

Petauroides volans (Diprotodontia: Pseudocheiridae)

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Abstract: *Petauroides volans* (Kerr, 1792) is a pseudocheirid marsupial with the common name greater glider. It is the largest and most conspicuous of the gliding possums and is 1 of the most numerous arboreal marsupials in the eucalypt forests of eastern Australia. Its gliding membranes are large and its thick, shaggy coat obscures the basic body form, making the animal appear much larger than it actually is. *P. volans* is nocturnal, arboreal, solitary, and folivorous and is dependent on large tree hollows for shelter. In Australia, *P. volans* has received particular attention because it is highly sensitive to the removal of old hollow-bearing trees during forestry practices such as clear-cutting. DOI: 10.1644/866.1.

Key words: arboreal marsupial, Australia, folivore, gliding, greater glider, hollows, marsupial, possum

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Petauroides Thomas, 1888

Petaurus Shaw, 1791: text to pl. 60.

Didelphis: Kerr, 1792:199. Part, not *Didelphis* Linnaeus, 1758.

Volucella: Bechstein, 1800:351. Not *Volucella* E. L. Geoffroy, 1764; and not *Volucella* Fabricius, 1794.

Phalanger: Lacépède, 1801:491. Not *Phalanger* Storr, 1780.

Phalangista: Desmarest, 1803:381. Not *Phalangista* É. Geoffroy Saint-Hilaire and Cuvier, 1795.

Petaurista: Desmarest, 1820:268. Not *Petaurista* Link, 1795.

Petauroides Thomas, 1888:163. Type species *Didelphis volans* Kerr, 1792, by monotypy.

Petaurides Ramsay, 1890:77. Subsequent misspelling of *Petauroides* Thomas, 1888.

Belideus: Anonymous, 1890:1030. Not *Belideus* Waterhouse, 1839.

Schoinobates: Iredale and Troughton, 1934:28. Not *Schoinobates* Lesson, 1842.

CONTEXT AND CONTENT. Order Diprotodontia, suborder Phalangeriformes, superfamily Petauroidea, family Pseudocheiridae, subfamily Hemibelideinae. The family Pseudocheiridae consists of 17 species within 6 genera (Groves 2005): *Hemibelideus*, *Petauroides*, *Petroseudes*, *Pseudocheirus*, *Pseudochirops*, and *Pseudochirulus*.

Petauroides volans (Kerr, 1792) Greater Glider

Didelphis volans Kerr, 1792:199. Type locality “New South Wales.”

Didelphis volucella Meyer, 1793:27. Type locality “Neusudwales” (= New South Wales).

Didelphis macroura Shaw, 1794:33. Type locality “New Holland” (= Australia).

Volucella nigra Bechstein, 1800:351. Type locality “Neuholland” (= Australia).

Volucella macroura: Bechstein, 1800:353. Name combination.



Fig. 1.—An adult *Petauroides volans* from Willi Willi National Park, New South Wales. Used with permission of the photographer P. German.

- Phalanger volans*: Lacépède, 1801:491. Name combination.
Phalangista volans: Desmarest, 1803:381. Name combination.
Petaurus macroura: Oken, 1816:1118. Name combination; unavailable name (International Commission on Zoological Nomenclature 1956, Opinion 417).
Petaurus niger: Oken, 1816:1119. Name combination; unavailable name (International Commission on Zoological Nomenclature 1956, Opinion 417).
Petaurus taguanoides: Desmarest, 1817:400. Type locality “Nouvelle-Hollande” (= Australia).
Petaurus macrourus: Desmarest, 1817:402. Name combination.
Petaurus peronii: Desmarest, 1817:404. Type locality “Nouvelle-Hollande” (= Australia).
Petaurista taguanoides: Desmarest, 1820:269. Name combination.
Petaurista macroura: Desmarest, 1820:269. Name combination.
Petaurista peronii: Desmarest, 1820:270. Name combination.
Phalangista macroura: Schinz, 1821:260. Name combination.
Petaurus didelphoides: Cuvier, 1825:129. Type locality “Australie.”
Petaurus maximus: Partington, 1837:424. Name combination.
Petaurus (Belideus) macrourus: Waterhouse, 1841:288. Name combination.
Petaurus (Petaurista) taguanoides: Waterhouse, 1846:322. Name combination.
Petaurus volans: O. Thomas, 1879:397. Name combination.
Petaurista volans: O. Thomas, 1885:728. Name combination.
Petauroides volans: O. Thomas, 1888:165. First use of current name combination.
Belideus cinereus: Anonymous, 1890:1030. Type locality “Bellenden Ker Ranges, North Eastern Queensland.”
Petaurides cinereus: Ramsay, 1890:78. Name combination.
Petauroides volans incanus: O. Thomas, 1923:247. Type locality “Eidsvold, Queensland.”
Petauroides volans armillatus: O. Thomas, 1923:248. Type locality “Coomooboolaroo Station, Queensland.”
Schoinobates volans: Iredale and Troughton, 1934:29. Name combination.

