kenya was 2.4 km<sup>2</sup> and for two juvenile ♀♀, 5.6 and 21.7 km<sup>2</sup> (Fuller *et al.* 1989), while range size over a 16-month period in the Bale Mountains of Ethiopia varied from 7.9 to 48.2 km<sup>2</sup> for adults and from 24.2 to 64.8 km<sup>2</sup> for subadults (Admasu *et al.* 2004a). Home-ranges of individuals within a social group tend to overlap, as reported by Van Lawick & Van Lawick-Goodall (1970), Khidas (1990) and Admasu *et al.* (2004a).

In Serengeti N. P. only the territorial pair does raised-leg urinations. These urination scent-marks are done in tandem on the same spot as the pair forage in their territory. Such scent-marks are considered to play an important role in territorial defence (Rosevear 1974). Affiliative behaviours like greeting ceremonies, grooming and group vocalizations are common in jackal social interactions (Van Lawick & Van Lawick-Goodall 1970, Golani & Keller 1975). Vocalization consists of a complex howl repertoire beginning with 2–3 simple low-pitch howls and culminating in a high-pitched staccato of calls. In Serengeti N. P. individuals give reciprocal howls

to locate their mates and family members. Families also occasionally group howl in response to neighbouring family howls.

In the Serengeti mating typically occurs from Oct to Dec (Moehlman 1983, 1986), and involves a copulatory tie that lasts for several minutes (Golani & Mendelssohn 1971, Golani & Keller 1975). Young are born in dens, which can take the form of existing earthen burrows of Aardvark *Oryzomys afer* or warthogs *Phacochoerus* spp., or rivulets, gullies, road embankments, drainage pipes and other man-made structures. Earthen dens may have 1–3 openings and are typically about 2–3 m long and 0.5–1 m deep. Young pups could be moved from 2–4 dens during their first 14 weeks of life (Jhala & Moehlman 2004).

In the Serengeti both parents and ‘helpers’ – offspring from previous litters – provision and guard the new pups. The ♂ also feeds his mate during her pregnancy and both the ♂ and the ‘helpers’ provision the ♀ during the period of lactation (Moehlman 1983, 1986, 1989, Moehlman & Hofer 1997). The ‘helpers’ are the offspring of the same ‘behavioural’ parents and thus may be full siblings to the young pups that they are provisioning and guarding. However, the paternity of the pups has not been checked genetically. The presence of helpers correlates with a higher pup survival (Moehlman 1986).

**Reproduction and Population Structure** In the Serengeti, pups may be born in most months of the year, but usually from Dec to Mar, coinciding with the wet season and the arrival of the migrating herds of Common Wildebeest, Plains Zebra and Thomson’s Gazelle (Moehlman 1983, 1986, 1989). In Egypt, wild-born litters have been recorded in Mar, Apr and May (Flower 1932). Females are typically monoestrous, but there is evidence in Tanzania of multiple litters (P. Moehlman pers. obs.). Gestation lasts about 63 days (Sheldon 1992). Litter-size ranges from 1 to 9, and Moehlman & Hofer (1997) give mean litter-size as 5.7. In Tanzania, Wyman (1967) reported an average of two pups emerging from the den at three weeks of age. Pups are born blind and their eyes open at approximately nine days and their teeth erupt at 11 days after birth (Moehlman & Hofer 1997). Lactation usually lasts for 8–10 weeks. Maximum longevity recorded in Serengeti N. P. is about 14 years (Moehlman & Hofer 1997).

**Predators, Parasites and Diseases** In East Africa, Spotted Hyaenas *Crocuta crocuta* have been observed to kill and feed on Golden Jackals (Kruuk 1972, Kingdon 1977). In Serengeti N. P., Golden Jackals will give a ‘warning yowl’ when Spotted Hyaenas approach their dens. The adult jackals will then chase the hyaenas and bite them on the rump/genitals.

The co-existence of three sympatric species of jackals (Golden, Black-backed and Side-striped) in East Africa is possibly due to resource partitioning in terms of foraging ecology and spatial and temporal habitat utilization and the high relative diversity of prey and predators in Africa (Fuller *et al.* 1989, Wayne *et al.* 1989b). Jackals often scavenge off the kills of larger predators like Lions *Panthera leo*, Leopards *P. pardus*, and Spotted Hyaenas (Van Lawick & Van Lawick-Goodall 1970, Kruuk 1972, Moehlman 1986).

In Serengeti N. P. blood serology of three animals had positive titres to canine parvovirus (n = 1), canine adenovirus (n = 2), canine coronavirus (n = 3) and canine herpesvirus (n = 2). All three individuals had negative titres to rabies virus, canine distemper, canine brucellosis, leptospirosis, rinderpest, African horse sickness

and Rift Valley fever (W. B. Karesh pers. comm.). During the 1994–95 distemper outbreak in the Serengeti, a single jackal tested positive for canine distemper (Roelke-Parker *et al.* 1996).

**Conservation** IUCN Category: Least Concern. CITES: Not listed.

Although the Golden Jackal is present in a number of protected areas across its wide range, including the Serengeti–Masai Mara–Ngorongoro complex, there is evidence that some populations are undergoing declines, as traditional land use practices (such as livestock rearing and dry farming) that were conducive to the survival of jackals and other wildlife, are being steadily replaced by industrialization and intensive agriculture (Jhala & Moehlman 2004). As with other jackal species, they are sometimes killed in indiscriminate predator control programmes.

### Measurements

*Canis aureus*

HB: 872 (822–893) mm, n = 9

T: 312 (290–347) mm, n = 9

HF c.u.: 200 (190–212) mm, n = 19

E: 112 (104–121) mm, n = 9

WT: 13 (10–15) kg, n = 4

Egypt (sexes combined; Osborn & Helmy 1980)

HB: 740, 785 mm, n = 2

T: 270, 280 mm, n = 2

E: 110, 110 mm, n = 2

WT: 6.3, 7.7 kg, n = 2

Tanzania (P. Moehlman pers. obs.)

**Key References** Fuller *et al.* 1989; Jhala & Moehlman 2004; Macdonald 1979a; Moehlman 1983, 1986, 1989; Moehlman & Hofer 1997.

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Golden Jackal *Canis aureus*.

**Canis mesomelas BLACK-BACKED JACKAL (SILVER-BACKED JACKAL)**

Fr. Chacal à chabraque; Ger. Schabrakenschakal

*Canis mesomelas* Schreber, 1775. Die Säugethiere 2 (14): pl. 95; text 1775, 3 (21): 370 [1976].

‘Vorgebirge der guten Hofnung’ [‘Cape of Good Hope’, South Africa].

Black-backed Jackal *Canis mesomelas*.

**Taxonomy** As many as six (Allen 1939) and five (Coetzee 1977) subspecies have been recognized. Meester *et al.* (1986) assigned all southern African material to the nominate subspecies. Considering the regional variation in the species, recognition of only two, geographically isolated, subspecies is followed here (and see Kingdon 1997, Walton & Joly 2003). Synonyms: *achrotes*, *arenarum*, *elgonae*, *mcmillani*, *schmidti*, *variegatoides*. Chromosome number:  $2n = 78$ , with all but two chromosomes acrocentric (Wallace 1977).

**Description** Fox-like in appearance, weighing between 6 and 13 kg (see Measurements). Diagnostic features are dark saddle, black, bushy tail and reddish head, flanks and limbs. Muzzle pointed with black nose. In common with other arid-adapted carnivores, ears are relatively large and constantly mobile. Flanks, legs, ears and head tawny to rufous-brown, belly and front of neck pale brown to beige. A black stripe mid-way up each flank slopes up obliquely from behind shoulder to top of rump; dark saddle is broadest at shoulders and tapers to narrow point at base of the tail. Anterior to this stripe, behind the shoulder, is a small vertical stripe, diffuse in some individuals. Above side markings, the back is interspersed with black and white hairs giving an overall silver appearance in mature animals (hence the alternative name Silver-backed Jackal). Juveniles and subadults have similar markings but are drabber and only gain mature pelage at around two years of age. Tail dark brown to black with distinctive black subcaudal marking; tip of tail black. Markings, especially side- and shoulder-stripes, are unique to each individual and can be used as features for individual identification. In the drier west and Namib coast in southern Africa winter coat is deep reddish-brown (particularly so in ♂♂). Distinctive side markings are likely to be signals to conspecifics, flanks being a focus for behaviours such as side-slammung (a common behaviour between dominant and subordinate

canids). Albinism may occur. Five digits on front feet; the first carries the dew-claw and is set well back from the remainder, not marking in the spoor; the hindfoot has four digits. The claws are relatively short, measuring about 150 mm over the curve. Black-backed Jackals have 6–8 nipples (Smithers 1971). Little obvious sexual dimorphism when seen in the field (Moehlman 1983, A. J. Loveridge pers. obs.) although ♂ is in fact slightly larger and heavier than ♀ (Smithers 1971, Rowe-Rowe 1978a, Stuart 1981; and see Measurements).

Skull elongated, braincase pear-shaped, rostrum narrow, supraoccipital crest well developed, bullae rounded and paroccipital processes fused to back of bullae; zygomatic arches broad and well developed; postorbital bars incomplete represented by blunt processes on the zygoma and frontals. Overall, skull and dentition more robust than in Side-striped Jackal *C. adustus* and Golden Jackal *C. aureus*, with outer upper incisors larger, and more pointed and caniniform.

**Geographic Variation***C. m. mesomelas*: southern Africa.*C. m. schmidti*: East Africa and Horn of Africa.

In southern Africa, slight variation in body size and weight has been recorded, with jackals from the former Cape Province, for example, slightly larger than those collected from Zimbabwe (see Measurements). In addition, Rautenbach (1982) found evidence of a clinal increase southwards in mean greatest skull length and suggested this could apply throughout the range of the species in southern Africa. The data of Stuart (1981) from the former Cape Province lend support to this finding. According to Van Valkenburgh & Wayne (1994), skulls of jackals from East Africa are shorter in total length and wider than skulls from southern Africa, and, likewise, animals in East Africa have longer and narrower carnassials and smaller upper and lower molar grinding areas than do animals in southern Africa. Sexual dimorphism also appears less evident, at least in male : female skull length ratio. Van Valkenburgh & Wayne (1994) suggested this was evidence of significant character displacement in East Africa where the species' range overlaps with that of both the Golden and Side-striped Jackal, and that this species is less sexually dimorphic when sympatric with other jackal species than when allopatric (and see Loveridge 1999).

**Similar Species**

*Canis adustus*. Lacks dark saddle and rich reddish colour of the flanks and limbs; tail not uniformly black, and with a white tip; white stripe along side, from shoulder to top of rump. Sympatric in parts of East Africa (see also Yalden *et al.* 1980), NE Namibia, N Botswana, C and S Zimbabwe, Mozambique, NE Limpopo Province and E Mpumalanga (South Africa), Swaziland and NE KwaZulu–Natal (South Africa); apparently parapatric in SW Angola (Crawford-Cabral 1993a).

*C. aureus*. Slightly larger and taller; saddle not so prominent; body colour golden sand to fawn, not russet-red. Sympatric in parts of East Africa.



**Distribution** Endemic to Africa; occurs in two separate populations, one in north-east and East Africa, the other in southern Africa. Entirely absent from Zambia and through much of central and Equatorial Africa (Ansell 1978). The disjunct distribution of this species is similar to that of the Aardwolf *Proteles cristatus* and Bat-eared Fox *Otocyon megalotis*. The two populations are separated by as much as 1000 km and their discontinuous distribution suggests that regions of dry *Acacia* bush and savanna, the preferred habitat of this species, once connected south-west Africa with the Horn of Africa (Coe & Skinner 1993).

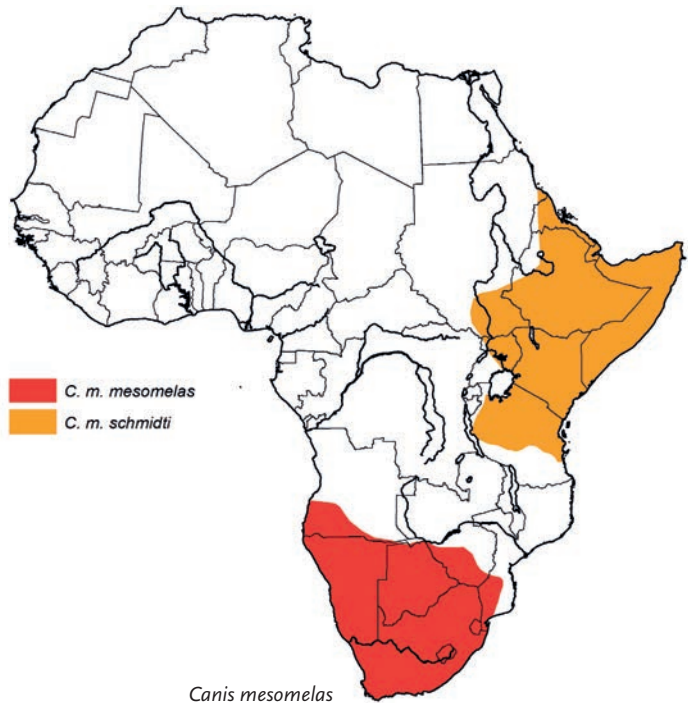
**Historical Distribution** Black-backed Jackal fossils are found in deposits in South Africa dating to at least 2 mya (Ewer 1956, Hendey 1974a), and there have been numerous palaeontological records in southern Africa over the past 30,000 years (Plug & Badenhorst 2001). Fossil remains have never been found north of Ethiopia, suggesting that they have always been restricted to sub-Saharan Africa. Commenting on remains of bones found in Bir Tarfawi and Bir Sahara, in the extreme south of Egypt, Gautier (1980) remarks ‘The material should be certainly ascribed to Golden Jackal *Canis aureus*, although the presence of the small jackal *Canis mesomelas*, a species today found toward the south in the Sudan, cannot be ruled out *a priori*.’

