MAMMALIAN SPECIES No. 715, pp. 1–9, 3 figs.

Canis mesomelas.

By Lyle R. Walton and Damien O. Joly

Published 30 July 2003 by the American Society of Mammalogists

Canis Linnaeus, 1758

Canis Linnaeus, 1758:38. Type species *Canis familiaris* (= *Canis lupus* Linnaeus).
Thos Oken, 1816:1037. Type species *Thos vulgaris* (= *Canis aureus* Linnaeus). Not available according to Opinion 417, International Commission on Zoological Nomenclature (Hemming 1956).
Vulpicanis Blainville, 1837:279. Type species *Canis aureus* Linnaeus.
Simenia Gray, 1868:494, 506. Type species *Canis simensis* Rüppell.
Lupulella Hilzheimer, 1906:363. Type species *Canis mesomelas* Schreber.
Schaeffia Hilzheimer, 1906:364. Type species *Canis adustus* Sundevall.

CONTEXT AND CONTENT. Order Carnivora, family Canidae. Seven species of the genus *Canis* are currently recognized: *C. adustus*, *C. aureus*, *C. latrans*, *C. lupus*, *C. mesomelas*, *C. rufus*, and *C. simensis* (Wozencraft 1993), although the validity of *C. rufus* is questioned (Clutton-Brock et al. 1976; Ewer 1973; Wayne 1993). Recent analysis of microsatellite DNA indicates *C. lupus lycaon* may warrant specific status as *C. lycaon* (Wilson et al. 2000). Also, analysis of mitochondrial DNA suggests that *Canis* is a paraphyletic group that should include *Cuon alpinus* (Vilà et al. 1999; Wayne et al. 1997). A key to species (Banfield 1974; Clutton-Brock et al. 1976; Hall and Kelson 1959; Smithers 1971) follows:

1 Condylobasal length >190 mm; body mass >26 kg 2
Condylobasal length ≤190 mm; body mass ≤26 kg 3
2 Condylobasal length >213 mm in males or >203 mm in females; relatively broad teeth; no conspicuous cingulum on outer edge of M1, specimen not from southeastern United States ..... *C. lupus*
Condylobasal length <235 mm in males or <215 mm in females; relatively narrow teeth; conspicuous cingulum present on outer edge of M1, specimen from southeastern United States ..... *C. rufus*
3 Specimen from North America ..... *C. latrans*
Specimen not from North America 4
4 Rostrum long; distance from posterior edge of alveolus of canine to posterior end of P3 (of both upper and lower jaws) > total length of P4 + M1 + M2 ..... *C. simensis*
Rostrum short; distance from posterior edge of alveolus of canine to posterior edge of P3 < total length of P4 + M1 + M2 5
5 Carnassials relatively small, length ≤83% of M1 + M2 and 130% of M2 + M3; tip of tail white; ears dark gray behind; dark stripe on either flank ..... *C. adustus*
Carnassials relatively large, length >83% of M1 + M2 and >130% of M2 + M3; tip of tail dark; ears reddish brown behind; no dark stripe on either flank 6
6 Flat postorbital process; dark saddlepatch sharply marked off from brighter rufous sides ..... *C. mesomelas*
Strongly convex postorbital process; no clearly defined saddlepatch ..... *C. aureus*

Canis mesomelas Schreber, 1775

Black-backed Jackal

Canis mesomelas Schreber, 1775:370. Type locality "Vorgebirge der guten Hofnung," South Africa, Cape Province, Cape of Good Hope.
Canis variegatoides Smith, 1833:87. Type locality "South Africa."
Canis schmidtii Noack, 1897:520. Type locality "Somaliland."
Lupulella mesomelas Hilzheimer, 1906:363. Elevation to generic status.
Canis mcmillani Heller, 1914:6. Type locality "Mtoto Andei Station, British East Africa, altitude 2,500 feet."
Canis elgonae Heller, 1914:6. Type locality "Uasin Gishu Plateau, British East Africa, altitude 8,000 feet."
Canis arenarum Thomas, 1926:295. Type locality "Berseba, central Great Namaqualand, South-West Africa."
Canis achrotes Thomas, 1926:295. Type locality "Rooibank, Kuiseb river, near Walvis Bay, coastal south-west Africa."

CONTEXT AND CONTENT. Context as above. Between 3 and 5 subspecies were recognized in Africa (Coetzee 1971; Ellerman et al. 1953; Lombaard 1971; Shortridge 1934). However, minor and inconsistent morphological and genetic differences and lack of a barrier to gene flow within the range of *C. mesomelas* (Wayne et al. 1990) suggest that many subspecies are not warranted (Meester et al. 1986). Consequently, 2 subspecies are recognized:

C. m. mesomelas Schreber, 1775:370, see above (*achrotes* Thomas, *arenarum* Thomas, and *variegatoides* Smith are synonyms).
C. m. schmidtii Noack, 1897:520, see above (*elgonae* Heller and *mcmillani* Heller are synonyms).

DIAGNOSIS. The black-backed jackal (Fig. 1) is a small canid distinguished from other members of the genus *Canis* by a dark saddle extending from neck to tail in bold contrast to the rufous head, flanks, and legs. Other distinguishing characters include tan coat; long, triangular foxlike ears; and black-tipped, rufous tail (Estes 1991; Stains 1975; Van de Merwe 1953a). Although *C. mesomelas* is longer and taller than the golden jackal (*C. aureus*), the skull of *C. mesomelas* is smaller (Bueler 1973; Sheldon 1992). In contrast to *C. mesomelas*, the side-striped jackal (*C. adustus*) has a white-tipped tail. *C. aureus* has mottled black and gray dorsal fur without an identifiable saddle (Nowak 1999).

GENERAL CHARACTERS. The black-backed jackal is a slender, long-legged jackal with large ears (Kingdon 1997). Head resembles that of a dog, with a pointed muzzle and erect, pointed

FIG. 1. Adult *Canis mesomelas* from the Amboseli Game Reserve, Kenya. Photograph courtesy of Mammal Images Library, American Society of Mammalogists, taken by J. G. Hall, 1973.

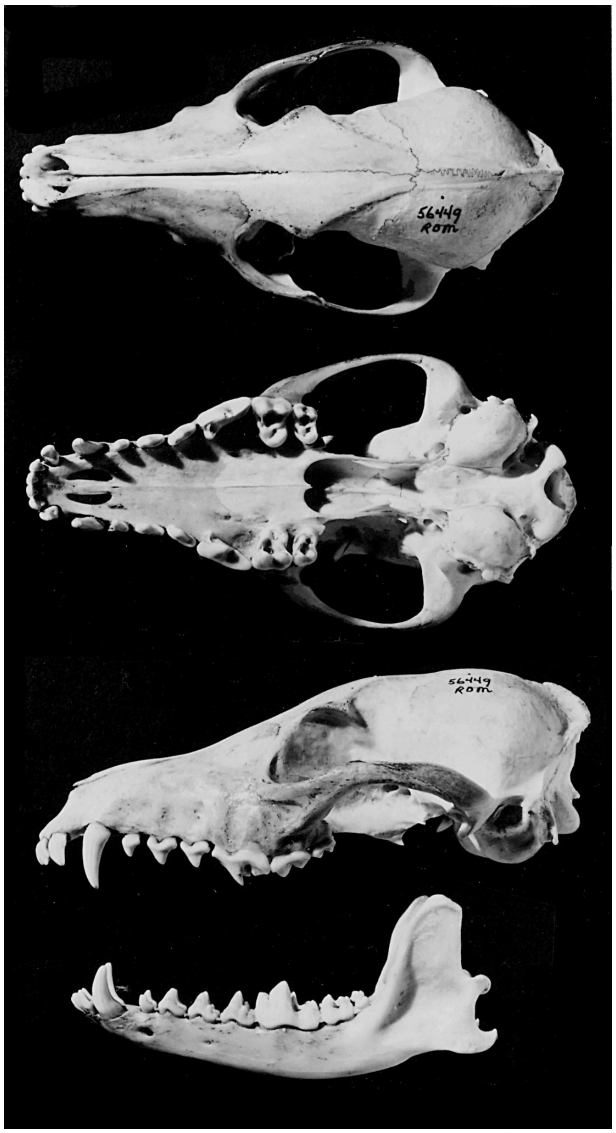

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Canis mesomelas* from Cape Province predator farm, Urolijkheid, near Robertson, South Africa (sex unknown, Royal Ontario Museum 56449, Toronto, Ontario, Canada). Greatest length of cranium is 159.8 mm.

ears (Smithers 1983). General color is reddish brown to tan, redder on flanks and legs. A well-defined black saddle-back, intermixed with silvery hair, extends from shoulders posteriorly to base of tail. Saddle narrows toward lumbar region to a point at crown of tail (Van de Merwe 1953a). Lips and fur on throat, chest, and inside of limbs are white. Tail is bushy and has a black tip, with black-and-white fur covering the basal third (Estes 1991; Smithers 1966). Guard hairs vary in length, from 60 mm at the shoulders to 40 mm at base of tail, increasing to 90 mm at tip of tail. Hair on face is 10–15 mm in length (Smithers 1983). Young are lead gray with an indistinct saddle (Estes 1991), although by 6 months of age the black-and-white saddle is evident and flanks, lumbar regions, and legs are characteristically rufous (Van de Merwe 1953a). Albinism may occur and the skin is a pale erythristic wash; further, the division between back and sides is indicated by a reddish line (Shortridge 1934). Front and hind feet have 5 and 4 digits, respectively, with claws measuring 15 mm along the curve (Smithers 1983).

