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Dasyurus viverrinus.

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Dasyurus viverrinus Shaw, 1800

Eastern Quoll

Didelphis maculata Anon, 1791:186. Type locality "neighbourhood of Port Jackson, N.S.W." (= New South Wales, Australia). Suppressed by International Commission on Zoological Nomenclature (1985).

Dasyurus viverrinus Shaw, 1800:491. Type locality "from Sydney region, N.S.W."

Dasyurus maugei Geoffroy, 1803:259. Type locality unknown (the discoverer, René Maugé, died in 1802 after visiting only southern Tasmania).

Dasyurus guttatus Desmarest, 1804:10. Type locality "from Australia (as Nouvelle-Hollande)."

Didelphis alboguttata Burmeister, 1854:340. Type locality "from Australia."

CONTEXT AND CONTENT. Order Dasyuromorphia, family Dasyuridae, subfamily Dasyurinae. *D. viverrinus* is monotypic.

DIAGNOSIS. *Dasyurus* are medium-sized marsupial carnivores distinguished from other Dasyurids by white spots on the pelage. *D. viverrinus* is distinguished from other *Dasyurus* by absence of a hallux on the hind foot.

GENERAL CHARACTERS. A medium-sized quoll, *D. viverrinus* has short legs and a tail 66% the length of head and body (Fig. 1). Eastern quolls have a finely tapered head and snout and thick neck. Ears are erect, of medium length with rounded tips, and are naked internally and covered externally with sparse, fine hair 2 mm long (Green 1967). Front feet have 5 toes and hind feet have 4. Foot pads are pink and lack ridges.

Body fur (mean length ca. 20 mm, guard hairs to 35 mm) is soft and dense, contrasting with coarser, longer (40–80 mm) tail fur and short (mean ca. 5 mm) fur on feet (Green 1967). Eastern quolls are either fawn color with pure white fur extending from under chin to front and hind feet and underside of tail, including the underbelly, or jet black except where grading to brownish on venter and underside of tail. Basal 75% of fur is slate gray in both color morphs. Hair tips are black in the black morph but either pure white or sandy yellow, tipped with black, in the fawn morph. Guard hairs are black. Fawn-colored individuals are most common throughout present and former range of the eastern quoll, comprising about 75% of the population. Both color morphs occur in the same litter. On either color morph, 60–80 irregularly shaped white spots, 5 to 20 mm in diameter, cover dorsal surface of the body, extending from top of head and cheeks to rump and to top of legs, but excluding tail. Vibrissae are black in black individuals and black, brown, or white in fawn individuals. Mystacial and genal vibrissae reach to 60 mm, with up to 25 and 8 in each set, respectively. Interramal vibrissae are up to 30 mm in length and supraorbital to 45 mm; each set contains 4 vibrissae (Green 1967).

Sexual size dimorphism is pronounced in eastern quolls. Adult male *D. viverrinus* in Tasmania are up to 1.5 times the mass of females and have stronger canines for their body size (Jones 1995, 1997). Average body mass is 1.1 kg for males and 0.7 or 0.8 kg for females (Green 1967; Jones 1995), although weights up to 1.9 kg for males and 1.1 kg for females are known (Bryant 1988a). Average and ranges of external measurements (in mm) of male and female *D. viverrinus*, respectively ($n = 21, 9$), from Tasmania are: total length, 568.8 (525–655), 535.2 (475–580); length of tail, 240.9 (200–280), 220.8 (173–240); length of hind foot, 69.4 (61–75), 64.1 (60–68); length of head, 92.5 (87–103), 83.9 (76–90); length of ear, 52.0 (49–57), 49.5 (46–51—Green 1967).

Skull is slightly rounded in profile with a broad tapering rostrum, so that it appears pear-shaped when viewed from above (Fig. 2). Rostrum is broader between lachrymal canals (mean 27.9 mm) than all other quolls except *D. maculatus* (Van Dyck 1987). Postorbital constriction is narrow, but not as extreme as in *D. maculatus.* Temporal fossae as well as sagittal and nuchal crests are enlarged. Jugals, but not frontals, have distinct postorbital processes. Palatine is fenestrated with 2 large and a number of fine holes. Jaw is not heavy. A ridge of bone between the mandibular condyle and dentary forms a shelf along ventral edge of masseteric fossa. Dental formula is i 4/3, c 1/1, p 2/2, m 4/4, total 42.

Average (and ranges) of cranial measurements (in mm) for male and female *D. viverrinus,* respectively ($n = 10$ of each sex), in Tasmania are: greatest length of skull, 81.9 (73.0–90.0), 74.1 (69.6–78.5); cranial breadth, 30.7 (26.5–33.3), 28.0 (26.6–29.5); zygomatic breadth, 47.1 (42.7–52.8), 42.0 (39.4–46.0); length of maxillary toothrow, 28.6, 26.9; length of molariform teeth in mandibular toothrow, 30.4; 28.1; maximal anterior–posterior diameter of upper canine, 3.9, 3.2 (further measurements in Green 1967; Jones 1995). Average cranial measurements for now extirpated male and female *D. viverrinus,* respectively ($n = 24, 18$), from Victoria and New South Wales are: greatest length of skull, 69.3, 63.7; maximal anterior–posterior diameter of upper canine, 3.2, 2.6 (Jones 1997). Male and female *D. viverrinus* from Tasmania are significantly larger and more dimorphic in the maximal anterior–posterior diameter of an upper canine than those from Victoria and New South Wales (Jones 1997).

