
Walker's

Carnivores of the World

Ronald M. Nowak

Introduction by
David W. Macdonald and
Roland W. Kays

The Johns Hopkins University Press
Baltimore and London

Contents

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Printed in the United States of America on acid-free paper
9 8 7 6 5 4 3 2 1

Portions of this book have been adapted from *Walker's Mammals of the World*, 6th edition, by Ronald M. Nowak,
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The Johns Hopkins University Press
2715 North Charles Street
Baltimore, Maryland 21218-4363
www.press.jhu.edu

CARNIVORES OF THE WORLD
David W. Macdonald and Ronald M. Nowak

Carnivores

Dogs, Wolves, Coyotes

Bears: Ursidae

Raccoons and Related Species

Weasels, Badgers, and Skunks

Civets, Genets, and Oryzomyids

Mongoose and Fossa

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Library of Congress Cataloging-in-Publication Data

Nowak, Ronald M.

Walker's carnivores of the world / Ronald M. Nowak ; introduction by David W. Macdonald and Roland W. Kays.

p. cm.

Portions of this book have been adapted from Walker's mammals of the world, 6th ed., by Ronald M. Nowak.

Includes bibliographical references and index.

ISBN 0-8018-8033-5 (hardcover : alk. paper)—ISBN 0-8018-8032-7 (pbk. : alk. paper)

1. Carnivora. 2. Carnivora—Classification. I. Nowak, Ronald M. Walker's mammals of the world. II. Title.

QL737.C2N69 2005

599.7—dc22

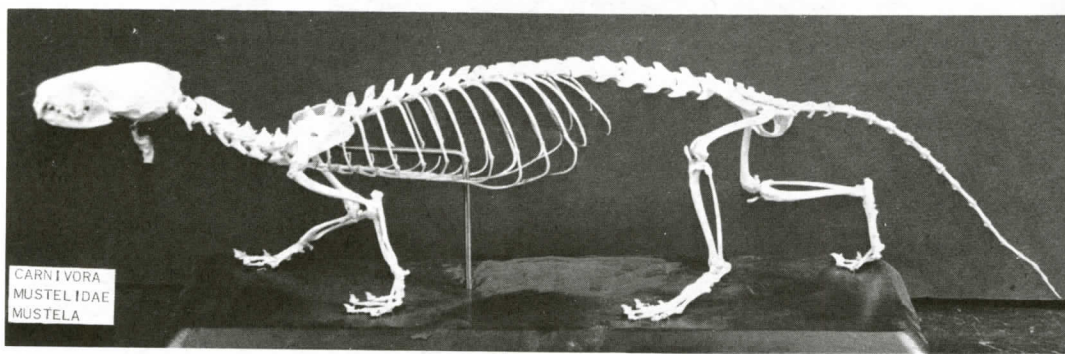
2004012073

A catalog record for this book is available from the British Library.

out difficulty. It feeds mainly on fruit but also hunts for insects and warm-blooded animals. Poglayen-Neuwall (1966) found that in captivity *Bassaricyon* required considerably more meat than *Potos*.

In the wild, *Bassaricyon* lives alone or in pairs. It is sometimes found in association with *Potos* as well as with opossums and douroucoulis (*Aotus*). It scent-marks with urine, perhaps for its own orientation or to attract the opposite sex (Poglayen-Neuwall in Grzimek 1990). Studies of captives by Poglayen-Neuwall (1966, 1989) found that *Bassaricyon* is less social than *Potos* and that two males could not be kept together. There was no definite breeding season, gestation lasted 73–74 days, and each of 16 births yielded a single offspring. The young weighed about 55 grams at birth, opened their eyes after 27 days, began taking solid food after 2 months, and attained sexual maturity at 21–24 months. One female remained reproductively active until 12 years and ultimately lived to be more than 25 years old.