Sexual dimorphism is evident, with males being larger and heavier than females (Bigalke and Rowe-Rowe 1969; Rowe-Rowe 1978; Smithers 1971). Male:female skull length ratios in South Africa and East Africa are 1.07 and 1.02, respectively, with the former ratio significantly different from 1 (Van Valkenburgh and

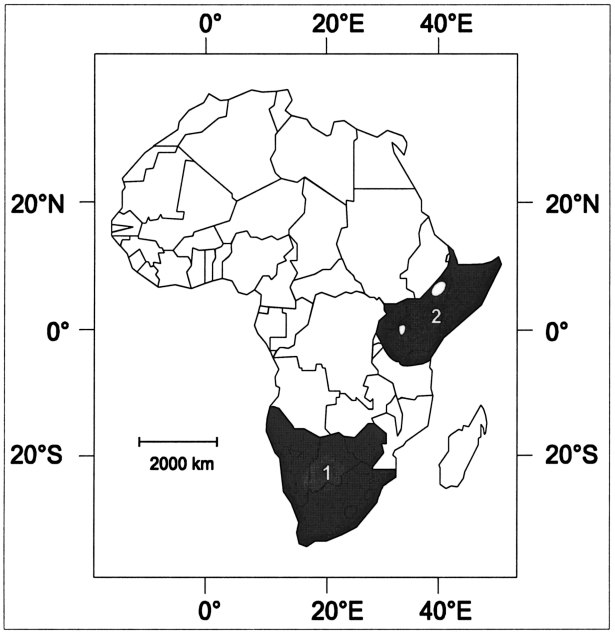

FIG. 3. Distribution of *Canis mesomelas* (modified from: Kingdon 1997; Skinner and Smithers 1990): 1, *C. m. mesomelas*; 2, *C. m. schmidtii*.

Wayne 1994). Body mass (in kg; range and *SD* in parentheses) of 123 adult males and 84 adult females from KwaZulu-Natal, respectively, averages 8.4 (6.4–11.4, 0.8) and 7.7 (5.9–10.0, 0.8—Rowe-Rowe 1978). Mean body measurements (in mm; range and *n* in parentheses) of adult male and female *C. mesomelas* (Rowe-Rowe 1978), respectively, are: length of head and body, 746 (711–812, 4), 688 (673–711, 5); length of tail, 321 (305–330, 4), 299 (267–318, 5); length of hind foot, 161 (152–165, 3), 155 (152–165, 5); and length of ear, 110 (102–114, 3), 106 (96–114, 5). Height at shoulder is 38–48 cm (Sheldon 1992).

Skull of *C. mesomelas* is elongated, with a pear-shaped braincase and narrow rostrum (Fig. 2). Sagittal crest is only apparent at back of skull, anteriorly dividing into 2 low ridges that end on postorbital bars (Smithers 1983). Skull size is similar to other jackals, with usual length of 141–147 mm (Van Valkenburgh and Wayne 1994) and mean adult cranial volume of 56 ml (*SD* 4.9, $n = 10$ adults—Sheppy and Bernard 1984). Cranial measurements (in mm; *SD*, range, and *n* in parentheses) of adult male and female black-backed jackals collected from the Transvaal, South Africa (Lombaard 1971), respectively, are: length of skull from basion to gnathion, 150.8 (4.2, 138.9–160.5, 120), 145.6 (4.2, 135.2–157.1, 135); length of skull from gnathion to junction of sagittal and lambdoid crests, 164.5 (4.4, 152.4–174.5, 122), 158.7 (4.4, 148.4–171.5, 137); width across widest portion of zygomatic arches at right angles to longitudinal axis of skull, 85.9 (3.2, 78.7–94.3, 118), 83.3 (2.7, 77.2–90.3, 136); palatal length from most anterior portion to gnathion, 81.3 (2.4, 75.2–87.8, 120), 78.5 (2.3, 73.2–83.9, 130); canine length from tip to base of enamel on labial side, 16.8 (1.1, 11.5–19.3, 114), 15.6 (1.3, 9.9–18.5, 132). Growth of skull asymptotes at ca. 4–6 months of age (Lombaard 1971). A clinal length increase is evident from north to south in the former Transvaal province of South Africa (Rautenbach 1982). Skulls of *C. mesomelas* from East Africa are shorter in total length and wider and less variable in 16 other measures than skulls from Southern Africa (Van Valkenburgh and Wayne 1994). Further, *C. mesomelas* has longer and narrower carnassials and smaller upper and lower molar grinding areas in East Africa than in southern populations (Van Valkenburgh and Wayne 1994). Additional measurements are provided by Lombaard (1971), Rautenbach (1982), Roberts (1954), and Stuart (1981).

DISTRIBUTION. The Mozambique or Rhodesian Gap (from the Zambesi to Tanzania) separates the 2 ranges of black-backed jackals (Kingdon 1997; Van den Brink 1973; Fig. 3). The northern subspecies, *C. m. schmidtii*, occupies southern Ethiopia, southern Sudan, Somalia, Kenya, Uganda, and northern Tanzania. *C. m.*

schmidti once extended into Egypt but was displaced by *C. aureus* and *C. adustus* (Van den Brink 1973). The range of the southern subspecies, *C. m. mesomelas*, extends from the Cape of Good Hope northward to Angola, Zimbabwe, and southern Mozambique (Sheldon 1992). *C. mesomelas* was absent from the highveld of Transvaal until ca. 1953 (Van de Merwe 1953a).

FOSSIL RECORD. Occupancy of eastern and southern Africa by the black-backed jackal for 2–3 million years is evident from early Pleistocene fossil deposits in Kenya, Tanzania, and South Africa (Savage 1978). Fossil specimens of *C. mesomelas* in the Transvaal Caves are roughly the same size as modern representatives, although nasal bones differ slightly in size (Ewer 1956). Specimens attributed to *C. antiquus* in these caves are likely representatives of *C. mesomelas* (Ewer 1956). Fossil specimens from the Cape Province of South Africa suggest that carnassial length of black-backed jackals tends to increase with south latitude (Klein 1986).

FORM AND FUNCTION. Baculum of *C. mesomelas* extends along entire length of penis. It is I-shaped, with a smooth surface. Urethral groove extends along midventral surface from head for ca. three-fourths length of baculum. Average lengths and weights of 20 bacula from males 1–5 years of age are 56.8 mm (range, 46.0–65.9) and 299 mg (range, 124–528), respectively (Lombaard 1971).

Female *C. mesomelas* have 8 mammae, although usually 6 produce milk, depending on size of litter (Van de Merwe 1953a). Left and right ovaries of a captive female black-backed jackal from South Africa were 8 by 10 by 15 mm and 6 by 8 by 15 mm, respectively, with a few small (3–4 mm in diameter) follicles (Appel et al. 1978). Uterine horns were each 80 mm in length with a diameter of 6 mm, and her uterus measured 40 mm in length and 8 mm in diameter. Serum estrone was <10 pg/ml, whereas estradiol and progesterone measured 34 pg/ml and 1.3 pg/ml, respectively; both levels consistent with normal proestrus (Appel et al. 1978).

Deciduous dental formula is i 3/3, c 1/1, p 3/3, with a permanent dental formula of i 3/3, c 1/1, p 4/4, m 2/3, total 42 (Lombaard 1971). Male : female canine diameter ratio was 1.10 and 1.07 in South Africa and East Africa, respectively, with both ratios significantly different from 1 (Van Valkenburgh and Wayne 1994). Dentition indices calculated for the black-backed jackal are: upper canine shape (mediolateral canine width/anteroposterior canine length), 60.5; premolar shape index (maximum mediolateral width of largest lower premolar/maximum anteroposterior length), 0.47; relative premolar size (maximum width of largest lower premolar/body weight$^{1/3}$), 2.24; relative blade length (ratio of anteroposterior length of trigonid measured along buccal margin/maximum M1 length), 0.66; relative grinding area (total grinding area of molars$^{1/2}$/total blade length of carnassial), 0.75 (Van Valkenburgh 1989).

Canis mesomelas has a thermoneutral zone of 22.5–27.5°C, with a resting metabolic rate of 134% of the basal metabolic rate predicted by body mass (Downs et al. 1991). Mean food volume (cm^3) in adult male and female black-backed jackal stomachs were 173 and 153 (range, 0–1,250 cm^3), respectively (Bothma 1966, 1971a), and may be ca. 10% of the body mass of an individual jackal (Grafton 1965). Mass of stomach contents from 5 black-backed jackals (3 males: 18 weeks, 4 and 5 years of age; 2 females: 24 weeks and 6 years of age) collected in the Addo Elephant National Park in 1977 ranged from 125.9 to 298.3 g. Heart girth measurements from 4 of these ranged from 35.0 to 44.0 cm (Hall-Martin and Botha 1980). Feeding trials conducted on 2 captive black-backed jackals showed that the same prey item is usually passed in the first 2 scats (mean = 2.8, n = 7) but may appear in up to 7 scats (Bowland and Bowland 1991).

The 3 jackal species of East Africa are unique among sympatric canids in degree of overlap in body size (Wayne et al. 1989). Other sympatric canid species generally diverge in body size by a factor of 2 or more, whereas *C. mesomelas*, *C. adustus*, and *C. aureus* each weigh ca. 7 kg (Wayne et al. 1989). However, in East Africa where the 3 species are sympatric, *C. mesomelas* exhibits significant character displacement such as changes in tooth shape (relative length of grinding molar and carnassial blade length) consistent with an increase in carnivory, reduced sexual dimorphism, and reduced morphological variability (Van Valkenburgh and Wayne 1994).