**Current Distribution** In north-east and East Africa from Sudan through Eritrea, Djibouti and Ethiopia, south to Kenya, E Uganda and N Tanzania. Southern range extends from SW Angola and Namibia through Botswana and S Zimbabwe to S Mozambique, Swaziland, Lesotho and South Africa, where they are mostly widespread (Crawford-Cabral 1993a, Lynch 1994, Monadjem 1998, Skinner & Chimimba 2005).

**Habitat** Occurs in a wide variety of habitats, from the arid coastal desert of Namibia and W South Africa (Dreyer & Nel 1990) to areas receiving more than 2000 mm of rainfall (Rowe-Rowe 1982). Occurs in montane grassland in the South African Drakensberg and Lesotho Maluti’s (above 3000 m) (Rowe-Rowe 1982, 1984, 1992a, Lynch 1994, N. Avenant pers. comm.) and in the alpine zone of Mt Kenya (3660 m; Young & Evans 1993), open savanna in Serengeti N. P., parts of Kenya, South Africa and Botswana (Kingdon 1977, Moehlman 1983, Fuller *et al.* 1989, Skinner & Chimimba 2005), woodland savanna mosaics in Zimbabwe and Mozambique (Smithers 1971, Loveridge & Macdonald 2002) and farmland. In most cases shows a preference for open habitats, tending to avoid dense vegetation. However, in Mokolodi G. R., Botswana, three radio-tracked Black-backed Jackals used bush savanna, mixed bushveld and agricultural land in preference to open grassland (Kaunda 2001).

Where more than one jackal species occurs in sympatry, the habitat is partitioned. Black-backed Jackals preferentially use either the grassland (when sympatric with the Side-striped Jackal, e.g. Hwange N. P., Zimbabwe), or *Acacia/Commiphora* woodland and long grassland (when sympatric with Golden and Side-striped Jackals, e.g. Laikipia and Serengeti; Kingdon 1977, Lamprecht 1978, Moehlman 1983, Estes 1991). In W Zimbabwe habitat partitioning is realized by aggressive encounters in which Black-backed Jackals displace Side-striped Jackals from grassland habitats into the less desirable woodland habitat (Loveridge & Macdonald 2002).

**Abundance** Generally common, especially in protected areas where suitable habitat occurs. In a wildlife area adjacent to Hwange N.



P. they occurred at densities of 53.9–79.1 per 100 km<sup>2</sup>, expanding to 68.3–97.1 per 100 km<sup>2</sup> during the breeding season (A. Loveridge pers. obs.). Rowe-Rowe (1984, 1992a) recorded densities of 40/100 km<sup>2</sup> in Giants Castle G. R., KwaZulu–Natal, and 10–20/100 km<sup>2</sup> in other areas of the province (Rowe-Rowe 1982, 1992a). In dry river beds in the SW Kalahari strip counts yield densities that vary from 0.09 to 1.3/km<sup>2</sup> (mean = 0.62), extrapolated to 62/100 km<sup>2</sup> (mean = 9–130) (J. A. J. Nel unpubl.). In Serengeti N. P., East Africa, Waser (1980) found densities of 0.5/km<sup>2</sup>. Densities of 22/km<sup>2</sup> have been reported at Cape Cross Seal Reserve, Namibia, perhaps because of superabundant resources there (Hiscocks & Perrin 1988). This density estimate for the Cape Cross population would only apply to the area in the immediate vicinity of the colony where the jackals aggregate at the seal colony to feed. In the surrounding West Coast Recreation Area where the jackals reside they are more dispersed (N. Jenner pers. comm.). Despite strenuous control measures (such as dog hunting, shooting, trapping and poisoning) in many farming areas of southern Africa this species has never been completely exterminated.

**Adaptations** Black-backed Jackals are relatively unspecialized canids and are well suited for an opportunistic life-style in a wide variety of habitats. They have a well-developed carnassial shear, with a longer premolar cutting blade than other jackal species, which suggests a greater tendency towards carnivory than other jackal species (Van Valkenburgh 1991, Van Valkenburgh & Koepfli 1993). Examination of kidney structure suggests that this species is well adapted to water deprivation (Loveridge 1999), which may explain its presence in the drier parts of the African continent. They apparently have a narrow thermoneutral zone (22.5–27.5 °C) above which thermal conductance – controlled by fur thickness, posture and piloerection – increases (Downs *et al.* 1991).

They show a high propensity for social learning (Nel 1999) and learn to avoid coyote getters (Brand & Nel 1997). Kingdon (1997) suggests that the Black-backed Jackal’s brighter, more contrasting



Lateral view of skull of Black-backed Jackal *Canis mesomelas*.

colouration is indicative of its less cryptic behaviour. In addition, Black-backed Jackals are reputed to be more aggressive than other species of jackal (Kingdon 1977, Estes 1991, Skinner & Chimimba 2005). Wyman (1967) found that this species was much more common than Golden Jackals at large carnivore kills in the Ngorongoro Crater, Tanzania, despite being less numerous in the area. Estes (1991) notes that Black-backed Jackals are more likely to attempt to feed on Lion *Panthera leo* and Spotted Hyaena *Crocuta crocuta* kills than other jackal species and that pups of this species become 'quarrelsome and unsocial' and are more likely to emigrate than Golden Jackal pups. Greater tendency towards aggressive behaviour is an adaptation that allows this species to oust the Side-striped Jackal from favourable habitat (Loveridge & Macdonald 2002).

**Foraging and Food** Opportunistic, generalist feeders. Kok & Nel (2004) found Black-backed Jackals to be more opportunistic and less specialized than sympatric felids (Wildcat *Felis silvestris* and Caracal *Caracal caracal*), reflecting phylogenetic adaptations to prey acquisition, and less specialized than the sympatric Cape Fox *Vulpes chama*. Diet varies according to food availability (Loveridge & Macdonald 2003, Skinner & Chimimba 2005). Numerous studies of dietary preferences have been undertaken, with dietary items generally including small to medium-sized mammals (e.g. murids, springhares *Pedestes* spp., young ungulates), reptiles, birds and birds' eggs, carrion and human refuse, as well as invertebrates (e.g. termites, grasshoppers) and plant matter (Roberts 1922, Bothma 1966a, 1971a, Smithers 1971, Stuart 1976, 1981, 1987, Kingdon 1977, Lamprecht 1978, Rowe-Rowe 1978a, 1983, Ferguson 1980, Dreyer & Nel 1990, Kok 1996, Kaunda & Skinner 2003, Klare *et al.* 2009). They also will feed on beached marine mammals, seals, fish, sea birds (e.g. Cape Cormorant *Phalacrocorax capensis* and Kelp Gull *Larus dominicanus*) and mussels on coasts (Nel & Loutit 1986, Avery *et al.* 1987, Nel *et al.* 1997, Oosthuizen *et al.* 1997, Kolar 2005).

The main feature of this species' foraging behaviour is flexibility and opportunism. Black-backed Jackals are largely nocturnal, but activity periods are extended well into the daylight hours in areas where they are free from persecution. In Hwange N. P. (Zimbabwe), Mokolodi G. R. (Botswana) and the Kalahari of South Africa, Black-backed Jackals exhibited peaks of activity in the evening and early morning (Ferguson *et al.* 1988, Kaunda 2000, Loveridge & Macdonald 2003). The large, mobile ears are used to locate quails, invertebrates and small mammalian prey in long grass. A leap, followed by an accurate pounce is employed to capture prey, guided by the sound, after the manner of a Red Fox *Vulpes vulpes* (Kingdon 1977, A.J. Loveridge & J.A.J. Nel pers. obs.).

Rowe-Rowe (1983) showed that, in the Drakensberg (South Africa), occurrence of carrion, rodent and ungulate prey in the diet closely corresponded to availability within the environment. In Hwange N. P., the diet changed from seasonally abundant invertebrates in the wet season to mammalian prey and carrion in

the dry season. Seasonally, temporally or locally abundant patches of food are exploited wherever possible. Ferguson *et al.* (1988) found that their activity closely approximates the activity cycles of local rodent prey. Black-backed Jackals on the Namib Desert coast of southern Africa scavenge extensively in the seal colonies, where marine refuse provides a rich resource base (Dreyer & Nel 1990) and where they have been seen to kill and eat neonate seal pups (e.g. Kolar 2005). Jackals especially favour the rich afterbirth. Outside the seal birthing period, jackals actively kill yearling and adult seals (N. Jenner pers. comm.). In Serengeti N. P. Black-backed Jackals exploited temporally abundant African Arvicanthus *Arvicanthus nilotica* (Moehlman 1983). On game ranches in the Northern Cape, South Africa, medium-sized ungulates, particularly Springbok *Antidorcas marsupialis*, make up a large proportion (up to 78% of biomass ingested) of Black-backed Jackal diet, and jackals may have significant impact on Springbok numbers in this area (Klare *et al.* 2009).

Black-backed Jackals are quick to respond to prey distress calls and often investigate the activities of large carnivores such as Lions and Spotted Hyaenas (A. Loveridge pers. obs.). They are recorded hunting cooperatively with Cheetahs *Acinonyx jubatus* (Eaton 1969), and, in the Namib, frequently occur in association with Brown Hyaenas *Hyaena brunnea* and may benefit by occasionally scavenging food items from the larger carnivore. Weak or unwary prey items are quickly capitalized upon; for instance, a pair of Black-backed Jackals in Hwange N. P. was, on two occasions, observed snatching young Chacma Baboons *Papio ursinus* that had strayed too far from the protection of the troop (A. Loveridge pers. obs.).

Commonly, pairs and small family groups are seen foraging together; for example, in the Ukhahlamba Drakensberg Park, KwaZulu-Natal, 78% of sightings (n = 872) were of single animals, 19% of pairs and only 3% of groups of three or four (Rowe-Rowe 1984). Less often large aggregations have been observed at particularly rich food resources. Groups of between 8 and 12 aggregate at large carcasses of herbivores, and more than 80 have been recorded at seal colonies on the Namib Desert coast (Oosthuizen *et al.* 1997), with jackals commuting up to 20 km from their denning or resting sites to access this resource (Jenner *et al.* 2011). Such aggregations are accompanied by aggressive behaviour between territorial individuals. However, in the SW Kalahari, where antelope carcasses are uncommon, pairs or groups of up to 30 individuals congregated at Common Eland *Tragelaphus oryx* or Gemsbok *Oryx gazella* carcasses and fed in succession, without much overt aggression (J. A. J. Nel pers. obs.). Mated Black-backed Jackal pairs will often cooperate in the capture of prey resulting in a higher success rate (Lamprecht 1978, Macdonald *et al.* 2004.). In Botswana, McKenzie (1990) found that, on occasion, they form 'packs' in order to hunt adult Impala *Aepyceros melampus*, and other authors have recorded several jackals taking adult antelope (Pienaar 1969, Van Lawick & Van Lawick-Goodall 1970, Sleicher 1973, Lamprecht 1978, Krofel 2008). Kamler *et al.* (2010) report an observation of a single Black-backed Jackal chasing and killing, by means of a throat bite, an apparently healthy adult Impala.

Caching of food is common (Lamprecht 1978), while on the Namib Desert coast accumulations of prey remains result in 'middens' as a result of animals carrying prey to feeding sites (Avery *et al.* 1987, Dreyer & Nel 1990).

This species will prey on livestock (especially juvenile goats and sheep) and is thus considered vermin in many livestock-producing

regions (Van der Merwe 1953). In some sheep-farming areas of KwaZulu–Natal, Black-backed Jackal predation may account for 3% of newborn lambs (Lawson 1989), equating to 2% of the total flock per year (Rowe-Rowe 1975a). In the Graaff Reinet and Nuwe Roggeveld areas losses amount to 3.9% (De Villiers 1979) and 2.4% (Vorster 1988), respectively, and on some individual farms, as high as 15–18% (Brand 1993). In N Botswana, 77% of domestic livestock losses to wild carnivores were due to Black-backed Jackal predation (Gusset *et al.* 2009). By contrast, in S Namibia, where controlled herding is practised, losses due to predation amount to only 0.3–0.5% (Brown 1988). Likewise, in villages bordering Serengeti N. P., where households lose 4.5% of their livestock annually to predators, Black-backed Jackals accounted for < 1% of incidents (Holmern *et al.* 2007).

**Social and Reproductive Behaviour** The monogamous mated pair is the basis for social structure. The pair bond appears to be life-long in most cases, and if one member of a pair dies the other will often lose its territory (Moehlman 1978, 1986, Estes 1991). However, on one occasion an immigrant ♀ was observed to displace the established ♀ in a territory, subsequently mating with the original territorial ♂ and giving birth to a litter of pups (A. Loveridge pers. obs.). Black-backed Jackals are territorial, using faeces and urine to demarcate their territorial boundaries (Kingdon 1977, Ferguson *et al.* 1983). A mated pair will often scent-mark in tandem, and Moehlman (1983) reports that one foraging pair tandem marked on 76% of observed marking incidents. Tandem marking advertises the presence of both members of the pair, and the pair will aggressively expel intruders. Vocalization by the territorial pair advertises occupancy of the territory and thereby reduces the number of aggressive encounters. Territories are spatially and temporally stable, but may fluctuate in size with season (Loveridge & Macdonald 2001) or where resource levels are widely variable between years (Moehlman 1983). In Hwange N. P., a mated pair of Black-backed Jackals is known to have held the same territory for at least four years (A. J. Loveridge pers. obs.). In Cape Cross Seal Reserve, jackals actively defend a territory during the breeding season. One mated pair has been recorded in the same breeding territory for at least four years (N. Jenner pers. comm.).