The IUCN now classifies *B. pauli* and *B. lasius* as endangered, estimating that each numbers fewer than 250 mature individuals, and *B. gabbi* and *B. beddardi* as near threatened. Glatston (1994) stated that those species, as well as *B. alleni*, are highly dependent on intact tropical forest and do not adapt readily to disturbed areas or secondary forest. They generally are found in a region where deforestation is rampant and seem to have become rare over much of their range.



Giant otter (*Pteronura brasiliensis*), photo by Bernhard Grzimek. Skeleton of mink (*Mustela vison*), photo by P. F. Wright of specimen in U.S. National Museum of Natural History.

CARNIVORA; Family MUSTELIDAE

Weasels, Badgers, Skunks, and Otters

This family of 25 Recent genera and 67 species occurs in all land areas of the world except the West Indies, Madagascar, Sulawesi and islands to the east, most of the Philippines, New Guinea, Australia, New Zealand, Antarctica, and most oceanic islands. One genus, *Enhydra*, inhabits coastal waters of the North Pacific. The sequence of genera presented here follows basically that of Simpson (1945), who recognized five subfamilies: the Mustelinae (weasels), with *Mustela*, *Vormela*, *Martes*, *Eira*, *Galictis*, *Lyncodon*, *Ictonyx*, *Poecilictis*, *Poecilogale*, and *Gulo*; the Mellivorinae (honey badger), with *Mellivora*; the Melinae (badgers), with *Meles*, *Arctonyx*, *Mydaus*, *Taxidea*, and *Melogale*; the Mephitinae (skunks), with *Mephitis*, *Spilogale*, and *Conepatus*; and the Lutrinae (otters), with *Lutra*, *Lutrogale*, *Lontra*, *Pteronura*, *Aonyx*, and *Enhydra*. A cladistic analysis of 46 morphological characters (Bryant, Russell, and Fitch 1993) generally supported these basic groupings but found the Melinae to be polyphyletic, with *Melogale* and perhaps *Taxidea* showing affinity with the Mustelinae and *Mydaus* showing some approach to the Mephitinae. Wozencraft (1989a) pointed out that *Taxidea* differs from

the other badgers sequentially (in V genus in a separ

The smallest (*Mustela nivalis*) 114–260 mm and members are t have a head and a weight of 22– larger than fem ted, or striped. ter in the north and slender in (*Gulo*) and in b pointed. The li claws are comp of badgers are l otters are usual anal scent glan baculum.

The skull is The dental form $\times 2 = 28-38$. cisors. The inci nines are elong reduced in num tween the later carnassials are ent, is reduced

Mustelids a ter in crevices elaborate burr partly on their er, slender for gait interspers forms proceed often sit on th are agile clim bers. Mustel scent, though developed. So ial, a few are aquatic anim badgers repor

Many mus as a defensiv pattern of bo white stripes. ing coloration and a remind the forms wi bled polecat (phasize this c ments when

Delayed in occurs in mar gestation is a tion the total in *Lutra cana*. The offspring young of *En* and in a mo mustelids. Th selves at abo year or 2. Th 5–20 years.

Mustelids keep rodents their fur.

the other badgers in critical basicranial characters, and subsequently (in Wilson and Reeder 1993) he placed that genus in a separate subfamily, the Taxidiinae.

The smallest member of this family is the least weasel (*Mustela nivalis*), which has a head and body length of 114–260 mm and a weight as low as 25 grams. The largest members are the otters *Pteronura* and *Enhydra*, which have a head and body length of around 1 meter or more and a weight of 22–45 kg. Male mustelids are about one-fourth larger than females. The pelage is uniformly colored, spotted, or striped. Some species of *Mustela* turn white in winter in the northern parts of their range. The body is long and slender in most genera but stocky in the wolverine (*Gulo*) and in badgers. The short ears are either rounded or pointed. The limbs are short and bear five digits each. The claws are compressed, curved, and nonretractile. The digits of badgers are large and heavy for burrowing. The digits of otters are usually webbed for swimming. Well-developed anal scent glands are present in most genera. Males have a baculum.

