



FAUNA *of* AUSTRALIA

21. DASYURIDAE

S.R. MORTON,
C.R. DICKMAN &
T.P. FLETCHER



Mulgara—*Dasyercus cristicauda* [K. Johnson]



Sandhill Dunnart—*Sminthopsis psammophila* [F. Knight/ANPWS]



Long-tailed Dunnart—*Sminthopsis longicauda* [F. Knight/ANPWS]



Fat-tailed Dunnart—*Sminthopsis crassicauda* [CSIRO Wildlife & Ecology]



Wongai Ningau—*Ningau ridei* [J. Wombey]



Giles' Planigale—*Planigale gilesi* [CSIRO Wildlife & Ecology]



Kowari—*Dasyercus byrnei* [L. Lim]



Western Quoll—*Dasyurus geoffroi* [M. Evans]

DEFINITION AND GENERAL DESCRIPTION

The family Dasyuridae is a member of the mammalian subclass Marsupialia and, within it, is placed in the order Polyprotodonta. Three families constitute the superfamily Dasyuroidea: the Dasyuridae, the Thylacinidae and the Myrmecobiidae. The Dasyuroidea comprises the basically insectivorous and carnivorous Australian marsupials. The family Dasyuridae contains by far the most species of dasyuroids.

All members of the Dasyuridae have four pairs of upper and three pairs of lower incisors. The possession of numerous incisors (polyprotodonty) immediately distinguishes the dasyurids from the primarily herbivorous marsupials, the wallabies, kangaroos, wombats, koala, possums and gliders, which possess only two pairs of lower incisors. In addition, dasyurids have at least four separately developed toes on their hind feet, a character distinguishing them from the polyprotodont bandicoots which possess hind feet with the second and third toes bound together (syndactyly). The Numbat, *Myrmecobius fasciatus*, (family Myrmecobiidae) possesses five molar teeth which are structurally simple and is distinguished, thereby, from the Dasyuridae, all of which have four pairs of upper and lower molars with well-developed cusps. The Thylacine, or Tasmanian Tiger, *Thylacinus cynocephalus* is placed in a separate family, the Thylacinidae, principally on the basis of peculiarities of its dental and cranial morphology and because, unlike dasyurids, it lacks epipubic bones (see Chapter 20).

Dasyurids are marsupials with five toes on the forefeet and four or five on the asyndactylous hind feet. When present, the inner rear toe (hallux) is always clawless. There are four pairs of upper and three pairs of lower incisor teeth, a single pair each of upper and lower canines, two or three pairs of premolars (of which the third upper pair is characteristically small) and four molars with many cusps. The dental characteristics of dasyurids reflect their insectivorous and carnivorous habits. The face of dasyurids has a long, pointed appearance when compared to the blunter faces of the diprotodont marsupials and the eutherian rodents. The pouch may be well developed or represented simply by raised ridges; the opening is directed either downward or backward. The number of nipples varies among the species from 4 to 12 and may vary within a species. There is considerable variation in size from the tiny Long-tailed Planigale, *Planigale ingrami* (Thomas 1906; 4 grams, the world's smallest marsupial) to the strongly-built Tasmanian Devil, *Sarcophilus harrisii*, but across this size range there is considerable uniformity of body shape and structure. The most obvious variation in external morphology occurs in the hind feet. Arboreal species have broad hind feet and a mobile hallux, whereas in those that are both terrestrial and arboreal the hind feet are longer and the hallux is reduced. The Kultarr, *Antechinomys laniger* exhibits the extreme in body shape; it has elongated hind legs and a bounding gait. Because of the overall uniformity of body shape among dasyurids, identification of species from external characteristics relies on size, hind foot morphology, tail length and colour patterns.

