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Dasyurus maculatus.

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Dasyurus E. Geoffroy, 1796

Viverra Kerr, 1792:170. Type species *V. maculatus*.
Dasyurus Geoffroy Saint-Hilaire, 1796:469. Type species *Didelphis maculata* (*Dasyurus maculatus*) Anon.
Nasira Harvey, 1841:210–211. Type species *Didelpha viverrina* (*Dasyurus viverrinus*) Shaw.
Dasyurinus Matschie, 1916:262. Type species of *Dasyurus geoffroii* Gould. Originally a subgenus of *Dasyurus*.
Dasyurops Matschie, 1916:262. Renaming of *Viverra maculata* Kerr (as *maculatus*). Originally a subgenus of *Dasyurus*.
Notoctonus Pocock, 1926:1082. Type species *Dasyurus geofroii* Gould (as *geoffroyi*).
Satanellus Pocock, 1926:1083. Type species *Dasyurus hallucatus* Gould.
Stictophonus Pocock, 1926:1083. Renaming of *Viverra maculata* Kerr.

CONTEXT AND CONTENT. Order Dasyuromorphia, family Dasyuridae, subfamily Dasyurinae. The genus *Dasyurus* has 6 living species (Groves 1993; Mahoney and Ride 1988). Polythetic cladistics, enzyme data, and structural evidence, which suggest that *D. hallucatus* is separate from and structurally ancestral to other quolls, support use of the genus *Satanellus* for this species (Archer 1982; Groves 1993; Kirsch and Archer 1982). A key to species (modified from Van Dyck 1987) follows:

1 No hallux on hind foot ..... *D. viverrinus*
Hallux on hind foot 2
2 White spots on tail ..... *D. maculatus*
Tail not spotted 3
3 Footpads with striations; I1 procumbent and separate from I2 4
Footpads without striations; I1 not procumbent and not separate from I2 5
4 Upper incisor row V-shaped; lower premolar row longer relative to lower toothrow (>21%); distribution northern Australia ..... *D. hallucatus*
Upper incisor row U-shaped; lower premolar row shorter relative to lower toothrow (≤21%); distribution New Guinea ..... *D. albopunctatus*
5 Hallux vestigial (≤3.5 mm); rostrum narrow between lachrymal canals (≤20.5 mm); body spots small (≤8.8 mm); ears small (≤45 mm); distribution New Guinea ..... *D. spartacus*
Hallux well developed (>3.5 mm); rostrum broad between lachrymal canals (>20.5 mm); body spots large (>8.8 mm); ears large (>45 mm); distribution northern Australia ..... *D. geoffroii*

Dasyurus maculatus (Kerr, 1792)

Spotted-tailed Quoll

Viverra maculata Kerr, 1792:170. Type locality not given.
Mustela novaehollandiae Meyer, 1793:27. Type locality not given.
Dasyurus macrourus Geoffroy Saint-Hilaire, 1803:259. Replacement name for *Viverra maculata*.
Dasyurus ursinus Leche, 1887:plate 18, figs. 4 and 5. Type locality unknown. This name is not invalidated by *Didelphis ursinus* Harris.
Dasyurus gracilis Ramsay, 1888:1296. Type locality "Bellenden Ker Range, Queensland, Australia."

CONTEXT AND CONTENT. Context as above. Two subspecies are recognized (Strahan 1995).

D. m. gracilis Ramsay, 1888:1296, see above.
D. m. maculatus (Kerr, 1792:170), see above (*macrourus* Geoffroy Saint-Hilaire, *novaehollandiae* (Meyer), and *ursinus* Leche are synonyms).

DIAGNOSIS. *Dasyurus* are medium-sized marsupial carnivores distinguished from all other dasyurids by white spots on their pelage. *D. maculatus* is the largest species of the genus (mean body weight of males : females of 3.5:1.8 kg for *D. m. maculatus* and 1.6:1.15 kg for *D. m. gracilis*, larger than the next largest quoll species, *D. geoffroii*, at 1.31:0.89 kg—Serena and Soderquist 1995) and is distinguished from all other quolls by presence of spots on its tail as well as body.

GENERAL CHARACTERS. *Dasyurus maculatus* is a medium-sized marsupial carnivore with short legs and a long tail, which is about equal to length of head and body (Fig. 1). Head and neck are stout, with strong jaws, and snout is slightly rounded. Small, delicate, and rounded ears are naked internally and have only sparse hair externally. Both front and hind feet have 5 toes, including a well-developed hallux on the hind feet. Foot pads, which extend to wrist and heel joints, are pink and ridged in this most arboreal quoll (Jones 1995).

Pelage is reddish-brown; individuals differ in darkness of coat but pelage does not vary seasonally, even in alpine areas, and no distinct molt is present. An orange-brown–colored oil is present on both skin and pelage. Spotted-tailed quolls have numerous coin-sized white spots on sides of body and dorsal surface of rump, on cheeks, down both fore and hind legs, and over the entire tail. Crown of head and shoulders are rarely spotted in *D. m. maculatus* but are usually so in *D. m. gracilis*. The ventral surface, also spotted and including chin and legs but excluding underside of tail, ranges in color from yellowish to grayish to creamy white in *D. m. maculatus* and from yellowish to black in *D. m. gracilis*. Guard hairs are ca. 15-mm long and straight: black on dorsum and cream on belly. Dorsal hairs are reddish brown in color, banded with white, and with a black tip. Ventral hairs are pale, gray at base with cream tips (Brunner and Coman 1974; Green and Scarborough 1990).

Sexual size dimorphism is pronounced. Adult males (mean = 3.5 kg, $n = 10$) of the southern subspecies, *D. m. maculatus*, are twice the mass of adult females (mean = 1.8 kg, $n = 9$) and have stronger canines and thicker necks (Jones 1995). Maximum sizes are 7 and 4 kg for males and females, respectively (Settle 1978).

FIG. 1. Adult male *Dasyurus maculatus maculatus* from Tasmania. Photograph by Dave Watts.

FIG. 2. Dorsal (female, #1988/1/55), ventral (female, #1986/1/17), and lateral (unknown sex, #1960/1/18) views of cranium and lateral (unknown sex, #1960/1/18) view of mandible of *Dasyurus maculatus maculatus* (Queen Victoria Museum and Art Gallery, Launceston, Tasmania). Photograph by John Leeming. Greatest length of skull #1988/1/55 is 88.9 mm.

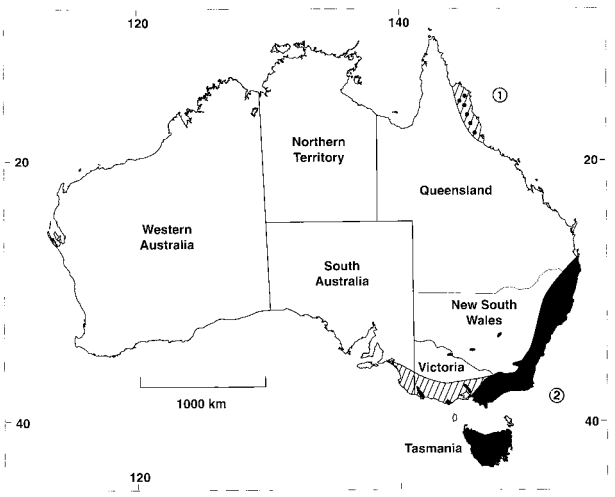

FIG. 3. Present (post-1970; black) and former (pre-1970; hatched) distribution of *Dasyurus maculatus* in Australia (Burnett 1993; Dickman and Read 1992; Edgar and Belcher 1995; Menkhorst 1995): 1. *D. m. gracilis* (north); 2. *D. m. maculatus* (south).

Males (mean = 1.6 kg, n = 25) of the northern Queensland subspecies, *D. m. gracilis*, are 50% heavier than females (mean = 1.15 kg, n = 24—Burnett 2000). Average and ranges of external measurements (in mm) of male and female *D. m. maculatus*, respectively (n = 10, 9), from Tasmania are: total length, 930 (840–1,000), 811 (745–870); length of tail, 433 (390–490), 386 (340–440); length of hind foot, 76.9 (70–81), 68.9 (54–78); length of head, 121 (110–131), 106 (99–107); length of ear, 45.9 (38–55), 43.4 (38–50). Average and ranges of external measurements (in mm) of male and female *D. m. gracilis*, respectively (n = 20–25 of each sex), from northern Queensland are: total length, 801 (670–950), 742 (680–840); length of tail, 388 (310–440), 357 (285–410); length of hind foot, 72.0 (66–80), 65.4 (59–71); length of head, 106 (92–130), 97 (87–130—Burnett 2000).