DISTRIBUTION. Once distributed in a broad band around southeastern mainland Australia, from eastern South Australia to the central coast of New South Wales (Godsell 1995; Fig. 3), the eastern quoll disappeared from its mainland range during the 20th Century. It disappeared first in South Australia, but persisted in western Victoria (ca. 1940) and in Melbourne (ca. 1946). The last known mainland population, from Nielson Park in the Sydney suburb of Vaucluse, disappeared as a result of combined effects of clearance of bush, a bushfire, and drought around 1964 (Nelson 1968; Troughton 1967).

The eastern quoll is now restricted to the island state of Tasmania where it occurs from sea level to 1,500 m, but is more common in the drier, eastern half of the state (Jones and Rose 1996; Rounsevell et al. 1991). It is absent from offshore islands except Bruny Island (where it may have been introduced—Maxwell et al. 1996).

FOSSIL RECORD. *Dasyurus viverrinus* occurs in many Pleistocene cave faunas of eastern and southern Australia, including regions that are now too arid for its survival (Archer et al. 1984; Morton et al. 1989). These include local faunas in Victoria Cave in southeastern South Australia, Pyramid's Cave in eastern Victoria, and both Russenden Cave and Eastern Darling Downs in south-

FIG. 1. *Dasyurus viverrinus* from Tasmania; fawn color morph, adult male. Photograph courtesy of Dave Watts.

FIG. 2. Dorsal (#1964/1/195), ventral (#1964/1/155), and lateral (#1964/1/183) views of cranium and lateral (#1964/1/183) view of mandible of *Dasyurus viverrinus* (Queen Victoria Museum and Art Gallery, Launceston, Tasmania). Photograph by John Leeming. Greatest length of skull (#1964/1/195) is 73.5 mm.

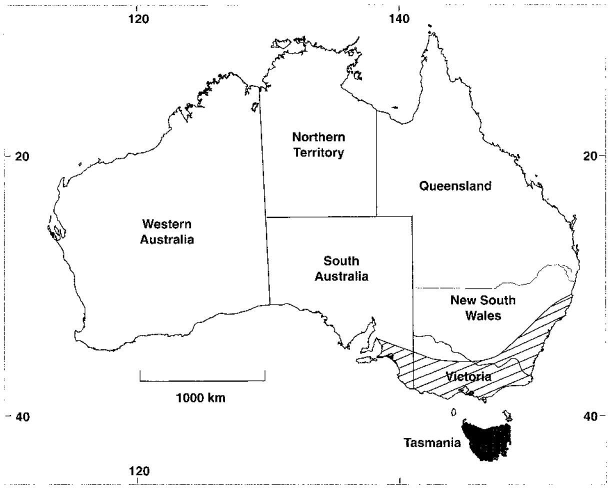

FIG. 3. Present (post-1966; black) and former (pre-1966; hatched) distribution of *Dasyurus viverrinus* in Australia (Godsell 1995).

eastern Queensland (Archer and Hand 1984; Archer et al. 1984; Wakefield 1967a, 1972).

Dasyurus viverrinus is well represented in Holocene sites. These include 8 sites in western Victoria (Fern Cave, Lower Glenelg; Natural Bridge, Mt. Eccles; Byaduk Caves; Mt. Hamilton; Bushfield; Tower Hill Beach; Swain's Cave, Mt. Porndon; and McEachern's Cave, Glenelg River), Pyramid's Cave in eastern Victoria, Flinders Island in Bass Strait (where it has never been recorded alive), and Nunamira and Bone Caves in southcentral Tasmania, where it was a minor prey species of aboriginal people (Cosgrove et al. 1990; Hope 1972; Wakefield, 1964, 1967a, 1967b, 1972).

FORM AND FUNCTION. Adult *D. viverrinus* undergoes partial molt during July–August, when in poor condition (Bryant 1988a); but complete molt is not recorded. Reflecting a carnivorous diet, incisor row is transverse and canines are large. Upper incisors are compressed laterally, degree of compression decreasing from I4 to I2 (Archer 1976); canines are ovoid in cross-section (Jones, in press; Jones and Stoddart 1998) and the 2 uncrowded premolars are slightly rounded. Slightly bulbous molar teeth of *D. viverrinus,* intermediate between the smallest, more insectivorous quolls and the carnivorous *D. maculatus,* have several features in common with *D. maculates:* paracone is reduced relative to increased metacone in upper molars with reverse in lower molars; slight longitudinal orientation of metacrista increasing meat-shearing ability; talonid in lower molars reduced (Archer 1976); relative length of metacrista is greater in *D. viverrinus* than in smaller, more insectivorous quolls (Jones 1995). Canine teeth overerupt during the animal's life. Wear and tear of the tooth can be used to judge the age of individuals. Rates of tooth fracture are equivalent to those of smaller species of quolls and lower than those of *D. maculatus* and Tasmanian devils (*Sarcophilus laniarius*—Werdelin 1987). Canine teeth break more frequently than other teeth (Jones 1995; Jones and Stoddart 1998).