Home-ranges differ between localities: in the Rift Valley in Kenya, home-ranges varied from 0.7 to 3.5 km<sup>2</sup>, with a mean of 1.8 km<sup>2</sup> (Fuller *et al.* 1989). In Zimbabwe home-ranges were larger in the cold dry season (1.05–1.3 km<sup>2</sup>) and smaller in the hot dry season (0.32–0.62 km<sup>2</sup>) (Loveridge & Macdonald 2001). In South Africa, home-range size averaged 18.2 km<sup>2</sup> (n = 14) in Giants Castle G. R. in the Drakensberg (Rowe-Rowe 1982), and 17.8 km<sup>2</sup> in the Northern Cape Province (Kamler *et al.* 2012). In Gauteng and North West Province, home-range size was 3.4–21.5 km<sup>2</sup> (mean 10.6 km<sup>2</sup>; n = 8) (Ferguson *et al.* 1983). Ranges of subadults varied considerably, from 1.9 to 575 km<sup>2</sup> (mean 85.2 km<sup>2</sup>, n = 11), with the largest ranges likely attained by dispersing individuals. In the more arid SW Kalahari, ranges were smaller, with adult ranges varying from 2.56 to 5.2 km<sup>2</sup> (mean 4.32 km<sup>2</sup>; n = 4) and subadult ranges from 4.04 to 8.8 km<sup>2</sup> (mean 6.32 km<sup>2</sup>; n = 4) (Ferguson *et al.* 1983). At Cape Cross Seal Reserve, average home-range size was 7.1 km<sup>2</sup> (range 3.2–13.2) or 24.9 km<sup>2</sup> (range 17.6–34) as calculated by the minimum area or modified minimum area methods (n = 4 in both cases). Here Black-backed Jackals did not defend their ranges, with home-ranges



Black-backed Jackal *Canis mesomelas* action drawing.

overlapping, and thus were not territorial (Hiscocks & Perrin 1988). At Cape Cross Seal Reserve home-range overlap is extensive around the seal colony. However, during the breeding season jackals actively defend and mark a territory (N. Jenner pers. comm.). In all other cases ranges were defended and mutually exclusive for pairs. Ferguson *et al.* (1983) reported that adults moved an average daily distance of 12 km.

In southern Africa the Black-backed Jackal is a very vocal species. A high-pitched, whining howl is used to communicate with group members and is often used to call the group together in the early evening. This may also function in territorial advertisement. Howling often stimulates the same behaviour in adjacent territories. A three- to five-syllable alarm call, consisting of an explosive yelp followed by a series of shorter high-pitched yelps, is used when disturbed and may be frantic and prolonged when mobbing a Leopard *Panthera pardus*. A low-pitched, gruff bark is used to warn pups of intruders near the den, and whines are used to call to pups. Kingdon (1997) notes the use of a 'clattering distress call' and a loud yelp when alarmed. Interestingly, Black-backed Jackals are much less vocal where they occur alongside the Golden Jackal in Serengeti N. P. in that they do not howl, and instead vocalize with yaps interspersed with howls. This is in contrast to their southern range where, in the absence of Golden Jackals, they howl in much the same way as Golden Jackals (Kingdon 1977, 1997, H. Kruuk pers. comm.). Elimination of the howl from the vocal repertoire of this species may serve to reduce the ambiguity of the signal, thereby limiting competition between these two species, and perhaps reducing instances of inter-specific territorial conflict.

Mating in this species is accompanied by increased vocalization and territoriality in both sexes (Skead 1973, Bernard & Stuart 1992, Loveridge & Macdonald 2001). The dominant individuals within the territory prevent same sex subordinates (usually offspring) from

mating by constant harassment. As with other canids, there is a copulatory tie after mating.

Pups are born in modified termitaria, disused burrows of Aardvark *Orycteropus afer* or other convenient burrows (less frequently caves or other crevices), often with multiple entrances. Jackals sometimes dig their own dens. At Cape Cross Seal Reserve jackals dig their own dens in salt-pans, dry river beds and under large boulders, but will also den in disused Brown Hyaena dens (N. Jenner pers. comm.). Jackals with pups will move dens several times during the first 4–5 months; the most likely explanation for this behaviour on the Namib coast is to reduce parasites (N. Jenner pers. comm.). The same den sites may be used from year to year. For the first three weeks the mother spends up to 90% of her time in the den with the pups; the ♂ and any helpers provision her during this time (Moehlman 1983). Parents and alloparents feed pups by regurgitation. Alloparental care is most fully documented for Black-backed Jackals in Serengeti N. P. (Moehlman 1978, 1983; but see also Ferguson *et al.* 1983). Alloparents guard the pups when the parents are foraging. One helper may increase the average number of pups surviving per mated pair from 1 to 3.3, and two helpers further increases survival to 4 pups (Moehlman 1979, 1983). Estes (1991) suggests that guarding of pups is more important in this species because they tend to den in thicker cover, allowing predators to approach the den more closely without detection. On the Namib coast, guarding helps protect pups from Brown Hyaena predation. Alloparents contribute to boundary defence and will actively protect young from intruding jackals (N. Jenner pers. comm.). Predators such as Spotted Hyaenas, approaching the den, are driven off by determined harassment, in some instances a pair of defending Black-backed Jackals will cooperate in this defence by alternately dashing in to nip the hindquarters of the intruder, before making a hasty escape (Moehlman 1983).

Juveniles disperse at one year of age, although some (24% in Serengeti; Moehlman 1983) may remain within their natal territory to act as helpers. In Hwange N. P., dispersal of five young Black-backed Jackals was documented (two ♀♀, three ♂♂). They dispersed over an average of  $2.8 \pm 2.05$  km, the maximum distance being 20 km. Two (one ♀, one ♂) dispersed to neighbouring territories where a vacancy existed, two (one ♀, one ♂) dispersed to nearby territories using only the periphery of the territory until they were later integrated into the group, and one floated between the natal territory and adjacent territories (A. Loveridge pers. obs.). Elsewhere dispersal distances of more than 100 km have been recorded, in one instance a ♂ dispersing 126 km over a 15-month period (Bothma 1971b, Ferguson *et al.* 1983).

**Reproduction and Population Structure** Mating generally occurs from late May to Aug and, following a gestation period of about 60 days, births occur from around Jul (sometimes Jun) to Oct (Wyman 1967, Fairall 1968, Kingdon 1977, Stuart 1981, Moehlman 1983, Bernard & Stuart 1992, Bingham & Purchase 2002, N. Jenner pers. comm.); later births were recorded in the Rift Valley in Kenya (Sep–Jan; Fuller *et al.* 1989). In the KwaZulu–Natal Drakensberg, Rowe-Rowe (1978a) recorded a peak in births in Jul. Bernard & Stuart (1992) suggested that summer births are timed to coincide with the reproductive season of important prey like the Southern African Vlei Rat *Otomys irroratus* and Mesic Four-striped Grass Rat *Rhabdomys dilectus*, and winter births with an increase in the availability of ungulate carcasses at the end of the winter dry season.

Litter-size ranges between one and nine (Wyman 1967, Rowe-Rowe 1978a, Bingham & Purchase 2002, N. Jenner pers. comm.); Bingham & Purchase (2002) found mean prenatal litter-size to be 4.6 (range 1–8) pups based on examination of foetuses and placental scars. Pups are born blind, open their eyes at days 8–10, first emerge from the den at three weeks, are weaned at 8–9 weeks, and are completely independent of the den at 14 weeks (Moehlman 1978, A. Loveridge pers. obs.). Permanent teeth start erupting at around 14–16 weeks of age, and are usually fully erupted at one year (Lombaard 1971, Bingham & Purchase 2003). Pups are able to hunt on their own at six months of age, but parents continue to occasionally groom and feed them (Moehlman 1983). They reach sexual maturity at about 11 months (Ferguson *et al.* 1983), but they seldom reproduce in their first year (Ferguson *et al.* 1983, Bingham & Purchase 2002).

Most pup mortality occurs in pups younger than 14 weeks (Moehlman 1987). On the Namib coast, where jackals have few predators, risk of mortality may be greatest during dispersal (post six months) (N. Jenner pers. comm.). It is unlikely that Black-backed Jackals live much beyond about seven years of age in the wild (Rowe-Rowe 1986, 1992a), though captives have lived more than 14 years (Nowak 1999, Weigl 2005).

**Predators, Parasites and Diseases** Main predator of adults is the Leopard (Turnbull-Kemp 1967). Four of 11 radio-collared Black-backed Jackals were killed and eaten by Leopards in a study in Hwange N. P. (A. Loveridge pers. obs.) and Estes (1967) observed 11 jackals taken by a single Leopard over the course of three weeks, and they may be a favourite Leopard prey item in some areas (Kingdon 1977). Other large predators, such as Spotted Hyaenas and Brown Hyaenas, may prey on unprotected pups (Van Lawick & Van Lawick-Goodall 1970, N. Jenner pers. comm.), as will the Ratel *Mellivora capensis* (Begg *et al.* 2003a), and Kamler *et al.* (2007) document several instances of predation on Black-backed Jackals by African Wild Dogs *Lycaon pictus*. There is also a record of them being preyed upon by Caracals *Caracal caracal* (Melville *et al.* 2004). Other predators include birds of prey; Van Lawick & Van Lawick-Goodall (1970) observed a Martial Eagle *Polemaetus bellicosus* fly away carrying a subadult Black-backed Jackal.

In Zimbabwe, seroprevalence of canine distemper virus, canine parvovirus and canine adenovirus (type 1) were 63.6%, 18.5% and 9.1%, respectively, in 22 Black-backed Jackals sampled (Spencer *et al.* 1999). Although jackals act as reservoirs for these diseases, susceptibility is not known. However, in Serengeti N. P. distemper is believed to have been the cause of several epidemics affecting Black-backed Jackals (Moehlman 1983). Black-backed Jackals are extremely susceptible to rabies, succumbing to the disease after an incubation period of between 15 and 17 days (Foggin 1988, Bingham *et al.* 1995). They are significant vectors of rabies in C southern Africa and are responsible for transmission of the disease to domestic stock (Foggin 1988, Bingham & Foggin 1993, Swanepoel *et al.* 1993, Bingham *et al.* 1999a). Seasonal peaks in rabies cases correspond closely to the mating season and dispersal periods when social disturbance is high (Loveridge & Macdonald 2001). The loss of livestock and the expense of vaccination make rabies economically significant in southern Africa. In some areas rabies control is undertaken by culling of wildlife, especially jackals, and is thus a major cause of mortality. However, rabies spread may be more restricted in stable populations

than in those disturbed by culling regimes. Rabies is rare in national parks, which may be due to the absence of domestic dogs (Cumming 1982) or to intact ecological processes and low disturbance (Foggin 1988, McKenzie 1993). Rabies in jackals is probably better controlled by oral vaccination techniques (e.g. Bingham *et al.* 1995, 1999a) and immunization of domestic dogs (Rhodes *et al.* 1998, Bingham *et al.* 1999a) than by culling (Loveridge & Macdonald 2001). If, as in other sympatric canids, behavioural avoidance and spatial segregation between species occurs, the contact rate (and hence the opportunity for transmission) may be low and reduced overall when jackals occur in sympatry (Loveridge 1999).

Black-backed Jackals have been recorded infected with internal parasites, including the trematode *Athesmia* (Hammond 1972), various cestodes (see list in Walton & Joly 2003) and protozoan parasites such as *Babesia canis* (Van Heerden 1980), *Ehrlichia canis* (Price & Karstad 1980) and *Sarcocystis* spp. (Wesemeier *et al.* 1995). Black-backed Jackals have also succumbed to sarcoptic mange (Keep 1970, Van Heerden 1980), particularly on the Namib coast (N. Jenner pers. comm.). Ectoparasites recorded on Black-backed Jackals include numerous ixodid ticks: *Amblyomma hebraeum*, *A. marmoreum*, *A. variegatum*, *Boophilus decoloratus*, *Haemaphysalis leachi*, *H. silacea*, *H. spinulosa*, *Ixodes pilosus*, *I. rubicundus*, *Rhipicephalus appendiculatus*, *R. evertsi*, *R. nuttalli*, *R. simus* and *R. zambeziensis* (Hall-Martin & Botha 1980, Horak *et al.* 1987, 2000).

**Conservation** IUCN Category: Least Concern. CITES: Not Listed.

Black-backed Jackals are persecuted for their role as livestock killers and as rabies vectors. Such efforts at population control appear largely ineffective (Rowe-Rowe 1986) and probably only succeed in producing a temporary reduction in local numbers. Bingham & Purchase (2003) note that productivity in this species is sufficiently high for rapid recovery following population crashes or extermination campaigns. There is now no significant trade in jackal products, although hunting and trapping for skins occurs in some areas, and body parts are used in traditional African medicine and clothing (N. Avenant pers. comm.). Populations of the species occur in numerous well-managed protected areas across their range, including Masai Mara (Kenya), Serengeti N. P. and Selous G. R. (Tanzania), Skeleton Coast N. P., Cape Cross Seal Reserve and Etosha N. P. (Namibia), Kgalagadi Transfrontier Park (Botswana, South Africa), Hwange N. P. (Zimbabwe) and Ukhahlamba-Drakensberg Park and Kruger N. P. (South Africa) (Loveridge & Nel 2004). Black-backed Jackals have been maintained in captivity for use in experiments testing rabies vaccine (Bingham *et al.* 1995), but are usually not a common zoo species.