Skull is broad, flat, and only slightly rounded in profile with a slender rostrum that, unlike other *Dasyurus*, is parallel between canines and molar teeth (Fig. 2). Spotted-tailed quolls have a long snout in relation to length of braincase (Werdelin 1986). A large temporalis muscle is accommodated by a large temporal fossa (formed by a narrow postorbital constriction, small braincase, and wide zygomatic arches) and by pronounced sagittal and nuchal crests (Jones 1995; Keast 1982; Werdelin 1986). Squamosal forms a broad shelf at posterior edge of temporal fossa where it sweeps out into the zygomatic arch. Frontals and jugals have distinct postorbital processes. Palatine is fenestrated with 2 large and several fine holes. Jaw is strong and a ridge of bone between mandibular condyle and dentary forms a shelf on ventral edge of masseteric fossa, for insertion of masseter. Dental formula is i 4/3, c 1/1, p 2/2, m 4/4, total 42.

Average cranial measurements (in mm) for *D. m. maculatus* from Tasmania, male and female, respectively (n = 10 of each sex), are: greatest length of skull, 104.5, 90.4; breadth of braincase, 12.0, 11.2; zygomatic breadth, 65.3, 56.0; length of maxillary toothrow, 34.0, 32.3; length of molariform teeth in mandibular toothrow, 36.7, 34.8; maximal anterior–posterior diameter of upper canine, 5.4, 4.3. Average cranial measurements (in mm, n = 3, 2) for male and female *D. m. gracilis*, respectively, are: greatest length of skull, 65.0, 62.6; maximal anterior–posterior diameter of upper canine, 2.9, 2.7 (Jones 1997).

Cranial measurements for female *D. m. maculatus* do not differ across their geographic range, but canine size and strength of males is less in Tasmania than on the mainland (Jones 1997). Skulls of *D. m. maculatus* exhibit no geographic differences in sexual size dimorphism of skull length, but Tasmanian populations are less dimorphic in canine strength than mainland populations. *D. m. gracilis* is less dimorphic in skull length and canine tooth size than *D. m. maculatus*.

DISTRIBUTION. The spotted-tailed quoll occurs in eastern Australia (Fig. 3) in the area that receives >600 mm of rain per year (Edgar and Belcher 1995; Mansergh 1984). Once widely distributed from southeastern Queensland, through eastern New South Wales, Victoria, southeastern South Australia and to the island state of Tasmania, the mainland range has been reduced by 50–90% because European settlement of Australia and, with the exception of Tasmania, populations are now fragmented (Maxwell et al. 1996). In southeastern Queensland, *D. m. maculatus* is rare; its range is fragmented and contracting (Watt 1993). In Victoria and New South Wales, *D. m. maculatus* occurs from the coast to snowline, above 1,500 m elevation, and inland to the western plains along the Murray River (Edgar and Belcher 1995). Its range in Victoria has more than halved and remaining populations are disjunct (Mansergh 1984). The magnitude of range decline in New South Wales appears to be less than in Victoria but the species is rare, particularly in the south (Edgar and Belcher 1995; Mansergh 1984). Probably never common in South Australia, it is now extremely rare or extirpated. In Tasmania, the spotted-tailed quoll is recorded most frequently in the north and west of the state correlating with seasonally reliable rainfall, from sea level to ca. 1,000 m, and less commonly from drier, climatically more variable, eastern parts (Jones and Rose 1996). Becoming extirpated on Flinders and King Islands in the 20th Century, spotted-tailed quolls are now absent from all Tasmanian offshore islands (Hope 1972).

In northern Queensland, *D. m. gracilis* occurs from sea level

to >1,500 m, although populations now occupy disjunct mountaintop rainforests within the Wet Tropics Area (Burnett 2000), probably stranded there following climatic warming over the past 5,000 years (Nix and Switzer 1991). *D. m. gracilis* is now restricted to 8 areas of high altitude (>900 m), having become extirpated in 3 biogeographic areas of the Wet Tropics Area (Burnett 1993).

FOSSIL RECORD. Earliest known unambiguous dasyurids are from the late Miocene to early Pliocene (Wroe 1997). A *D. maculatus*–like form is known from the Kutjamarpu local fauna of the Wipijiri formation in South Australia (Archer 1982). *Glaucodon ballaratensis* Stirton, from the Plio-Pleistocene site of Smeaton in Victoria, is ancestral to and structurally intermediate between *D. maculatus* and *Sarcophilus laniarius* (= *harrisii*—Archer 1982). The only known extinct representative of *Dasyurus*, *D. dunmalli* is placed as the sister taxon to *D. maculatus* in a monophyletic clade together with *D. albopunctatus* and *D. hallucatus* (Wroe and Mackness 1998).

Dasyurus maculatus occurs in many Pleistocene cave faunas of eastern Australia, including regions that are now too arid for its survival (Archer et al. 1984; Morton et al. 1989). These include local faunas of Victoria Cave and Mount Gambier Caves, both in southeastern South Australia, and McEachern's Cave in southwestern Victoria (Archer and Hand 1984; Archer et al. 1984; Wakefield 1967a).

Dasyurus maculatus is well represented among numerous Holocene sites. These include Fromm's Landing local fauna in South Australia, 6 sites in western Victoria (Fern Cave, Lower Glenelg; Mt. Hamilton; Bushfield; Tower Hill Beach; Swain's Cave, Mt. Porndon; McEachern's Cave, Glenelg River); King, Flinders, Deal, and Cape Barren Islands in Bass Strait; and southern Tasmania (Archer and Hand 1984; Hope 1972; Wakefield 1964, 1967a).

Dasyurus maculatus occurred in 65% and *D. viverrinus* in 95% of 17 Pleistocene and Holocene cave deposits in Victoria (Wakefield 1964, 1967a, 1967b). *D. maculatus* was more common than *D. viverrinus* in southwestern Victoria and the Otway Ranges, areas where *D. maculatus* still remains (Mansergh 1983).

FORM AND FUNCTION. Reflecting a carnivorous diet, upper incisor row is transverse and canines are large. Upper incisors are compressed laterally with degree of compression decreasing from I4 to I2 (Archer 1976). Canines are ovoid in cross-section (Jones, in press; Jones and Stoddart 1998). Two premolars (ancestrally 4 premolars) are slightly rounded but the premolar tooth row is not crowded. Slightly bulbous molar teeth can withstand powerful bite forces and have several features which adapt them for carnivory: reduced anterior cusp (paracone) relative to a larger middle cusp (metacone) in upper molars, with the reverse occurring in lower molars; point of maximum metacrista shear shifted posteriorly and carnassial notch in lower molars shifted toward tongue, giving a slight longitudinal orientation of metacrista, thus increasing meat-shearing ability; reduced crushing area (talonid) in lower molars (Archer 1976); greater relative length of meat-shearing blade (metacrista) than in smaller, more insectivorous quolls (Jones 1995). Canine teeth markedly overerupt; in old individuals, dentine–enamel junctions may be near tip of canine. Tooth wear can be used to age individuals. *D. m. maculatus* has much higher rates of tooth fracture than other *Dasyurus*. Canine teeth break more frequently than other teeth (Jones 1995; Jones and Stoddart 1998).

The spotted-tailed quoll has short metatarsals (Jones, in press; Keast 1982) and metacarpals (Keast 1982) compared to rest of limb, suggesting it is a slow runner (Jones, in press). In relation to spine length, front legs (69%) and hind legs (91%) are longer than those of similar-sized mustelids and shorter than those of canids, but are equivalent to those of other carnivorous marsupials. Forelimbs are much shorter (76%) than hind limbs. Neck (26% of spine length) is shorter than that of mustelids, canids, and thylacinids, but longer than that of *Antechinus* (Keast 1982). *Dasyurus maculatus* has a nictitans gland but no Harderian gland associated with the nictitating membrane of the eye (Sakai and van Lennep 1984).