ONTOGENY AND REPRODUCTION. Black-backed jackals are monogamous (Moehlman 1983; Wyman 1967). They reach sexual maturity at 11 months, although in the wild only adults ≥2 years of age breed (Ferguson et al. 1983; Moehlman 1979). Gestation lasts 60–65 days (Van der Merwe 1953a). Parturition (April–February) varies regionally (Van der Merwe 1953a) and is likely related to habitat and food availability (Bernard and Stuart 1991; Moehlman 1987). In the Rift Valley of Kenya, parturition is from September to January, though 1 female was lactating as early as 5 August (Fuller et al. 1989). In northern Tanzania and Kwa-Zulu-Natal, parturition occurs from June to September (Moehlman 1983; Rowe-Rowe 1978; Wyman 1967). In South Africa, parturition occurs August–October (Fairall 1968; Ferguson et al. 1983). In the National Zoological Gardens of South Africa, *C. mesomelas* parturition lasted from mid-August to mid-November (Brand 1963). In the London Zoological Gardens, parturition of 4 litters occurred in March–April (Zuckerman 1953). Females may produce 2 litters per year (Van der Merwe 1953a), but evidence for this is lacking.

Litter size ranges from 1 to 9 but is usually 3–6 (Bingham and Purchase 2002; Brand 1963; Rowe-Rowe 1978, 1984, 1992; Wyman 1967). Pups are born blind and begin to open their eyes by days 8–10 (Moehlman 1987; Van der Merwe 1953a). They begin to eat regurgitated food from adults at 3 weeks and are weaned by 8–10 weeks (Lombaard 1971; Moehlman 1979, 1987; Van der Merwe 1953a).

In 2 captive pups (1 male, 1 female) no deciduous teeth were present at birth, although by 3 weeks all 14 of the deciduous teeth had erupted. Upper and lower permanent premolars erupt at 14.5 weeks with the last permanent tooth (M3) beginning to erupt at 23.5 weeks. Within 6–12 months all permanent teeth are fully erupted (Lombaard 1971).

Pups are born in underground burrows and do not emerge from underground dens until ca. 3 weeks of age. However, pups spend most of their time in the den until ca. 7 weeks of age. By 12–14 weeks, pups leave the dens and begin to forage with adults (Moehlman 1979, 1987; Van der Merwe 1953a). Most pup mortality occurs in pups <14 weeks of age, with a sex ratio of surviving pups >14 weeks ca. 1:1 (Moehlman 1979, 1983, 1987). Only 1–3 pups survive >14 weeks of age (Moehlman 1987; Rowe-Rowe 1982, 1984, 1986). In the Serengeti Plains of Tanzania, ca. 24% of surviving pups stay with the family unit (instead of dispersing at 10–11 months of age) for the first 1.5–2 years (Moehlman 1979, 1987).

ECOLOGY. Black-backed jackals are opportunistic predators and scavengers. They are omnivorous and feed on whatever is most abundant and easily obtained (Grafton 1965; Rowe-Rowe 1976, 1983; Sheldon 1992). Where surface water is available, black-backed jackals drink regularly. However, in some areas such as the southwest and central Kalahari, *C. mesomelas* survives where surface water may not be available for up to 9 months of the year (Smithers 1971; Van der Merwe 1953a).

Canis mesomelas diet may consist of the mammals from the orders Artiodactyla (including domestic stock in some regions), Carnivora, Insectivora, Lagomorpha, and Rodentia. Other foods include amphibians, birds, fish, invertebrates such as the Arachnida, Coleoptera, Crustacea, Diplopoda, Diptera, Hymenoptera, Isoptera, Myriapoda, Orthoptera, Pelycopoda, reptiles, and plant material from both cultivated and wild sources (Bothma 1971a; Bothma et al. 1984; Grafton 1965; Lamprecht 1978; Nel et al. 1997). Carrion is an important food source, although its importance varies regionally and temporally (Avery et al. 1987; Bothma 1971a; Grafton 1965; Smithers 1971; Wyman 1967).

In South Africa, antelope, carrion, hares, hoofed domestic stock (particularly sheep), insects, and rodents are major food sources (Bothma 1971a; Kok 1996; Stuart 1981). Impala (*Aepyceros melampus*) and springbok (*Antidorcas marsupialis*) are the main species of antelope consumed, although duiker (*Sylvicapra grimmia*), reedbuck (*Redunca arundinum*), and steenbok (*Raphicerus campestris*) may be eaten (Bothma 1971a). Small mammals of the genera *Aethomys*, *Cryptomys*, *Hystrix*, *Leggada*, *Mastomys*, *Mus*, *Otomys*, *Pedetes*, *Praomys*, *Rhabdomys*, *Tatera*, and *Xerus* are consumed (Bothma 1971a; Grafton 1965). Carnivores such as mongooses (Viverridae), polecats (Mustelidae), wild cats (Felidae), and domestic dogs and cats have been identified from stomachs of *C. mesomelas*. Domestic animals such as pigs, goats, sheep, and poultry have been identified, with sheep making up the majority of the domestic intake (Bothma 1971a; Grafton 1965). Lizards, snakes,

and tortoises may be eaten as well. Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Odonata, and Orthoptera may be consumed when available. Insects may make up an entire meal and be an important food item when abundant (Bothma 1971a; Grafton 1965; Hall-Marten and Botha 1980; Smithers 1971). Domestic plant material including groundnuts and grapes, wild grasses, seeds, berries, and fruit may be important food items when abundant (Bothma 1971a; Grafton 1965; Smithers 1971). Eleven stomachs from the Kalahari Gemsbok Park contained (by volume) 63.4% insects, 12.2% rodents, 11.2% carrion, 5.4% reptiles, 5.0% arachnids, 1.4% grass, 0.6% wild fruit, 0.4% birds, and 0.4% bark of shrubs and trees (Bothma 1966).

Diet of the black-backed jackal on the Namib Desert coast consists primarily of marine birds, mammals, fish, and insects. The Cape and whitebreasted cormorants (*Phalacrocorax capensis*, *P. carbo*), jackass penguin (*Spheniscus demersus*), Cape fur seal (*Arctocephalus pusillus*), sea catfish (*Tachysurus feliceps*), and insects (Orthoptera and Coleoptera) are the most common items in the diet (Avery et al. 1987; Hiscocks and Perrin 1987; Oosthuizen et al. 1997; Stuart 1976; Stuart and Shaughnessy 1984).

The black-backed jackal diet was compared among nature reserves and sheep farming areas in KwaZulu-Natal. Stomachs contained (by volume) 58% wild and 52% domestic carrion, 36% and 10% wild antelope and mammals, and 4% and 32% domestic sheep, respectively. Small amounts of birds, reptiles, invertebrates, and grass were also detected (Rowe-Rowe 1976). Diet of black-backed jackals in the Natal Drakensberg consists mostly of small mammals (55%) such as *Amblysomus hottentotus*, *Cryptomys*, *Dendromus*, *Myosorex varius*, *Otomys irroratus*, and *Rhabdomys pumilio*; medium-sized mammals (9%) such as *Ichneumia albicauda*, *Ictonyx striatus*, *Lepus saxatilis*, *Procavia capensis*, *Pronolagus crassicaudatus*, and *Thryonomys swinderianus*; and antelope (11%) such as *Damaliscus dorcas*, *Ourebia ourebi*, *Pelea capreolus*, *Redunca fulvorufula*, *Taurotragus oryx*, and *Tragelaphus scriptus*. Domestic mammals, birds, reptiles, and insects make up a small part of the diet in this region (Rowe-Rowe 1983).

Black-backed jackals may compete with aardwolves (*Proteles cristatus*), bat-eared foxes (*Otocyon megalotis*), Cape foxes (*Vulpes chama*), golden jackals, side-striped jackals, and spotted hyenas (*Crocuta crocuta*). In the Namib Desert, enough separation in the diet, use of space, and activity occurs to allow coexistence of aardwolves, bat-eared foxes, Cape foxes, and black-backed jackals (Bothma et al. 1984). Where the 3 jackal species are sympatric, segregation of habitat and temporal activity limit intraspecific competition (Fuller et al. 1989). In the Serengeti Plains of Tanzania, golden and black-backed jackals use different habitats; *C. mesomelas* typically inhabits the brush woodlands whereas *C. aureus* inhabits the adjacent shortgrass plains (Moehlman 1983). Further, whelping seasons differ with *C. mesomelas* whelping during the dry season (July–September), whereas *C. aureus* gives birth during the wet season (December–March). The diets of the 2 jackal species (*C. mesomelas* and *C. aureus*) are similar, and interspecific dominance relationships between the 2 species vary (Lamprecht 1978; Wyman 1967).