The skull is usually sturdy and has a short facial region. The dental formula is: (i 3/2–3, c 1/1, pm 2–4/2–4, m 1/1–2) $\times 2 = 28$ –38. *Enhydra* is the only genus with 2 lower incisors. The incisors of mustelids are not specialized, the canines are elongate, the premolars are small and sometimes reduced in number, and a constriction is usually present between the lateral and medial halves of the upper molar. The carnassials are developed. The second lower molar, if present, is reduced to a simple peg.

Mustelids are either nocturnal or diurnal and often shelter in crevices, burrows, and trees. Badgers usually dig elaborate burrows. Mustelids move about on their digits or partly on their digits and partly on their soles. The smaller, slender forms usually travel by means of a scampering gait interspersed with a series of bounds. The larger, stocky forms proceed in a slow, rolling, bearlike shuffle. Mustelids often sit on their haunches to look around. Many genera are agile climbers, and otters and minks are skillful swimmers. Mustelids are mainly flesh eaters. They hunt by scent, though the senses of hearing and sight are also well developed. Some species occasionally feed on plant material, a few are omnivorous, and otters subsist mainly on aquatic animals. *Mustela*, *Pocilogale*, *Gulo*, and certain badgers reportedly store food.

Many mustelids use the secretions of their anal glands as a defensive measure. Some genera have a contrasting pattern of body colors; for example, skunks have black and white stripes. This pattern is thought to be a form of warning coloration associated with the fetid anal gland secretion and a reminder that the animal is better left alone. Some of the forms with contrasting body colors, such as the marbled polecat (*Vormela*) and certain skunks, expose and emphasize this contrasting pattern by means of bodily movements when they are alarmed.

Delayed implantation of the fertilized eggs in the uterus occurs in many genera. The actual period of developmental gestation is about 30–65 days, but with delayed implantation the total period of pregnancy is as long as 12.5 months in *Lutra canadensis*. There is usually a single litter per year. The offspring are usually tiny and blind at birth. The young of *Enhydra*, however, are born with their eyes open and in a more advanced stage than the young of other mustelids. The young of most genera can care for themselves at about 2 months and are sexually mature after a year or 2. The potential longevity in the wild is generally 5–20 years.

Mustelids sometimes kill poultry, but they also help to keep rodents in check. Many species are widely hunted for their fur.

The geological range of this family is early Oligocene to Recent in North America, Eocene to Recent in Europe, middle Oligocene to Recent in Asia; early Pliocene to Recent in Africa; and late Pliocene to Recent in South America (Stains 1984).

CARNIVORA; MUSTELIDAE; Genus MUSTELA Linnaeus, 1758

Weasels, Ermines, Stoats, Minks, Ferrets, and Polecats

There are 5 subgenera and 17 species (Alberico 1994; Coetzee in Meester and Setzer 1977; Corbet 1978; Corbet and Hill 1992; Ellerman and Morrison-Scott 1966; E. R. Hall 1951, 1981; Izor and de la Torre 1978; Izor and Peterson 1985; Lekagul and McNeely 1977; Schreiber et al. 1989; Van Bree and Boeadi 1978; Youngman 1982):

subgenus *Grammogale* Cabrera, 1940

- M. felipei* (Colombian weasel), known by five specimens from western Colombia and northern Ecuador;
- M. africana* (tropical weasel), Amazon Basin of Brazil, eastern Ecuador, and northeastern Peru;

subgenus *Mustela* Linnaeus, 1758

- M. erminea* (ermine, or stoat), Scandinavia and Ireland to northeastern Siberia and the western Himalayan region, Japan, Alaska and northern Greenland to northern New Mexico and Maryland;
- M. nivalis* (least weasel), most of the Palaearctic region from western Europe and Asia Minor to northeastern Siberia and Korea, parts of China and northern Viet Nam, Great Britain, several Mediterranean islands, Japan, northwestern Africa, Egypt, Alaska, Canada, north-central conterminous United States, Appalachian region;
- M. frenata* (long-tailed weasel), southern Canada to Guyana and Bolivia;
- M. altaica* (mountain weasel), southern Siberia to the Himalayan region and Korea;
- M. kathiah* (yellow-bellied weasel), Himalayan region to southern China and northern Viet Nam, Hainan;