Penis of *D. maculatus* has a fleshy appendage (Woolley and Webb 1977). No baculum is present. Sperm of *D. maculatus* are large, with a long flagellum, and long, thin nucleus (Harding et al. 1982). In *D. maculatus*, head of spermatozoan is rod-like and pivoted at point of insertion of the neck (Bishop and Austin 1957; Harding et al. 1979). At 15–19 days, scrotum is detectable anterior to penis (Hill and Hill 1955). Scrotal skin is thin and covered with finer and sparser hair than rest of body, probably to aid cooling.

During the breeding season, the rear-opening pouch, formed by enlargement of lateral folds, develops (whether the female is lactating or not) into a glandular pocket-like area (Fleay 1940). Six mammae are arranged in 2 curved lateral rows. Pouch folds nearly enclose the young while they are very small and permanently attached to nipples.

Dasyurus maculatus has a relatively short alimentary canal without a cecum (Hill and Rewell 1955). Feces have a distinctive oily pungent odor; are twisted cylinders 50–70-mm long; often have 1 end pointed; and contain fur, feathers, and bone fragments (Triggs 1996).

Blood from 2 males *D. maculatus* had abundant enzymes (except serum amylase). *D. maculatus* has the second highest serum acid phosphotase activity (20.14 μmol *p*-nitrophenol formed/min/ml plasma) recorded for any mammal. This value is ca. 100 times higher than other marsupials except *Sarcophilus laniarius* (Parsons and Guiler 1972; Sallis and Guiler 1977). Cortisol is the major corticosteroid (Oddie et al. 1976). One male *D. maculatus* had peripheral plasma cortisol concentrations of 9.6×10^{-7} *M*, the highest association constant for cortisol binding among 16 dasyurids (Bradley 1982). Aldosterone is present in peripheral blood of *D. maculatus* (Scoggins et al. 1970).

Although 1.5–3.5 times more sensitive than other quoll species, *D. maculatus* is twice as tolerant to 1080 (sodium fluoroacetate) poison as badger, *Taxidea taxus*, and 4 times more tolerant than feral cats, *Felis catus* (McIlroy 1981). Body temperatures of 2 *D. maculatus* ranged from 32.2 to 34.3°C (Brown 1909).

ONTOGENY AND REPRODUCTION. *Dasyurus maculatus* is a seasonal breeder, with vaginal smears indicating a cycle of ca. 21 days (Settle 1978). The spotted-tailed quoll is facultatively monestrous, reproducing synchronously each winter but able to return to estrus if conception fails or a litter is lost (Lee et al. 1982). Breeding season is midwinter (June/July) but females, which enter estrus for 3 days at a time, may do so as early as April (Edgar 1983). Gestation is ca. 3 weeks, and young first appear in the pouch from early July to as late as 10 August in Victoria (Fleay 1940; Troughton 1954b). In the wild, pouch young have been observed in *D. m. gracilis* only between June and September inclusive (Burnett 2000), and in *D. m. maculatus* in July and September. Lactating females have been trapped from October to December inclusive (Jones 1995). In captivity in the northern hemisphere, *D. maculatus* still enters estrus in winter, between December and February (Collins et al. 1993). In wild *D. m. gracilis*, litter sizes range from 2 to 6; mean number of young attaching to the 6 nipples is 5.3. Average number weaned each year, crudely represented by number of enlarged nipples in the female's pouch, is 4.6, representing a preweaning mortality of at least 13% (Burnett 2000).

Young measure 7 mm at birth, but grow to 35 mm by 4 weeks of age (Fleay 1940). At 7 weeks, dark brown fur emerges, first on the large and well-formed head; and eyes begin to open (Collins 1973; Settle 1978). At 12 weeks, spots and abdomen are pinkish, but a few weeks later they are white (Fleay 1940). Beyond 12 weeks, young are increasingly lively. From 14 weeks onward, they eat food brought by the mother. By 18–21 weeks, young are entirely independent and self-supporting, but they are still only 33% the size of the mother (Troughton 1954b). Pronounced sexual dimorphism becomes apparent at this stage. Although sexually mature at 12 months, full size is not attained until 2 years of age (Fleay 1940).

Sex ratio of litters born in captivity is close to unity (Settle 1978), as are those born in the wild in northern Queensland (Burnett 2000). Sex ratio of adults in the wild is also close to unity (Burnett 2000; Jones 1995), although male *D. m. maculatus* are often caught more readily than females and nearly all individuals killed on the road and in traps are male (Green and Scarborough 1990; Jones 1995; Mansergh 1983). Male and female *D. m. gracilis* have been caught in equal numbers (both as total number of captures and total number of individuals—Burnett 2000).

Life span of *D. maculatus* is short compared to placental carnivores of similar size (Burnett 2000; Cockburn 1997). In a wild population of *D. m. gracilis*, no animal lived for >36 months (Burnett 2000). In captivity, although most *D. m. maculatus* live between 3 and 4 years (Collins 1973), 1 lived for 6 years and 3 months (Mitchell 1911). Females >3 years produced no litters, but males up to 5.5 years of age have sired young (Collins et al. 1993).

ECOLOGY. Spotted-tailed quolls occur in a wide range of habitats, including wet scrub and coastal heathland, but are most common in wet forest types (rainforest and closed eucalypt forest—Edgar and Belcher 1995; Green and Scarborough 1990; Jones 1995; Jones and Rose 1996; Rounsevell et al. 1991). Records on farmland are invariably near forest areas (Green and Scarborough 1990; Mansergh 1984). *D. m. gracilis* is restricted to unfragmented rainforest. Ninety percent of 95 locality records are from this habitat type; the remainder is from wet sclerophyll and human-modified environments very close to unfragmented rainforest (Burnett 2000).

Spotted-tailed quolls are moderately arboreal. *D. m. maculatus* moves up to 200 linear meters on logs; ca. 11% of the distance they travel is above ground (Jones 1995). Adept at climbing high into trees, they can capture possums and sleeping birds at night (Jones 1995), including tree-roosting domestic hens (Fleay 1948). Seventeen percent of daytime radio locations of *D. m. gracilis* were of quolls in rainforest canopy and 1 individual was observed traveling between adjacent trees through the canopy (Burnett 2000). The high proportion of arboreal prey in the diet of the spotted-tailed quoll also indicates an arboreal habit (Burnett 2000; Jones and Barmuta 2000).

Spotted-tailed quolls eat a variety of prey species, including insects, crayfish, lizards, snakes, birds, domestic poultry, small mammals, platypus, rabbits, arboreal possums, macropods, and wombats (Alexander 1980; Belcher 1995; Burnett 2000; Jones and Barmuta 1998; Troughton 1954a). Plant material in scats is probably incidental. *D. maculatus* has killed pademelons (*Thylogale*) and small wallabies (*Macropus*), but larger animals, including tree kangaroos, feral pigs, cattle, and dingoes, are almost certainly scavenged (Burnett 2000; Green and Scarborough 1990; Jones 1995). With few adaptations for bone consumption, only bones of small prey are consumed. Spotted-tailed quolls scavenge less frequently than sympatric *D. viverrinus* and *Sarcophilus laniarius* in Tasmania, but are common scavengers at roadkills, campsites, and houses (Jones 1995). Most important dietary items in terms of biomass are medium-sized (0.5–4.5 kg) marsupials (especially arboreal species), including brushtail (*Trichosurus vulpecula*) and ringtail (*Pseudocheirus peregrinus*) possums, bandicoots, *Perameles nasuta*, and musky rat kangaroos (*Hypsiprymnodon moschatus*—Alexander 1980; Belcher 1995; Burnett 2000; Jones and Barmuta 1998). Male *D. m. maculatus* eat significantly larger prey than females. Males eat possums, macropods, and wombats, whereas females consume small mammals, possums, birds, and invertebrates (Jones and Barmuta 1998). Subadults eat smaller prey than either adult females or males (Belcher 1995). Diet differs seasonally in some locations (Alexander 1980; Belcher 1995; Burnett 2000) but not in others (Jones and Barmuta 1998).

Average annual population mortality or emigration in *D. m. gracilis* is 59% and 34% for males and females, respectively, >3 years. Twenty-three percent of females lived for 2 years and 13% for 3 years. Comparable figures for males were 11% and 0%, respectively; no male lived for 3 years (Burnett 2000).