Eastern quolls have short metatarsals compared with rest of limb (Jones 1995). Foot pads are not ridged in *D. viverrinus* (Jones 1995). *D. viverrinus* has a nictitans gland but no Harderian gland associated with the nictitating membrane (Sakai and van Lennep 1984).

Penis of *D. viverrinus* (and of all *Dasyurus*) species has a fleshy appendage (Woolley and Webb 1977). No baculum is present. Penis lies against ventral wall of cloaca when flaccid but when erect is everted, with a curved base, to stand parallel to ventral surface.

Eastern quolls have testes with relatively few, large seminiferous tubules that produce few but large sperm (Bedford et al. 1984; Setchell 1977; Woolley 1975). Luminal surface of epithelium is lined with stereocilia (Harding et al. 1982). Accessory glands of males comprise 3 pairs of Cowper's glands and 1 elongated tripartite prostate gland; each part performs a function similar to separate eutherian glands (Tyndale-Biscoe and Renfree 1987). Glands fluctuate in size throughout the year, reaching maximal weights before the breeding season (Fletcher 1985). Scrotal skin is thin and sparsely covered with finer hair than elsewhere.

In gross morphology and ultrastructure, sperm of *D. viverrinus* are indistinguishable from those of *S. laniarius.* Long axis of sperm head of mature sperm, in the proximal third of the epididymis, is supported at a 60–90° angle to axis of tail by a conical cytoplasmic droplet (Fletcher 1977, 1985; Hughes 1982; Woolley 1975). A helical fiber network develops in the midpiece during epididymal transit (Harding et al. 1977).

Body weight, scrotal width, luteinizing hormone, and testosterone levels fluctuate seasonally. In Tasmania, adult males increase in body weight from 1.1 to 1.48 kg during December–March but lose 16–31% of total body weight during May–June (midwinter) during the mating period, which is when luteinizing hormone and testosterone levels are reaching their peaks (Bryant 1986, 1992; Godsell 1983). Scrotal size is maximal during April–May, then decreases by an average of 10.3 mm or 49% in width and 6.7 mm or 38% in height between May and November. Spermatogenesis commences well in advance of mating (Fletcher 1977), but regression of the reproductive system is evident by the time of mating, and by September testes have regressed and sperm production has ceased (Bryant 1988a).

Female *D. viverrinus* have sperm storage crypts throughout the oviductal isthmus (Bedford et al. 1984). Placenta of *D. viver-*

rinus differs from that of most marsupials; although the allantois becomes apposed to the chorion, it degenerates and comes to lie as a vestigial structure in the extraembryonic coelom and does not become part of the placenta (Hill 1900). Development of mammary glands begins during the first half of pregnancy.

Females have 6–8 teats in a shallow pouch formed by enlargement of lateral folds. Pouch is lined with sparse hair 25–30 mm long (Green 1967). Teat number varies geographically, with 6 in Tasmania (Bryant 1988a; Godsell 1983), and 6 or 8 in Victoria (Fleay 1935; Hill and O'Donoghue 1913). Each teat has 6 ducts (galactophores). Pouch changes in depth and glandulosa during the breeding season (Bryant 1988a). Only mammary glands to which young initially attach, enlarge and lactate; the others regress quickly. Teats associated with active glands grow during lactation as young grow, enlarging from 2–3 to 10 mm (O'Donoghue 1911). Number of enlarged teats and number of young in nests are correlated (Godsell 1983). Pouches and mammary glands regress after December, but suckled teats remain elongated and protrude from the contracted pouch entrance. By February, the parous pouch is shallow with little obvious mammary development (Bryant 1988a). Adult females gain 12% in weight during January–May; lose weight during the mating period, averaging 721 g ± 90 *SE* when young are born; and do not increase in weight until young are deposited in dens around August (Bryant 1988a). These are small fluctuations compared to males.

In addition to ductus arteriosus and interatrial communication in the heart, *D. viverrinus* has a large interventricular communication and incomplete septation of the outflow tract (Runciman et al. 1995). A detailed description of dorsal thalamus and thalamic projections to parietofrontal neocortex of the brain is available (Haight and Neylon 1981a, 1981b). *D. viverrinus* has a simple and relatively short alimentary canal, without a cecum (Hill and Rewell 1955). The hindgut, which is undivided into colon and rectum, is also relatively short and simple (Mitchell 1905). Pungent and dark brown scats, 30–50 mm long, have a diagnostic overlain curl at 1 end and are a straight cylinder if packed with insect remains or twisted if containing fur (Triggs 1996).

Basal metabolic rate of *D. viverrinus* (2.46 $M^{-0.75}$—MacMillen and Nelson 1969) is slightly higher than mean value (2.33 $M^{-0.75}$) of marsupials (Dawson and Hulbert 1970). Digestible energy required for maintenance is 545 kJ $kg^{-0.75}$ day^{-1}, or 6.30 $W/kg^{-0.75}$, or about 2.5 times the calculated basal metabolic rate. Daily water turnover is 128 ml $W^{0.82}$ ± 11 *SD* and only 5% of water influx of captive *D. viverrinus* is derived from drinking water (Green and Eberhard 1979).