### Measurements

#### *Canis mesomelas*

HB (♂♂): 721 (680–755) mm, n = 39  
 HB (♀♀): 673 (640–725) mm, n = 52  
 T (♂♂): 329 (280–365) mm, n = 39  
 T (♀♀): 314 (250–370) mm, n = 52  
 HF c.u. (♂♂): 161 (150–179) mm, n = 39  
 HF c.u. (♀♀): 160 (140–180) mm, n = 52  
 E (♂♂): 109 (90–115) mm, n = 39  
 E (♀♀): 99 (80–115) mm, n = 52  
 WT (♂♂): 7.9 (6.8–9.5) kg, n = 39

WT (♀♀): 6.6 (5.5–10.0) kg, n = 52  
 Zimbabwe (Smithers 1983)

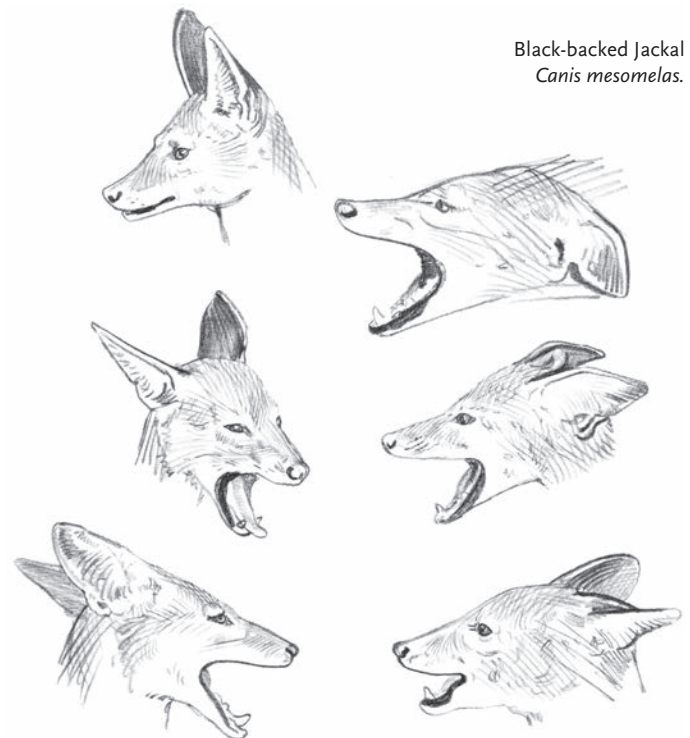
HB (♂♂): 785 (690–900) mm, n = 65  
 HB (♀♀): 745 (650–850) mm, n = 42  
 T (♂♂): 326 (270–395) mm, n = 70  
 T (♀♀): 316 (260–381) mm, n = 45  
 HF c.u. (♂♂): 160 (130–185) mm, n = 66  
 HF c.u. (♀♀): 156 (140–180) mm, n = 43  
 E (♂♂): 109 (90–132) mm, n = 68  
 E (♀♀): 104 (80–120) mm, n = 41  
 WT (♂♂): 8.2 (5.9–12.0) kg, n = 59  
 WT (♀♀): 7.4 (6.2–9.9) kg, n = 42

Northern Cape, Western Cape and Eastern Cape, South Africa (Stuart 1981)

Other mean measurements recorded include: 8.4 kg for ♂♂ (range 6.4–11.4; n = 123) and 7.7 kg for ♀♀ (range 5.9–10.0; n = 84) in Ukhahlamba-Drakensberg Park, KwaZulu-Natal (Rowe-Rowe 1978a); and 8.2 kg for ♂♂ (range 5.0–9.3; n = 26) and 7.6 kg for ♀♀ (range 6.3–8.5; n = 19) in the former Transvaal (Rautenbach 1982). At Cape Cross Seal Reserve, jackals are slightly larger than in other parts of southern Africa and ♂♂ weigh 10.3 (7.5–13.3) kg, n = 28, and ♀♀ weigh on average 8.7 (7.0–10.7) kg, n = 29 (N. Jenner pers. comm.); Stutterheim (in litt.) recorded weights for ♂♂ of 9.7 (8.4–10.5) kg, n = 7, and for ♀♀ 8.7 (6.9–10) kg, n = 12. In East Africa, average weight of ♂♂ and ♀♀ is around 8.5 kg (7–13.5 kg) (Kingdon 1977).

**Key References** Dreyer & Nel 1990; Ferguson 1980; Loveridge 1999; Loveridge & Macdonald 2001, 2002, 2003; Moehlman 1979, 1983, 1986; Rowe-Rowe 1982; Skinner & Chimimba 2005.

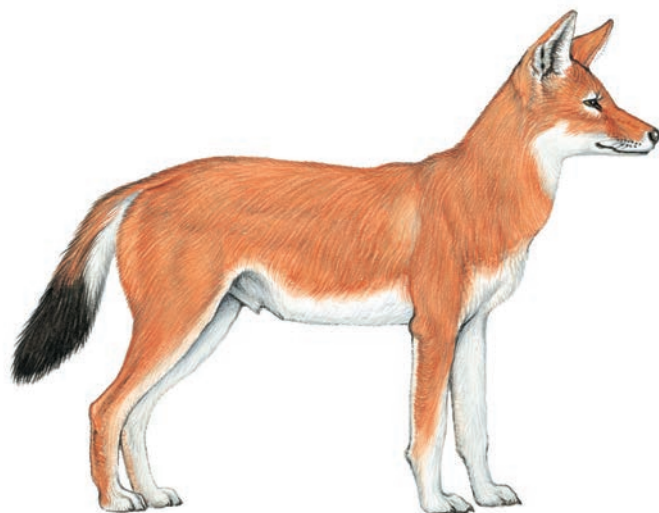
Andrew J. Loveridge & Jan A. J. Nel



**Canis simensis ETHIOPIAN WOLF (SIMIEN FOX)**

Fr. Loup d'Abyssinie; Ger. Aethiopienfuchs

*Canis simensis* Rüppell, 1835. Neue Wirbelt. Fauna Abyssin. Gehörig. Säugeth.  
1: 39, pl. 14. 'in der Bergen von Simen' [Simen Mountains, Ethiopia, ca. 13° 15' N, 38° 00' E].

Ethiopian Wolf *Canis simensis*.

**Taxonomy** The most distinct species in the genus *Canis*. Clutton-Brock *et al.* (1976) suggested close affinity with Side-striped Jackal *Canis adustus* and *Dusicyon* spp., and the species was placed in a separate genus *Simenia* by Gray (1868). Although it has been called the Simien or Simenian Fox, the Ethiopian Wolf is not closely linked to the *Vulpes* group (Clutton-Brock *et al.* 1976). Rook & Azzaroli Puccetti (1997) suggested a close relationship with jackals. Phylogenetic analysis using mitochondrial DNA sequencing suggested that *Canis simensis* is more closely related to the Grey Wolf *C. lupus* and the Coyote *C. latrans* than to any African canid (Gottelli *et al.* 1994). It may be an evolutionary relict of a grey wolf-like ancestor crossing to northern Africa from Eurasia (Gottelli *et al.* 1994), where fossils of wolf-like canids are known from the late Pleistocene (Kurtén 1968). Microsatellite and mitochondrial DNA variability is small relative to other canid species, suggesting small population sizes may have characterized its recent evolution (Gottelli *et al.* 2004). There is no fossil record of *C. simensis*. Two subspecies have been recognized (Coetzee 1977). Synonyms: *citernii*, *sinus*, *walgie*. Chromosome number: not known.

**Description** Medium-sized canid with reddish coat with distinctive white markings, long legs and elongate muzzle, resembling a large German Shepherd dog in conformation and size (Sillero-Zubiri & Gottelli 1994). Overall colour tawny-rufous (ochre to rusty-red), with dense whitish to pale ginger underfur. Throat, chest and underparts white. Distinctive white band around ventral part of neck; inner aspect of limbs white. Face, upper part of slender muzzle and dorsal surface of ears red. Ears broad and pointed, and directed forward; thickly fringed with long white hairs growing inward from the edge, whereas inside of pinnae is almost naked. Tail furry; anterior part white underneath. Rufous colour of coat continues in a short strip down back of tail, becoming a black strip connecting to

a thick black brush of guard hairs, which have black tips. No evident seasonal variation in coat colour, but contrast of white markings against the red coat increases with age and social rank in both sexes. Very long and slender legs. Forefoot has five toes; hindfoot has four toes. Limb posture is digitigrade. Male Ethiopian Wolves are larger than ♀♀ (20% larger in body mass). Female's coat generally paler than male's; during breeding and pregnancy coat turns pale yellow and becomes woolly, and tail turns brownish and loses much of its hair. There are eight nipples, but often only six are functional.

Skull elongated with a slender elongate nose. Facial length 58% of total skull length. Skull very flat in profile, with only a shallow angle between frontals and nasals. Neurocranium low and narrow, thick and almost cylindrical. Interparietal crest slightly developed. Teeth, especially premolars, small and widely spaced. Sharply pointed canines average 19 mm long (14–22 mm) and carnassials are relatively small (Sillero-Zubiri & Gottelli 1994). Lower third molar occasionally absent.

**Geographic Variation**

*C. s. simensis*: north-west of the Rift Valley. Nasal bones consistently shorter than those from the southern race.

*C. s. citernii*: south-east of the Rift Valley.

Dalton (2001) identified differences in the craniomorphology of wolves on both sides of the Rift Valley, but mtDNA analysis from a larger sample of individuals does not lend any support to subspecies recognition of northern and southern clades (Gottelli *et al.* 2004).

**Similar Species**

*Canis aureus*. Smaller, with relatively shorter legs; lacks distinctive reddish coat, white underparts, throat, chest, and tail markings of the Ethiopian Wolf. Other jackals (*C. mesomelas*, *C. adustus*) share same differences, but are not sympatric with Ethiopian Wolves.

**Distribution** Endemic to Africa; confined entirely to the Ethiopian Highlands, where species is restricted to a few mountain ranges of afroalpine grasslands and heathlands, between 6° N and 14° N.

**Historical Distribution** There are no recent records of the species at altitudes below 3000 m, although specimens were collected at 2500 m from Gojjam (where the species is now extinct – Marino 2003a) and north-western Shoa at the beginning of the century (Yalden *et al.* 1980). Its range restricted altitudinally by increasing agricultural pressure and small populations in Gosh Meda and Mt Guna recently became extinct (Marino 2003a, Marino *et al.* 2011). Reports from Chercher and North Sidamo are either erroneous or suggest further recent extinctions. There is no evidence that Ethiopian Wolves ever occurred in Eritrea.

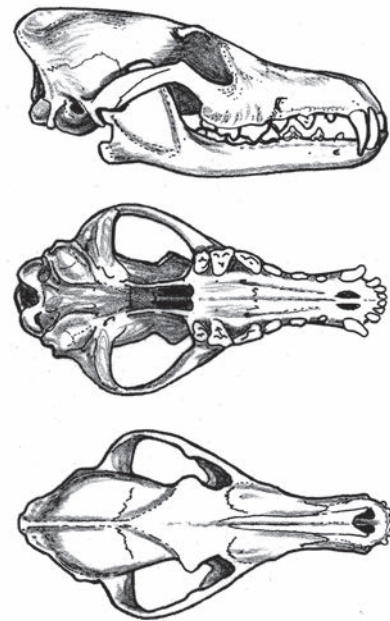
*Canis simensis*

**Current Distribution** Confined to seven mountain ranges of the Ethiopian Highlands, at altitudes of 3000–4500 m (Gottelli & Sillero-Zubiri 1992, Marino 2003a). Wolf populations occur both sides of the Rift Valley: the Simen Mts, North and South Wollo highlands and Menz to the north; and Arsi Mts, Bale Mts and West Bale to the south.

**Habitat** A very localized endemic species, confined to isolated pockets of afroalpine grasslands and heathlands where they prey on afroalpine rodents. Suitable habitats extend from above the treeline at about 3200 m, up to 4500 m, with some montane grasslands at 3000 m. However, subsistence agriculture extends up to 3500–3800 m in many areas, restricting wolves to higher ranges (Marino 2003b). Rainfall at high altitude varies between 1000 and 2000 mm/year, with one pronounced dry period from Dec to Feb/Mar.

Ethiopian Wolves utilize all afroalpine habitats, but prefer open areas with short herbaceous and grassland communities where rodents are most abundant, along flat or gently sloping areas with deep soils and poor drainage in parts. Prime habitats in the Bale Mts are characterized by short herbs (*Alchemilla* spp.) and grasses and low vegetation cover, a community maintained in continuous succession as a result of Giant Root-rat *Tachyoryctes macrocephalus* burrowing activity. Other good habitats include tussock grasslands (*Festuca* spp., *Agrostis* spp.), high-altitude scrubs dominated by *Helichrysum* spp. and short grasslands in shallow soils. In northern parts of the range, plant communities characterized by a matrix of 'guassa' tussock grasses (*Festuca* spp.), 'cherenfi' bushes (*Euryops pinifolius*) and giant lobelias (*Lobelia rhynchopetalum*) sustain high rodent abundance and are preferred by Ethiopian Wolves. Ericaceous moorlands (*Erica* and *Phillipia* spp.) at 3200–3600 m are of marginal value, with open moorlands with patches of herbs and grasses being relatively good habitat.

**Abundance** With only 400–450 individuals surviving (Gottelli & Sillero-Zubiri 1992, Marino 2003a, Marino *et al.* 2011), this distinctive carnivore is considered the rarest canid in the world (Sillero-Zubiri &

Lateral, palatal and dorsal views of skull of Ethiopian Wolf *Canis simensis*.

Marino 2004). More than half of the species' population (220–300) live in Bale Mts N. P., where density is positively correlated with density of rodent prey and negatively with vegetation height (Sillero-Zubiri & Gottelli 1995a, Marino 2003b). Not more than 110–150 Ethiopian Wolves persist north of the Rift Valley with less than 75 in Simien (Marino *et al.* 2011).

Highest densities are found in short afroalpine herbaceous communities (1.0–1.2 adults/km<sup>2</sup>); lower densities are found in *Helichrysum* dwarf-scrub (0.2/km<sup>2</sup>), and in ericaceous heathlands and barren peaks (0.1/km<sup>2</sup>). Ethiopian Wolves also are present at low density (0.1–0.2/km<sup>2</sup>) in montane grasslands at lower altitudes. Elsewhere, overall wolf density is relatively lower. In Menz, wolf density was estimated at 0.2 animals per km<sup>2</sup> (Tefera Ashenafi *et al.* 2005). Census data indicate higher abundance in North Wollo (0.20 ± 0.20 sightings per km), intermediate in Arsi and Guna (0.10 ± 0.11 and 0.10 ± 0.14, respectively), and lower in South Wollo and Simien (0.08 ± 0.13 and 0.06 ± 0.11, respectively) (Marino 2003b).

**Adaptations** The legs are strikingly long and slender, seemingly suitable for coursing in open country. The muzzle is long, and the small, well-spaced teeth suggest morphological adaptation to feeding on rodents. They have an unusually good sense of smell, and bolt more readily at scent than sight of man. The guard hairs are short and the underfur is thick, providing protection at temperatures as low as –15 °C. Ethiopian Wolves do not use dens to rest at night, and during the breeding season only pups and nursing ♀♀ use the den. Wolves sleep in the open, alone or in groups, curled up, with the nose beneath the tail. Several animals may sleep close together. During the cold nights in the dry season, a 'bed' is carefully prepared from a pile of vegetation debris, the product of Giant Root-rat activity. During the day they take frequent naps, usually resting on their sides. Occasionally, they seek shelter from the rain under overhanging rocks and behind boulders (Sillero-Zubiri 1994).