The longest straight-line movement recorded for *D. m. maculatus* is 17.5 km in 2 years for a male (Guiler 1969) marked as a newly weaned juvenile. This movement may represent dispersal. Along 10-km trapping lines, resident male and female *D. m. maculatus* moved a maximum of 8,000 and 2,000 m, respectively (Jones 1995); male and female *D. m. gracilis* moved a maximum of 6,650 and 2,600 m, respectively (Burnett 2000). Between successive captures, male and female *D. m. gracilis* moved an average of 1,350 and 661 m, respectively (range up to 6,100 and 2,450 m). Movements >1,000 m within a 24-h period recorded by radiotracking are common for resident females (Burnett 2000).

Home ranges of male *D. m. maculatus* are 580–875 ha, with a minimum core area of exclusive space at least 128 ha (Watt 1993). Home ranges of female *D. m. gracilis* average 124.8 ha (range 90–188 ha). Female *D. m. gracilis* exhibit longer residency than males, although 50% of both sexes in a trapped population were transients (Burnett 2000).

Character displacement has occurred in response to the number of competitors. Spotted-tailed quolls in Tasmania, with 3 competitors (*D. viverrinus, S. laniarius, Thylacinus cynocephalus*), have smaller values for canine tooth strength and temporalis muscle size than those on the mainland of Australia with only 1 competitor (*D. viverrinus*—Jones 1997). Patterns of dietary overlap and behavioral dominance among *D. viverrinus, D. maculatus,* and *S. laniarius* suggest that interspecific competition may explain why spotted-tailed quolls are comparatively rare in Tasmania (Jones 1995; Jones and Barmuta 1998). A high degree of dietary overlap with foxes, cats, and wild dogs suggests that competition with these introduced carnivores may be significant in mainland Australia (Belcher 1994).

Dasyurus m. maculatus has been reported as an occasional prey for *S. laniarius* and the masked owl, *Tyto novaehollandiae,* in Tasmania (Jones 1995; Mooney 1993), and the dingo and domestic dog in southern Australia (Brunner and Wallis 1986; Green and Scarborough 1990; Wallis and Brunner 1984). Large amounts of *D. m. maculatus* fur are occasionally found in spotted-tailed quoll scats (Alexander 1980; Jones 1995). A juvenile spotted-tailed quoll was killed by a house cat and an adult spotted-tailed quoll was killed by the owner of a kitten the quoll was attempting to kill (Burnett 2000). A spotted-tailed quoll has been recorded killing a large male cat (Troughton 1943). *D. m. gracilis* is an occasional prey item in the diet of the wedge-tailed eagle, *Aquila audax,* and the dingo, and is probably also taken by large pythons, *M. amethystine* and *M. spilotes* (Burnett 1996). In Tasmania, spotted-tailed quolls avoid encounters with adult Tasmanian devils but will chase away from carcasses subadult Tasmanian devils, which are larger than themselves. A fight between an adult spotted-tailed quoll and a subadult devil at a carcass resulted in severe injuries to both and the probable death of the quoll (Jones 1995).

At least 23 species of endoparasites are known from spotted-tailed quolls, including 5 flukes (Trematoda), 4 tapeworms (Cestoda), 14 nematodes (Nematoda), and 1 protozoan (Obendorf 1993; Spratt 1991). Wombats, macropods, and possums are common intermediate hosts. A severe host reaction has been recorded from tissue infested with the plerocercoid of *Spirometra erinacei* (Obendorf 1993). *Trichinella pseudospiralis,* a nematode with high prevalence in eastern and spotted-tailed quolls and Tasmanian devils, is probably endemic to Tasmania and is maintained through carrion feeding and cannibalism (Obendorf et al. 1990). *Salmonella,* most commonly *S. mississippi,* is frequently found in feces of *D. maculatus* (Obendorf 1993).

The 10 species of known ectoparasites include 1 species of mite (Laelapidae), 2 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 spotted-tailed quolls in Tasmania, burrows into the skin, causing irritation and hair loss (Obendorf 1993; Pearse 1981).

Degenerative skeletal conditions, including hind limb paralysis caused by prolapsed thoraco-lumbar intervertebral discs and osteoarthritis, are common in old, free-living spotted-tailed quolls (Obendorf 1993). Broken canine teeth are seen more frequently in spotted-tailed quolls than in any other species of quoll, Tasmanian devil, or thylacine. The most common infectious disease of captive spotted-tailed quolls is cutaneous myobacterial infection, often as a consequence of bite wounds inflicted on females by copulating males (Raymond et al. 2000; Tell et al. 1993). Incidence of tumors in captive spotted-tailed quolls is high (Tell et al. 1993) and multiple proliferative lesions have been reported (Canfield et al. 1990). Many diseases in captive animals can be traced to either inappropriate diets or to the extended lifespan of captive individuals (Obendorf 1993; Tell et al. 1993).

Spotted-tailed quolls are difficult to breed in captivity. Critical prerequisites are natural photoperiods, separation of individuals before the breeding season, and generous feeding of males before and during the breeding season to prevent fighting as well as preventing males from killing females. Other important factors are a varied and balanced diet and a structurally complex enclosure, with soil substrate and a diversity of hollow logs, pipes, rocks and limbs for dens, runways, climbing, and digging (Collins et al. 1993; Conway 1988). Excellent climbing ability means that roof netting is essential. Although on display at a number of wildlife parks and zoos, only 2 captive breeding colonies were viable in 2000 (Trowunna Wildlife Park, Tasmania; Featherdale Wildlife Park, Sydney, both Australia).

Spotted-tailed quolls are trapped in wire cage traps baited with meat held on a hook in the rear of the trap (Jones 1995) or placed at the back of the trap on the floor behind a treadle (Burnett 2000). Male *D. m. maculatus* are more trappable than females (Green and Scarborough 1990; Jones 1995; Mansergh 1983) although sexes of *D. m. gracilis* are equally trappable (Burnett 2000). Spotted-tailed quolls can be handled in a sack or in a clear restraining tube (Collins et al. 1993; Jones 1995). The small and delicate ears are

easily damaged by ear tags, so ear tattoos are more effective in marking individuals for study. *D. m. maculatus* has been sedated with valium; Jurox vitamin B complex and vitamin E are used to reduce capture-related myopathy (Watt 1993). *D. m. gracilis* is effectively anesthetized with the inhalant Forthane (isofluorane—Burnett 2000). Because of the stout neck, radio-collars are positioned just behind the ears (and must be monitored carefully to prevent abrasion) or radiotags, glued to fur on the rump, are used. Whip antennae are usually destroyed within a few months.

BEHAVIOR. Although predominantly nocturnal, spotted-tailed quolls, especially juveniles and females with large young in the den, are frequently active during daylight hours and often emerge from and return to the den in daylight (Burnett 2000; Edgar and Belcher 1995; Fleay 1940; Green and Scarborough 1990; Watt 1993). In captivity, *D. maculatus* is most active at dusk and dawn, but activity periods are strongly influenced by feeding times (Collins et al. 1993; Conway 1988; Settle 1978).

Spotted-tailed quolls rest during the day in dens, which may be underground burrows, caves, rock crevices, tree hollows, and hollow logs or in human structures such as under houses and in sheds (Edgar and Belcher 1995; Jones 1995; Watt 1993). Male *D. m. maculatus* use 1–3 dens (Watt 1993). In captivity, females dig and construct nests in underground chambers (Collins and Conway 1986; Conway 1988). Natal nest sites of *D. m. gracilis* include hollow tree roots and rock fissures (Burnett 2000).

Spotted-tailed quolls move in both a walk and a bounding gait (Fleay 1932) along the ground. Although trails are not used extensively, *D. m. maculatus* uses fallen logs as runways wherever possible (Jones and Barmuta 2000) and uses roads for foraging and scent marking (Burnett 2000). *D. maculatus* climbs vertical tree trunks, including climbing down head first, travels on even the thin outer branches, and crosses between contiguous tree canopies (Burnett 2000; Fleay 1940; Jones 1995; Troughton 1943). Lacking large feet or furred foot pads, *D. maculatus* has difficulty moving in deep snow (Jones et al. 1997).