Eastern quolls do not routinely enter torpor and have a daily rhythm of body temperature (amplitude 1.1°C), with temperatures rising each evening, early in the activity period, remaining high during the night, and then declining while resting in the den (Jones et al. 1997). Body temperatures of 3 free-ranging males averaged 36.5°C, but ranged from 33.5 to 38.6°C (Jones et al. 1997), similar to the 36.7°C obtained for 2 captive adult females at 30°C (MacMillen and Nelson 1969). Body temperature increases at running speeds of 3–4 km^{-1}, but in contrast to eutherians, *D. viverrinus* stores 33% of the heat and later dissipates >50% by means of evaporation (Baudinette 1982).

Normal ranges of hematological values, red cell enzymes, and metabolic intermediates for *D. viverrinus* are available (Melrose et al. 1987, 1990; Parsons et al. 1971). Eastern quolls have high concentrations of hemoglobin (17 ± 1 g/100 ml^{-2}), high hematocrits (0.48 ± 0.3 g), and low hemoglobin oxygen affinity (Hallam et al. 1995). They have higher levels of phosphofructokinase, glyceraldehyde dehydrogenase, and phosphoglycerate kinase and lower levels of enolase and 2,3-diphosphoglycerate than other marsupials (Melrose et al. 1990).

Adrenal function and blood hormone levels indicate that eastern quolls do not experience major stress during the breeding season. However, red cell disorders, seasonal weight loss, and perhaps high free cortisol and testosterone levels may act synergistically to lower autoimmune response and thus to increase susceptibility to parasitic infection or disease. Such factors may contribute to increased mortality of adults after the breeding season (Bryant 1988a).

Cortisol is the major corticosteroid (McDonald 1977), comprising 85–87% of total peripheral plasma corticosteroid (Godsell 1983). Male *D. viverrinus* had peripheral plasma cortisol concentrations of 3.2–5.6 μg/100 ml, compared with 7.0 μg/100 ml in females (Weiss and Richards 1971). Adrenocorticotropic hormone appears to be the prime regulator of glucocorticoid production in eastern quolls (Weiss and Richards 1971).

Increased free cortisol in males is not associated with a decrease in plasma corticosteroid-binding globulin, and cortisol and testosterone levels are not highly correlated (Bryant 1988a). Testosterone secretion in males is controlled by luteinizing hormone, secretions of both occurring episodically rather than in pulses (Bryant 1992). Sex-hormone–binding globulin is not present; testosterone is bound to albumin with high capacity and low affinity (Bradley 1982). Thus, during the breeding season, body tissues are exposed to high concentrations of free steroids, leading to increased aggressive behavior (Lee and Cockburn 1985; Lee et al. 1977).

In females, luteinizing hormone concentrations increase progressively in April and May to reach highest levels in June, then drop in July before returning to baseline levels for the rest of the year (Bryant 1988a). Progesterone levels show a similar pattern in females of all ages. Both luteinizing hormone and progesterone levels were highest at the time of mating in some females. By contrast, prolactin levels of yearling and older females increase throughout lactation and decline during late lactation and weaning (Bryant 1988a).

Dasyurus viverrinus is relatively tolerant to the poison compound 1080 (sodium monofluoroacetate): 4 times more tolerant than the ferret (*Mustela putorius*) and 9 times more tolerant than the feral cat, *Felis catus* (McIlroy 1981).

ONTOGENY AND REPRODUCTION. Eastern quolls are facultatively monestrous, breeding synchronously each winter but are able to return to estrus if they fail to conceive or lose a litter early in the season (Fletcher 1985; Lee and Cockburn 1985). *D. viverrinus* has a promiscuous mating system. Breeding occurs in winter, with most births between May and July, depending on location (Bryant 1988a; Godsell 1982a; Green 1967; Green and Eberhard 1983). In Tasmania, most young become independent around November (spring), when food abundance is high (Godsell 1983).

Proestrus lasts 4–10 days and is recognized by increasing moistness of pouch region and swelling of vulva, both of which reach maximum development at estrus which lasts 1, rarely up to 3 days (Hill and O'Donoghue 1913; Sandes 1903). During follicular growth, oocytes remain in prophase of the first maturation division, the completion of the same (and accompanying extrusion of first polar body) has been described by Hill (1910) and Hill and O'Donoghue (1913). Live spermatozoa can be found in oviducts for up to 14 days after coitus (Hill and O'Donoghue 1913).

Estrous cycle is 37 days (Fletcher 1985). Ovulation is spontaneous and occurs 4–7 days after estrus (Hill 1910; Hill and O'Donoghue 1913). Ca. 3 days after ovulation, the ruptured follicle becomes the corpus luteum, producing high concentrations of progesterone from days 13 to 19, when blastocyst expansion occurs and embryogenesis proceeds to full term (Tyndale-Biscoe and Renfree 1987). Progesterone remains at elevated levels until 8 h before parturition, when it falls rapidly to basal levels (Tyndale-Biscoe and Renfree 1987). Luteal phase comprises 60% of the estrous cycle and is followed by a follicular phase leading to next estrus and ovulation. Pregnancy is accommodated within the luteal phase and parturition coincides with corpus luteum regression. If lactation follows, the subsequent follicular phase is suppressed, and the corpus luteum regresses into a corpus albicans (Tyndale-Biscoe and Renfree 1987). Growth and development of corpus luteum is the same in pregnant and nonpregnant female quolls (O'Donoghue 1912).