**Foraging and Food** Pack members forage and feed alone on small prey, contradicting the general trend in carnivores for grouping and

cooperative hunting. In the Bale Mts they are most active during the day feeding chiefly upon diurnal small mammals of the high-altitude afroalpine grassland community, such as the endemic Giant Root-rat (300–930 g), grass rats (*Arvicanthis blicki*, *Lophuromys melanonyx*, *L. flavopunctatus*, *Otomys typus*) and Starck's Hare *Lepus starcki*. Murid rodents accounted for 96% of all prey occurrences in faeces in Bale (Sillero-Zubiri & Gottelli 1995a). Elsewhere, Giant Root-rats are absent and the smaller African Root-rat *Tachyoryctes splendens* becomes an important component of the wolf diet (Malcolm 1997, Marino 2003b). Occasionally, Ethiopian Wolves were observed feeding on goslings and eggs, Rock Hyraxes *Procapra capensis*, and young of the Common Duiker *Sylvicapra grimmia*, Bohor Reedbuck *Redunca redunca* and Mountain Nyala *Tragelaphus buxtoni* (Sillero-Zubiri & Gottelli 1995a, Malcolm 1997, C. Sillero-Zubiri pers. obs.). Leaves of sedge (*Carex monostachya*) are occasionally ingested, probably to assist digestion or control parasites.

Ethiopian Wolves will take carrion or feed on carcasses; in fact a sheep carcass is the most successful bait for trapping. The local name 'Jeedala fardaa' – the horse's jackal – refers to the habit of following mares and cows about to deliver and eating the afterbirth. In areas of grazing in Bale Ethiopian Wolves were often seen foraging among herds of cattle, a tactic that may aid in ambushing rodents out of their holes, by using the herd as a mobile hide (Sillero-Zubiri 1994).

Ethiopian Wolves are mostly diurnal. Peaks of foraging activity in Bale suggest that they synchronize their activity with that of rodents above the ground (Sillero-Zubiri *et al.* 1995a, b). There is little nocturnal activity, with wolves seldom moving far from their evening resting site. They are more crepuscular and nocturnal where human interference is severe.

Digging out prey is common, mostly to catch Giant Root-rats, with the effort expended varying from a few scratches at a rat hole to the total destruction of a set of burrows. Sometimes digging serves to reach a nest of grass-rats. Kills often are cached and later retrieved. Rich food patches are carefully explored by wolves walking slowly, pausing frequently to investigate holes or to locate the rodents by hearing. Once a prey is located, the wolf moves stealthily towards it, taking short steps, and freezing, sometimes with its belly pressed flat to the ground. The quarry is grabbed with the mouth after a short dash. A stalk can last from seconds to up to one hour, in the case of a Giant Root-rat. Occasionally, wolves run in zig-zags across rat colonies picking up the rodents in passing.

Until recently, Ethiopian Wolves in Bale were unmolested by humans and did not appear to be regarded as a threat to sheep and goats, which are sometimes left unattended during the day (Gottelli & Sillero-Zubiri 1992). Only two instances of predation upon lambs were recorded during 1800 hours of foraging observation (Sillero-Zubiri & Gottelli 1994). Losses to wolves in the southern highlands were dismissed by herders as unimportant when compared with damage by Golden Jackals *Canis aureus* and Spotted Hyenas *Crocuta crocuta*. In N Ethiopia, Ethiopian Wolves have been persecuted in the past due to their reputation as predators of sheep and goats; livestock predation is reported as important in the heavily populated areas of Wollo and Simien (Marino 2003b).

**Social and Reproductive Behaviour** Ethiopian Wolves live in packs, a discrete and cohesive social unit that communally shares and defends an exclusive territory. Packs of 3–18 adults (mean 6)

congregate for social greetings and border patrols at dawn, noon and evenings, and to rest together at night, but break up to forage individually in the morning and early afternoon. Peaks of foraging activity suggest that wolves synchronize their activity with that of rodents above the ground. There is little nocturnal activity, with wolves seldom moving far from their evening resting site.

Annual home-ranges of eight packs monitored for four years averaged 6.0 km<sup>2</sup>, with some overlap in home-ranges. Home-ranges in an area of lower prey biomass averaged 13.4 km<sup>2</sup> (n = 4) (Sillero-Zubiri & Gottelli 1995b). Overlap and aggressive encounters between packs were highest during the mating season. Dispersal movements are tightly constrained by the scarcity of suitable habitat. Males do not disperse and are recruited into multi-male philopatric packs; some ♀♀ disperse at two years of age and become 'floaters', occupying narrow ranges between pack territories until a breeding vacancy becomes available (Sillero-Zubiri *et al.* 2004b). Dead breeding ♀♀ typically are replaced by a resident daughter.

Adult Ethiopian Wolves hunt alone but travel in packs when patrolling to advertise and maintain their territories. All pack members, independent of social rank, regularly scent-mark territory boundaries, via urine posts, scratching and deposition of faeces on conspicuous sites (mounds, rocks, bushes) (Sillero-Zubiri & Macdonald 1998). More often only adults of both sexes take part, led by one of the dominant pair, usually the ♀. Vocalizations also play a role in territory defence. Aggressive interactions with neighbouring packs are common, highly vocal and always end with the smaller group fleeing from the larger (Sillero-Zubiri *et al.* 2004b).

Calls can be grouped into two categories: alarm calls, given at the scent or sight of man, dogs, or unfamiliar wolves, start with a 'huff' (rapid expulsion of air through mouth and nose), followed by a quick succession of high-pitched 'yelps' (a series of 4–5 'yeahp-yeahp-yeahp-yeahp') and 'barks'. 'Yelps' and 'barks' can be also given as contact calls, and often attract nearby pack mates. Greeting calls include a 'growl' of threat, a high-frequency 'whine' of submission, and intense 'group yip-howls', given at the reunion of pack members and advertise pack size, composition and position. A lone howl and a group howl are long-distance calls used to contact separate pack members and can be heard up to 5 km away. Howling by one pack of wolves may stimulate howling in adjacent packs. Communal calls mustered pack members before a border patrol (Sillero-Zubiri & Macdonald 1998).

Many postures and habits of the Ethiopian Wolf are typical of other social canids. It grooms itself by licking and nibbling and by reciprocating attention of others. It laps water with its tongue. Wolves often wade streams and swim across narrow rivers when necessary. Ethiopian Wolves remain playful throughout their lives, particularly male siblings.

Precopulatory behaviour by the dominant ♀ includes an increase in the scent-marking rate, play soliciting, food-begging towards the dominant ♂ and agonistic behaviour towards subordinate ♀♀. The receptive period is synchronized in sympatric ♀♀ to less than two weeks (Sillero-Zubiri *et al.* 1998). Courtship may take place between adult members of a pack or with members of neighbouring packs. After a short courtship, which primarily involves the dominant ♂ permanently accompanying the ♀, the pair copulate over a period of 3 to 5 days. Copulation involves a tie lasting up to 15 min. Other ♂♂ may stand by a tied pair with no signs of aggression. Mate





Ethiopian Wolf *Canis simensis* dominance display.

preference is shown, with the ♀ discouraging attempts from all but the pack's dominant ♂, by either defensive snarls or moving away; she is receptive to any visiting ♂ from neighbouring packs. Up to 70% of matings ( $n = 30$ ) involved ♂♂ from outside the pack (Sillero-Zubiri *et al.* 1996a, 2004b).

During the breeding season social gatherings are more common and take place next to the den. Intense, energetic and noisy greetings that occur primarily when groups form or before tandem-marking patrols seem to be an important component in keeping cohesion and friendly relations within the pack. Other common interactions are food-sharing, allogrooming, nibbling and playing, which involves chasing, ambushing and mock fighting. Strong affiliative ties are developed between siblings during the first months of their life. Vicious play-fighting during the first weeks outside the den may determine the establishment of rank between siblings. Hierarchies among pack members are well established with frequent displays of dominance and subordination; a dominance rank develops among adults of each gender; shifts in rank may occasionally take place in ♂♂ but not among ♀♀ (Sillero-Zubiri *et al.* 2004b).

**Reproduction and Population Structure** The dominant ♀ of each pack gives birth once a year between Oct and Jan (Sillero-Zubiri *et al.* 1998, 2004b). Gestation, based on the time from last day of mating to parturition, lasts 60–62 days. Pups are born with their eyes closed and without teeth, in a den dug by the ♀ in open ground, under a boulder or inside a rocky crevice. Five and six placental scars were counted in the uteri of two ♀♀. A seven-week-old unborn litter comprised three female and two male foetuses, averaging 122 g. A ten-day-old female pup had a mass of 650 g. The natal coat is charcoal grey with a buff patch in chest and inguinal regions. Two to seven pups emerge from the den after three weeks. At this time, the dark natal coat begins to be replaced by the pelage typical of the species. Pups are regularly shifted between dens, up to 1300 m apart. In eight out of 18 natal dens watched, a subordinate ♀ assisted the mother in suckling the pups (Sillero-Zubiri *et al.* 2004b). At least 50% of extra nursing ♀♀ showed signs of pregnancy and may have lost or deserted their own offspring before joining the den of dominant ♀.

Development of the young is divisible into three stages: (1) early nesting (Week 1 to Week 4), when the young are entirely dependent on milk; (2) mixed nutritional dependency (Week 5 to Week 10), when milk is supplemented by solid foods regurgitated by all pack members until pups are completely weaned; and (3) postweaning dependency (Week 10 to Month 6), when the pups subsist almost entirely on solid foods supplied by helpers. Adults have been observed providing food to juveniles up to one year old. Juveniles will join adults in patrols as early as six months of age, but will not urinate with raised leg until 11 months if male or 18 months if female. Yearlings have 80–90% of adult body mass. Full adult appearance is attained at two years. Both sexes become sexually mature during their second year. Only about 60% of ♀♀ breed successfully each year (Sillero-Zubiri *et al.* 1996a). A ♂ in Bale lived to 15 years, but 8–10 is the norm (C. Sillero-Zubiri pers. obs.).

Adult sex ratio in packs is biased toward ♂♂ 1.8 : 1 ( $n = 59$ ), with small family groups closer to 1 : 1 (Sillero-Zubiri & Gottelli 1995b).

**Predators, Parasites and Diseases** No known predators, but unattended young may be taken by Spotted Hyaenas or Verreaux's Eagles *Aquila verreauxi*. Attacks of the Tawny Eagle *Aquila rapax* directed at small pups result in swift defence by guarding adults. The high densities and diversity of raptors (12 recorded species in Bale), many of which have been observed to feed on small mammals, are likely to pose the greatest competitive threat to Ethiopian Wolves. In addition, free-ranging domestic dogs, Golden Jackals and Servals *Leptailurus serval* may also feed upon the same prey species, and, therefore, will compete when food resources are limited. There is interference competition with domestic dogs, which will actively chase away Ethiopian Wolves from large carcasses. The Ratel *Mellivora capensis* is also a possible competitor for food and burrows (Sillero-Zubiri 1996).

The most widespread disease to affect Ethiopian Wolves is rabies, and is the main cause of mortality, killing whole wolf packs and accounting for a major population decline in Bale Mts with losses of up to 77% in 1991–92 (Sillero-Zubiri *et al.* 1996b, Haydon *et al.* 2002, Randall *et al.* 2006). In 2003–2004 and 2008–2009, rabies epizootics had a similar impact; the outbreaks were contained through parental vaccination (Randall *et al.* 2004, 2006, Johnson *et al.* 2010). Elsewhere, rabies has been reported in domestic dogs, livestock, people and wolves (Marino 2003b). The level of rabies awareness amongst people in the highlands, and the frequency of the reports, suggests high incidence across the highlands. In Bale, dogs travel regularly with their owners in and out of wolf range, and are in contact with many other dogs that are attracted to garbage and carrion in villages, and they may provide the vehicle for pathogens such as rabies or distemper to reach their wild relatives (Haydon *et al.* 2002). The risk of transmission, however, will depend on the probability of contact between wolves and dogs, which varies with grazing regimes in high-altitude pastures, dog husbandry and the spatial distribution of wolf habitat in relationship to settlements. High-density populations of Ethiopian Wolves are particularly vulnerable to decline due to rabies (Marino *et al.* 2006). A population viability model indicates that disease-induced population fluctuations and extinction risks can be markedly reduced with the vaccination against rabies of a relatively small

proportion of wolves (Haydon *et al.* 2002). Randall *et al.* (2006) present an integrated management strategy for rabies in Ethiopian Wolves combining long-term population monitoring, disease surveillance, conventional and emergency vaccination programmes, and advanced modelling techniques.

Other causes of mortality in Ethiopian Wolves include starvation of juveniles between weaning and one year of age, road kills and shooting. At least four animals have been killed by vehicles in Bale since 1988. Two others have been shot from the road and another two were left with permanent limps from collisions with vehicles.

Ethiopian Wolves are free of ectoparasites, perhaps because of the cold mountain climate; none were found on any of over 300 animals handled (C. Sillero-Zubiri pers. obs.). Nematodes and trematodes were present in faeces and carcasses, including *Taenia pisiformis* (M. Anwar pers. comm.).

**Conservation** IUCN Category: Endangered B1ab(iii,v); C1+2a(i), D. CITES: Not listed.

The Ethiopian Wolf is less common and less widely distributed now than in the past (Yalden *et al.* 1980, Marino 2003a). The main causes of this decline are loss of habitat to agriculture and grazing, disease, hybridization with domestic dogs and human persecution.