Canis mesomelas may be infected with pathogens such as rabies virus, canine parvovirus, canine distemper virus, canine adenovirus, a tick-borne disease-causing pathogen *Ehrlichia canis* (Alexander et al. 1994; Rowe-Rowe 1984; Spencer et al. 1999), and African horse sickness virus (Alexander et al. 1994; Binepal et al. 1992). In addition, spores of *Bacillus anthracis* have been isolated from *C. mesomelas* scats in Etosha National Park, Namibia (Lindeque and Turnbull 1994). Black-backed jackals are an important rabies vector in Africa and have been associated with epidemics (Bingham and Foggin 1993; Bingham et al. 1999a, 1999b; Courtin et al. 2000; McKenzie 1993; Swanepoel et al. 1993). Jackal rabies appears to cycle every 4–8 years with seasonal variation being explained by rainfall patterns and social behavior (Bingham and Foggin 1993; Courtin et al. 2000; Loveridge and Macdonald 2001). In Zimbabwe, *C. mesomelas* is able to maintain rabies independently of other species (Bingham et al. 1999b). Epidemics may be effectively controlled through oral vaccination (Bingham et al. 1993, 1995, 1999c). However, long-term control of rabies in jackals will not be effective unless populations of domestic dogs are immunized (Bingham et al. 1999c; Rhodes et al. 1998). Tetracycline compounds as biomarkers to identify vaccinated animals in bait-delivered vaccination programs cannot be used in jackals in Zimbabwe due to naturally occurring fluorescence in femur sections (Bingham et al. 1994). Immunoperoxidase techniques applied to formalin-fixed brain tissue can be used to positively identify rabies antigen in *C. mesomelas* (Last et al. 1994).

Canis mesomelas also may be infected with the following parasites: trematodes *Athesmia* (Hammond 1972); cestodes *Dipylidium caninum*, *Echinococcus granulosus*, *Joyeuxialla echinorhyncoides*, *J. pasqualei*, *Mesocestoides lineatus*, *Taenia erythraea*, *T. hydatigena*, *T. jackhalsi*, *T. mulitceps*, *T. pungutchui*, and *T. serialis*; nematodes *Ancylostoma braziliense*, *A. caninum*, *A. martinaglia*, *A. somaliense*, *A. tubaeforme*, and *Physaloptera praeputialis* (Iori and Lanfranchi 1996; Macchioni 1995; Macpherson et al. 1983; Round 1968; Van der Merwe 1953a); and protozoans *Babesia canis*, *Ehrlichia canis*, *Hepatozoon canis*, *Rickettsia canis*, *Sarcocytis*, *Toxoplasma gondii*, and *Trypanosoma congolense* (Price and Karstad 1980; Van der Merwe 1953a; Van Heerden 1979, 1980; Wesemeier et al. 1995). Ectoparasites such as mites that cause sarcoptic mange (Hiscocks and Perrin 1987); ticks *Amblyomma hebraeum*, *A. marmoreum*, *A. nymphs*, *A. variegatum*, *Boophilus decoloratus*, *Haemaphysalis leachii*, *H. silacea*, *H. spinulosa*, *Hyelomma*, *Ixodes pilosus*, *I. rubicundus*, *Rhipicephalus appendiculatus*, *R. evertsi*, *R. sanguineus*, and *R. simus* (Hall-Martin and Botha 1980; Horak et al. 1987; Price and Karstad 1980; Van der Merwe 1953a); and fleas *Ctenocephalides cornatus*, *Echidnophaga gallinacea*, and *Synosternus caffer* (Van der Merwe 1953a) may also infect *C. mesomelas*. In some parts of its range, canine distemper, rabies, and sarcoptic mange may contribute to local declines in *C. mesomelas* populations (Keep 1970; McKenzie 1997; Rowe-Rowe 1992).

Black-backed jackals can live up to almost 14 years in captivity (Flower 1931), with adults in the wild probably only reaching 6–8 years (Moehlman 1987; Rowe-Rowe 1982). Small pups are vulnerable to any predator large enough to carry them away, but eagles are probably the main threat and are able to carry off even subadults (Van Lawick and Van Lawick-Goodall 1970). Other than humans, the main predator of adults is the leopard (*Panthera pardus*—Schaller 1972).

Home-range size varies throughout the year, being greatest during the mating season (Loveridge and Macdonald 2001). Average home-range size of radio-collared adult *C. mesomelas* in the Transvaal of South Africa was 10.6 km^2 (n = 8) and ranged from 3.4 to 21.5 km^2 (Ferguson et al. 1983). Home ranges of mated pairs overlapped only slightly and other mated pairs were excluded, although home ranges of immature animals overlapped extensively with adult pairs (Ferguson et al. 1983). Territories are defended and trespassing adult pairs are chased away by the mated pair, with most aggression occurring between members of the same sex (Ferguson et al. 1983; Moehlman 1987; Wyman 1967). However, immature *C. mesomelas* are tolerated and may hunt unmolested (Ferguson et al. 1983; Loveridge and Macdonald 2001). Territories in the Serengeti Plains, Tanzania, are held throughout the year and a pair may hold a territory for their lifetime (Moehlman 1983). Territoriality breaks down around watering holes and where carcasses are locally or seasonally abundant (Ferguson et al. 1983; Moehlman 1983; Nel 1984; Oosthuizen et al. 1997). At the Reenen Bay seal colony, Namibia, 78 jackals were observed at the carcass of a Cape fur seal pup (Oosthuizen et al. 1997).

Minimum seasonal range sizes of *C. mesomelas* (n = 6) in the Rift Valley of Kenya during June–August did not vary predictably by sex or age and averaged 1.8 km^2, with a range of 0.7–3.5 km^2 (Fuller et al. 1989). In the Cape Cross Seal Reserve, Namibia, average home ranges (April–July) were 7.1–24.9 km^2 (Hiscocks and Perrin 1988). Considerable home range overlap occurred suggesting that black-backed jackals in this region are not territorial (Hiscocks and Perrin 1988).

In the Giant's Castle Game Reserve in the Natal Drakensberg, South Africa, average home range size was 18.2 km^2 (n = 10; SE = 3.0). Mated pairs had overlapping home ranges which did not overlap with home ranges of other mated pairs, although as in the Transvaal, immature animals were tolerated within the mated pair's home range (Rowe-Rowe 1982).

Black-backed jackals travel on footpaths and roads at 10 km/h (Van der Merwe 1953a). Daily distances moved by adult and immature *C. mesomelas* averaged ca. 12 and 8 km, with males and females averaging 9.2 and 8.6 km, respectively (Ferguson et al. 1983, 1988).

Population estimates of *C. mesomelas* can be derived from helicopter surveys (van Hensbergen et al. 1996). *C. mesomelas*

occurs at densities of 0.3–0.4 jackals/km² in Giant's Castle Game Reserve in the Natal Drakensberg (Rowe-Rowe 1982) to 22 (*SD* = 2.2) jackals/km² in the Cape Cross Seal Reserve, Namibia (Hiscocks and Perrin 1988). Sex ratio in the former reserve was likely 1:1, and the population was estimated to comprise 25% breeding adults, 25% young of the year, and 50% nonbreeding adults and subadults during 1978–1980 (Rowe-Rowe 1984).

Black-backed jackals occupy a wide range of habitats from veld upland and mountains (>3,000 m above sea level) to coastal desert (Kingdon 1997; Rowe-Rowe 1976, 1986, 1992). Six radiocollared black-backed jackals in the Rift Valley of Kenya were most often found in closed woodland habitat, with mean habitat use significantly different among *C. adustus*, *C. aureus*, and *C. mesomelas* (Fuller et al. 1989). In the Mikumi National Park, Tanzania, *C. mesomelas* occurred significantly less than expected in grassland <1 m in height within 600 m of a major highway (Newmark et al. 1996).

Black-backed jackals may be captured with padded steel-jawed traps (Bothma 1971b; Fuller et al. 1989; Rowe-Rowe and Green 1981), snares, greyhounds, cage-type live traps, or by digging out dens (Bothma 1971b), and may be immobilized with a tranquilizer dart fired from a gun (Fuller et al. 1989). Black-backed jackals may be anesthetized with ketamine hydrochloride alone (Bingham et al. 1995; Hiscocks and Perrin 1988) or in combination with promazine hydrochloride or acetylpromazine (Fuller et al. 1989; Rowe-Rowe and Green 1980, 1981). Age of black-backed jackals can be determined by tooth eruption; replacement and wear criteria; cementum annuli layers in upper permanent canines; growth curves of eye-lens weight; baculum weight and length; X-rays of distal epiphyses of humerus, radius, and ulna; and body measurements and weights combined with cranial measurements (Butynski 1975; Lombaard 1971).

Populations of black-backed jackals are sometimes controlled because of their reputation for killing livestock and of their role as a rabies vector. Explosive-propelled cyanide guns (Bothma 1971c; Brand and Nel 1997; Brand et al. 1995; Ferguson 1986), hunting with dogs (Grafton 1965; Rowe-Rowe 1975), poisoned baits (Grafton 1965), fencing (Heard and Stephenson 1987; Thomson 1999), and trapping all have been used to manage this species. *C. mesomelas* may be hunted throughout the year in South Africa (Ginsberg and Macdonald 1990).

BEHAVIOR. Average daily activity for *C. mesomelas* was 20% and 48%, monitored by motion sensors and changes in signal integrity, respectively (Fuller et al. 1989). Daily activity budgets vary throughout the whelping period and with the presence or absence of nonbreeding helpers within the family unit (Moehlman 1983). Activity patterns are variable and animals may be active at any time throughout the 24-h period. However, *C. mesomelas* is most active near sunrise and sunset, coinciding closely with activity patterns of their mammalian prey. In areas where they are heavily persecuted by humans, black-backed jackals may become strictly nocturnal (Bueler 1973; Ferguson et al. 1988; Fuller et al. 1989; Hiscocks and Perrin 1988; Rowe-Rowe 1978). Increased activity at night occurs during periods with an intermediate amount of moonlight, with lowest nighttime activity occurring during the full and new moon phases. Adult jackals started moving earlier in the evening and ceased movement later in the morning than did immature animals (Ferguson et al. 1988).