CONTEXT AND CONTENT. Context as for genus. The genus *Petauroides* is monotypic, and 2 subspecies are currently recognized (Flannery 1994; McKay 1988, 2008):

- P. v. volans* Kerr, 1792:199. See above.
P. v. minor Collett, 1887:829. Type locality “Herbert Vale,” Queensland; *cinereus* (Anonymous), and *armillatus* O. Thomas, are synonyms.

NOMENCLATORIAL NOTES. The taxonomic history of *Petauroides volans* has been recently reviewed (Maloney and Harris 2008). Originally, taxonomic affinity was suggested to

be with *Didelphis* (Phillip 1789). However, generic distinction was needed and although *Volucella* Bechstein, 1800, and *Petaurista* Desmarest, 1820, were offered, they were soon found to be already occupied. Later, Thomas (1888) advanced *Petauroides*, but then Iredale and Troughton (1934) argued that *Schoinobates* Lesson, 1842, antedated *Petauroides*. The name *S. volans* then remained in use for around 50 years. However, McKay (1982) found that the name *Schoinobates* was unavailable for Australian marsupials and that *Petauroides* must stand.

Among a long list of synonyms for *P. volans* in Thomas (1888), the name *Phalangista petaurista* Geoffroy Saint-Hilaire, 1803, is not synonymous with *P. volans* because the original description represents the yellow-bellied glider (*Petaurus australis*). Two other names (*Petaurus leucogaster* Mitchell, 1838, and *Petaurista leucogaster* Gray, 1841) listed in Thomas (1888) as synonymous with *P. volans* probably represent the squirrel glider (*Petaurus norfolcensis*—see Maloney and Harris 2008).

The genus name means *Petaurus*-like; the specific name is derived from the Latin word *volare* meaning to fly (McKay 2008; Strahan 1981). Vernacular names used include black flying opossum, flying opossum, long-tailed opossum, large-tailed *Petaurista*, Peron’s *Petaurista*, white-bellied flying squirrel, gray flying squirrel, large-tailed flying squirrel, taguan flying opossum, taguan flying phalanger, greater flying phalanger, brill, flying phalanger, great flying opossum, flying squirrel, dusky glider, and greater glider-possum (see Maloney and Harris 2008). Stability was achieved in 1980 when a committee of the Australian Mammal Society formalized it as greater glider. Known Aboriginal names for this animal include poong-goong and warnda (Fleay 1947).

DIAGNOSIS

Petauroides volans is the only gliding member of the family Pseudocheiridae. It is the largest gliding marsupial, distinguished from other Australian gliders (families Acrobatidae and Petauridae) by a patagium attached to the elbow of the forearm instead of to the outer digit of the manus (Johnson-Murray 1987; McKay 1988). Another diagnostic feature of *P. volans* is an elongated tail that is much longer than the body.

GENERAL CHARACTERS

Petauroides volans (Figs. 1 and 2) is a medium-sized, arboreal marsupial with large gliding membranes, short head, short, pointed muzzle, and large, erect, oval-shaped ears that are furred externally but naked inside. The tail is long and evenly bushy, pendulous, and with a small naked area on the ventral surface at the tip (Fleay 1933; Marlow



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Petauroides volans*, from Gosford, New South Wales, collected on 13 July 1979 and donated to the Australian Museum by the Taronga Zoo Trust (museum



Fig. 3.—Black and white color morphs of *Petauroides volans*. Studio photo taken in Canberra, Australia. Used with permission of the photographer E. Beaton.

1962; McKay 1988). The thick, shaggy coat obscures the basic body form making the animal appear much larger than it actually is (Flannery 1994). However, the ventral sides of the membranes have a lower density of hair (Rübsamen et al. 1984). Illustrations showing the arrangement of the hair also have been published (Boardman 1943, 1945). The hairs are fine and soft and eye-shaped in cross section (guard hairs maximum diameter = 35 μ m; maximum length = 60 mm—Brunner and Triggs 2002). Fur color is highly variable ranging from jet black to dark chocolate through gray and mottled to white (Fig. 3; Comport et al. 1996; Flannery

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registration number M6640). Greatest length of skull is 61.4 mm. Used with permission of the photographer K. S. Maloney.