The highlands of Ethiopia are among the most densely populated agricultural areas within Africa. Habitat destruction and soil degradation have steadily reduced the afroalpine ecosystems, which increasingly resemble islands. Sixty per cent of all land above 3200 m has been converted into farmland, and all populations below 3700 m are particularly vulnerable to further habitat loss, especially if the areas are small and of relatively flat relief (Marino 2003b). Extensive overgrazing by livestock probably depresses rodent populations significantly, and in some areas habitat is threatened by proposed development of commercial sheep farms.

Human persecution is currently less severe than in the past and associated with conflicts over livestock losses (Marino 2003a). Some Ethiopian Wolf populations have been exterminated due to their reputation as predators of sheep and goats. Local people in Simien regard them as a menace to sheep, and report that they would come near the pens at night. In many regions, people living close to wolves believe numbers are recovering through successive years of good breeding and less persecution. Still, the degree of conflict due to predation determines the negative attitudes to wolves in some regions and resulting persecution (Marino 2003a). In the past, sport hunters occasionally killed Ethiopian Wolves, but no hunting is currently permitted and the species is protected by national law. Most of the range of the two largest populations, i.e. Bale and Simien, is protected within National Parks. There are no reports of exploitation for fur or other purposes, although parts of wolf skins were seen used as saddle pads (C. Sillero-Zubiri pers. obs.). There are no animals in captivity.

In western areas of Bale some Ethiopian Wolves had pale-coloured coats, heavily built bodies and kinky tails (Gottelli *et al.* 1994). One melanistic ♀ was heavier than any other ♀ captured, did not belong to any pack, and gave birth outside the breeding season; she twice lost her offspring after birth. Mitochondrial DNA restriction fragments and microsatellite alleles concluded that hybridization

occurred in areas with sympatric dogs, and was due only to crosses between female Ethiopian Wolves and male domestic dogs (Gottelli *et al.* 1994). Although hybrids are confined to parts of Bale, they may threaten the genetic integrity of the wolf population. Following hybridization, a population may be affected by outbreeding depression, or reduction in fitness, although to date this does not seem to have taken place in Bale.

Ethiopian Wolves have been monitored since 1983. The IUCN SSC Canid Specialist Group produced an action plan for the Ethiopian Wolf (Sillero-Zubiri & Macdonald 1997), providing a detailed strategy for the conservation and management of remaining wolf populations. This plan advocated immediate action on three fronts – education, wolf population monitoring and rabies control in domestic dogs – to conserve the afroalpine ecosystem and its top predator. As a result, the Ethiopian Wolf Conservation Programme (EWCP) was established in 1995 by the University of Oxford with support from the Born Free Foundation, UK. Its overall aim is to protect the afroalpine ecosystem and many of its rare highland endemic plants and animals through better management in Bale and the establishment of other conservation areas in Arsi, Menz and Wollo. The EWCP has taken a number of important steps, including: (1) a dog vaccination campaign in Bale and north Ethiopia; (2) sterilization programme for domestic dogs and hybrids in Bale; (3) community and school education programme; (4) strengthening the capacity of protected areas – funding patrolling and infrastructure; (5) surveys to determine the persistence and status of all populations of wolves; (6) monitoring of all wolf populations; (7) wolf vaccination interventions to mitigate rabies epizootics in the Bale Mts; and (8) setting up the Ethiopian Wolf Conservation Committee within Ethiopia as a national steering committee for dealing with conservation issues (see Sillero-Zubiri & Marino 2004). A conservation strategy and National Action Plan for the conservation of Ethiopian Wolves is now in place (IUCN SSC Canid Specialist Group 2011).

## Measurements

### *Canis simensis*

HB (♂♂): 963 (928–1012) mm, n = 18  
 HB (♀♀): 919 (841–960) mm, n = 8  
 T (♂♂): 311 (290–396) mm, n = 18  
 T (♀♀): 287 (270–297) mm, n = 8  
 HF c.u. (♂♂): 199 (193–209) mm, n = 18  
 HF c.u. (♀♀): 187 (170–197) mm, n = 8  
 E (♂♂): 108 (100–119) mm, n = 18  
 E (♀♀): 104 (95–110) mm, n = 8  
 WT (♂♂): 16.2 (14.2–19.3) kg, n = 18  
 WT (♀♀): 12.8 (11.2–14.2) kg, n = 8  
 Bale Mts, Ethiopia (Sillero-Zubiri & Gottelli 1994)

**Key References** Gottelli & Sillero-Zubiri 1992; Gottelli *et al.* 1994, 2004; Haydon *et al.* 2002; IUCN SSC Canid Specialist Group 2011; Marino 2003a; Sillero-Zubiri & Gottelli 1994, 1995; Sillero-Zubiri & Macdonald 1997; Sillero-Zubiri & Marino 2004; Sillero-Zubiri *et al.* 1996a, b, 2004.

Claudio Sillero-Zubiri

## GENUS *Lycaon* African Wild Dog

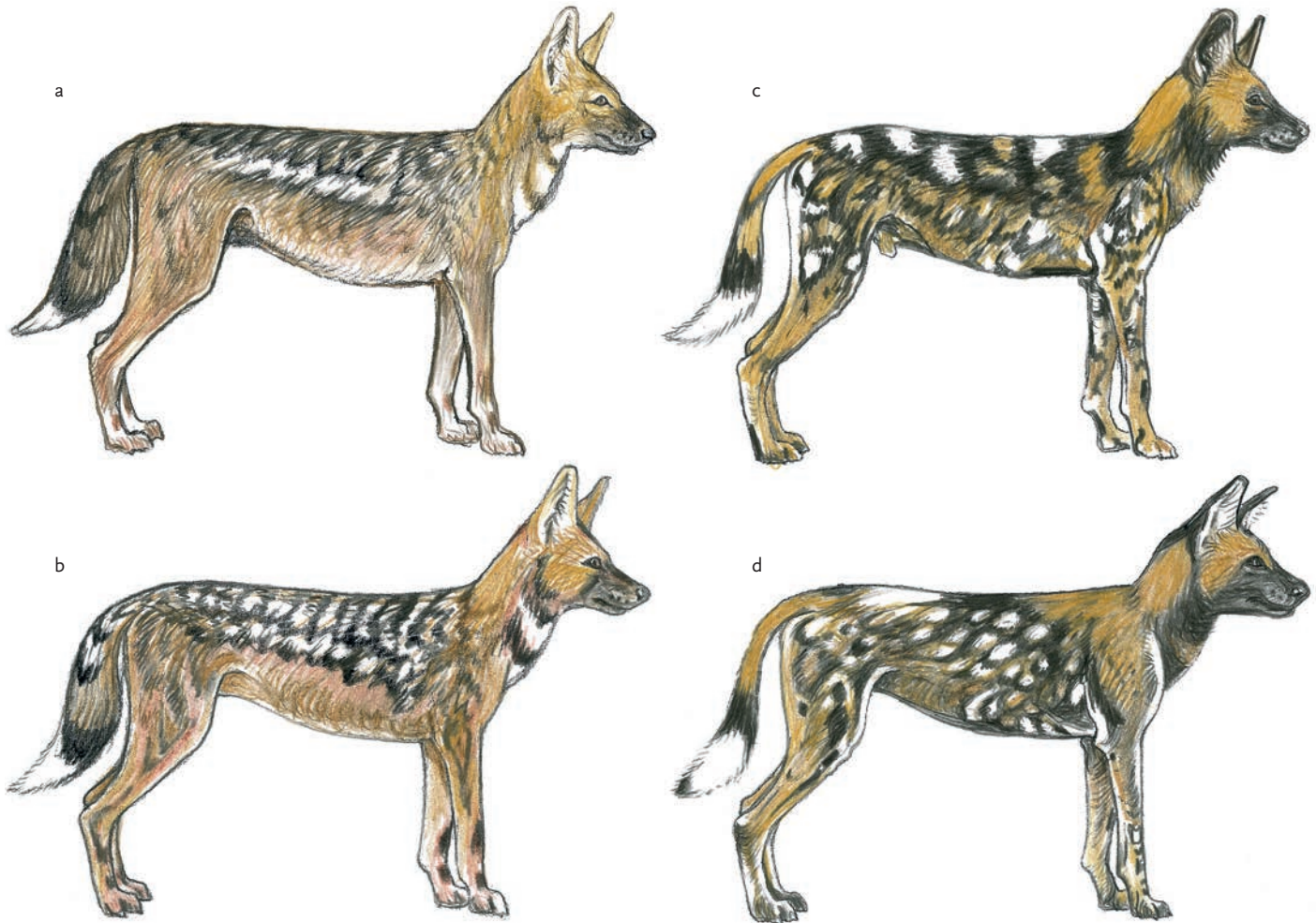
*Lycaon* Brookes, 1827. In: Griffith *et al.* Anim. Kingd. 5: 151.

The genus *Lycaon* was first identified by Brookes in 1827 after revising an earlier description by Temminck (1820) who identified a specimen as *Hyaena picta*. Extant *Lycaon* are known only from sub-Saharan Africa with fossil evidence of early forms of *Lycaon* identified in Africa from 3 to 2 mya. However, fossil evidence of *Lycaon* from the late middle Pleistocene also exists from localities outside of sub-Saharan Africa and includes a *Lycaon* specimen from Israel (Stiner *et al.* 2001) and possibly *Lycaon*-like fossils in Europe (Kurtén 1968; but see Stiner *et al.* 2001).

Studies by Matthew (1924, 1930) and Simpson (1945) placed *Lycaon* within the subfamily Simocyoninae. This was largely based on a modification of the carnassial tooth or blade-like lower molar with a unicuspid talonid (trenchant heel) possessed only by three extant canid genera (all monospecific); *Lycaon* (the African Wild Dog), *Cuon* (the Asian Dhole) and *Speothos* (the South American Bush

Dog). These hypercarnivorous canids have teeth specifically adapted for processing meat unlike other canid genera that are adapted more for omnivory (Van Valkenburgh 1989). More recent analyses of morphological and molecular genetic data reject the monophyly of the Simocyoninae. These data strongly support *Lycaon* as a distinct genus associated with the wolf-like canids, which include species in the genus *Canis* (wolves, coyotes, jackals, domestic dog) and *Cuon* (Clutton-Brock *et al.* 1976, Van Gelder 1978, Wayne & O'Brien 1987, Girman *et al.* 1993, Tedford *et al.* 1995, Wayne *et al.* 1997). The combination of molecular evidence (Wayne *et al.* 1997) and a review of palaeontological evidence (Rook 1994) suggests that *Lycaon* may be the sister taxon to the wolf-like canids and one of its most basal lineages.

Derek J. Girman



Pelage pattern formation in African Wild Dog *Lycaon pictus*. (a) Generalized, semi-cryptic formation in genus *Canis*, as expressed in various jackals and wolves. (b) Similar pattern becoming more conspicuous through enhanced tonal contrast. (c) *Lycaon* pelage in which *Canis*-like format has been dislocated but elements are still perceptible. (d) *Lycaon* pelage in which dislocation has generated typical 'marbling' (individual from Longido, N Tanzania).



**Geographic Variation** African Wild Dogs in East Africa are smaller than those in southern Africa and were originally believed to represent distinct subspecific populations. African Wild Dogs in north-east Africa also tend to be predominantly black with small white and yellow patches, while dogs in southern Africa are more brightly coloured with a mix of brown, black and white. However, on the basis of genetic analysis, no subspecies are currently recognized (Girman & Wayne 1997, Girman *et al.* 2001).

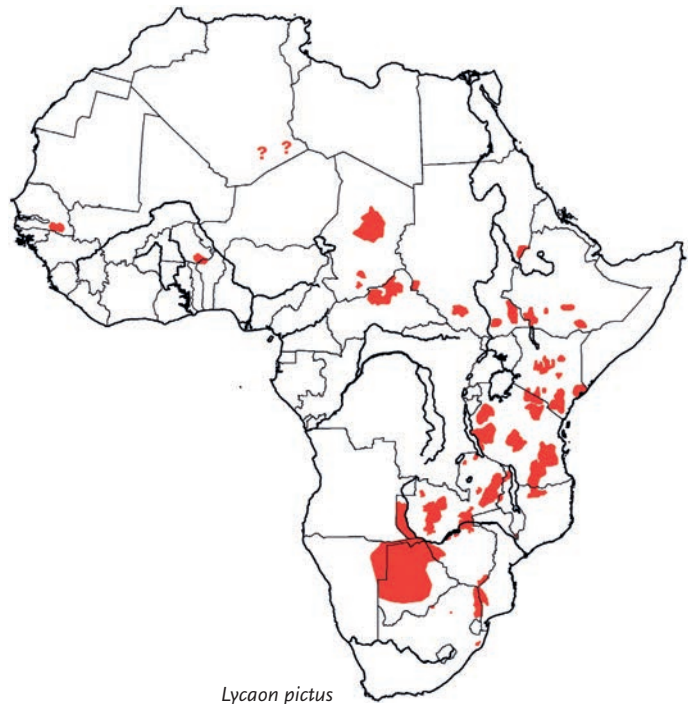
**Similar Species** Spotted Hyaenas *Crocuta crocuta*, Striped Hyaenas *Hyaena hyaena* and even jackals (*Canis* spp.) and feral domestic dogs are occasionally misidentified as African Wild Dogs, but all are only distantly related and morphologically distinct.

**Distribution** Endemic to Africa; formerly distributed throughout sub-Saharan Africa, from desert (Lhotse 1946) to mountain summits (Thesiger 1970). In North Africa occurred as disjunct populations in S and SW Algeria; there are no confirmed records from Libya, but they persisted (as vagrants) in Egypt until the late 1800s (Osborn & Osbornová 1998). Probably absent only from lowland rainforest and the most arid deserts (Schaller 1972).