More eggs and embryos are produced than can be accommodated by 6 (or 8) teats (e.g., 35 females averaged 20 embryos—Hill and O'Donoghue 1913; O'Donoghue 1912). Comparatively large eggs of *D. viverrinus* are ca. 290 μm in diameter, and include 3 egg membranes: zona pellucida (ca. 1.6 μm), mucoid coat (15–22 μm), and shell membrane (2–8 μm—Selwood and Young 1983). All membranes remain intact while cleavages produce a 4.5–5.0-mm unilaminar blastocyst (bypassing the morula stage of development—Hill 1910). Next, the formative area of the embryo differentiates and endoderm cells appear, forming a 5–6-mm bilaminar blastocyst by ca. day 15. Development proceeds quickly during the last third of pregnancy, with parturition at 19–24 days (mean = 21.2—Fletcher 1977; Green and Eberhard 1983; Sandes 1903; Tyndale-Biscoe and Renfree 1987).

Young remain in the pouch permanently attached to teats for

60–65 days and continue development in a den until weaned at 150–165 days. They grow from crown-rump lengths of 4, 8, 10, 15–17, 18–19, 24–28, and 36–38 mm at 1, 3, 7, 21, 28, 42, and 56 days, respectively (Bryant 1988a; Hill and Hill 1955). Mean body weights increase from 12.5 mg at birth (Hill and O'Donoghue 1913) to 4.2, 21.5–21.9, 84.1–88.8 g at 45, 65, and 85 days, respectively. Sexual dimorphism becomes apparent at ca. 100 days. Weights of males and females average 202.8 and 181.9 g at 105 days, 465.8 and 379.2 g at 135 days, and 652.8 and 472.1 g at 155 days, respectively (Merchant et al. 1984). Scrotum is visible at 21 days; pigmentation and fur are visible at 51–59 days; eyes open at ca. 79 days; tooth eruption begins at ca. 90 days and is complete at ca. 177 days. From 85 days, when they are well furred, until they are independent, young forage at night with their mother, often clinging to her back but becoming increasingly coordinated and independent. They are capable of killing by 100 days and eat solid food at ca. 105 days. Young of both sexes are sexually mature and fully grown in their first year: ≤12 months (Bryant 1988a; Collins 1973; Godsell 1983; Merchant et al. 1984; Nelson and Smith 1971).

Significant changes in milk constituents and plasma prolactin concentrations occur when young vacate the pouch. Prolactin concentration initially increases 3–4-fold, but later progressively decreases as consumption of solid food increases (Green et al. 1987; Hinds and Merchant 1986). Mass-specific milk consumption rates, mass gain, and daily energy intake are intermediate to low for marsupials but the large number of young produced potentially places a high burden on the mother in late lactation (Green et al. 1997). Mortality at this stage is difficult to assess as survivors use vacant teats; teat regression results from earlier mortality (Green et al. 1997; Merchant et al. 1984).

Litter size in both wild and captive Tasmanian populations is usually 6 (Godsell 1983; Green 1967; Sandes 1903), although 8 was recorded in Victoria (Fleay 1932). Litter size decreases with age of female. Growth rates are comparable in litters of 2 and 6. Mortality in both sexes is low before weaning but high (40–80%) in first 6 months of independent life (Godsell 1983).

Life span of *D. viverrinus* is relatively short compared to placental carnivores of comparable size (Cockburn 1997; Godsell 1982a; Lee and Cockburn 1985). Although eastern quolls can live up to 7 years in captivity (average 2 years 4 months—Collins 1973; Mitchell 1911), longevity in the wild probably is 3–4 years (Bryant 1988a; Godsell 1982a, 1983). In any year, breeding females comprise ca. 66% yearlings and most of the rest are 2 year olds (Godsell 1983).

ECOLOGY. In Tasmania, the eastern quoll is found in most habitats (including grassland, sedgeland, heathland, alpine habitats, grassy woodland, dry [open] and wet [closed] eucalypt forests, and temperate rainforest), but it is more abundant in the drier eastern half and prefers open habitats, reaching its highest population densities on grasslands or where farmland is adjacent to eucalypt forest (Andrews 1968; Blackhall 1980; Driessen et al. 1991; Godsell 1982a, 1983; Hocking and Guiler 1983; Jones and Barmuta 2000; Jones and Rose 1996; Rounsevell et al. 1991; Taylor et al. 1985). Population densities in open eucalypt forest increase for 5–10 years after major fires (Driessen et al. 1991; Hocking and Guiler 1983). Lacking special adaptations for climbing, eastern quolls are mostly terrestrial (Jones 1995).