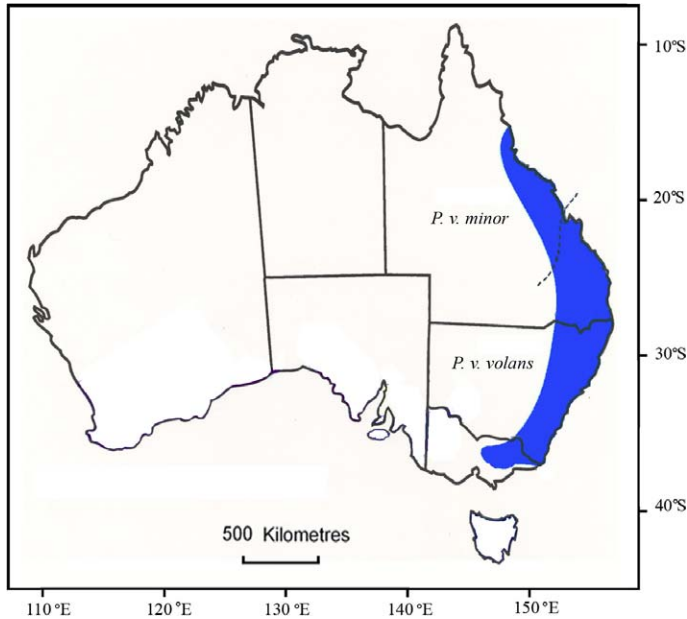


Fig. 4.—Geographic distribution of *Petauroides volans*. Adapted from Eyre (2004), Kavanagh (2004), van der Ree et al. (2004), and Winter et al. (2004).

1994). *P. v. minor* differs morphologically from *P. v. volans* by being less variable in color, smaller in mass (700–900 g versus 1,000–1,700 g) and by having a more slender body with shorter ears and tail (Comport et al. 1996). Females are generally physically larger than males (Flannery 1994; Kavanagh and Wheeler 2004). Ranges for standard external measurements (mm) from 4 male and 5 female specimens in the Australian Museum were: length of head and body (males 390–419, females 398–428); length of tail (males 438–498, females 484–525); length of hind foot (males 43–52, females 49–54); length of ear (males 42–49, females 44–48—Flannery 1994).

On the forefoot, there are 5 toes with the 1st and 2nd opposable to the others. The hind foot has 5 toes with the 1st opposable and the 2nd and 3rd syndactylous (Flannery 1994; Marlow 1962; McKay 1988). All toes (except the hallux on the hind foot) have strong recurved claws for grasping onto bark (Flannery 1994; Johnson-Murray 1987; Marlow 1962). Another general character of *P. volans* is a peculiar musty smell resulting from its cloacal glands and urine dribbling (Comport et al. 1996; Fleay 1933, 1947; Henry 1984; Tyndale-Biscoe and Smith 1969a).

DISTRIBUTION

The distribution of *Petauroides volans* encompasses eucalypt forests throughout eastern mainland Australia from southeastern Victoria to northeastern Queensland (Fig. 4). The southern subspecies, *P. v. volans* inhabits temperate and subtropical areas from near Gippsland in

Victoria to southeastern Queensland (Eyre 2004, 2006; Henry 1995; Kavanagh 2004; van der Ree et al. 2004). The northern subspecies, *P. v. minor*, occurs in the wet-dry tropical region of northeastern Queensland, north from about the Tropic of Capricorn to around Cairns (Comport et al. 1996; Winter et al. 2004).

FOSSIL RECORD

Petauroides volans has been recorded from at least 8 late Pleistocene or Holocene fossil sites in southeastern Australia. Sites in Victoria include Murrindal Cliffs (Wakefield 1960a), Pyramids Cave (Wakefield 1960b, 1967, 1972), Grampians Owl Cave (Marshall 1985), and Mitchell River National Park (Bilney et al. 2006). Sites in New South Wales include Marble Arch (Hall 1975), Nettle Cave (Morris et al. 1997), Upper Mangrove Creek, and Barrenjoey Peninsula (Recher et al. 1993). In South Australia, *P. volans* is recorded from Robertson Cave near Naracoorte (Reed and Bourne 2000), but there are no modern records from this state, indicating a late Pleistocene range contraction. Today, the nearest populations to Naracoorte are in central Victoria, about 300 km to the east.