Spotted-tailed quolls stalk their prey, walking or running forward when the prey has its head down and stopping when its head is raised (Troughton 1943). Spotted-tailed quolls pounce or leap on their prey, depending on whether it is small or large, and kill it with a bite at base of skull or top of neck (Fleay 1932; Green and Scarborough 1990; Jones 1995; Troughton 1954a). Forelegs are used in prey capture. Small prey, such as skinks, are pinned with forepaws before they are killed (Green and Scarborough 1990). Sleeping birds, including domestic hens, and possums are caught in trees at night. The spotted-tailed quoll sometimes knocks sleeping birds off the branch with a forepaw, catching and killing them on the way to the ground (Jones 1995; Troughton 1954a). Spotted-tailed quolls leap onto the back of large prey, such as pademelons (*Thylogale*), and grip with all 4 legs while biting the neck. The bite is positioned with lower canines near vertebral column and upper canines toward throat (Jones 1995). Grasping forepaws, vibrissae on the wrists, and the ability of quolls to reach into small mammal live traps and extract prey suggest that spotted-tailed quolls extract prey from dens or other refuges (Burnett 2000).

Home ranges of male *D. m. maculatus* overlap although each male maintains an exclusive core area (Watt 1993). Home ranges of female *D. m. gracilis* have little overlap, but ranges of males probably overlap more (Burnett 2000). *D. m. maculatus* may share dens during the breeding season (Watt 1993). In captivity, both sexes mate with several different individuals in succession (Collins et al. 1993). After mating, females are aggressive toward males and this intensifies as birth approaches (Collins et al. 1993; Conway 1988). Males show no parental care. In 1 case, a male brought food to his young (Settle 1978), but this behavior was probably an artifact of a captive-bred brother–sister pair. Dispersal is male-biased (Firestone, in press).

Olfactory and auditory signals are more important than visual communication in *D. maculatus*. Foraging behavior, including sniffing of the ground as they move (Green and Scarborough 1990) and the ability to pick up the cross-trail of a rabbit (Fleay 1932), suggest a keen sense of smell. During intraspecific encounters, spotted-tailed quolls sniff nose to nose and males sniff the rumps of females in estrus. Face washing, besides cleaning, may function as self-marking behavior, as mouth and ear secretions are smeared on the head (Croft 1982; Eisenberg and Golani 1977). Communal latrines are present in some populations but not in others (Kruuk and Jarman 1995). Latrines typically are found in rocky creek beds, at the bases of cliffs, and on roads (Belcher 1995; Burnett 2000; Kruuk and Jarman 1995). Visits to latrines occur throughout the night, with activity peaks during the breeding season (Belcher 1994). Defecation is often accompanied by cloacal dragging (Burnett 2000).

Vocalizations are infrequent in *D. maculatus* but are given in all social interactions, including agonistic, mating, and maternal care (Settle 1978). During agonistic encounters with other spotted-tailed quolls or when disturbed by humans, spotted-tailed quolls emit gutteral huff, cough, and hissing sounds and abrupt, piercing screams likened to a short blast of a circular saw (Croft 1982; Fleay 1932, 1940, 1948). In captivity, males greet other spotted-tailed quolls with slightly opened jaws and low-pitched hissing sounds (Fleay 1940). Females in estrus vocalize with a soft, repeated "cp–cp–cp" sound heard only during this time (Collins et al. 1993; Settle 1978). Females and young call to each other with a muffled string of "chh–chh" (females) or "echh–echh" (young) sounds (Collins et al. 1993; Croft 1982). Juveniles vocalize frequently when fighting and the mother may warn them with a hissing sound when they clamber over her (Collins and Conway 1986; Conway 1988).

Agonistic behavior in *D. maculatus* involves both vocal and open-mouth behavioral threats. In the latter, the mouth is opened wide, displaying their teeth to the opponent; ears are laid back; and eyes are narrowed (Croft 1982; Fleay 1948). Males fight each other in vigorous tumbles, grasping each other with forepaws, kicking with hind feet, biting, and screeching (Jones 1995).

Females vocalize when in estrus and readily accept a male's mounting attempts; both behaviors are unique to spotted-tailed quolls. On meeting a mate, a receptive female spotted-tailed quoll moves about slowly, pausing occasionally with head lowered and rump raised. The male follows the female, sniffs the cloacal region, and vocalizes with a series of staccato cries. The "cp–cp–cp" vocalization of the female causes the male to reduce the volume of his vocalizations. During copulation, the male grasps the female's body with the forearms, often palpating her abdomen and stroking her sides. The male holds the back of the female's neck during copulation, occasionally releasing his bite to lick the female's neck (both behaviors are unique, among dasyurids, to spotted-tailed quolls—Croft 1982; Settle 1978). This grip results in lacerations to the neck and shoulders in both wild and captive spotted-tailed quolls and occasionally in the death and subsequent partial consumption of captive females (Croft 1982; Fleay 1940; Settle 1978). Females develop a swollen neck region during estrus (Croft 1982). Throughout copulation, the female crouches with head low and eyes half-closed (Settle 1978), vocalizing frequently (Collins et al. 1993; Fleay 1940). Copulation is prolonged and lasts from several hours to 24 h (Collins et al. 1993).

During parturition, *D. maculatus* stands quietly for about 1.5 h with the hindquarters raised and the tail curled beside her (Fleay 1940). For the first 3 weeks of pouch life, females elevate their hindquarters as they walk. Females with pouch young rest on their sides or crouch with hind legs raised so that no pressure is on the pouch. Nest-building behavior becomes pronounced at 4 weeks (Conway 1988). Mobility of a female with large pouch young is reduced (Fleay 1940) and, after young emerge permanently from the pouch, she spends long periods of time in the nest (Conway 1988).

At 50–60 days, before their eyes open, young locate siblings and mother by calling (the female replies), by moving around the nest, and by curling up next to warm objects. These behaviors cease by 70 days when eyes open. Agonistic play behavior between litter mates and self-grooming, by scratching the head with the hind foot, start at this time. By 90 days, social play is well developed and involves stalking, chasing, wrestling, and playing with objects, accompanied by much vocalizing (Conway 1988; Croft 1982; Settle 1978). A female does not carry young on her back but will tolerate them climbing on her while in the nest (Conway 1988; Settle 1978) or clinging to her back with teeth and claws if frightened (Fleay 1948). Sometimes a female will stalk her young, pinning them to the ground while gently biting them. This behavior is observed in play, if the young have strayed too far or are persistent in jumping on her (Collins and Conway 1986; Conway 1988). As young grow, they stray farther and the female recalls them with a soft clucking sound (Collins and Conway 1986). Beyond 100 days, the female spends progressively less time with her offspring and displays more aggression toward them (Conway 1988). By 95 days, young can kill a mouse (*Mus musculus*) within 5 s of its introduction into an

enclosure, despite no previous experience with live prey (Settle 1978); by 8 months young spotted-tailed quolls can kill adult rabbits (*Oryctolagus cunniculus*—Collins et al. 1993).

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

Based on 32 loci from 32 species of dasyurids, *Dasyurus* (with *Sminthopsis*) was genetically most diverse, with 55% of loci showing differences (Baverstock et al. 1982). Nearly every study of phylogenetic relationships among the quolls (morphometric, serologic, and genetic) has proposed a different phylogeny (Archer 1976; Baverstock et al. 1982; Kirsch 1977; Krajewski et al. 1994, 1997; Parsons and Guiler 1972; Van Dyck 1987; Wroe and Mackness 1998). Molecular sequencing studies support the monophyletic nature of the quolls, 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 populations of spotted-tailed quolls show distinct genetic differentiation from all mainland populations, sufficient for subspecific classification. The evolutionary history of this species is not reflected in morphological characters, which separate *D. m. gracilis* from both mainland and Tasmanian populations of *D. m. maculatus*. *D. m. gracilis* and mainland *D. m. maculatus* are distinct only at the level of genetic management units (Firestone et al. 1999). Populations >50-km apart are sufficiently different to be considered as genetic management units (Firestone, in press).

CONSERVATION STATUS. Because the range of *D. m. maculatus* has declined 50–90% since European settlement, it is now classified as vulnerable to extinction (IUCN 1996; Maxwell et al. 1996). Because total number is small (<1,000), populations are disjunct and a number have become extinct (3/11 biogeographic areas—Burnett 2000), *D. m. gracilis* is classified as endangered (IUCN 1996; Maxwell et al. 1996). *D. maculatus* is especially susceptible to decline because it is a climatic and habitat specialist, occurs in naturally low population densities, is subject to competition from native and introduced carnivores, has large space requirements, a short life span, and low lifetime fecundity (Jones et al., in press). The major threats are fragmentation and loss of habitat, which affect prey availability, hunting ability, and increase contact with humans (Jones et al., in press). Human-induced mortality factors include persecution by farmers (because quolls kill poultry), motor vehicles, poisoning from 1080 baits laid to control wild canids and cats, secondary poisoning from control programs for rabbits, and perhaps ingestion of toxic cane toads, *Bufo marinus* (Belcher 1998; Burnett 1997; Jones et al., in press). Competition from introduced predators, i.e., foxes, cats, and dogs, may further exacerbate these factors (Belcher 1994; Burnett 2000; Green and Scarborough 1990; Jones et al., in press).