**Current Distribution** African Wild Dogs have disappeared from much of their former range (Fanshawe *et al.* 1997, Woodroffe *et al.* 2004, IUCN SSC 2008, 2009). In North Africa, they may still survive in S Algeria, but there is no recent information; they were last recorded in the Tassili N. P. in 1996 (K. de Smet pers. comm.). The species is virtually eradicated from West Africa, where populations survive in Niokolo-Koba N. P. in Senegal and in the protected areas complex between Niger, Benin and Burkina Faso (Lamarque 2004, P. Chardonnet pers. comm.). African Wild Dogs are similarly greatly reduced in central Africa, where the only surviving populations are known in N Central African Republic and Chad. In north-east Africa they survive in good numbers only in parts of Ethiopia and S Sudan. The largest populations remain in southern Africa (especially N Botswana/W Zimbabwe/E Namibia) and parts of East Africa (particularly S Tanzania and N Mozambique). Important but relatively isolated populations, persist in C Zambia (Kafue N. P.), C Kenya (Laikipia and Samburu) and E South Africa (Kruger N. P.) (IUCN SSC 2008, 2009).

African Wild Dogs are known, or presumed, to be extinct, or near-extinct, in Burundi, Cameroon, Congo, Côte d'Ivoire, DR Congo, Eritrea, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Mali, Nigeria, Rwanda, Sierra Leone, Swaziland, Togo and Uganda (updated from Fanshawe *et al.* 1997, Woodroffe *et al.* 2004).

**Abundance** Historical records indicate that African Wild Dog populations have always existed at relatively low densities, with very occasional historical reports of large aggregations (e.g. Cumming 1850). Today they are rarely seen even in the few protected areas where they are relatively common. Density estimates vary widely for the few populations comparatively unconstrained by fences or human population expansion. These range from a low of 0.5 adults/100 km<sup>2</sup> in some areas associated with the dry Kalahari Desert in C Botswana and NE Namibia, to a high of 3.5–4.6 adults/100 km<sup>2</sup> in NW Botswana and the Selous G. R. in Tanzania (Woodroffe *et al.* 2004). Relatively small and somewhat more fragmented populations persist in several additional parts of their former range with densities that vary between these extremes. The cur-

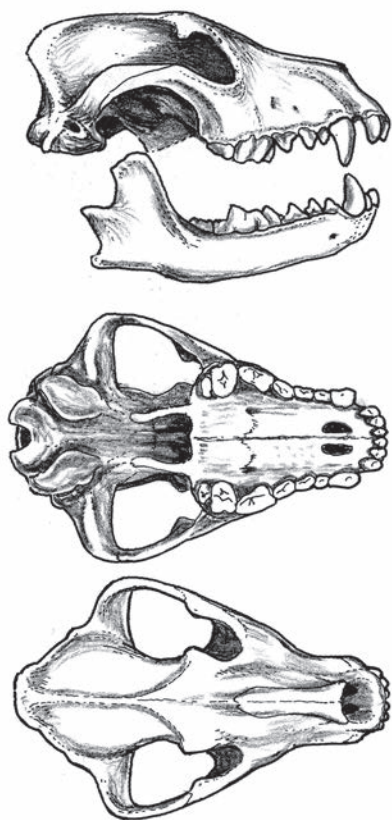


*Lycaon pictus*

rent population of free-ranging African Wild Dogs remaining in Africa has been estimated at less than 8000 individuals, in ~750 packs, with the largest populations in N Botswana/E Namibia/W Zimbabwe/S Angola (~2500) and in S Tanzania/N Mozambique (1300). These estimates are based primarily on density estimates from studied populations, on knowledge of presence elsewhere and on habitat characteristics.

**Habitat** African Wild Dogs occupy a range of habitats, including short-grass plains, semi-desert, bushy savannas, woodlands and upland forest. While early studies in Serengeti N. P., Tanzania, led to the belief that they were primarily an open plains species, more recent data indicate that they reach their highest densities in thick bush and woodland habitats (e.g. Selous G. R., Tanzania; Mana Pools N. P., Zimbabwe; and N Botswana). African Wild Dogs have been recorded in desert (Lhotse 1946), montane (Thesiger 1970) and coastal scrub and woodland habitats (Temminck 1820). Several relict populations occupy dense upland forest (e.g. Harenna Forest, Ethiopia; Ngare Ndare Forest, Kenya), and they are also the only mammal species, other than humans, known to have reached the summit of Kilimanjaro at 5895 m (Thesiger 1970, Grimshaw *et al.* 1995) and are recorded from 4250 m on Mt Kenya (Young & Evans 1993) and 4050 m on the Sanetti Plateau in Ethiopia (Dutson & Sillero-Zubiri 2005). It appears that their current distribution is limited primarily by human activities (which they avoid; Woodroffe 2011a), the availability of prey, and disease, rather than by the loss of a specific habitat type.

**Adaptations** The teeth are adapted to holding and slicing and show a much lesser function of grinding than in some other canids. The outer upper incisors are larger than the central ones, heavily built and recurved; they wear to sharp edges to assist the short, sharp-pointed canines in holding prey. The outer incisors in the lower jaw are less well developed. The back portion of the lower first molar is sectorial, adding to the slicing ability of the carnassial mechanism. The crushing function is performed by the second upper molar and



Lateral, palatal and dorsal views of skull of African Wild Dog *Lycaon pictus*.

the lower second and third molars that are less developed than the remainder of the teeth (Skinner & Chimimba 2005).

One of the most striking peculiarities of African Wild Dogs is their extraordinary tri-coloured mottle pattern, which is never the same in any two individuals and is almost without precedent in a wild mammal, although it does resemble the artificially selected polymorphisms of several domestic animal species. The conspicuous white tail-tip resembles a flag, and playing pups try to bite the white tip while chasing one another (Kuhme 1965a). Bold patterns have also been interpreted as helping scattered pack members to keep in visual contact and maintain group cohesion (Schaller 1972). Other authors have suggested that the main function of individual variation in colour is to aid recognition within the pack (Ewer 1973). Although it appears conspicuous to the human eye this type of patterning has been interpreted as camouflage by some observers because it breaks up the body's contours. Its adaptive value has also been linked to the social disciplines that maintain pack cohesion (Kingdon 1977).

African Wild Dogs can run at speeds of up to 60 km/h, and are specially adapted to deal with the heat stress that this involves (Taylor *et al.* 1971).

**Foraging and Food** African Wild Dogs are cursorial predators that opportunistically hunt medium-sized antelope. Many of the common prey species are more than twice their size, the average weighing around 50 kg, and may be as large as 200 kg (Creel & Creel 2002). In most areas where African Wild Dogs persist in relatively large numbers, their principal prey are Impala *Aepyceros melampus*, comprising, for example, around 54% of their prey in Selous G. R. (Creel & Creel 2002), more than 80% of their diet in Moremi G. R. in

N Botswana (McNutt 1996a) and as much as 94% of their diet in Kruger N. P. (Pienaar 1969, Reich 1981, Mills & Biggs 1993, Mills & Gorman 1997). In some habitats (and sometimes even in areas where Impala populations are not necessarily low), several other species take over as primary prey. These vary with habitat type and region but include in particular Greater Kudu *Tragelaphus strepsiceros* and Springbok *Antidorcas marsupialis* in southern Africa, and Thomson's Gazelle *Eudorcas thomsonii* and Common Wildebeest *Connochaetes taurinus* in East Africa (Estes & Goddard 1967, Schaller 1972, Fanshawe & FitzGibbon 1993, Creel & Creel 1995); for example, in Aitong, Kenya, Thomson's Gazelle made up 67% of prey compared with only 17% Impala (Fuller & Kat 1990). Similarly, in Kafue Valley, Zambia, Impala made up only 2% of kills whereas Common Duiker *Sylvicapra grimmia* and Common Reedbuck *Redunca arundinum* made up half their prey in about equal parts, with Lichtenstein's Hartebeest *Alcelaphus buselaphus lichtensteini* accounting for about 15% (Mitchell *et al.* 1965).

African Wild Dogs will chase, but rarely kill, larger species, such as Eland *Tragelaphus oryx*, Roan *Hippotragus equinus* and African Buffalo *Syncerus caffer*. More typically, calves of these species are targeted when encountered. Small antelopes, especially Common Duiker, dikdik *Madoqua* spp. and Steenbok *Raphicerus campestris*, are important in some areas. Warthogs *Phacochoerus* spp. are taken in some populations. In Samburu and Laikipia Districts, Kenya, dikdik made up 70% of the biomass consumed by African Wild Dogs, with Impala comprising 11% (Woodroffe *et al.* 2007b). African Wild dogs also opportunistically capture relatively smaller prey such as small carnivores like Bat-eared Foxes *Otocyon megalotis* (Rasmussen 1996), Black-backed Jackals *Canis mesomelas* (Kamler *et al.* 2007) or Banded Mongooses *Mungos mungo* (Creel & Creel 2002), hares, springhares *Pedetes* spp., francolins, lizards and even eggs, but these constitute a small proportion of their diet.

African Wild Dogs travel and hunt in packs. Hunts typically take place around the first and last hour of daylight and are preceded by a 'social rally' or 'greet' believed to alert and collect the pack in anticipation of departure (Kuhme 1964b, 1965a, Kingdon 1977). Occasionally, hunts can begin before dawn or extend after dusk. They commonly also hunt on moonlit nights. Typical capture is as follows: one dog bites and holds the quarry, usually at the flank, and other pack members help pull it to ground and quickly kill it by disembowelling. In some hunts, usually involving large prey, one pack member may effectively immobilize the prey by biting and holding its nose while others make the kill. Hunts can appear to be highly coordinated events, but in many areas, particularly typical woodland habitats with dense brush understorey, packs tend to split during hunts with individual dogs opportunistically chasing and often bringing down prey alone. In the Selous, successful chase distances varied from 50 m to as much as 4.6 km (n = 304, Creel & Creel 2002).

Although hunting is not necessarily cooperative, feeding at kills, in contrast, is highly coordinated and cooperative. In general, prey is consumed rapidly – Van Lawick & Van Lawick-Goodall (1970) recorded the consumption of a Thomson's Gazelle in 15 minutes – and quietly by the entire pack with several individuals pulling against others to facilitate the rending of the carcass. When pups are travelling with the pack a system of priority of access is given to the youngest first and reinforced by the dominant pair. Otherwise, all members of the pack eat together rapidly and leave a carcass after eating. If they have left pups somewhere, they return to the pups and regurgitate meat to them. Caching of food has also been recorded (Malcolm 1980).

Hunting success is relatively high in comparison with some other large carnivore species. In Serengeti N. P. 44% of hunts ( $n = 666$ ) were successful (see Creel & Creel 2002, based on pooled data from studies of Schaller 1972, Malcolm & Van Lawick 1975, Fuller & Kat 1990, Fanshawe & FitzGibbon 1993), which is the same as hunting success of animals in Selous G. R. (Creel & Creel 2002). Hunting success also varies with prey; in their study in the Selous, Creel & Creel (2002) noted that Impala were not only hunted most often (40% of hunts) and killed most often (54%), but also yielded the highest hunting success (64%). Zebra, on the other hand, provided the most mass per kill, but were rarely killed, with a probability of killing (7%) far lower than other species (presumably because zebra are dangerous to hunt).

As a result of social hunting, each pack member has a higher foraging success (measured as kg killed per km chased) than it would if it hunted alone: hunting success increased from 42% in packs of three adults to 67% in packs of 20 adults while the mass of prey killed increased from 16 kg to 40 kg and the distance chased decreased from 1.1 km to 0.5 km, accordingly (Creel & Creel 1995). Small packs are more selective in their hunting decisions, likely because they are not as effective as larger packs in hunting larger prey (Creel & Creel 2002). Larger packs are able to utilize larger, more profitable prey species (e.g. Common Wildebeest; Creel & Creel 2002), and are better able to defend their kills against scavenging hyaenas (Fanshawe & FitzGibbon 1993; though see Carbone *et al.* 1997). African Wild Dogs themselves very rarely scavenge (Mills & Biggs 1993), although they have been observed appropriating kills of Leopards *Panthera pardus*, Lions *P. leo* and Spotted Hyaenas (Kruuk 1972, Creel & Creel 1995).

Consumption rates in the wild vary from 1.2 to 5.9 kg/dog/day. In East Africa, a pack of 17–43 African Wild Dogs killed an average of at least three animals per day (independent of size or composition of the pack), consuming 1.7 kg/dog/day (Fuller & Kat 1990), which compares favourably with the findings of Creel & Creel (2002) in the Selous (where food consumption averaged between 2.0 and 2.5 kg/dog/day). Observations in the Selous suggest an animal can consume 8–9 kg in one sitting (Creel & Creel 2002).

**Social and Reproductive Behaviour** African Wild Dogs are intensely social animals, spending virtually their entire lives in close association with other dogs (e.g. Kuhme 1965a, McCreery 2000). They are obligate social breeders that live in a close kin-related pack. A pack, then, rather than a pair of individuals, should be considered the basic reproductive unit within the population. A pack, defined by its potential for reproduction, is rarely static in membership for extended periods. Rather, pack membership typically changes throughout the year due to relatively high rates of mortality, dispersal and high variance in reproductive success. By definition a pack may be as small as a pair, but packs with fewer than four adults often dissolve or extinguish following unsuccessful attempts to rear pups through to one year. In Botswana, of 11 packs comprising fewer than four adults, only one (a pair) successfully raised pups to one year. Three had pups but lost them all to other predators before they were four months old. No pack of the 10 small packs that failed survived to attempt a second litter (J. W. McNutt pers. obs.). In contrast, in Kenya three packs of 3–4 adults all successfully raised pups and grew in size, although their reproductive success was lower than that of larger packs (Woodroffe 2011b). The low success of small packs provides empirical evidence of an Allee effect for African Wild Dogs that should

be incorporated into population viability estimates for all populations (Courchamp *et al.* 2000, 2002, Courchamp & Macdonald 2001; but see Buettner *et al.* 2007). Pack size varies between populations and also within populations over time (average range 5.9–13.2 from six studied populations), but the cumulative average pack falls roughly on the median: 9–10 adults, including yearlings ( $n = 221$  pack-years) (Woodroffe *et al.* 2004). Packs greater than 30 adults and yearlings have been recorded in the comparatively large remaining populations in Botswana (max. = 36) and Tanzania (max. = 44). In the past, much larger, but very rare aggregations have been reported. In the nineteenth century packs of several hundred dogs were recorded in South Africa (Cumming 1850). In the 1920s an aggregation travelling across Masailand in S Kenya was estimated in the region of 500 dogs as described by Blixen (1937).