Black-backed jackal society is made up of a hierarchical family group (Kingdon 1997). The basic social unit is the mated pair and their offspring. A strong pair bond exists between the mated pair and they may remain together for up to 8 years (Moehlman 1983). Four components of black-backed jackal social organization are: the mated pair which is territorial; progeny of the year; nonbreeding helpers; and solitary nonbreeding, nonterritorial animals (Moehlman 1979; Rowe-Rowe 1982). Group size ranges from 1 to 8 individuals and may vary seasonally (Rowe-Rowe 1978, 1982, 1984). Parents and siblings are protective of pups and may attack predators if they approach the den (Kingdon 1997; Moehlman 1979).

Black-backed jackals have a well-developed social life, and behavior patterns during social interactions show no major departures from the typical canine sequences (Ferguson 1978; Kleiman 1967). Allogrooming is common within a jackal pair and consists of 1 member of the pair grooming the other between and behind the ears, as well as side of neck, back, forelegs, and anal area. Interactions within a pair are predominantly friendly, whereas interactions between nonpair members are mainly agonistic (Ferguson 1978). Body-slamming is used to signal dominance to a submissive animal. The dominant animal swings its hindquarters through an arc of at least 120°, hitting the submissive animal on the forelegs and torso to throw the submissive animal off balance and onto its side (Ferguson 1978).

Adult black-backed jackals scent mark with urine or feces, often on conspicuous objects like grass tufts or rocks (Ferguson et al. 1983). While foraging together, jackal pairs scent mark twice as often as solitary foragers. This tandem marking advertises that both members of the pair are in residence (Moehlman 1987).

Black-backed jackals opportunistically hunt in groups when appropriate prey is available (Moehlman 1987). Success rate (kills/attempt × 100) of attacking *C. mesomelas* on Thomson's gazelles (*Gazella thomsonii*) is 67% if 2 jackals are involved compared with 16% if only 1 jackal is involved (Wyman 1967). However, success rates of black-backed jackal attacks on Thomson's gazelle fawns (75%) by an individual or a pair were equal (Lamprecht 1978). Cooperative groups of jackals have a better chance of defending and feeding on a carcass (Moehlman 1987). *C. mesomelas* was successful in 60% of observed Cape hare (*Lepus capensis*), spring hare (*Pedetes capensis*), and gazelle fawn (*Gazella thomsonii*, *G. granti*) hunts in the Serengeti (Lamprecht 1978). Caching behavior occurs (Lamprecht 1978; Wyman 1967).

Black-backed jackals can kill adult antelope such as kudu (*Tragelaphus strepisiceros*), oribi (*Ourebia ourebi*), Sharpe's grysbuck (*Raphicerus sharpei*), steenbok, and Thomson's gazelle (Hirst 1969; Lamprecht 1978; Pienaar 1969). Newborn lambs of small antelope, young wildebeest (*Connochaetes taurinus*) calves, and zebra (*Equus burchelli*) foals may also be killed by groups of black-backed jackals (Pienaar 1969). Circumstantial evidence suggests black-backed jackal raid ostrich (*Struthio camelus*) nests (Hall-Martin and Botha 1980).

The method used most frequently by *C. mesomelas* to hunt Thomson's gazelles involves trotting toward the victim, gradually increasing speed to a fast gallop, and then grabbing the gazelle at any available part such as rear leg, flank, neck, or muzzle. The kill is primarily accomplished by a throat bite that suffocates the animal (Wyman 1967); however, black-backed jackals have also been observed to kill by tearing open the abdomen (Lamprecht 1978; Wyman 1967).

Cooperative hunting occurs between cheetahs (*Acinonyx jubatus*) and the black-backed jackal (Eaton 1969). Black-backed jackals also associate with lions (*Panthera leo*) and may follow lion prides to scavenge kills (Smithers 1971; Van der Merwe 1953a, 1953b).

On farms, the black-backed jackal is a problem, particularly during lambing season (Bothma 1971a; Lawson 1989; Rowe-Rowe 1975, 1976). *C. mesomelas* does not generally attack cattle, although cows during parturition may be attacked (Skead 1973). In a 440-km study area in KwaZulu-Natal, sheep losses to *C. mesomelas* were 0.05% of the sheep population and occurred mostly during the dry season (winter and spring) when flocks were lambing (Rowe-Rowe 1975). Thirteen percent of 395 sheep killed in a sheep farming area in KwaZulu-Natal were killed by *C. mesomelas*, 83% by domestic dogs, 2% by *Felis caracal*, and 2% by unknown predators (Roberts 1986). Predation on sheep by black-backed jackals occurs primarily by a throat bite (Rowe-Rowe 1975; Van der Merwe 1953a). The flank of the sheep is opened first, followed by consumption of flesh and skin of the flank, heart, liver, some ribs, haunch of hind leg, and sometimes stomach and its contents (possibly milk in young lambs). In older lambs, the main portions eaten are usually heart and liver (Rowe-Rowe 1975). Usually only 1 lamb per night is killed in any 1 place but sometimes 2 and occasionally 3 may be killed (Rowe-Rowe 1975).

Black-backed jackals on the Namib Desert coast carry whole or parts of captured and scavenged prey to specific feeding sites. Accumulations of prey debris form well-defined middens associated with low, vegetated, coastal hummocks. This behavior is unique to coastal populations of *C. mesomelas* (Avery et al. 1984, 1987; Dreyer and Nel 1990).

Black-backed jackals dig dens but commonly use uninhabited dens made by aardvarks (*Orycteropus afer*—Van der Merwe 1953a, 1953b). Dens may be located in termite mounds, in rock crevices, in tall vegetation, near the edge of the bush, or in the bush itself

(Van der Merwe 1953a; Wyman 1967). Females may share a den with porcupines (Hystricidae—Van der Merwe 1953a).

The male of a mated pair provides food for the female for 1–2 weeks postparturition (Nel 1984). Both members of the mated pair assist in feeding the young (Ferguson et al. 1983; Wyman 1967). However, as many as 3–4 other adult helpers may assist in feeding and guarding the pups (Ferguson et al. 1983; Loveridge and Macdonald 2001; Moehlman 1979, 1987). Helpers are usually nonbreeding adult siblings ca. 11–20 months old. Addition of helpers correlates with improved protection, provisioning, and survival of pups (Moehlman 1979, 1981, 1983, 1987; Montgomerie 1981). When 1 of the adults returns from hunting, the pups approach the adults keeping their muzzles to the corner of the adults mouth, wag their tails vigorously, with the ears back against the neck. Adults regurgitate meat for pups (Wyman 1967).

The litter starts to venture out of the den at 3 weeks but remains very close to the natal den until ca. 12 weeks (Ferguson et al. 1983; Lombaard 1971). Young jackals remain within relatively restricted areas for the first year, usually in vicinity of the den.

Dispersal from natal areas usually occurs at ca. 1 year of age (Ferguson et al. 1983; Loveridge and Macdonald 2001; Van der Merwe 1953a). One male captured in the western Transvaal, South Africa, dispersed 126 km (straight line distance) during 15 months (Ferguson et al. 1983). Another male jackal (6 months old) moved 103 km in 8 months (Bothma 1971b).

Acoustic communication is elaborate and may consist of growls, whines, cackles, barks, yaps, and howls (Sheldon 1992). A variety of vocalizations have been identified: a drawn out "nyah-h-h-h- yah yah-yah," a short sharp "yah yah yah," a soft "wuf," and numerous other grunts, cries, and growls. The interpretation and number of calls is variable (Bueler 1973; Roberts 1954; Shortridge 1934; Van der Merwe 1953a). Most calling occurs between sunset and sunrise, and peak calling occurs in June, July, and August (Skead 1973).

CONSERVATION STATUS. The International Union for Conservation of Nature and Natural Resources (IUCN) and the Convention on International Trade in Endangered Species of Wild Flora and Fauna have not listed the black-backed jackal as a vulnerable or threatened species. *C. mesomelas* is an adaptable carnivore found at relatively high densities in many parts of Africa, and despite increasing urbanization and agricultural expansion black-backed jackals coexist with humans. Thus, no conservation measures are recommended by the IUCN (Ginsberg and Macdonald 1990). However, in local areas where disease is prevalent or human efforts are made to eradicate the black-backed jackal, population declines and perhaps even local extirpations may occur (Keep 1970; McKenzie 1997; Rowe-Rowe 1978, 1992).

GENETICS. *Canis mesomelas* possesses a uniform karyotype with a diploid number of 78 chromosomes. All but 2 chromosomes are acrocentric, with the exceptions being a large unpaired submetacentric and a very small, unpaired submetacentric (Wallace 1977). Analysis of mitochondrial DNA of 64 free-ranging individuals from East Africa indicates that *C. mesomelas* shows high variability (i.e., sequence divergence) among a low number of genotypes (Wayne et al. 1990). Mitochondrial DNA analysis also showed large sequence divergence in *C. mesomelas* from sympatric *C. adustus* and *C. aureus*, indicating divergence 2.3–4.5 million years ago (Wayne et al. 1989).