REMARKS. *Dasyurus* is the combined form of the Greek words *dasys*, which means shaggy or hairy, and *oura*, referring to the tail (Strahan 1981). The specific name, *maculatus*, is a Latin word meaning spot or spotted. Other vernacular names include spot-tailed quoll, tiger quoll, and tiger cat.

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LITERATURE CITED

ALEXANDER, D. 1980. Diet of the tiger quoll (*Dasyurus maculatus* Kerr) in an area of New England National Park, northeastern New South Wales. Bachelor of Natural Resources thesis, University of New England, Armidale, New South Wales, Australia, 92 pp.

ARCHER, M. 1976. The dasyurid dentition and its relationships to that of didelphids, thylacinids, borhyaenids (Marsupicarnivora) and peramelids (Peramelina: Marsupialia). Australian Journal of Zoology, Supplementary Series 39:1–34.

ARCHER, M. 1982. Review of the dasyurid (Marsupialia) fossil record, integration of data bearing on phylogenetic interpretation, and suprageneric classification. Pp. 397–443 in Carnivorous marsupials (M. Archer, ed.). Royal Zoological Society of New South Wales, Sydney, Australia 2:397–804.

ARCHER, M., G. CLAYTON, AND S. HAND. 1984. A checklist of Australasian fossil mammals. Pp. 1027–1087 in Vertebrate zoogeography and evolution in Australasia (M. Archer and G. Clayton, eds.). Hesperian Press, Carlisle, Western Australia.

ARCHER, M., AND S. HAND. 1984. Background to the search for Australia's oldest mammals. Pp. 517–565 in Vertebrate zoogeography and evolution in Australasia (M. Archer and G. Clayton, eds.). Hesperian Press, Carlisle, Western Australia.

BAVERSTOCK, P. R., M. ARCHER, M. ADAMS, AND B. J. RICHARDSON. 1982. Genetic relationships among 32 species of Australian dasyurid marsupials. Pp. 641–650 in Carnivorous marsupials (M. Archer, ed.). Surrey Beatty & Sons Pty, Limited, Chipping Norton, New South Wales, Australia 2:397–804.

BELCHER, C. A. 1994. Studies on the diet of the tiger quoll, *Dasyurus maculatus*. Master's thesis, LaTrobe University, Bundoora, Victoria, 116 pp.

BELCHER, C. A. 1995. Diet of the tiger quoll *Dasyurus maculatus* in East Gippsland, Victoria. Wildlife Research 22:341–357.

BELCHER, C. A. 1998. Susceptibility of the tiger quoll, *Dasyurus maculatus*, and the eastern quoll, *D. viverrinus*, to 1080-poisoned baits in control programmes for vertebrate pests in eastern Australia. Wildlife Research 25:33–40.

BISHOP, M. W. H., AND C. R. AUSTIN. 1957. Mammalian spermatozoa. Endeavour 16:137–150.

BRADLEY, A. J. 1982. Steroid binding proteins in the plasma of dasyurid marsupials. Pp. 651–657 in Carnivorous marsupials (M. Archer, ed.). Surrey Beatty & Sons Pty, Limited, Chipping Norton, New South Wales, Australia 2:397–804.

BROWN, A. E. 1909. The tuberculin test in monkeys: with notes on the temperature of mammals. Proceedings of the Royal Society of London 81–90.

BRUNNER, H., AND B. J. COMAN. 1974. The identification of mammalian hair. Inkata Press, Melbourne, Victoria, Australia.

BRUNNER, H., AND L. R. WALLIS. 1986. Roles of predator scat analysis in Australian mammal research. Victorian Naturalist 103:79–87.

BURNETT, S. 1993. The conservation status of the tiger quoll, *Dasyurus maculatus gracilis* in north Queensland. Report for Queensland Department of Environment and Heritage March: 1–15.

BURNETT, S. 1996. Successful foraging by the wedge-tailed eagle in tropical rainforest. Emu 96:277–280.

BURNETT, S. 1997. Colonising cane toads cause population declines in some Australian vertebrate predators: reliable anecdotal information and management implications. Pacific Conservation Biology 3:65–72.

BURNETT, S. 2000. The ecology and endangerment of the spotted-tailed quoll, *Dasyurus maculatus gracilis*. Ph.D. dissertation, James Cook University of North Queensland, Townsville, Australia, 303 pp.

CANFIELD, P. J., W. J. HARLEY, AND G. L. REDDACLIFF. 1990. Spontaneous proliferations in Australian marsupials—a survey and review. 2. Dasyurids and bandicoots. Journal of Comparative Pathology 103:147–158.

COCKBURN, A. 1997. Living slow and dying young—senescence in marsupials. Pp. 163–174 in Marsupial biology: recent research, new perspectives (N. Saunders and L. Hinds, eds.). University of New South Wales Press, Sydney, Australia.

COLLINS, L., AND K. CONWAY. 1986. A quoll by any other name. Zoogoer January–February:14–16.

COLLINS, L., ET AL. 1993. Captive management and husbandry procedures for tiger quolls (*Dasyurus maculatus*). Pp. 47–54 in The biology and management of Australasian carnivorous marsupials (M. Roberts, J. Carnio, G. Crawshaw, and M. Hutchins, eds.). Metropolitan Toronto Zoo and the Monotreme and Marsupial Advisory Group of the American Association of Zoological Parks and Aquariums, Toronto, Ontario, Canada.

COLLINS, L. R. 1973. Monotremes and marsupials. A reference for

zoological institutions. Smithsonian Institution Press, Washington, D.C.

CONWAY, K. 1988. Captive management and breeding of the tiger quoll. International Zoo Yearbook 27:108–119.

CROFT, D. B. 1982. Communication in the Dasyuridae (Marsupialia): a review. Pp. 291–309 in Carnivorous marsupials (M. Archer, ed.). Surrey Beatty & Sons Pty, Limited, Chipping Norton, New South Wales, Australia 1:1–396.

DICKMAN, C. R., AND D. G. READ. 1992. The biology and management of the arid zone in NSW. New South Wales National Parks and Wildlife Service Species Management Report 11: 1–112.

EDGAR, R. 1983. Spotted-tailed quoll. Pp. 18–19 in The Australian Museum complete book of Australian mammals. First edition (R. Strahan, ed.). Angus and Robertson, Sydney, New South Wales, Australia.

EDGAR, R., AND C. BELCHER. 1995. Spotted-tailed quoll. Pp. 67–69 in The mammals of Australia. Second edition (R. Strahan, ed.). Australian Museum/Reed Books, Sydney, New South Wales.

EISENBERG, J. F., AND I. GOLANI. 1977. Communication in metatheria. Pp. 575–599 in How animals communicate (T. A. Sebeok, ed.). Indiana University Press, Bloomington.

FIRESTONE, K. B. In press. The application of genetic research to conservation management in dasyurids. In Predators with pouches: the biology of carnivorous marsupials (M. E. Jones, C. R. Dickman, and M. Archer, eds.). CSIRO Publishing, Melbourne, Victoria, Australia.

FIRESTONE, K. B., M. S. ELPHINSTONE, W. B. SHERWIN, AND B. A. HOULDEN. 1999. Phylogeographical population structure of tiger quolls *Dasyurus maculatus* (Dasyuridae: Marsupialia), an endangered carnivorous marsupial. Molecular Ecology 8: 1613–1625.

FLEAY, D. 1932. The rare dasyures (native cats). Victorian Naturalist 49:63–69.

FLEAY, D. 1940. Breeding of the tiger cat. Victorian Naturalist 56: 158–163.

FLEAY, D. 1948. Australia's marsupial tiger cat. Wildlife 1948: 459–464.

GEOFFROY SAINT-HILAIRE, É. 1796. Dissertation sur les animaux à bourse (*Didelphis*, L.). Magasin Encyclopaedique 3(12): 445–472.