Both ♂♂ and ♀♀ emigrate from their natal packs in groups, with ♀♀ typically dispersing a year earlier than ♂♂. As with most mammals, ♂♂ disperse further than ♀♀, which often establish reproductive territories that incorporate part of their natal area (McNutt 1996a). Packs are formed when small same-sex subgroups (usually full siblings and litter-mates) leave their natal group and join subgroups of the opposite sex from other packs (McNutt 1996a, McCreery & Robbins 2001). In a new pack, therefore, the ♀♀ (mean = 2) are typically closely related to one another, but not to the ♂♂, and the ♂♂ (mean = 3–4) are closely related to one another, but not to the ♀♀. Offspring produced by the dominant pair are, therefore, typically related to all adults in the pack. In this sense most African Wild Dog packs represent an extended kin group, within which all dogs are closely related to others in the pack. However, it is not uncommon (25% of observed packs in Botswana) for packs to have an adult unrelated to any of the others as a consequence of stochastic events affecting subgroup membership among packs in transition, especially adoption of unrelated pups (McNutt 1996b, McNutt *et al.* 2008). As a result, inferences cannot be made safely about the kin relationships within any pack without a thorough knowledge of the history of the pack members. Occasionally, new packs form by fission of large packs, with some of the original founders of both sexes emigrating together in a secondary dispersal event. In such situations pups might remain with the natal pack or join the secondary dispersal group, irrespective of the whereabouts of their parents. The priority of access to meat in favour of the youngest animals (and reinforced by the dominant pair, as mentioned earlier) has implications for social structure. Older ♂♂ that had been designated as dominant have been recorded being replaced, after serious fighting, by young ♂♂ (Creel & Creel 2002). The susceptibility of adults to coercion (notably to regurgitate meat) by very young animals and a tendency for adult ♂♂ from the youngest cohorts to achieve dominant status has been called the ‘youth first protocol’ (Burrows 2004).

African Wild Dogs have large home-ranges for their body size and the mean is 606 km<sup>2</sup> ( $n = 50$  packs) across habitats. However, these ranges vary widely between habitats (probably with prey density and availability) from 150 km<sup>2</sup> in the lowveld savanna woodlands of Kruger N. P. ( $n = 20$  packs; Fuller *et al.* 1992a) to more than 2000 km<sup>2</sup> in the arid habitats of southern Africa, such as the Kahalari (J. W. McNutt pers. obs.), where prey populations live at comparatively low densities and are widely dispersed, and in Serengeti N. P. where migratory prey is only seasonally abundant. During the 3–4 months while feeding young pups at a den, packs are

confined to relatively small areas (50–200 km<sup>2</sup>), but the rest of the year a pack ranges widely within their much larger territory.

Although neighbouring African Wild Dog packs overlap along boundaries, African Wild Dogs should be considered territorial. They rarely enter other packs' core areas and they defend their ranges infrequently but aggressively, occasionally with fatal consequences, against intruders and unrelated neighbours. The large territories of packs translate into very low population densities typical for the species. Even packs that inhabit protected areas may travel extensively outside reserve borders, where they encounter conflict with human activities and threats such as roads, snares and livestock and game farmers likely to persecute them. African Wild Dogs of both sexes emigrating from their natal packs may range over extremely wide areas compared with territory sizes. Dispersing African Wild Dogs have been tracked over hundreds of kilometres (Fuller *et al.* 1992b), a characteristic that could account for the occasional reports of single animals, or single-sex groups from countries such as Uganda, DR Congo and Swaziland, where there have been no resident populations for several decades. It can also account for the occasional re-colonization of formerly occupied habitats such as the Serengeti ecosystem, Laikipia and Savé Valley in Zimbabwe.

African Wild Dogs have a complex communication system, including a number of unique vocalizations (Robbins 2000), as well as olfactory communication both within and between packs (Van Heerden 1981, M. Parker pers. comm.). Territory boundaries appear to be predominantly communicated through scent-marking with faecal and urine marks by the dominant pair. Semio-chemical communication is also important in maintaining pack cohesion during hunting in bush habitats. Most vocalizations are for intra-pack communication and are generally high frequency, and relatively low in volume and broadcast quality. Food-begging calls are typically twittering. Whines combine with body postures to suggest an appeasing function and yelps denote the anticipation of food. Broadcast inter-pack vocalizations such as the howls typical of other canids (e.g. wolves, coyotes, jackals) are rare in African Wild Dogs and only occur in the specific context of direct interactions between residents and intruders. This rare vocalization is a howl-like duet projected at the ground by the resident pack's dominant pair immediately following inter-pack encounters (J. W. McNutt pers. obs.). Even the commonly described intra-pack contact call, or 'hoo call' used to regroup a dispersed pack or a lost individual is only used conservatively, perhaps to minimize chances of alerting other large predators such as Lions and Spotted Hyaenas to their location (Webster *et al.* 2010).

In a pack larger than two adults the reproductive pair consists of the dominant ♂ and the dominant ♀ (Frame *et al.* 1979, Malcolm & Marten 1982). In most African Wild Dog packs, the dominant ♀ is the mother of all the pups, although two or even three ♀♀ may breed on some occasions. Similarly, the dominant ♂ fathers most of the pups but multiple paternity has been reported (Girman *et al.* 1997). All pack members are involved in caring for the pups and dominant ♂♂ are usually no more assiduous in caring for pups than are other ♂♂ in the pack (Malcolm & Marten 1982). There is some evidence to suggest that pup survival is higher in large packs where there are more helpers to assist with their care (Creel *et al.* 1997).

The advantages in terms of survival and reproduction associated with larger packs, including increased hunting success, appears to predispose African Wild Dogs to an unusual willingness to adopt pups irrespective of their relatedness. Adoption (provisioning and protection) of pups



African Wild Dogs *Lycaon pictus* action drawings. Note the solicitation-like postures during 'social rallies' (right foreground).

by free-ranging animals carries few costs to an average pack preying on medium-sized prey, and the predisposition has provided important management options for isolated populations and for African Wild Dogs living in conflict with domestic livestock (McNutt 1996b).

Pups are born in an underground den that they use for the first three months of life. Such dens are usually those of Aardvark *Oryzomys afer*, and are often enlarged and modified by Cape Porcupines *Hystrrix africae australis* or Spotted Hyaenas. Dens may also take the form of small caves or other suitable structures in rocky formations. The mother is confined to the den during early lactation, and is reliant on other pack members to provision her during this time. Pack members feed the mother, and, starting from about four weeks of age, the pups by regurgitating solid pieces of meat. Some pack members also 'baby-sit' the pups, and chase predators off while the remainder of the pack is away hunting. These adults sometimes join the pups in begging for food when the provisioners return.

**Reproduction and Population Structure** Births occur roughly annually. In southern Africa, pups are born between Apr and Sep, with a peak during the dry season in late May and early Jun. Following a gestation period of approximately 71–73 days (J. W. McNutt pers. obs.), ♀♀ whelp large litters for their body size, averaging 8–11 and occasionally as many as 21 pups (Fuller *et al.* 1992b). Birth-weight is approximately 300–350 g and pups are born blind. Pups are generally fully weaned by eight weeks but continue to use a den for refuge until 12–16 weeks of age. African Wild Dogs reach sexual maturity in their second year of life, and it is common for ♀♀ to first reproduce at this age though ♂♂ commonly delay another year (McNutt 1996a). However, reproductive suppression of subordinates of both sexes means that disproportionately few of those that live to reproductive age ever reproduce directly (Creel *et al.* 1997).



African Wild Dog populations have been widely reported to have male-biased sex ratios both at birth and among adult populations. Although some populations occasionally show deviations in favour of female pups (Fuller *et al.* 1992a), long-term observations (McNutt & Silk 2008) statistically support the male-biases first reported in Serengeti N. P. by Frame *et al.* (1979).

In Kruger N. P. and N Botswana, no African Wild Dog has survived more than 11 years, and most dogs studied in Selous lived six years or less (Creel & Creel 2002). In captivity, record longevity is 15 years (Weigl 2005). Annual age-specific adult mortality is generally quite high for African Wild Dogs compared with other large carnivore species (range 20–57%), but it varies with other demographic characteristics such as fecundity, litter-size and pup survival among populations. Pup mortality during the first year of life is relatively high, and averages around 50% in most populations. However, mean litter-size and variance in pup survivorship vary widely among populations. Juvenile survival has been shown to be an important variable in a population's long-term growth and stability (Creel *et al.* 2004), although adult mortality is also important. Buettner *et al.* (2007) investigated the influence of rainfall and pack size on juvenile survival from den emergence to 12 months of age in Kruger N. P. (based on data on 30 packs monitored over a period of 15 years), and found that past rainfall significantly influenced pup survival up to nine months of age, such that pups benefited from preceding dry periods. The positive effects of pack size on juvenile survival only became evident for pups older than nine months. Consequently, survival of juveniles as well as adults has been flagged as a focal point for assessing population status and conservation action.

**Predators, Parasites and Diseases** Competition with larger predators has a major impact on African Wild Dog behaviour and population biology (Creel & Creel 1996, 2002, Mills & Gorman 1997). There is a large degree of dietary overlap between African Wild Dogs and Spotted Hyaenas and Lions (see Creel & Creel 2002), and the latter two species will steal kills from African Wild Dogs, particularly in open areas, such as the Serengeti and Ngorongoro Crater, where such kills are easily located (Kruuk 1972, Fanshawe & FitzGibbon 1993). Loss of kills to other predators is much less common in well-wooded ecosystems (such as Kruger and the Selous). For example, Fanshawe & FitzGibbon (1993) found that Spotted Hyaenas were present at over 85% of all kills of Common Wildebeest and Thomson's Gazelle in Serengeti N. P. (24.5% of which were appropriated by hyaenas); on the other hand, Creel & Creel (1996), in the more densely vegetated Selous, reported their occurrence at only 18% of kills (of which only 2% were appropriated by hyaenas).

The high metabolic rate of African Wild Dogs means that prey loss to competitors has the potential to seriously impact their energy balance: a model based on data from Kruger suggested that dogs must spend about 3.5 hours/day hunting in order to meet their energy requirements but would need to increase this to some 12 hours if they lost 25% of their food (Gorman *et al.* 1998). Despite earlier suggestions (Fanshawe & FitzGibbon 1993), the benefits of increased group size for the purpose of defending the carcass against kleptoparasites such as Spotted Hyaenas might be countered by increasing intra-specific competition for food as pack size increases. Small groups would probably be particularly vulnerable to kleptoparasitism, because they would not be able to consume enough food before the hyaenas

appropriated the kill, and medium-sized groups may, therefore, be most effective to meet energy and nutritional demands (Carbone *et al.* 1997). As such African Wild Dogs seem to fare well where interference competition is minimal. However, where Spotted Hyaena density is high and visibility good, hyaenas can accumulate at kills in sufficient numbers to negatively impact foraging success (Creel & Creel 2002).

The degree of competition between African Wild Dogs and Lions is less clear, but predation by Lions (outside the context of kills) is a principal cause of natural mortality in African Wild Dogs. Lion predation accounted for 9% of 45 known-cause deaths in Selous (Creel & Creel 1996, 2002), 33% of 57 deaths in Kruger (Van Heerden *et al.* 1995), and 50% of 14 deaths in Moremi (McNutt 1995). An attempt to reintroduce African Wild Dogs to Etosha N. P. in Namibia failed because they were hunted out by a pride of Lions over a period of weeks (Scheepers & Venzke 1995). Away from kills, Spotted Hyaenas also occasionally kill dogs of all ages (Ginsberg *et al.* 1995, Creel & Creel 2002, J. W. McNutt & R. Woodroffe pers. obs.), and Leopards and African Rock Pythons *Python sebae* have also been recorded killing animals.

Competition with larger carnivores could help explain the ranging behaviour of African Wild Dogs. While larger predators tend to occur at higher densities where prey species are relatively abundant, African Wild Dogs (like Cheetahs *Acinonyx jubatus*) tend to avoid these areas. Because they range in areas of comparatively low prey densities, they tend to occupy ranges effectively requiring greater travel distances during hunting. Naturally wide-ranging behaviour, and a preference for areas with reduced large predator densities, can explain in part why African Wild Dogs are often found in habitats outside of protected areas. As a result of changes in Lion and Spotted Hyaena populations, some habitats with suitable prey populations can become marginal or completely unsuitable for African Wild Dogs.

In addition to inter-specific competition, adults and pups have been killed in inter-pack clashes. Intra-specific competition caused 69% of known-cause deaths in Selous through conflict within and between packs (Creel & Creel 1998).

Infectious disease can also play an important role in the dynamics of some African Wild Dog populations. Pups appear to be particularly susceptible, with 26% of pup deaths attributed to disease in some populations (Woodroffe *et al.* 2007a). Many of the pathogens infecting African Wild Dogs are common canine pathogens that also infect domestic dogs and other wild canids, such as jackals and foxes. Some, such as canine coronavirus, adenovirus and herpesvirus, probably have little effect on populations: a high proportion of healthy adults show evidence of past exposure to these infections (Woodroffe & Ginsberg 1997, Alexander *et al.* 2010). At the opposite extreme, rabies virus can have major population impacts, especially in small populations. Rabies has been implicated in the 'disappearance' (see Marsden *et al.* 2012) of the African Wild Dog population in the Serengeti ecosystem on the Kenya–Tanzania border in 1990–91 (Gascoyne *et al.* 1993, Burrows 1995, Kat *et al.* 1995) and has hindered the re-establishment of packs in Madikwe G. R., South Africa (Hofmeyr *et al.* 2000, 2004) as well as killing animals reintroduced to Etosha N. P. in Namibia (Scheepers & Venzke 1995). Evidence suggests that rabies similarly caused the deaths of several packs in N Botswana in 1995 and 1996 (J. W. McNutt pers. obs.) and in N Kenya in 2005 (R. Woodroffe pers. obs.).

African Wild Dog populations cannot maintain rabies infection: rates of contact between packs are so low that all pack members would