Eastern quolls eat a wide range of foods: mammals, birds, lizards and snakes, terrestrial crayfish, adult and larval insects, earthworms, grass, and fruit (Blackhall 1980; Godsell 1983; Green 1967; Jones 1995). Prey >1.5 kg are probably scavenged, although eastern quolls can kill large domestic hens (Troughton 1943). With no dental adaptations for bone crushing, only bones of small prey are eaten. In the wild, eastern quolls commonly scavenge on carcasses and they dart around feeding Tasmanian devils to find small pieces of flesh. Tasmanian devils may benefit eastern quolls by opening tough-skinned carcasses (Jones 1995). On farmland interspersed with forest, insect larvae are important in the diet all year, although species abundance change according to emergence time (Blackhall 1980; Godsell 1983). Insect larvae are primarily Coleoptera, such as *Aphodius* and *Paropsis* and Lepidoptera, including army worms (Noctuidae) and corbie grubs (Hepialidae: *Oncopera intricata, O. rufobrunnae*). In October and February, the southern army worm (*Persectania ewingi*) moves en masse at night across pastures and occurs in large quantities in eastern quoll scats (Godsell 1983). Fruits, especially blackberries, are eaten in summer (Blackhall 1980; Godsell 1983) and vegetation, mostly grass, is consumed year round in small quantities, even when grass-dwelling insects are scarce (Blackhall 1980; Godsell 1983; Jones 1995). In subalpine habitat (ca. 900 m), small mammals and birds comprise 50% of the diet, a higher proportion than that found at lower altitudes, the remainder comprising larger mammals (possums and macropods), reptiles, insects, and terrestrial crayfish. No insects are consumed in winter in alpine areas, but otherwise diets between seasons and sexes are similar (Jones and Barmuta 1998).

Eastern quoll populations fluctuate seasonally, reaching high densities in early summer (November–December) as the annual cohort of juveniles is weaned and declining to a minimum, largely because of juvenile mortality (although adult and juvenile mortality rates are similar), in August (Godsell 1982a, 1983). Female survival is high except in summer, when young are weaned and range more widely. Males range more widely during the winter mating season, after which mortality increases substantially. Sex ratio of pouch young is not different from unity, but that of trapped juveniles is 1:1.95 males : females. Sex ratio again approaches unity by 10 months after weaning. Population turnover is high (Godsell 1982a, 1983).

Significant dietary overlap between eastern quolls and female and subadult spotted-tailed quolls suggests that interspecific competition is an active force in communities of sympatric dasyurid carnivores in Tasmania (Jones 1995, 1997; Jones and Barmuta 2000). Competition with feral cats may also occur.

Eastern quolls, both adult and juvenile, are taken in small numbers by masked owls, *Tyto novaehollandiae* (Mooney 1993). Other potential predators in Tasmania include spotted-tailed quolls, Tasmanian devils, introduced cats, and humans (they may be dispatched by landowners). Both devil and eastern quoll scats have been found packed with eastern quoll fur (Blackhall 1980; Jones 1995). Wild eastern quolls show a greater degree of vigilance than do Tasmanian devils, consistent with a higher risk of predation (Jones 1998). Wild juvenile male Tasmanian eastern quolls, tested in a captive enclosure with vocalizations of predators, responded to masked owl, Tasmanian devil, and cat vocalizations by reducing activity (Smith 1999). Adult males responded to owl and Tasmanian devil calls by increasing vigilance. Introduced red fox (*Vulpes vulpes*) vocalizations elicited a response similar to controls suggesting that foxes were not perceived as a predation threat. Red foxes were a major factor in the extirpation of eastern quolls on mainland Australia but are absent in Tasmania (Smith 1999). Aboriginal people in Tasmania may have occasionally preyed on *D. viverrinus* (Cosgrove et al. 1990).

At least 21 species of endoparasites occur in eastern quolls, including 5 flukes (Trematoda), 5 tapeworms (Cestoda), and 11 nematodes (Nematoda—Obendorf 1993; Spratt 1991). Wombats, macropods, and possums are common intermediate hosts (Obendorf 1993). The high incidence of *Trichinella pseudospiralis,* a nematode probably endemic to Tasmania, is maintained through carrion feeding and cannibalism in eastern and spotted-tailed quolls and the Tasmanian devil (Obendorf et al. 1990). *Salmonella,* most commonly *S. mississippi,* is frequently found (70% of cases) in feces of Tasmanian dasyurid carnivores, including the eastern quoll (Obendorf 1993).

Known ectoparasites include 5 species of mites (Laelapidae), 3 ticks (Ixodidae), and 7 species of fleas (Siphonaptera—Green 1989; Green and Scarborough 1990). The larval stage of *Uropsylla tasmanica,* found in thylacines, Tasmanian devils, and eastern quolls in Tasmania, burrows into the skin, causing irritation and hair loss (Obendorf 1993; Pearse 1981).