FORM AND FUNCTION

Dental formula is $i\ 3/1, c\ 1/0, p\ 3/1, m\ 4/4$, total 34 (Fig. 2; Maloney and Harris 2008). Further descriptions of the form and function of the dentition are available (Archer 1984; Hume 1999; Lindenmayer 2002; Menkhorst and Knight 2001; Smith 1971; Springer 1993; Tate 1945; Triggs 1996; Turnbull et al. 1987). The pouch is well developed, opens anteriorly (type 5—Russell 1982) and contains 2 teats (McKay 1988; Tyndale-Biscoe and Renfree 1987). Brain mass to body mass ratio is small compared to that of other possums and gliders (Haight and Nelson 1987; Sanderson 2004). The erythrocytes have moderate central paleness, with mild anisocytosis (unequal size), and neutrophils have 3–6 nuclear lobes composed of coarsely clumped chromatin (Clark 2004; Viggers and Lindenmayer 2001). Basal respiratory frequency is 18 breaths/min (Rübsamen et al. 1984). The natural frequency of urination is 4–12 times per day (Foley and Hume 1987b). Total body surface area is 2,664, 2,895, and 2,910 cm^2 for animals with masses of 1,100, 1,230, and 1,140 g, respectively, and for these animals the patagium accounted for 41%, 49%, and 46% of the total surface areas (Rübsamen et al. 1984). The anatomy of the male reproductive system closely resembles that of other marsupials, but there are only 2 pairs of Cowper's glands (Smith 1969). Testicular size is about 8.3–15.2 mm depending on breeding condition (Viggers and Lindenmayer 2001). In females, Woffian ducts are present, ovaries are slightly flattened, and the lateral vaginae unite posteriorly with the urethra to form a urogenital sinus (Smith 1969).

The musculature of the patagium in *P. volans* has been described from dissected specimens (Johnson-Murray 1987; see also Haswell 1886). The patagium can be used by *Petauroides volans* to reduce heat loss by increasing the insulation around the body and also as a heat sink in hot weather by changing postures and reducing the effective surface area (Rübsamen et al. 1984). Body temperature is relatively constant at ambient temperatures (T_a) between 5°C and 20°C ($\bar{X} = 35.4^\circ\text{C} \pm 0.4^\circ\text{C SD}$; $n = 22$ —Rübsamen et al. 1984). When body temperature rose above 38°C (at $T_a > 40^\circ\text{C}$) intense licking of extremities and the ventral body surface was observed (Rübsamen et al. 1984).

Petauroides volans is close to the lower limit of body weight at which mammals could be expected to sustain a strictly folivorous diet, and for this reason the species' nutrition, digestion, and metabolism have been of particular interest to animal physiologists (Dash 1988; Foley 1987; Foley and Hume 1987a, 1987b; Foley et al. 1987, 2004; Hume 1982, 1999, 2004; Hume et al. 1984; McIlwee et al. 2001). Various strategies are used to cope with the high-fiber, low-nutrient diet and the metabolic burden of detoxifying secondary plant compounds including selective retention of fine particulate digesta in the oversized cecum (Foley and Hume 1987a; Hume 1999). This reduces fecal nitrogen losses and decreases the gut-filling effects of bulk indigestible fiber (Foley and Hume 1987a). Basal metabolic rate is about 2.39 W/kg^{0.75} and field metabolic rate is about 6.64 W/kg^{0.75} (where $W = 87.72 \text{ kJ/day}$ —Foley 1987; Hume 1999; see also Rübsamen et al. 1984). For maintenance of zero nitrogen balance, captive *P. volans* required 700 mg/kg^{0.75} daily on a dietary basis, or 560 mg/kg^{0.75} on a truly digestible basis on foliage of *Eucalyptus radiata* that is high in terpenes, which elevates urinary nitrogen loss (Foley 1987; Foley and Hume 1987b). Requirements are lower in koalas, but these were determined with animals fed foliage of *E. punctata*, a species low in terpenes, and in phenolics (which elevate fecal nitrogen loss—Hume 1999). In free-living *P. volans*, the pattern of foliage selection is suggested to be related to foliar concentrations of nitrogen, and more particularly to the ratio of nitrogen to acid-detergent fiber (i.e., cellulose and lignin—Hume 1999; Kavanagh and Lambert 1990). Water turnover rates in free-living *P. volans* averaged 87 ml kg^{-0.75} day⁻¹, with about 58% of the water required provided by consumed leaves (Foley et al. 1990). About 21 ml/day of free water is needed by *P. volans* to remain in water balance (Foley et al. 1990; Hume 1999), and this is presumably obtained from dew condensation on leaf surfaces (Rübsamen et al. 1984).

ONTOGENY AND REPRODUCTION

There is some plasticity in the mating system of *Petauroides volans* (monogamous, polygamous, or polygynous—Comport et al. 1996; Lindenmayer and Lacy 1995;

Norton 1989; Pope et al. 2004) depending on habitat suitability and population density. One progeny is produced annually (monotocous—Smith 1969; Tyndale-Biscoe and Smith 1969a), although up to 50% of female *P. volans* do not breed in any given year, and juvenile mortality may reach about 20% by 1 year of age (Tyndale-Biscoe and Smith 1969a). Although physiologically polyestrous, breeding is restricted to a very brief period in February–May (Henry 1984; Smith 1969; Tyndale-Biscoe and Smith 1969a). The males are spermatogenic only during the brief breeding season and the testes regress after May (Baldwin et al. 1974; Kerle 2001; Smith 1969), so that females that fail to breed at the 1st estrus, or those that subsequently lose their young, do not conceive again during that year (Tyndale-Biscoe and Renfree 1987).