subgenus *Lutreola* Wagner, 1841

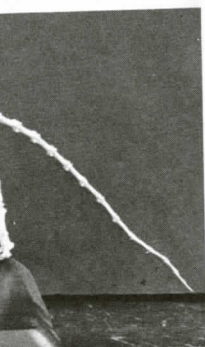
- M. lutreola* (European mink), France to western Siberia and the Caucasus;
- M. sibirica* (Siberian weasel), eastern European Russia to eastern Siberia and Thailand, Japan, Taiwan;
- M. lutreolina* (Indonesian mountain weasel), southern Sumatra, Java;
- M. nudipes* (Malaysian weasel), Malay Peninsula, Sumatra, Borneo;
- M. strigidorsa* (back-striped weasel), Nepal to northern Viet Nam;

subgenus *Vison* Gray, 1843

- M. vison* (American mink), Alaska, Canada, conterminous United States except parts of Southwest;
- M. macrodon* (sea mink), formerly on Atlantic coast from New Brunswick to Massachusetts;

unks, and

67 species occurs in the West Indies, Madagascar, most of the Philippines, Zealand, Antarctica, and *Enhydra*, inhabits the sequence of genera of Simpson (1945), Mustelinae (weasels), *Galictis*, *Lyncodon*, *Gulo*; the Mellivorinae (badgers), *Melinae* (badgers), *Urocyon*, *Spilogale*, and *Lutra*, *Lutro*, *Enhydra*. A cladistic analysis (Bryant, Russell, 1989) of these basic groupings is phylogenetic, with *Melogale* sister to the Mustelinae, and *Taxidea* differs from



by P. F. Wright of

gale in ceremonial costumes or as ornaments, and the Zulu people reportedly use its skin and other parts for medicinal purposes.

CARNIVORA; MUSTELIDAE; Genus *GULO*
Pallas, 1780

Wolverine

The single species, *G. gulo*, originally occurred from Scandinavia and Germany to northeastern Siberia, throughout Alaska and Canada, and as far south as central California, southern Colorado, Indiana, and Pennsylvania (Corbet 1978; E. R. Hall 1981). Although Hall treated the North American populations as a separate species, *G. luscus*, he indicated that there was evidence supporting their recognition as a subspecies of *G. gulo*.

Head and body length is 650–1,050 mm, tail length is 170–260 mm, shoulder height is 355–432 mm, and weight is 7–32 kg. Females average 10 percent less than males in linear measurements and 30 percent less in weight (E. R. Hall 1981). The fur is long and dense. The general coloration is blackish brown. A light brown band extends along each side of the body from shoulder to rump and joins its opposite over and across the base of the tail. *Gulo* resembles a giant marten, with a heavy build, a large head, relatively small and rounded ears, a short tail, and massive limbs (Stroganov 1969). Females have four abdominal and four inguinal mammae (Pasitschniak-Arts and Larivière 1995).

The wolverine occurs in the tundra and taiga zones. It may be found in forests, mountains, or open plains. For shelter it may construct a rough bed of grass or leaves in a cave or rock crevice, in a burrow made by another animal,

or under a fallen tree (Banfield 1974; Stroganov 1969). Most maternal dens in Finland were found in holes under the snow (Pulliainen 1968). *Gulo* is mainly terrestrial, the usual gait being a sort of loping gallop, but it can climb trees with considerable speed and is an excellent swimmer. It has a keen sense of smell but apparently poor eyesight and indifferent hearing. It seems to be unexcelled in strength among mammals of its size and has been reported to drive bears and cougars from their kills. It is largely nocturnal but is occasionally active in daylight. In the far north, where there are periods of extended light or darkness, the wolverine reportedly alternates 3- to 4-hour periods of activity and sleep. In winter it has been known to cover up to 45 km in a day. It can maintain a gallop for a lengthy period, sometimes moving 10–15 km without rest (Stroganov 1969). In mountainous areas it moves to lower elevations during winter (Pasitschniak-Arts and Larivière 1995). Juveniles normally disperse 30–100 km from their natal range, and an individual marked on 6 March 1981 was found 378 km away on 29 November 1982 (Gardner, Ballard, and Jessup 1986).