HISTORY OF DISCOVERY

The first known report of a dasyurid by Europeans dates from April, 1770, when Captain Cook's party reported footprints like those of a polecat or weasel in the vicinity of Botany Bay (Mahoney & Ride 1984; Whitley 1970). The animal which made these tracks was almost certainly a *Dasyurus*, two species of which occurred in the vicinity at the time of European settlement. Cook and his party did not actually see a *Dasyurus* until their ship, the *Endeavour*, was beached at Endeavour River in north Queensland, where Cook's naturalists recorded a

spotted quadruped ‘of the viverra kind’ and ‘resembling a polecat’ (Mahoney & Ride 1984). Based on this specimen or specimens, the species *Mustela quoll* Zimmermann, 1777 was described as a member of the eutherian order Carnivora and was mentioned again by Zimmermann in subsequent publications (1780, 1783). The specimen was lost, like so much of the valuable material collected on Cook's voyage, and Zimmermann's name consequently was suppressed by the International Commission on Zoological Nomenclature. The species probably referred to by this name is that currently known as the Northern Quoll, *Dasyurus hallucatus* (Mahoney & Ride 1984), a species which remains abundant in coastal north Queensland. The term quoll, a literation of an Aboriginal word variously reported as dekol, taquol, jaquol or je-quoll, is believed to originate from the word dhigul used for *D. hallucatus* by people of the Guugu Yimidhirr tongue. Although it disappeared from scientific literature, quoll remains in use as a common name for *Dasyurus* species.

After white settlement at Sydney in 1788, two species of spotted ‘opossums’, ‘martins’ or ‘rats’ were mentioned in accounts of the colony (Mahoney & Ride 1984). The use of the term opossum indicates that in some cases the marsupial nature of reproduction in *Dasyurus* was recognised. One species, the Tiger Quoll, *Dasyurus maculatus*, was described as a member of a genus of Carnivora, *Viverra*. Other authors described the same species in similar genera, for example *Mustela novaehollandiae*. The second species, the Eastern Quoll, *Dasyurus viverrinus*, was described as a member of the American marsupial genus, *Didelphis*. Both species were quickly included in the genus *Dasyurus* (from the Greek, ‘hairy tail’), but taxonomic distinction above the generic level was not advocated until 1820, when Goldfuss recognised the Australian carnivorous marsupials as the tribe Dasyurini. Waterhouse (1841a) elevated the group to familial level, thereby establishing Dasyuridae Goldfuss, 1820 (for a detailed history and references, see Archer 1982a).

As in most other groups of Australian mammals, considerable taxonomic rearrangement occurred before the genera familiar to us today were established. The second species of dasyurid to be described, the Brush-tailed Phascogale, *Phascogale tapoatafa*, was placed initially with the Tiger Quoll in the genus *Viverra*. Both species were later listed as members of the American opossum genus *Didelphis*, together with the Eastern Quoll, and then all three were transferred to *Dasyurus*. The naming of *Phascogale* Temminck, 1824 removed the Brush-tailed Phascogale from *Dasyurus* and created a genus to which many of the smaller dasyurids were assigned throughout the 19th Century. Interestingly, two of the first dasyurid species to be described were given names of Aboriginal origin – quoll and tapoatafa – but virtually all subsequently described species have scientific names of European derivation. Only within the past ten years have Aboriginal words been used once more as the basis for dasyurid names. Similarly, despite some early interest in Aboriginal knowledge of dasyurids (for example, H.H. Finlayson in central Australia, Finlayson 1961; and D.F. Thomson in northern Australia, Dixon & Huxley 1985), the detailed observations of these superb naturalists have only recently begun to be recorded (Burbidge & Fuller 1979; Johnson & Roff 1982).

Only two more currently recognised species of dasyurids, both from Tasmania, were described in the early years of European settlement. The Swamp Antechinus, *Antechinus minimus*, was placed initially in *Dasyurus*. The genus *Antechinus* Macleay, 1841 was not established until many years later. The largest dasyurid, the Tasmanian Devil, *Sarcophilus harrisii*, was first described in 1808, but nomenclatural problems necessitated later redefinition. Commencing in the late 1830s, there was a 20-year period during which large numbers of new species and genera of dasyurids were described. Many names later proved to be invalid, particularly the genera, but the taxonomic activity increased the number of species currently accepted to about 20. Prominent

among the describers was John Gould, the great English naturalist and artist, who named seven dasyurids that are still recognised as valid species. During this period, the first fossil dasyurid, *Sarcophilus laniarius*, also was described.