Length of the estrous cycle and gestation period in *P. volans* is unknown (Kerle 2001). Births are known to occur between April and June, and the newborns stay in the pouch until 4 months of age, long after their eyes are open and they are well furred (Smith 1969; Tyndale-Biscoe and Renfree 1987). For the next 3 months suckling young are carried on the mother's back (but not when gliding—Henry 1984) or are left in a den while the mother forages (Russell 1982; Tyndale-Biscoe and Renfree 1987). Weaning occurs in January when animals are about 7.5 months of age and they may become independent as early as 9 months (Henry 1984; Smith 1969; Tyndale-Biscoe and Smith 1969a). Dispersal occurs at about 12 months of age (Lindenmayer and Lacy 1995). Sexual maturity is reached at 18–24 months (Russell 1984; Tyndale-Biscoe and Renfree 1987; Tyndale-Biscoe and Smith 1969a). Maximum life span is 12–15 years (Lindenmayer 1997; Lindenmayer and Lacy 1995; Tyndale-Biscoe and Smith 1969a).

Embryonic development has been studied through various stages including as a 2-celled ovum (blastomeres = 37 by 38 by 117 μm), unilaminar blastocyst stage (shell diameter = 0.24–3.4 mm), and trilaminar stage (shell diameter = 4.4 mm—Bancroft 1973). This work established that it is not possible to visually determine the sex of newborns. Neonates have a mass of about 273 mg (Tyndale-Biscoe and Renfree 1987). The gonad was 1st recognizable as a developing testis in a pouch young of head length 8.5 mm, and as a developing ovary at head length 9.3 mm (Hill 1951). When the pouch fetus reaches a crown–rump length of about 33 mm, the body is still naked, but the rhinarium is defined, syndactyly on the pes can be observed, and claws are present on the digits (Hill 1951). At about 55 mm crown–rump length, the body is still naked, but a patagium is obvious, and sparse hairs are present on the muzzle (Hill 1951).

ECOLOGY

Population characteristics.—Population densities in suitable habitat vary from 0.5 to 3.8 animals/ha (Comport et al.

1996; Henry 1984; Kavanagh and Lambert 1990; Kehl and Borsboom 1984). The patchy distribution and variable population abundance is attributed primarily to differences in foliar nutrient levels (Braithwaite 1983; Comport et al. 1996; Kavanagh and Lambert 1990), and the presence and density of suitable tree hollows (Eyre 2006; Henry 1995; Lindenmayer et al. 1990). Other factors affecting the presence and abundance of *Petauroides volans* include soil fertility, eucalypt tree species, forest age and structural complexity, disturbance history, and predator abundance (Braithwaite 1983; Eyre 2006; Kavanagh 1988; Kavanagh and Lambert 1990; Lindenmayer et al. 1990; Lunney 1987; Wormington et al. 2002).

Petauroides volans inhabits a variety of types of eucalypt forest, from low, open forests on the coast to tall forests on the ranges and even low woodlands west of the Great Dividing Range (Flannery 1994). However, in many parts of its range it appears to be most common in high-elevation, tall, wet eucalypt forests (Bennett et al. 1991; Eyre 2004, 2006; Kavanagh et al. 1995; Maloney and Harris 2006; van der Ree et al. 2004). Scant information is available on the dispersal of young *P. volans* (McCarthy and Lindenmayer 1999a); presumably some inherit a part of their mother's range (Henry 1995). Adult males are believed to be antagonistic to their male offspring and may drive them away at an early age (Tyndale-Biscoe and Smith 1969a), causing many deaths among young males. This could be the cause of the female-biased sex ratio (about 1:1.56) that characterizes at least some populations of *P. volans* (Henry 1984, 1995; Lindenmayer and Lacy 1995; Tyndale-Biscoe and Smith 1969a).

Space use.—Home-range estimates are typically 1.2–4.1 ha (Comport et al. 1996; Henry 1984; Kavanagh and Wheeler 2004; Kehl and Borsboom 1984; Pope et al. 2004), with those of males usually larger than those of females (Comport et al. 1996; Henry 1984; Pope et al. 2004; Smith et al. 2007). However, in southern Queensland, males of *Petauroides volans* have been recorded using large home ranges of up to 19.3 ha (Eyre 2004; Smith et al. 2007). Home ranges may overlap both within and between the sexes but animals closely associate with each other only during the breeding season (Comport et al. 1996; Henry 1995; Kavanagh and Wheeler 2004; Pope et al. 2004; Smith et al. 2007; Tyndale-Biscoe and Smith 1969a).