GEOFFROY SAINT-HILAIRE, É. 1803. Note sur les espèces du genre dasyure. Bulletin de le Scientifique Société de Philomathematique du Paris 3(81):258–259.

GREEN, R. H. 1989. The ectoparasitic mites of Tasmanian vertebrate animals. Records of the Queen Victoria Museum, Launceston 98:1–25.

GREEN, R. H., AND T. J. SCARBOROUGH. 1990. The spotted-tailed quoll *Dasyurus maculatus* (Dasyuridae, Marsupialia) in Tasmania. The Tasmanian Naturalist 100:1–15.

GROVES, C. P. 1993. Order Dasyuromorphia. Pp. 29–37 in Mammal species of the world, a taxonomic and geographic reference (D. E. Wilson and D. A. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C.

GUILER, E. R. 1969. Colour change in the marsupial tiger cat. Nature 221:758.

HARDING, H. R., F. N. CARRICK, AND C. D. SHOREY. 1979. Special features of sperm structure and function in marsupials. Pp. 289–303 in The spermatozoan (D. W. Fawcett and J. M. Bedford, eds.). Urban and Schwarzenberg, Inc., Baltimore, Maryland.

HARDING, H. R., P. A. WOOLLEY, C. D. SHOREY, AND F. N. CARRICK. 1982. Sperm ultrastructure, spermiogenesis and epididymal sperm maturation in dasyurid marsupials: phylogenetic implications. Pp. 659–673 in Carnivorous marsupials (M. Archer, ed.). Royal Zoological Society of New South Wales, Sydney, Australia 2:397–804.

HARVEY, J. B. 1841. A sketch of the natural history of Port Lincoln. South Australian Magazine 1:210–212.

HILL, J. P., AND W. C. O. HILL. 1955. The growth-stages of the pouch-young of the native cat (*Dasyurus viverrinus*), together with observations on the anatomy of the new-born young. Transactions of the Zoological Society of London 28:349–425.

HILL, W. C. O., AND R. E. REWELL. 1955. The caecum of monotremes and marsupials. Transactions of the Zoological Society of London 28:185–240.

HOPE, J. H. 1972. Mammals of the Bass Strait islands. Proceedings of the Royal Society of Victoria 85:163–196.

IUCN 1996. IUCN red list of threatened animals (M. Baillie and B. Groombridge, eds.). International Union for the Conservation of Nature and Natural Resources Species Survival Commission, Gland, Switzerland.

JONES, M. E. 1995. Guild structure of the large marsupial carnivores in Tasmania. Ph.D. dissertation, University of Tasmania, Hobart, Tasmania, Australia, 143 pp.

JONES, M. E. 1997. Character displacement in Australian dasyurid carnivores: size relationships and prey size patterns. Ecology 78:2569–2587.

JONES, M. E. In press. Predators, pouches and partitioning: ecomorphology and guild structure of marsupial and placental carnivores. In Predators with pouches: the biology of carnivorous marsupials (M. E. Jones, C. R. Dickman, and M. Archer, eds.). CSIRO Publishing, Melbourne, Victoria, Australia.

JONES, M. E., ET AL. In press. Carnivore concerns: problems, issues and solutions for conserving Australia's marsupial carnivores. In Predators with pouches: the biology of carnivorous marsupials (M. E. Jones, C. R. Dickman, and M. Archer, eds.). CSIRO Publishing, Melbourne, Victoria, Australia.

JONES, M. E., AND L. A. BARMUTA. 1998. Diet overlap and abundance of sympatric dasyurid carnivores: a hypothesis of competition? Journal of Animal Ecology 67:410–421.

JONES, M. E., AND L. A. BARMUTA. 2000. Niche differentiation among sympatric Australian dasyurid carnivores. Journal of Mammalogy 81:434–447.

JONES, M. E., G. GRIGG, AND L. BEARD. 1997. Body temperatures of Tasmanian devils (*Sarcophilus harrisii*) and eastern quolls (*Dasyurus viverrinus*) through an alpine winter. Physiological Zoology 70:53–60.

JONES, M. E., AND R. K. ROSE. 1996. Preliminary assessment of distribution and habitat associations of the spotted-tailed quoll (*Dasyurus maculatus maculatus*) and eastern quoll (*D. viverrinus*) in Tasmania to determine conservation and reservation status. Nature Conservation Branch, Parks and Wildlife Service. Report to the Tasmanian Regional Forest Agreement Environment and Heritage Technical Committee, November: 1–68.

JONES, M. E., AND D. M. STODDART. 1998. Reconstruction of the predatory behaviour of the extinct marsupial thylacine. Journal of Zoology, London 246:239–246.

KEAST, A. 1982. The thylacine (Thylacinidae, Marsupialia): how good a pursuit carnivore? Pp. 675–684 in Carnivorous marsupials (M. Archer, ed.). Surrey Beatty & Sons Pty, Limited, Chipping Norton, New South Wales, Australia 2:397–804.

KERR, R. 1792. The animal kingdom, or zoological system, of the celebrated Sir Charles Linnaeus; class 1. Mammalia; being a translation of that part of the Systema Naturae, as lately published with great improvements by Professor Gmelin, together with numerous additions from more recent zoological writers and illustrated with copperplates. J. Murray, London, United Kingdom 1:1–400.

KIRSCH, J. A. W. 1977. The comparative serology of Marsupialia, and a classification of marsupials. Australian Journal of Zoology, Supplementary Series A 52:1–152.

KIRSCH, J. A. W., AND M. ARCHER. 1982. Polythetic cladistics, or when parsimony's not enough: the relationships of carnivorous marsupials. Pp. 595–619 in Carnivorous marsupials (M. Archer, ed.). Surrey Beatty & Sons Pty, Limited, Chipping Norton, New South Wales, Australia 2:397–804.

KRAJEWSKI, C., J. PAINTER, L. BUCKLEY, AND M. WESTERMAN. 1994. Phylogenetic structure of the marsupial family Dasyuridae based on cytochrome *b* DNA sequences. Journal of Mammalian Evolution 2:25–35.

KRAJEWSKI, C., J. YOUNG, L. BUCKLEY, P. A. WOOLLEY, AND M. WESTERMAN. 1997. Reconstructing the evolutionary radiation of dasyurine marsupials with cytochrome *b*, 12S rDNA, and protamine P1 gene trees. Journal of Mammalian Evolution 4: 217–236.

KRUUK, H., AND P. J. JARMAN. 1995. Latrine use by the spotted-tailed quoll (*Dasyurus maculatus*: Dasyuridae, Marsupialia) in its natural habitat. Journal of Zoology, London 236:345–349.

LECHE, W. 1887. Dr. H. G. Bronn's Klassen und Ordnungen des Thier-reichs wissenschaftlich dargestellt in Wort und Bild. Säugethiere: Mammalia. C. F. Winter'sche Verlagshandlung, Leipzig, Germany.

LEE, A. K., P. WOOLLEY, AND R. W. BRAITHWAITE. 1982. Life history strategies of dasyurid marsupials. Pp. 1–11 in Carnivorous marsupial (M. Archer, ed.). Surrey Beatty & Sons Pty, Limited, Chipping Norton, New South Wales, Australia 1:1–396.

MAHONEY, J. A., AND W. D. L. RIDE. 1988. Dasyuridae. Pp. 14–33 in Mammalia, zoological catalogue of Australia (J. L. Bannister, J. H. Calaby, L. J. Dawson, J. K. Ling, J. A. Mahoney, G. M. McKay, B. J. Richardson, W. D. L. Ride, and D. W. Walton, eds.). Australian Government Printing Service, Canberra, Australian Capital Territory.

MANSERGH, I. 1983. Notes on the capture period of the tiger quoll (*Dasyurus maculatus*) in Victoria. Victorian Naturalist 100: 32–33.

MANSERGH, I. 1984. The status, distribution and abundance of *Dasyurus maculatus* (tiger quoll) in Australia, with particular reference to Victoria. Australian Zoologist 21:109–122.

MATSCHIE, P. 1916. Die Verbreitung der Beuteltiere auf Neuguinea mit einigen Bemerkungen über ihre Einteilung in Untergattungen. Mitteilungen. Zoologisches Museum in Berlin 8:259–308.