The diet includes carrion, the eggs of ground-nesting birds, lemmings, and berries. Large mammals such as reindeer, roe deer, and wild sheep are taken mainly in winter, when the snow cover allows *Gulo* to travel faster than its prey. Most large mammals, however, are obtained in the form of carrion. Small rodents may be chased, pounced upon, or dug out of the ground (Pasitschniak-Arts and Larivière 1995). Caches of prey or carrion are covered with earth or snow or, sometimes, wedged in the forks of trees.

Gulo occurs at relatively low population densities (Van Zyll de Jong 1975). In Scandinavia the estimates vary from 1/200 sq km to 1/500 sq km. An adult male there has a territory that may be as large as 2,000 sq km in winter, and individuals of the same sex are not tolerated within it. Territories are regularly marked, mainly by secretions from anal

scent glands but each male are and their young. Ovaskainen 19

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Wolverine (*Gulo gulo*), photo by James K. Drake.

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scent glands but also with urine. Within the territory of each male are the territories of three or four adult females and their young (Kruska in Grzimek 1990; Pulliainen and Ovaskainen 1975).

Somewhat different information was derived from studies in Montana (Hornocker 1983; Hornocker and Hash 1981; Koehler, Hornocker, and Hash 1980). A study area of 1,300 sq km there contained a minimum population of 20 wolverines. Average yearly home range was 422 sq km for males and 388 sq km for females; however, individuals sometimes left their ranges, and females occupied much smaller areas while they were nursing young. There was extensive overlap between the ranges of both the same and the opposite sexes, and no territorial defense was observed. The extensive marking was considered not to define a territory but rather to identify the area being utilized at a given time.

Investigations in arctic Alaska indicated that females generally exclude one another from their home ranges but males tolerate the presence of females (Gipson 1985). In south-central Alaska, Whitman, Ballard, and Gardner (1986) determined annual home range to average 535 sq km for males and 105 sq km for females with young. Annual ranges in Yukon were found to be 209–69 sq km for males and 76–269 sq km for females (Banci and Harestad 1990).

The wolverine is solitary except during the breeding season. Females are monestrous and apparently give birth about every two years. Mating usually occurs from late April to July, but implantation of the fertilized eggs in the uterus is delayed until the following November to March, with births from January to April. The usual number of young per litter is two to four, and the range is one to five. Active gestation lasts 30–40 days. The young weigh 90–100 grams at birth, nurse for 8–10 weeks, separate from the mother in the autumn, and attain adult size after 1 year. Sexual maturity comes in the second or third year of life (Banci and Harestad 1988; Banfield 1974; Grzimek 1975; Pulliainen 1968; Rausch and Pearson 1972; Stroganov 1969). A captive female approximately 10 years of age gave birth after a pregnancy of 272 days (Mehrer 1976). Another captive wolverine lived 17 years and 4 months (Jones 1982).

The pelt of the wolverine is not used widely in commerce but is valued for parkas by persons living in the Arctic because it accumulates less frost than other kinds of fur. During the 1976–77 trapping season 1,922 skins were reported taken in Canada, Alaska, and Montana. The average selling price was about \$182 (Deems and Pursley 1978). In 1983–84 the take was 1,377, with an average value of \$77.16 (Novak, Obbard, et al. 1987). In 1991–92, 591 skins were taken in Alaska and sold at an average price of \$235 (Linscombe 1994). Fur trapping has contributed to a decline in the numbers and distribution of the wolverine, but a more important factor may be human consideration of the genus as a nuisance. In Scandinavia it was intensively hunted, often for bounty, because of alleged predation on domestic reindeer. Throughout its range the wolverine came into conflict with people by following traplines and devouring the fur bearers it found and by breaking into cabins and food caches and spraying the contents with its strong scent.