Very large hollows in a trunk or branch of tall, large-diameter trees are used for denning (Kavanagh and Lambert 1990; Kavanagh and Wheeler 2004; Lindenmayer 1997; Lindenmayer et al. 1991, 2004). Typically, 4–20 different dens are used by individual animals within their home range (Comport et al. 1996; Smith et al. 2007). Den selection by *P. volans* is influenced by a wide range of factors (Comport et al. 1996; Lindenmayer et al. 1990). Hollows develop extraordinarily slowly in Australian eucalypts, with figures most often quoted as minimum times of 150–260 years from germination to the beginning of hollow development (see Smith et al. 2007 and references therein).

Diet.—*Petauroides volans* is a selective arboreal folivore, feeding almost exclusively on young leaves and flower buds of a few favored *Eucalyptus* species in each particular locality (Bennett et al. 1991; Comport et al. 1996; Kavanagh and Lambert 1990; Marples 1973). *Eucalyptus radiata* is a widely preferred species in Victoria (Henry 1995), and *P. volans* is thought to prefer *E. viminalis* in southeastern New South Wales (Kavanagh and Lambert 1990), and *E. acmenoides* in northeastern Queensland (Comport et al. 1996). Other important diet species include *E. fastigata*, *E. globoidea*, *E. moluccana*, *E. regnans*, and *E. tereticornis* (Eyre 2004, 2006; Fleay 1933, 1947; Henry 1995; Kavanagh and Wheeler 2004; Le Souef and Burrell 1926; Maloney and Harris 2006; Smith et al. 2007). There are occasional feeding observations on noneucalypts (e.g., *Acacia* and *Amyema*) but these are infrequent and are not considered to represent the primary diet (Cunningham et al. 2004; Henry 1995; Le Souef and Burrell 1926; Lindenmayer 2002; Maloney and Harris 2006; Troughton 1957). Analysis of stomachs collected from freshly killed *P. volans* ($n = 133$) provided estimates of daily food intake for adults ($>1,000$ g) as 20 g dry weight or 108 kcal (Marples 1973). Feeding rates were about 2.8 g dry weight/h or 6 kg dry weight $\text{ha}^{-1} \text{year}^{-1}$ (3.2×10^4 kcal $\text{ha}^{-1} \text{year}^{-1}$ —Marples 1973). In 1 laboratory study, mean dry matter intake was recorded as 44 g $\text{kg}^{-0.75} \text{day}^{-1}$ (Foley 1987; see also McIlwee et al. 2001).

Diseases and parasites.—Various ticks and mites have been recorded as parasitic on *Petauroides volans* including *Ascospogonastia rattus*, *Campylochiroopsis dolichurus*, *Campylochirus antechinus*, *C. sthenophallus*, *Choristopsylla ochi*, *Domrownysus dentatus*, *Guntheria peregrina*, *Haemolaelaps ulixes*, *Ornithonyssus petauri*, *Sclerochiroides mirabilis*, *Trichosurolaelaps fallax*, *T. marra*, *T. striatus*, and *Trixacarus caviae* (Domrow 1987, 1992; Domrow and Lester 1985; Dunnet and Mardon 1974). Mites have been implicated in the death of some *P. volans* (Fleay 1933, 1947). Internal parasites recorded include *Austroxyuris finlaysoni*, *Bertiella mawsonae*, *B. petaurina*, *Cercopithifilaria johnstoni*, *Marsupostrongylus minesi*, and *Paraustroxyuris parvus* (Beveridge 1978; Beveridge and Spratt 1996; Johnston and Mawson 1938; Mawson 1964; Spratt et al. 1990). *Chlamydia* is reported for *P. volans* but it does not appear to compromise breeding success as it has done in some populations of koalas (Lindenmayer 2002).

Interspecific interactions.—An important predator of *Petauroides volans* is the powerful owl (*Ninox strenua*), which may feed exclusively on *P. volans* in some areas (Kavanagh 1988). Over a 3-year period, 2 individuals of *N. strenua* were suggested to have reduced 80 *P. volans* to only 7 individuals (Kavanagh 1988). Other predators such as the domestic cat (*Felis catus*), dingo (*Canis lupus dingo*), domestic dog (*C. lupus familiaris*), and red fox (*Vulpes vulpes*) occasionally catch *P. volans* on the ground or consume remains after primary predation by other animals (Coman and Brunner 1972; Kavanagh 1988; Maloney and Harris 2006; Robertshaw and

Harden 1985; Tyndale-Biscoe and Smith 1969b). There are also predation records for wedge-tailed eagle (*Aquila audax*), spotted-tail quoll (*Dasyurus maculatus*), sooty owl (*Tyto tenebricosa*), lace monitor (*Varanus varius*), and carpet python (*Morelia spilota*—Belcher et al. 2007; Bilney et al. 2006; Jarman et al. 2007; Lindenmayer 2002; Maloney and Harris 2006; Weavers 1989).