Degenerative skeletal conditions, including hindlimb paralysis caused by prolapsed thoraco-lumbar intervertebral discs, are common in old, free-living eastern quolls (Obendorf 1993), as are broken canine teeth (Jones 1995). Degenerative lesions of the central nervous system, leading to paralysis and blindness, occur in aged captive individuals (Holz and Little 1995). Neoplasms, including multiple and carcinogenic, occur in wild and in aged captive individuals (Canfield and Cunningham 1993; Canfield et al. 1990; Twin and Pearse 1986). Eastern quolls have red blood cells with a structure and metabolism similar to pathologic red cells characteristic of human hemolytic disease (Melrose et al. 1987). Many diseases in captive animals can be traced to inappropriate diets or to extended life spans of captive individuals (Obendorf 1993).

Eastern quolls are maintained and bred in captivity. Several individuals of both sexes can be housed together, except in the breeding season when males fight and after parturition when females compete for dens. Overcrowding can cause stress, reducing male testosterone secretion, and interfering with dominance. A varied, balanced diet and a complex (preferably outdoor) enclosure that provides a variety of daytime secluded resting sites are important (Bryant 1988b). Eastern quolls climb and dig in captivity, so roofing and buried mesh are essential (Godsell 1982b).

BEHAVIOR. Eastern quolls are nocturnal, becoming active at or shortly after dark and remaining active for an average of 8 hours year round despite changing day length (Jones et al. 1997). Circadian rhythm is maintained in captivity on a 14L:10D cycle and in total dark, but becomes longer in constant light (Kennedy et al. 1990).

Dens are mostly in underground burrows (use of rabbit burrows is not recorded), but can be in natural rock piles or fallen trees, or in man-made structures, including buildings, rubbish tips, and bulldozed earth. Burrow entrances are often at the bases of rotting tree stumps or under bushes where soil is less compacted. Dens are mostly in forest adjacent to pasture, but are sometimes in open grassland (Godsell 1983; Jones 1995). Underground burrows range from simple tunnels (with no nests) to complex interconnecting tunnels with 1 or occasionally more nests. Both sexes use multiple dens, usually l–5 (but up to 12) and frequently change dens on successive days. Den use is related to proximity to feeding areas, except from July to October when females occupy only 1 den with their young. Den sharing is uncommon, apart from mother and young. Males generally avoid sharing dens, but related females sometimes do. In captivity, only females dig or construct dens, or use grass to line nest boxes (Godsell 1983).

Eastern quolls move with a bounding gait, usually across country. They climb logs and fallen branches but do not climb trees regularly (Jones and Barmuta 2000). Their light weight and splayed front feet enable them to move easily in snow (Jones et al. 1997).

Prey is stalked at a walk or a run, usually from rear or side when making use of cover (Eisenberg and Leyhausen 1972; Pellis and Nelson 1984). Prey is pinned with forepaws while bites are administered, initially to thorax or rear if prey is moving, with killing bites puncturing skull. A headshake that involves rotation in opposite direction to that of eutherian carnivores enhances penetration of the canines (Pellis and Nelson 1984). Using forepaws to manipulate prey, *D. viverrinus* sits on its hind legs and starts eating at the head (Eisenberg and Leyhausen 1972; Fleay 1932; Pellis and Nelson 1984). Absence of feeding holes indicates that invertebrate prey is caught on surface (Godsell 1983).

Eastern quolls are solitary, maintaining mean interindividual distances of >200 m when foraging. Avoidance behavior is mediated by visual, auditory, and perhaps olfactory cues. Associations are evident only among related females and mother and young. Eastern quolls are loosely collected into "neighborhoods" of (related or unrelated) individuals that use the same area (Godsell 1983).

Home ranges of *D. viverrinus* overlap extensively. Although each individual has a core area of intensive use that is avoided by neighboring residents, defense of exclusive territories is not evident. Females share their range with their litters. Mean home range of males (44 ha) is larger and varies more in size, in relation to body weight of individual males, than mean home ranges of females (35 ha). Home range size of males increases significantly in the May–June mating season. The slight November–January increase in mean home range size of females is associated with weaning of young and period of highest population density. Most males and some females disperse from their natal home ranges (Godsell 1983).

Olfactory and auditory signals are more important than visual communication in *D. viverrinus*. In captivity, eastern quolls show a number of scent-marking behaviors, including deliberate defecation and micturation (urine dribble); sternal, ventral, and cloacal rubbing; and face washing (Bryant 1988a; Croft 1982; Eisenberg and Golani 1977). Frequencies of scent-marking, face-washing, and pouch-cleaning behaviors increase in estrous females (Bryant 1988a). Males sniff female genitals and deposit scent marks, often rubbing against and mock copulating with the latter. Except for young in captivity that defecate at the edge of the nest or at one end of a tunnel (covered with grass by the female), eastern quolls are not known to use latrines. Wild adults deposit scats singly and randomly (Godsell 1983).

Infrequent vocalizations are part of threat defense by subordinate individuals in intrasexual agonistic encounters (Godsell 1983). Vocalizations by adults are variations on guttural hissing and coughs, including spat-hissing preceded by staccato hissing in rapid succession (Croft 1982; Fleay 1932, 1935). A short, sharp shriek, higher in pitch and not as loud as that of *D. maculatus*, is sometimes emitted as a contact or alarm call (Jones 1996). Mother and young call to each other after young have detached from the teats at 9 weeks of age. Mother's call is an "er-chuck, er-chuck," whereas young utter a soft "shish–shish–shish" (Croft 1982; Fleay 1935; Godsell 1983).