REMARKS. The black-backed jackal is also known as the gray, silver, or saddle-backed, red, and even golden jackal (Shortridge 1934; Van der Merwe 1953a). Other names include: chacal à chabraque (French); Schabrackenschakal (German); Rooijakkals (Afrikaans); Ekwee (Ateso); Kwee (Karamojong); Nhyewe (Kigogo); Nchewe (Kihehe); Ngewe (Kikinga); Gedala (Kiliangulu); Mola (Kinyatura); Kewe (Kisagara); Bweha Nyakundu, Bweha Shaba (Kiswahili); Muzozo (Kitaita; Ginsberg and Macdonald 1990); impungushe, ikhanka (Zulu; Rowe-Rowe 1978); and Phokoje (Tswana; Smithers 1971). The genus name *mesomelas* is derived from *meso,* meaning middle, and *melas,* meaning black.

L. R. Walton was supported by a University of Saskatchewan Graduate Teaching Fellowship. D. O. Joly was supported by a University of Saskatchewan Graduate Scholarship and subsequently a Natural Sciences and Engineering Research Council of Canada Postgraduate Scholarship. Y. T. Hwang, T. K. Fuller, and D. T. Rowe-Rowe reviewed earlier drafts of this manuscript. We gratefully acknowledge assistance from M. Thomson and Y. Pancheshnikov in obtaining interlibrary loans and from A. Gardner in finding synonym authors.

LITERATURE CITED

Alexander, K. A., P. W. Kat, R. K. Wayne, and T. K. Fuller. 1994. Serologic survey of selected canine pathogens among free-ranging jackals in Kenya. Journal of Wildlife Diseases 30: 486–491.

Appel, G., J. Olsen, and B. Lasley. 1978. Clinical, anatomical and hormonal observations on the genital tract of a South African black-backed jackal (*Canis mesomelas mesomelas*). Der Zoologische Garten 48:65–68.

Avery, G., D. M. Avery, S. Braine, and R. Loutit. 1984. Bone accumulation by hyaenas and jackals: a taphonomic study. South African Journal of Science 80:186–187.

Avery, G., D. M. Avery, S. Braine, and R. Loutit. 1987. Prey of coastal black-backed jackal *Canis mesomelas* (Mammalia: Canidae) in the Skeleton Coast Park, Namibia. Journal of Zoology (London) 213:81–94.

Banfield, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Ontario, Canada.

Bernard, R. T. F., and C. T. Stuart. 1991. Correlates of diet and reproduction in the black-backed jackal. South African Journal of Science 88:292–294.

Bigalke, R. C., and D. T. Rowe-Rowe. 1969. An analysis of the results of hunting black-backed jackals over a five year period in Natal. Lammergeyer 10:70–80.

Binepal, V. S., B. N. Wariru, F. G. Davies, R. Soi, and R. Olubayo. 1992. An attempt to define the host range for African horse sickness virus (Orbivirus, Reoviridae) in east Africa, by a serological survey in some Equidae, Camelidae, Loxodontidae, and Carnivore. Veterinary Microbiology 31:19–23.

Bingham, J., and C. M. Foggin. 1993. Jackal rabies in Zimbabwe. Onderstepoort Journal of Veterinary Research 60:365–366.

Bingham, J., C. M. Foggin, A. I. Wandeler, and F. W. G. Hill. 1999a. The epidemiology of rabies in Zimbabwe. 1. Rabies in dogs (*Canis familiaris*). Onderstepoort Journal of Veterinary Research 66:1–10.

Bingham, J., C. M. Foggin, A. I. Wandeler, and F. W. G. Hill. 1999b. The epidemiology of rabies in Zimbabwe. 2. Rabies in jackals (*Canis adustus* and *Canis mesomelas*). Onderstepoort Journal of Veterinary Research 66:11–23.

Bingham, J., A. Kappeler, F. W. G. Hill, A. A. King, B. D. Perry, and C. M. Foggin. 1995. Efficacy of SAD (Berne) rabies vaccine given by the oral route in two species of jackal (*Canis mesomelas* and *Canis adustus*). Journal of Wildlife Diseases 31:416–420.

Bingham, J. C., R. Matema, A. Kappeler, and F. W. G. Hill. 1994. Naturally occurring tetracycline-like fluorescence in sections of femur from jackals in Zimbabwe. Veterinary Records 135:180–182.

Bingham, J., and G. K. Purchase. 2002. Reproduction in the jackals *Canis adustus* Sundevall, 1846, and *Canis mesomelas* Schreber, 1778 (Carnivora: Canidae), in Zimbabwe. African Zoology 37:21–26.

Bingham, J., C. L. Schumacher, F. W. G. Hill, and A. Aubert. 1999c. Efficacy of SAG-2 oral rabies vaccine in two species of jackal (*Canis adustus* and *Canis mesomelas*). Vaccine 17: 551–558.

Bingham, J., et al. 1993. Oral rabies vaccination of jackals: progress in Zimbabwe. Onderstepoort Journal of Veterinary Research 60:477–478.

Blainville, H. M. D. de. 1837. Rapport sur un mémoire de M. Jourdan concernant deux nouvelles espèces de mammifères de l'Inde. Annales des Sciences Naturelles, Zoologie et Biologie Animale, séries 2, 8:270–281.

Bothma, J. Du P. 1966. Notes on the stomach contents of certain carnivora (Mammalia) from the Kalahari Gemsbok Park. Koedoe 9:37–39.

Bothma, J. Du P. 1971a. Food of *Canis mesomelas* in South Africa. Zoologica Africana 6:195–203.

Bothma, J. Du P. 1971b. Notes on movement by the black-backed jackal and the aardwolf in the western Transvaal. Zoologica Africana 6:205–207.

Bothma, J. Du P. 1971c. Control and ecology of the black-backed jackal in the Transvaal. Zoologica Africana 6:187–193.

Bothma, J. Du P., J. A. J. Nel, and A. MacDonald. 1984. Food niche separation between four sympatric Namib desert carnivores. Journal of Zoology (London) 202:327–340.

Bothma, J. Du P, A. G. W. Steyn, and S. H. C. Du-Toit. 1976. Determination of sample size in feeding habits studies using the black-backed jackal in the western Transvaal. South African Journal of Wildlife Research 6:129–132.

Bowland, J. M., and A. E. Bowland. 1991. Differential passage rates of prey components through the gut of serval *Felis serval* and black-backed jackal *Canis mesomelas*. Koedoe 34:37–39.

Brand, D. J. 1963. Records of mammals bred in the National Zoological Gardens of South Africa during the period 1908 to 1960. Proceedings of the Zoological Society of London 140: 617–659.

Brand, D. J., N. Fairall, and W. M. Scott. 1995. The influence of regular removal of black-backed jackals on the efficiency of coyote getters. South African Journal of Wildlife Research 25:44–48.

Brand, D. J., and J. A. J. Nel. 1997. Avoidance of cyanide guns by black-backed jackal. Applied Animal Behaviour Science 55:177–182.

Bueler, L. E. 1973. Wild dogs of the world. Stein and Day Publishers, New York.

Butynski, T. M. 1975. Ageing black-backed jackal pups in Botswana. Journal of the Southern African Wildlife Management Association 5:39–42.

Clutton-Brock, J., G. B. Corbet, and M. Hills. 1976. A review of the family Canidae, with a classification by numerical methods. Bulletin of the British Museum (Natural History), Zoology Series 29:117–199.

Coetzee, C. G. 1971. Order Carnivora. Pp. 8.1–8.42 in The mammals of Africa: an identification manual (J. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D.C.

Courtin, F., T. E. Carpenter, R. D. Paskin, and B. B. Chomel. 2000. Temporal patterns of domestic and wildlife rabies in central Namibia stock-ranching area, 1986–1996. Preventive Veterinary Medicine 43:13–28.

Downs, C. T., J. M. Bowland, A. E. Bowland, and M. R. Perrin. 1991. Thermal parameters of serval *Felis serval* (Felidae) and blackbacked jackal *Canis mesomelas* (Canidae). Journal of Thermal Biology 16:277–279.

Dreyer, H. van A., and J. A. J. Nel. 1990. Feeding-site selection by black-backed jackals on the Namib Desert coast. Journal of Arid Environments 19:217–224.

Eaton, R. L. 1969. Cooperative hunting by cheetahs and jackals and a theory of domestication of the dog. Mammalia 33:87–92.

Ellerman, J. R., T. C. S. Morrison-Scott, and R. W. Hayman. 1953. Southern African mammals 1758 to 1951: a reclassification. British Museum (Natural History), London, United Kingdom.

Estes, R. D. 1991. The behavior guide to African mammals: including hoofed mammals, carnivores, primates. University of California Press, Berkeley.

Ewer, R. F. 1956. The fossil carnivores of the Transvaal caves: Canidae. Proceedings of the Zoological Society of London 126: 97–119.

Ewer, R. F. 1973. The carnivores. Cornell University Press, Ithaca, New York.

Fairall, N. 1968. The reproductive seasons of some mammals in the Kruger National Park. Zoologica Africana 3:189–210.

Ferguson, J. W. H. 1978. Social interactions of black-backed jackals *Canis mesomelas* in the Kalahari Gemsbok National Park. Koedoe 21:151–162.

Ferguson, J. W. H. 1986. Human factors affecting the efficiency and selectivity of the coyote-getter in jackal control. South African Journal of Wildlife Research 16:145–149.

Ferguson, J. W. H., J. S. Galpin, and M. J. De Wet. 1988. Factors affecting the activity patterns of black-backed jackals *Canis mesomelas*. Journal of Zoology (London) 214:55–69.