Miscellaneous.—*Petauroides volans* has been maintained in the laboratory (Foley 1987; Foley and Hume 1987a, 1987b; McIlwee et al. 2001; Nagy et al. 1990; Rübssamen et al. 1984) and hand-raised orphaned individuals are occasionally maintained in zoos (Fleay 1933, 1947). However, *P. volans* is not regarded as a good display animal and for this reason there has not been a serious attempt to establish the species in captivity (George 1990). Moreover, arboreal folivores are difficult to maintain in captivity on natural diets, and it has not been possible to maintain *P. volans* on artificial diets (Foley and Hume 1987b; Troughton 1957).

Petauroides volans can be relatively difficult to capture because it is active high above the ground (Henry 1984; Kavanagh and Lambert 1990; Tyndale-Biscoe and Smith 1969a). In addition, *P. volans* is difficult to lure into traps because its diet of eucalypt leaves is widely available (Pope et al. 2004). Previously, animals have been netted from dens (Henry 1984), shaken from low branches with a long pole (Comport et al. 1996; Russell 1980), or caught on the ground after using a rifle to prune branches on which animals perched (Henry 1984; Kavanagh and Wheeler 2004; Kehl and Borsboom 1984; Pope et al. 2004; Smith et al. 2007). Another accepted method for detecting *P. volans* involves “stag-watching,” which involves scanning the crowns of trees that may have suitable cavities before, during, and after dusk and identifying species by behavior, silhouette, or call (Lindenmayer 2002; Lindenmayer et al. 1990; Smith et al. 1989). However, by far the most widely employed census technique is spotlighting, in which reflected eyeshine or body shape of an animal is detected by a handheld, high-powered light beam (Comport et al. 1996; Eyre 2006; Henry 1984; Kavanagh 1984, 1988; Kavanagh and Lambert 1990; Lindenmayer et al. 2001; Maloney and Harris 2006; Smith et al. 2007; Wintle et al. 2005). In this species, the eyeshine is highly reflective and a brilliant white color (Lindenmayer 2002; McKay 1988; Menkhorst and Knight 2001; Russell 1980).

Fecal pellets are reddish brown, small, often irregularly shaped, and very dry, and have little or no odor (Flannery 1994; Triggs 1996). They are found in large numbers under den trees, because *P. volans* defecates soon after emerging from the den (Triggs 1996).

BEHAVIOR

Petauroides volans is mainly solitary but a den may be shared with a mate during the breeding season (Comport et

al. 1996; Cunningham et al. 2004; Fleay 1933; Henry 1984; Kavanagh and Lambert 1990). The young stay with the female until they disperse (Fleay 1933). Individuals in adjacent home ranges may actively avoid each other, and when social interactions do occur they are generally nonaggressive. However, agonistic behavior has occasionally been observed between males and between females (Comport et al. 1996; Henry 1984).

Of 1,107 behavioral observations at Taravale Station near Paluma, in northeastern Queensland (Comport et al. 1996), 2 individuals were observed together in a tree only on 78 occasions (7.0%) and these mainly occurred in November and December. Social interactions observed included nasal-ing, mutual sniffing, climbing over the top of another, and sitting beside a consort (see Comport et al. 1996).

Petauroides volans is strictly nocturnal and does not emerge from its sleeping dens before sunset (mean emergence time = 36 min after sunset \pm 2 SD; n = 59—Lindenmayer et al. 1990). However, for about 30% of animals the emergence time is more than 1 h after dusk (Lindenmayer et al. 1990; Smith et al. 1989). During the day, *P. volans* usually chooses a large, old tree, nesting in a hollow high up in the trunk, which it sometimes lines with leaves and strips of bark (Fleay 1947; Triggs 1996; Troughton 1957). Sleeping animals typically adopt a curled posture, with the tail wound around the body (Rübssamen et al. 1984). Frequently changing den sites may be due to predator or parasite avoidance or a mechanism to maintain their home range (Comport et al. 1996).

A number of secondary sources (Flannery 1994; Kerle 2001; McKay 1983) indicate that horizontal distances of up to 100 m are able to be covered in a single glide, and animals can turn, in midglide, through a 90° arc (no primary source found). Note that Wakefield (1970) disputes some of what has been written about the gliding ability of *P. volans*, and suggests that some observations may actually be attributable to the yellow-bellied glider. Glides by *P. volans* are usually undertaken from the top of one tree to the lower trunk of another (Fleay 1947). *P. volans* reduces the force of impact by stalling just before landing and the tail may be used for steering (Fleay 1933; McKay 1988, 2008). A “clap” may be heard as an animal lands on the bark (Le Souef and Burrell 1926), and scratchings on the bark from repeated landings can sometimes be detected (Fleay 1933, 1947; McKay 2008). Because the patagium reaches only the elbow, not the wrist, its gliding posture is unique among other gliders (Flannery 1994; Fleay 1947). When gliding, the forelimbs are folded and the wrists tucked under the chin, and the general shape of the patagium when outstretched is triangular (Fleay 1933, 1947; Johnson-Murray 1987; Troughton 1935). Walking is extremely clumsy and slow, and is described as an undulating gallop (Fleay 1947; Troughton 1935).