In Europe *Gulo* is now found only in parts of Scandinavia, where it is very rare, and northern Russia (Pasitschniak-Arts and Larivière 1995; Smit and Van Wijngaarden 1981). Only 120–50 individuals remain in Norway; although legally protected, they are regularly killed in response to claims of attacks on the increasing numbers of sheep being allowed to graze in mountainous areas (Be-

vanger 1992). The genus has disappeared over most of eastern and south-central Canada (Van Zyll de Jong 1975). It is classified as vulnerable by the IUCN and has been designated as endangered in eastern Canada. By the early twentieth century the wolverine also had been nearly eliminated in the conterminous United States. One population, however, held out and subsequently increased in the mountains of northern and eastern California, and another population reestablished itself in western Montana. Since 1960 there have been numerous reliable reports from Washington, Oregon, Idaho, Wyoming, and Colorado and a few questionable records in Minnesota, Iowa, and South Dakota (Birney 1974; Blus, Fitzner, and Fitzner 1993; Field and Feltner 1974; Johnson 1977; Nead, Halfpenny, and Bissell 1985; Nowak 1973; Schempf and White 1977). The U.S. Fish and Wildlife Service recently was petitioned to add the wolverine in the conterminous United States to the List of Endangered and Threatened Wildlife but decided against such a measure (Nordstrom 1995), seemingly in contradiction of the IUCN classification and the whole history of the species. The subspecies *G. g. katschemakensis* of Alaska's Kenai Peninsula now numbers only about 50 individuals and reportedly continues to decline because of an excessively long hunting season (Schreiber et al. 1989).

CARNIVORA; MUSTELIDAE; Genus MELLIVORA Storr, 1780

Honey Badger, or Ratel

The single species, *M. capensis*, originally occurred from Palestine and the Arabian Peninsula to Turkmenistan and eastern India and from Morocco and lower Egypt to South Africa (Coetzee in Meester and Setzer 1977; Corbet 1978).

Head and body length is 600–770 mm, tail length is usually 200–300 mm, and shoulder height is usually 250–300 mm. Kingdon (1977) listed weight as 7–13 kg. The upper parts, from the top of the head to the base of the tail, vary from gray to pale yellow or whitish and contrast sharply with the dark brown or black of the underparts. Completely black individuals, however, have been found in Africa, particularly in the Ituri Forest of northern Zaire. The color pattern of the honey badger has been interpreted as being a warning coloration because it makes the animal easily recognizable. Females have two pairs of mammae.

The body is heavily built, the legs and tail are relatively short, the ears are small, and the muzzle is blunt. The large forefeet are armed with very large, strong claws. The hair is coarse and quite scant on the underparts. The skin is exceedingly loose on the body and very tough. The skull is massive and the teeth are robust. Anal glands secrete a vile-smelling liquid. This combination of characters provides an effective system of deterrence and defense.

Mellivora is very difficult to kill. Except on the belly the skin is so tough that a dog can make little impression. The ratel can twist about in its skin, so it can even bite an adversary that has seized it by the back of the neck. Porcupine quills and bee stings have little effect, and snake fangs are rarely able to penetrate. *Mellivora* seems to be devoid of fear, and it is doubtful that any animal of equivalent size can regularly kill it. It may rush out from its burrow and charge an intruder, especially in the breeding season. Horses, antelopes, cattle, and even buffalo have been attacked and severely wounded in this manner.

The honey badger occupies a variety of habitats, mainly in dry areas but also in forests and wet grasslands. It lives among rocks, in hollow logs or trees, and in burrows. Its