MAXWELL, S., A. A. BURBIDGE, AND K. MORRIS. 1996. The action plan for Australian marsupials and monotremes. Report for the International Union for the Conservation of Nature and Natural Resources Species Survival Commission, Australasian Marsupial and Monotreme Specialist Group, 234 pp.

MCILROY, J. C. 1981. The sensitivity of Australian animals to 1080 poison. II. Marsupial and eutherian carnivores. Australian Wildlife Research 8:385–399.

MENKHORST, P. 1995. Mammals of Victoria. Oxford University Press, Oxford, United Kingdom.

MEYER, F. A. A. 1793. Systematisch-summarische uebersicht der neuesten zoologischen entdeckungen in Neuholland und Afrika. Nebst zwey andern Zoologischen Abhandlungen. Dykischen Buchhandlung, Leipzig, Germany, 27 pp.

MITCHELL, P. C. 1911. On longevity and relative viability in mammals and birds; with a note on the theory of longevity. Proceedings of the Royal Society of London (Biology) 1911:425–548.

MOONEY, N. 1993. Diet of the masked owl in Tasmania: past and present. Pp. 160–174 in Australian raptor studies (P. Olsen, ed.). Australian Raptor Association, Royal Australian Ornithologists Union, Melbourne, Victoria.

MORTON, S. R., C. R. DICKMAN, AND T. P. FLETCHER. 1989. Dasyuridae. Pp. 560–582 in Fauna of Australia (D. W. Walton and B. J. Richardson, eds.). Australian Government Publishing Service, Canberra, Australian Capital Territory.

NIX, H. A., AND M. A. SWITZER. 1991. Kowari 1. Rainforest animals. Atlas of vertebrates endemic to Australia's wet tropics. Australian National Parks and Wildlife Service, Canberra, Australian Capital Territory.

OBENDORF, D. L. 1993. Diseases of dasyurid marsupials. Pp. 39–46 in The biology and management of Australasian carnivorous marsupials (M. Roberts, J. Carnio, G. Crawshaw, and M. Hutchins, eds.). Metropolitan Toronto Zoo and the Monotreme and Marsupial Advisory Group of the American Association of Zoological Parks and Aquariums, Toronto, Ontario, Canada.

OBENDORF, D. L., ET AL. 1990. *Trichinella pseudospiralis* infection in Tasmanian wildlife. Australian Veterinary Journal 67: 108–110.

ODDIE, C. J., ET AL. 1976. Blood corticosteroids in Australian marsupial and placental mammals and one monotreme. Journal of Endocrinology 69:341–348.

PARSONS, R. S., AND E. R. GUILER. 1972. Observations on the blood of the marsupial tiger cat, *Dasyurops maculatus* (Kerr) [Dasyuridae]. Comparative Biochemistry and Physiology 43A: 935–939.

PEARSE, A. M. 1981. Aspects of the biology of *Uropsylla tasmanica* Rothschild (Siphonaptera). Master's thesis, University of Tasmania, Hobart, Tasmania, Australia, 195 pp.

POCOCK, R. I. 1926. The external characters of *Thylacinus, Sarcophilus,* and some related marsupials. Proceedings of the Zoological Society of London 1926:1,037–1,084.

RAMSAY, E. P. 1888. Notes on the fauna of the Bellenden-Ker Ranges. Proceedings of the Linnaean Society of New South Wales, Second Series 3:1295–1299.

RAYMOND, J. T., L. TELL, M. BUSH, D. K. NICHOLS, F. Y. SCHULMAN, AND R. J. MONTALI. 2000. Subcutaneous atypical mycobacteriosis in captive tiger quolls (Dasyurus maculatus). Veterinary Pathology 37:137–142.

ROUNSEVELL, D. E., R. J. TAYLOR, AND G. J. HOCKING. 1991. Distribution records of native terrestrial mammals in Tasmania. Wildlife Research 18:699–717.

SAKAI, R., AND E. W. VAN LENNEP. 1984. The Harderian gland in Australian marsupials. Journal of Mammalogy 65:159–162.

SALLIS, J. D., AND E. R. GUILER. 1977. Unusual plasma acid phosphotase activity in two species of Tasmanian marsupials. Pp. 327–335 in The biology of marsupials (B. Stonehouse and D. Gilmore, eds.). The Macmillan Press Ltd, London, United Kingdom.

SCOGGINS, B. A., ET AL. 1970. The physiological and morphological response of mammals to changes in their sodium status. Pp. 577–600 in Hormones and the environment (G. K. Benson and J. G. Phillips, eds.). Cambridge University Press, Cambridge, United Kingdom.

SERENA, M., AND T. SODERQUIST. 1995. Western quoll. Pp. 62–64 in The mammals of Australia. Second edition (R. Strahan, ed.). Australian Museum/Reed Books, Sydney, New South Wales.

SETTLE, G. A. 1978. The quiddity of tiger quolls. Australian Natural History 19:164–169.

SHARMAN, G. B. 1961. The mitotic chromosomes of marsupials and their bearing on taxonomy and phylogeny. Australian Journal of Zoology 9:38–60.

SPRATT, D. M. 1991. A catalogue of the Australasian monotremes and marsupials and their recorded helminth parasites. Records of the South Australian Museum, Monograph Series 1: 1–105.

STRAHAN, R. 1981. A dictionary of Australian mammal names. Angus and Robertson Publishers, Sydney, New South Wales, Australia.

STRAHAN, R. 1995. The mammals of Australia. Second edition. Australian Museum/Reed Books, Sydney, New South Wales.

TELL, L., R. MONTALI, S. CITINO, M. BUSH, Y. SCHULMAN, AND L. COLLINS. 1993. Pathological findings in tiger quolls (*Dasyurus maculatus*) at the National Zoological Park. Pp. 55–60 in The biology and management of Australasian carnivorous marsupials (M. Roberts, J. Carnio, G. Crawshaw, and M. Hutchins, eds.). Metropolitan Toronto Zoo and the Monotreme and Marsupial Advisory Group of the American Association of Zoological Parks and Aquariums, Toronto, Ontario, Canada.

TRIGGS, B. 1996. Tracks, scats and other traces. A field guide to Australian mammals. Oxford University Press, Melbourne, Victoria, Australia.

TROUGHTON, E. 1943. Furred animals of Australia. Angus and Robertson, Sydney, New South Wales, Australia.

TROUGHTON, E. 1954a. The marsupial "tiger" cat. The Australian Museum Magazine 11:168–170.

TROUGHTON, E. 1954b. The marsupial "tiger cat." Birth and growth in captivity. The Australian Museum Magazine 11:200–202.

VAN DYCK, S. 1987. The bronze quoll, *Dasyurus spartacus* (Marsupialia: Dasyuridae), a new species from the savannahs of Papua New Guinea. Australian Mammalogy 11: 145–156.

WAKEFIELD, N. A. 1964. Recent mammalian sub-fossils of the basalt plains of Victoria. Proceedings of the Royal Society of Victoria 77:419–425.

WAKEFIELD, N. A. 1967a. Mammal bones in the Buchan district. Victorian Naturalist 84:211–214.

WAKEFIELD, N. A. 1967b. Preliminary report on McEachern's Cave, S. W. Victoria. Victorian Naturalist 84:363–383.

WALLIS, R., AND H. BRUNNER. 1984. Predator scat analysis–availability of packing yarn and a report on an unusual dog scat from east Gippsland. Victorian Naturalist 101:79.

WATT, A. 1993. Conservation status and draft management plan for *Dasyurus maculatus* and *D. hallucatus* in southern

Queensland. Report for Queensland Department of Environment and Heritage and The Department of the Environment, Sport and Territories, October:1–132.

WERDELIN, L. 1986. Comparison of skull shape in marsupial and placental carnivores. Australian Journal of Zoology 34:109–117.

WOOLLEY, P., AND S. J. WEBB. 1977. The penis of dasyurid marsupials. Pp. 307–323 in The biology of marsupials (B. Stonehouse and D. Gilmore, eds.). The Macmillan Press Ltd, London, United Kingdom.

WROE, S. 1997. A re-examination of proposed morphology-based synapomorphies for the families of Dasyuromorphia (Marsupialia): part I, Dasyuridae. Journal of Mammalian Evolution 4: 19–52.

WROE, S., AND B. R. MACKNESS. 1998. Revision of the Pliocene dasyurid, *Dasyurus dunmalli* (Dasyuridae: Marsupialia). Memoirs of the Queensland Museum 42:605–612.

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