Petauroides volans tends to rest, feed, and den in the uppermost strata of the forest canopy (Bennett et al. 1991;

Cunningham et al. 2004; Kavanagh and Lambert 1990; Lindenmayer 1997). Feeding behavior involves grasping a branchlet with 1 forepaw and drawing it toward the mouth (Kavanagh and Lambert 1990). Most of its energy budget is spent resting (40.4%) and feeding (33.0%), and a much smaller amount is spent moving (12.5%) and grooming (5.5%—Comport et al. 1996; see also Kehl and Borsboom 1984). This species has no loud vocalizations and is generally silent (Borsboom 1982; Wakefield 1970), and scent-marking is probably the principal method of remote communication (Comport et al. 1996; Flannery 1994; Henry 1984; Kerle 2001; Russell 1984).

GENETICS

Petauroides volans has XY/XX sex determination and the diploid number (2n) is 22 (Agar 1923; McKay 1984; McQuade 1984). However, variations in the morphology of the X and Y chromosomes have been found to occur, such that 2–6 supernumerary (or B) chromosomes may be present (Hayman and Martin 1965, 1969; McQuade et al. 1994; Murray et al. 1979).

A number of molecular studies indicate that *P. volans* forms a monophyletic group with the ringtail possums (family Pseudocheiridae) including *Pseudocheirus* (Baverstock et al. 1987, 1990; Kirsch 1968, 1977) and *Hemibelideus* (McQuade 1984; Springer 1993; Springer et al. 1992). Previously, *P. volans* was grouped in the Petauridae (McKay 1988). Divergence of *Petauroides* and *Pseudocheirus* occurred about 36 million years ago, and divergence of *Petauroides* and *Hemibelideus* about 18 million years ago (Springer et al. 1992). Genetic analysis of metapopulation structure in fragmented landscapes has been used to examine the response of *P. volans* to disturbance (see Lindenmayer et al. 1999a; Taylor et al. 2002, 2007).

CONSERVATION

The species is rated as “Least Concern” on the 2010 *International Union for Conservation of Nature and Natural Resources Red List of Threatened Animals* (International Union for the Conservation of Nature and Natural Resources 2010), and is not listed as a threatened species federally within Australia or in state-based legislation in Queensland, New South Wales, or Victoria. However, in the Eurobodalla local government area of New South Wales 1 population is considered endangered because it is disjunct, isolated, and faces future habitat loss due to urban and rural residential development (New South Wales Scientific Committee 2006). A change in official status from “Common” to “Rare or Vulnerable” is suggested for another isolated population at Gilbert Range, northern Queensland (Winter et al. 2004).

Petauroides volans can be locally common in its preferred habitat. However, in many areas of its current distribution logging operations take place (Eyre 2006; Henry 1995), and the impact can be severely detrimental to this species (Goldingay and Daly 1997; Kavanagh et al. 1995; Tyndale-Biscoe and Smith 1969b). This is because *P. volans* depends on the canopy of mature forest for its fastidious diet and because it has small home ranges and high site fidelity, poor dispersal ability, a low reproductive rate, and it requires large tree hollows (Henry 1995; Hume 1999; Kavanagh 2000; Kavanagh et al. 1995; Kavanagh and Wheeler 2004; Lindenmayer et al. 1990, 1999a; Tyndale-Biscoe and Smith 1969b). It can survive in remnant eucalypt patches, but not in the large-scale exotic Monterey pine (*Pinus radiate*) stands that have been established for plantation forestry in southeastern Australia (Lindenmayer 2004; Lindenmayer and Lacy 1995; Lindenmayer et al. 1999a; Pope et al. 2004; Tyndale-Biscoe and Smith 1969b). The conflict between the conservation of *P. volans* and timber harvesting has led to much recent work on predictive population modeling (Eyre 2006; Lindenmayer and Lacy 1995; Lindenmayer et al. 1995, 1999a, 1999b; McCarthy and Lindenmayer 1999a, 1999b; McCarthy et al. 2001; Possingham et al. 1994; Stockwell et al. 1990; Tyre et al. 1998). These studies have examined various issues pertaining to conservation of *P. volans*, including probability of extinction, metapopulation dynamics, patch occupancy, and the design of appropriately-sized nature reserves.

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