A second upsurge in discovery of new species occurred in the period 1890-1910, resulting largely from collections made by travellers, naturalists and scientists in inland and northern Australia. The most important describers were W. Baldwin Spencer, Professor of Biology at the University of Melbourne, who worked in central Australia, and Oldfield Thomas, a mammalogist at the British Museum (Natural History) in London, who obtained material from many collectors in Australia (and, indeed, from all over the world). A quiet period ensued from 1910 to 1970, during which only about four currently recognised species were described. From 1970 until the present, however, there have been some 10 new species of dasyurids described and many generic rearrangements have taken place or been foreshadowed. Research into the systematics of dasyurids is, therefore, more intensive than in most other families of Australian marsupials and undoubtedly more species remain to be described.

Study of other aspects of dasyurid biology lagged well behind systematic work. Initially, investigations focused on homologies and succession of teeth in order to facilitate taxonomic understanding and to determine the relationships of the Dasyuridae (Thomas 1887b). Then, interest grew in the reproduction and embryology of dasyurids. Research was led by J.P. Hill, a demonstrator in biology at the University of Sydney in the 1890s, who maintained Eastern Quolls in captivity and assembled an extensive series of reproductive organs and early developmental stages from nearly 100 females. On his return to Great Britain, Hill and his co-workers published detailed accounts of the reproductive cycle and embryology of the Eastern Quoll (Hill 1900b, 1910; Sandes 1903; O'Donoghue 1911, 1912; Hill & O'Donoghue 1913; Hill & Hill 1955). In accordance with the spirit of the times, interest in the dasyurids was justified in terms of advancing eutherian research: 'we might reasonably hope, in view of the generally admitted (primitive) relationships of the Marsupialia, that a knowledge of their early development would aid us in the interpretation of that of Eutheria' (Hill 1910, p. 5). Hill's collections and notebooks remain of considerable value to present-day students of reproduction (Fletcher 1985; Selwood 1982). Most of the limited research on the Dasyuridae until 1950 was anatomical, although physiological studies were begun. An increasing amount of work was conducted in Australia as local universities became established, although European biologists remained important contributors (Martin 1902; Beddard 1908; Flynn 1910; MacKenzie 1918a, 1918b, 1919a; Sonntag 1921b; Pearson 1944b; Pearson & de Bavay 1951, 1953). Anatomical work culminated in the monographic studies of Tate (1947b) and Jones (1949).

Throughout the first half of the century, interest in the dasyurids as part of the Australian environment was kept alive by a few workers, notably David Fleay of the Sir Colin MacKenzie Sanctuary in Victoria (Fleay 1934, 1935), Frederic Wood Jones of the University of Adelaide and Hedley Herbert Finlayson of the South Australian Museum (Jones 1923a; Finlayson 1933a), Ludwig Glauert of the Western Australian Museum (Glauert 1933) and Ellis Troughton of the Australian Museum in Sydney (Troughton 1941). This limited attention to whole animal biology blossomed in the 1960s after studies of the Brown Antechinus, *Antechinus stuartii*, suggested that it had a surprisingly limited breeding period of only a couple of weeks each year (Horner & Taylor 1959; Marlow 1961). Subsequent laboratory and field work on *Antechinus* species confirmed these observations (Woolley 1966; Wood 1970) and led to a substantial expansion in research into many aspects of dasyurid biology, particularly ecological. The increase in field studies, together with survey work stemming from increased public awareness of conservation, in turn stimulated

the upsurge in systematic work referred to above. Knowledge of the Dasyuridae is now increasing rapidly, as evidenced by the recent publication of a substantial body of review papers (Archer 1982b).

MORPHOLOGY AND OESTRUS PHYSIOLOGY

Morphology

In their body plan, dasyurids resemble some of the eutherian Insectivora (shrews) and Carnivora (cats and weasels). Uniformity within the Dasyuridae is demonstrated by maintenance of proportions between limbs, skulls and axial skeletons of species across the size range of the family (Keast 1982). The digestive tracts of dasyurids all appear to be simple and without diverticula or specialisation. The small and large intestines are short and there is no caecum. Like eutherian carnivores, dasyurids eat food of high digestibility and so require only a simple digestive system (Hume 1982). The circulatory system, respiratory system, nervous system and sense organs do not diverge from the basic marsupial structure, except that many of the desert-dwelling species have quite large eyes and pinnae to enhance sight and hearing. Specialised exocrine glands occur and are mentioned in discussion of olfactory communication.