Ferguson, J. W. H., J. A. J. Nel, and M. J. De Wet. 1983. Social organization and movement patterns of black-backed jackals *Canis mesomelas* in South Africa. Journal of Zoology (London) 199:487–502.

Flower, M. S. S. 1931. Contributions to our knowledge of the duration of life in vertebrate animals. V. Mammals. Proceedings of the Zoological Society of London 1931:145–234.

Fuller, T. K., A. R. Biknevicius, P. W. Kat, B. Van Valkenburgh, and R. K. Wayne. 1989. The ecology of three sympatric jackal species in the Rift Valley of Kenya. African Journal of Ecology 27:313–323.

Ginsberg, J. R., and D. W. Macdonald. 1990. Foxes, wolves, jackals, and dogs. An action plan for the conservation of canids. IUCN/SSC Canid Specialist Group and Wolf Specialist Group, Gland, Switzerland.

Grafton, R. N. 1965. Food of the black-backed jackal: a preliminary report. Zoologica Africana 1:41–53.

Gray, J. E. 1868. Notes on the skulls of the species of dogs, wolves, and foxes (Canidae) in the collection of the British Museum. Proceedings of the Zoological Society of London 1868:492–525.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Ronald Press Company, New York.

Hall-Martin, A. J., and B. P. Botha. 1980. A note on feeding habits, ectoparasites and measurements of the black-backed jackal *Canis mesomelas* from ADDO Elephant National Park. Koedoe 23:157–162.

Hammond, J. A. 1972. On Athesmia (Trematoda: Dicrocoeliidae) from jackals in Tanzania. Journal of Helminthology 46:175–184.

Heard, H. W., and A. Stephenson. 1987. Electrification of a fence to control the movements of black-backed jackals. South African Journal of Wildlife Research 17:20–24.

Heller, E. 1914. New subspecies of mammals from equatorial Africa. Smithsonian Miscellaneous Collections 63:1–12.

Hemming, F. (ed.). 1956. Opinion 417. Opinions and declarations rendered by the International Commission on Zoological Nomenclature 14(1):1–42.

Hilzheimer, M. 1906. Die geographische Verbreitung der Afrikanischen Grauschakale. Zoologischer Beobachter 47:363–373.

Hirst, S. M. 1969. Predation as a regulating factor of wild ungulate populations in Transvaal Lowveld nature reserve. Zoologica Africana 4:199–230.

Hiscocks, K., and M. R. Perrin. 1987. Feeding observations and diet of black-backed jackals in an arid coastal environment. South African Journal of Wildlife Research 17:55–58.

Hiscocks, K., and M. R. Perrin. 1988. Home range and movements of black-backed jackals at Cape Cross Seal Reserve, Namibia. South African Journal of Wildlife Research 18:97–100.

Horak, I. G., A. J. Guillarmod, L. C. Moolman, and V. De Vos. 1987. Parasites of domestic and wild animals in South Africa. XXII. Ixodid ticks on domestic dogs and on wild carnivores. Onderstepoort Journal of Veterinary Research 54:573–580.

Iori, A., and P. Lanfranchi. 1996. Contribution to the knowledge of helminthofauna of wild mammals of Somalia. Parassitologia 38:511–515.

Keep, M. E. 1970. Sarcoptic mange in the black-backed jackal *Canis mesomelas*. Lammergeyer 12:72.

Kingdon, J. 1997. The Kingdon field guide to African mammals. Academic Press, San Diego, California.

Kleiman, D. G. 1967. Some aspects of social behavior in the Canidae. American Zoologist 7:365–372.

Klein, R. G. 1986. Carnivore size and quaternary climatic change in southern Africa. Quaternary Research 26:153–170.

Kok, O. B. 1996. Dieetsamestelling van enkele karnivoorsoorte in die Vrystaat, Suid-Afrika. South African Journal of Science 92:393–398.

Lamprecht, J. 1978. On diet, foraging behaviour and interspecific food competition of jackals in the Serengeti National Park, East Africa. Zeitschrift für Säugetierkunde 43:210–223.

Last, R. D., J. E. Jardine, M. M. E. Smit, and J. J. Van Der Lugt. 1994. Application of immunoperoxidase techniques to formalin-fixed brain tissue for the diagnosis of rabies in southern Africa. Onderstepoort Journal of Veterinary Research 61: 183–187.

Lawson, D. 1989. The effects of predators on sheep farming in

Natal: an opinion survey. South African Journal of Wildlife Research 19:4–10.

LINDEQUE, P. M., AND P. C. B. TURNBULL. 1994. Ecology and epidemiology of anthrax in the Etosha National Park, Namibia. Onderstepoort Journal of Veterinary Research 61:71–83.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Stockholm, 1:1–824.

LOMBAARD, L. J. 1971. Age determination and growth curves in the black-backed jackal, *Canis mesomelas* Schreber, 1775 (Carnivora: Canidae). Annals of the Transvaal Museum 27: 135–181.

LOVERIDGE, A. J., AND D. W. MACDONALD. 2001. Seasonality in spatial organization and dispersal of sympatric jackals (*Canis mesomelas* and *C. adustus*): implications for rabies management. Journal of Zoology (London) 253:101–111.

MACCHIONI, G. 1995. Ancylostoma Genettae, A. Protelesis, A. Somaliense: three new species from wild Carnivora in the Somali Republic. Parassitologia 37:219–228.

MACPHERSON, C. N. L., L. KARSTAD, P. STEVENSON, AND J. H. ARUNDEL. 1983. Hydatid disease in the Turkana District of Kenya. III. The significance of wild animals in the transmission of *Echinococcus granulosus*, with particular reference to Turkana and Masailand in Kenya. Annals of Tropical Medicine and Parasitology 77:61–73.

MCKENZIE, A. A. 1993. Biology of the black-backed jackal *Canis mesomelas* with reference to rabies. Onderstepoort Journal of Veterinary Research 60:367–371.

MCKENZIE, A. A. 1997. Black-backed jackal *Canis mesomelas*. Pp. 198–199 in The complete book of southern African mammals (G. Mills and L. Hes, eds.). Struik Winchester, Cape Town, South Africa.

MEESTER, J. A. J., I. L. RAUTENBACH, N. J. DIPPENAAR, AND C. M. BAKER. 1986. Classification of southern African mammals. Transvaal Museum Monograph 5:1–359.

MOEHLMAN, P. D. 1979. Jackal helpers and pup survival. Nature 277:382–383.

MOEHLMAN, P. D. 1981. Why do jackals help their parents? Reply to Montgomerie. Nature 289:824–825.

MOEHLMAN, P. D. 1983. Socioecology of silverbacked and golden jackals (*Canis mesomelas* and *Canis aureus*). Pp. 423–453 in Advances in the study of mammalian behavior (J. F. Eisenberg and D. G. Kleiman, eds.). Special Publication, American Society of Mammalogists 7:1–753.

MOEHLMAN, P. D. 1987. Social organization in jackals. American Scientist 75:366–375.

MONTGOMERIE, R. D. 1981. Why do jackals help their parents? Nature 289:824–825.

NEL, J. A. J. 1984. Behavioural ecology of canids in the southwestern Kalahari. Koedoe Supplement 27:229–235.

NEL, J. A. J., A. J., R. LOUTIT, J. DU P. BOTHMA. 1997. Prey use by black-backed jackals along a desert coast. South African Journal of Wildlife Research 27:100–104.

NEWMARK, W. D., J. I. BOSHE, H. I. SARIKO, AND G. K. MAKUMBULE. 1996. Effects of a highway on large mammals in Mikumi National Park, Tanzania. African Journal of Ecology 34: 15–31.

NOACK, T. 1897. Ostafrikanische Schakale. Zoologischer Anzeiger 20:517–521.

NOWAK, R. M. 1999. Walker's mammals of the world. Sixth edition. John Hopkins University Press, Baltimore, Maryland 2: 1–836.

OKEN, L. 1815–1816. Lehrbuch der Naturgeschichte. Zoologie. August Schmid und Comp., Jena, Germany 3:1–1270.

OOSTHUIZEN, W. H., ET AL. 1997. Variation in jackal numbers at the Van Reenen Bay seal colony with comment on likely importance of jackals as predators. South African Journal of Wildlife Research 27:26–29.

PIENAAR, U. DE V. 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. Koedoe 12:108–176.

PRICE, J. E., AND L. H. KARSTAD. 1980. Free-living jackals (*Canis mesomelas*)—potential reservoir hosts for *Ehrlichia canis* in Kenya. Journal of Wildlife Diseases 16:469–473.

RAUTENBACH, I. L. 1982. Mammals of the Transvaal. Ecoplan Monograph, Pretoria, South Africa 1:1–211.

RHODES, C. J., R. P. D. ATKINSON, R. M. ANDERSON, AND D. W. MACDONALD. 1998. Rabies in Zimbabwe: reservoir dogs and the implications for disease control. Philosophical Transactions of the Royal Society of London, Biological Sciences 353: 999–1010.

ROBERTS, A. 1954. The mammals of South Africa. Second edition. Central News Agency, Johannesburg, South Africa.

ROBERTS, D. H. 1986. Determination of predators responsible for killing small livestock. South African Journal of Wildlife Research 16:150–152.

ROUND, M. C. 1968. Checklist of the helminth parasites of African mammals of the orders Carnivora, Tubulidentata, Proboscidea, Hyracoidea, Artiodactyla, and Perissodactyla. Commonwealth Agricultural Bureaux, Bucks, United Kingdom.