Agonistic behavior involves both vocal and visual threats (Croft 1982; Godsell 1983), including open mouth displays, hissing, interlocking jaws while standing on hind legs, stalks (slow approach, staring, with head lowered), lunges, and chases (usually lasting 5–15 s, but sometime as long as 30 s). Submissive behavior, involving either fleeing or crouching with head lowered and turned away, usually ends an aggressive episode. Agonistic behavior increases during the mating season among males, and in females during courtship, after copulation, and when they have large pouch young (Godsell 1983).

Estrous females show increased agitation, including pacing, tail-lifting, and guttural calls (Bryant 1988a). Courting males follow and sniff estrous females, who are frequently agonistic, resulting in prolonged chases. During copulation, the male grips the female's body with his forelegs and her neck with his teeth, resulting in wounds on her neck (Croft 1982; Eisenberg 1977; Godsell 1983). During copulation, which lasts for up to 5 h with bouts of thrusting and resting, the female crouches passively with rump raised and tail to one side, and the male clasps her abdomen (Eisenberg 1977; Godsell 1983). Both sexes mate several times during the breeding season (often with different partners), but females become increasingly agonistic toward males (Godsell 1983). Evidence that the female has mated includes fur loss and matting on neck, blood in urine, and a mucous discharge (Bryant 1988a). Once estrus is past, males display no further sexual behavior, nor any evidence of pair bonding or paternal behavior (Godsell 1983). Captive males establish nonlinear dominance hierarchies. Dominant males interfere with, but do not prevent, subordinates from mating (Godsell 1983).

Before parturition, the female becomes quiet and grooms the pouch area (Godsell 1983). Mother and young sniff each other but allogrooming has not been recorded (Bryant 1988a). Play behavior among both young and females includes chasing, wrestling, wrestling in bipedal posture, and mouth-to-mouth grappling (Croft 1982; Fleay 1932, 1935; Godsell 1983; Nelson and Smith 1971). Juvenile *D. viverrinus* first show agonistic behavior (open-mouth threats) at 13 weeks (Godsell 1983), and after independence, hiss and run to avoid meeting adults (Godsell 1983).

GENETICS. *Dasyurus viverrinus* has a diploid chromosome number of 14. Autosomes consist of 3 pairs of large metacentrics or submetacentrics, 1 pair of medium-sized metacentrics, and 2 pairs of smaller chromosomes, 1 of which may have a satellited short arm. X chromosome is a small metacentric and Y chromosome is even smaller (Sharman 1961).

Based on electrophoresis of 32 loci on 32 species of dasyurids, *Dasyurus* (with *Sminthopsis*) is most diverse, with 55% of polymorphic loci (Baverstock et al. 1982). Nearly every study of phylogenetic relationships among the quolls, morphometric, serological, and genetic, has proposed a different phylogeny (Archer 1976; Baverstock et al. 1982; Kirsch 1977; Krajewski et al. 1994, 1997; Van Dyck 1987; Wroe and Mackness 1998). Molecular sequencing studies support quoll monophylly, the basal separation of northern quolls from all other quolls, and the close relationships between *D. geoffroii* and the New Guinea quolls (Firestone, in press; Krajewski et al. 1997). Tasmanian eastern quolls have moderate levels of genetic diversity and widely spaced populations are sufficiently genetically distinct to be regarded as separate management units for conservation (Firestone, in press).

CONSERVATION STATUS. Having declined in range by 50–90% since European settlement of Australia, eastern quolls are classified as vulnerable to extinction (ESPA 1992). *D. viverrinus* has been extirpated over its entire mainland range in the 20th Century; the last sighting was in 1964, although there have been unsubstantiated sightings in northern New South Wales since the mid-1970s. Possible causes of extinction on the mainland were predation by and competition from introduced red foxes, disease (possibly toxoplasmosis introduced with placental carnivores, such as cats—Corbett 1995; Wood-Jones 1923), animal damage control (eastern quolls prey on domestic poultry—Nelson 1968), and hunting (Jones et al., in press). In the late 19th Century, 2,000–5,000 skins were exported to England each year (Batey 1907). The possibility of reestablishing eastern quolls to suitable habitat on the mainland where red foxes are controlled by baiting programs is being explored (Maxwell et al. 1996).

Although eastern quolls are widespread and locally common in Tasmania (numbers in Tasmania increased from 1975 to 1990—Driessen and Hocking 1992), their distribution and abundance is not well understood (Maxwell et al. 1996—Vertebrate Advisory Committee 1994). Eastern quolls are susceptible to road mortality, resulting in local decline (Jones 2000), juveniles may be susceptible to cats, and would be vulnerable to introduction of red foxes in Tasmania (Smith 1999).

REMARKS. *Dasyurus* is from the Greek *dasys* meaning shaggy or hairy, and *oura* meaning tail; the specific name, *viverrinus,* is from the Latin *viverra*, meaning ferret (Strahan 1981). This refers to the shaggy-tailed yet ferret-like appearance of the eastern quoll. Other vernacular names for *D. viverrinus* are native cat and eastern native cat.

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