ROWE-ROWE, D. T. 1975. Predation by black-backed jackals in a sheep-farming region of Natal. Journal of the Southern African Wildlife Management Association 5:79–81.

ROWE-ROWE, D. T. 1976. Food of the black-backed jackal in nature conservation and farming areas in Natal. East African Wildlife Journal 14:345–348.

ROWE-ROWE, D. T. 1978. The small carnivores of Natal. Lammergeyer 25:1–48.

ROWE-ROWE, D. T. 1982. Home range and movements of black-backed jackals in an African montane region. South African Journal of Wildlife Research 12:79–84.

ROWE-ROWE, D. T. 1983. Black-backed jackal diet in relation to food availability in the Natal Drakensberg. South African Journal of Wildlife Research 13:17–23.

ROWE-ROWE, D. T. 1984. Black-backed jackal population structure in the Natal Drakensberg. Lammergeyer 32:1–7.

ROWE-ROWE, D. T. 1986. The black-backed jackal: know your problem animal. Wildlife Management Technical Guides for Farmers 15:1–2.

ROWE-ROWE, D. T. 1992. The carnivores of Natal. Natal Parks Board, Pietermaritzburg, South Africa.

ROWE-ROWE, D. T., AND B. GREEN. 1980. Ketamine and acetylpromazine for black-backed jackal immobilization. South African Journal of Wildlife Research 10:153.

ROWE-ROWE, D. T., AND B. GREEN. 1981. Steel-jawed traps for live capture of black-backed jackals. South African Journal of Wildlife Research 11:63–65.

SAVAGE, R. J. G. 1978. Carnivora. Pp. 249–267 in Evolution of African mammals (V. J. Maglio and H. B. S. Cooke, eds.). Harvard University Press, Cambridge, Massachusetts.

SCHALLER, G. B. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press, Illinois.

SCHREBER, J. C. D. 1775. Die Säugthiere in Abbildungen nach der Natur, mit Beschreibungen. Wolfgang Walther, Erlangen, Germany.

SHELDON, J. W. 1992. Wild dogs. The natural history of the nondomestic Canidae. Academic Press, San Diego, California.

SHEPPY, K., AND R. T. F. BERNARD. 1984. Relative brain size in the mammalian carnivores of the Cape Province of South Africa. South African Journal of Zoology 19:305–308.

SHORTRIDGE, G. C. 1934. The mammals of South West Africa. William Heinemann Ltd., London, United Kingdom.

SKEAD, D. M. 1973. Incidence of calling in the black-backed jackal. Journal of the Southern African Wildlife Management Association 3:28–29.

SKINNER, J. D., AND R. H. N. SMITHERS. 1990. The mammals of the southern African subregion. University of Pretoria, South Africa.

SMITH, A. 1833–1834. An epitome of African zoology; or, a concise description of the objects of the animal kingdom inhabiting Africa, its islands and seas. South African Quarterly Journal 2:16–32, 49–64, 81–96, 113–128, 145–160, 169–192, 209–224, 233–248.

SMITHERS, R. H. N. 1966. The mammals of Rhodesia, Zambia and Malawi. Collins Clear-Type Press, London, United Kingdom.

SMITHERS, R. H. N. 1971. The mammals of Botswana. Mardon Printers (Pvt.) Ltd., Salisbury, Rhodesia.

SMITHERS, R. H. N. 1983. The mammals of the southern African subregion. University of Pretoria, South Africa.

SPENCER, J. A., J. BINGHAM, R. HEATH, AND B. RICHARDS. 1999. Presence of antibodies to canine distemper virus, canine parvovirus and canine adenovirus type 1 in free-ranging jackals

(*Canis adustus* and *Canis mesomelas*) in Zimbabwe. Onderstepoort Journal of Veterinary Research 66:251–253.

STAINS, H. J. 1975. Distribution and taxonomy of the Canidae. Pp. 3–26 in The wild canids: their systematics, behavioral ecology and evolution (M. W. Fox, ed.). Robert E. Kreiger Publishing Company, Inc., Malabar, Florida.

STUART, C. T. 1976. Diet of the black backed jackal (*Canis mesomelas*) in the central Namib desert, south west Africa. Zoologica Africana 11:193–205.

STUART, C. T. 1981. Notes on the mammalian carnivores of the Cape Province, South Africa. Bontebok 1:1–58.

STUART, C. T., AND P. D. SHAUGHNESSY. 1984. Content of *Hyaena brunnea* and *Canis mesomelas* scats from southern coastal Namibia. Mammalia 48:611–612.

SWANEPOEL, R., ET AL. 1993. Rabies in southern Africa. Onderstepoort Journal of Veterinary Research 60:325–246.

THOMAS, O. 1926. On mammals from Ovamboland and the Cunene River obtained during Capt. Shortridge's third Percy Sladen and Kaffrarian Museum Expedition into South-West Africa. Proceedings of the Zoological Society of London 1: 285–312.

THOMSON, G. R. 1999. Alternatives for controlling animal diseases resulting from interactions between livestock and wildlife in southern Africa. South African Journal of Science 95: 71–76.

VAN DEN BRINK, F.-H. 1973. Distribution and speciation of some carnivores. Mammal Review 3:85–95.

VAN DER MERWE, N. J. 1953a. The jackal. Fauna and Flora 4: 1–83.

VAN DER MERWE, N. J. 1953b. The coyote and the black-backed jackal. A comparison of certain similar characteristics. Fauna and Flora 3:44–51.

VAN HEERDEN, J. 1979. Transmission of canine ehrlichiosis to the wild dog *Lycaon pictus* (Temminck) and black-backed jackal *Canis mesomelas* (Schreber). Journal of the South African Veterinary Association 50:245–248.

VAN HEERDEN, J. 1980. The transmission of *Babesia canis* to the wild dog *Lycaon pictus* (Temminck) and black-backed jackal *Canis mesomelas* (Schreber). Journal of the South African Veterinary Association 51:119–120.

VAN HENSBERGEN, H. J., M. P. S. BERRY, AND J. JURITZ. 1996. Helicopter-based line-transect estimates of some southern African game populations. South African Journal of Wildlife Research 26:81–87.

VAN LAWICK, H., AND J. VAN LAWICK-GOODALL. 1970. Innocent killers. Houghton Mifflin, Boston, Massachusetts.

VAN VALKENBURGH, B. V. 1989. Carnivore dental adaptations and diet: a study of trophic diversity within guilds. Pp. 410–434 in Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York.

VAN VALKENBURGH, B., AND R. K. WAYNE. 1994. Shape divergence associated with size convergence in sympatric East African jackals. Ecology 75:1567–1581.

VILÀ, C., J. E. MALDONADO, AND R. K. WAYNE. 1999. Phylogenetic relationships, evolution, and genetic diversity of the domestic dog. Journal of Heredity 90:71–77.

WALLACE, C. 1977. Chromsome analysis in the Kruger National Park—the chromosomes of the saddle-backed jackal (*Canis mesomelas*). Koedoe 20:193–195.

WAYNE, R. K. 1993. Molecular evolution of the dog family. Trends in Genetics 9:218–224.

WAYNE, R. K., E. GEFFEN, D. J. GIRMAN, K. P. KOEPFLI, L. M. LAU, AND C. R. MARSHALL. 1997. Molecular systematics of the Canidae. Systematic Biology 46:622–653.

WAYNE, R. K., B. VAN VALKENBURGH, P. W. KAT, T. K. FULLER, W. E. JOHNSON, AND S. J. O'BRIEN. 1989. Genetic and morphologic divergence among sympatric canids. Journal of Heredity 80:447–454.

WAYNE, R. K., ET AL. 1990. Large sequence divergence among mitochondrial DNA genotypes within populations of eastern African black-backed jackals. Proceedings of the National Academy of Sciences 87:1772–1776.

WESEMEIER, H. H., K. ODENING, G. WALTER, AND I. BOCKHARDT. 1995. The black-backed jackal (Carnivora: Canidae) in Namibia as intermediate host of two Sarcocytis species (Protozoa: Sarcocystidae). Parasite 2:391–394.

WILSON, P. J., ET AL. 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. Canadian Journal of Zoology 78:2156–2166.

WOZENCRAFT, W. C. 1993. Order Carnivora: Canidae. Pp. 279–282 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C.

WYMAN, J. 1967. The jackals of the Serengeti. Animals 10:79–83.

ZUCKERMAN, S. 1953. The breeding seasons of mammals in captivity. Proceedings of the Zoological Society of London 122: 827–950.

Associate editors of this account were ELAINE ANDERSON and SERGE LARIVIÈRE. Editor was VIRGINIA HAYSSEN.

LYLE R. WALTON, DEPARTMENT OF BIOLOGY, UNIVERSITY OF SASKATCHEWAN, 112 SCIENCE PLACE, SASKATOON, SASKATCHEWAN S7N 5E2, CANADA. Present address: WILDLIFE RESEARCH AND DEVELOPMENT SECTION, ONTARIO MINISTRY OF NATURAL RESOURCES, HIGHWAY 101 EAST, POSTAL BAG 3020, SOUTH PORCUPINE, ONTARIO P0N 1H0, CANADA. DAMIEN O. JOLY, DEPARTMENT OF BIOLOGY, UNIVERSITY OF SASKATCHEWAN, 112 SCIENCE PLACE, SASKATOON, SASKATCHEWAN S7N 5E2, CANADA. Present address: USGS NATIONAL WILDLIFE HEALTH CENTER, 6006 SCHROEDER ROAD, MADISON, WISCONSIN 53711.