Important morphological differences are evident among dasyurid species. Two major trends are: increasing strength of teeth and jaws as the diet becomes more carnivorous (reaching maximum development in the Tasmanian Devil); and, evolution of a suite of characteristics (such as evacuated palates and altered molar cusp patterns) in small, desert-dwelling species as, for example, in the Fat-tailed Dunnart, *Sminthopsis crassicaudata* (Archer 1976a). Equally important differences can be seen in the structure of the pouch. Four general types of pouch can be defined on the basis of the arrangement of nipples and the extent to which the pouch is covered by skin folds, but there is no apparent correlation between pouch type and habitat, body size, litter size or duration of lactation (Woolley 1974). One noticeable morphological feature highly developed among dasyurids is caudal fat storage. Fat tails occur in desert-dwelling species of *Dasyurus*, *Pseudantechinus* and *Sminthopsis*. These allow increased fat storage where energy supplies are particularly uncertain, while allowing unhindered manoeuvrability during hunting (Morton 1980a).

Respiration and Energy Metabolism

Martin's (1902) work on body temperatures and metabolic rates of monotremes, marsupials and eutherians partly fostered the notion that marsupials were primitive mammals. Marsupial body temperatures were found to be intermediate between those of eutherians and monotremes. Further work showed that standard metabolic rates (oxygen consumption at rest) of dasyurids were indeed about 70% of those found in eutherian mammals of comparable size (MacMillen & Nelson 1969; Dawson & Hulbert 1970;). The reduced body temperature and standard metabolic rate do not extrapolate to intermediate energetic capacities. For example, the Paucident Planigale, *Planigale gilesi* and the Kowari, *Dasyuroides byrnei*, both found in arid regions, are able to increase their metabolic rates eight to nine times when held at temperatures from 5 to -10°C (Dawson & Dawson 1982). At -10°C, the Kowari was able to maintain its body temperature for at least 4 hours. The much smaller Paucident Planigale maintained normal body temperature for 3 hours at 0°C, but body temperature fell at -10°C. The largest extant dasyurid, the Tasmanian Devil, has a similar ability to thermoregulate by greatly increasing metabolic rate (Nicol & Maskrey 1980). Although acclimation to cold may have exaggerated the abilities of the dasyurids in these experiments (Reynolds & Hulbert 1982), it seems likely that

their higher metabolic scope is not an artifact. In two of these studies, rodents included for comparative purposes could not boost metabolism as greatly as the dasyurids. Thus, despite having a lower standard metabolic rate than eutherians of comparable size, dasyurids have a greater ability to increase their metabolic rates and maintain body temperature when exposed to cold.

Many eutherian mammals, when exposed to cold, generate heat by non-shivering thermogenesis in brown adipose tissue and skeletal muscle in response to the release of noradrenaline. Injection of noradrenaline into cold-exposed and warm-exposed Brown Antechinuses had no effect on metabolic rate (Reynolds & Hulbert 1982), suggesting that non-shivering thermogenesis may not be mediated by noradrenaline in dasyurids (Wallis 1982). Despite lack of knowledge about the cause of greater metabolic scope, it is clear that the phenomenon also allows dasyurids to exercise at a higher rate than would be expected on the basis of their standard metabolic rates (Baudinette 1982).

Torpor is a further widespread response to cold and to food shortage in dasyurids. When entering torpor, small dasyurids adopt a sleeping posture, lower their breathing and heart rates, and allow their body temperature to drop by up to 20°C (Wallis 1982). Torpor may last up to 10 hours and can reduce energy expenditure by a considerable amount. Most dasyurids probably experience torpor, although its depth, duration and regularity vary markedly (Nicol 1982; Wallis 1982). The occurrence of torpor in the wild has been studied only in the Fat-tailed Dunnart. In this species torpor appears to be used infrequently and only during the colder months of the year (Morton 1978a).

Excretion and Water Metabolism

The kidneys of dasyurids display no peculiarities of structure or function compared with other insectivorous mammals. Most dasyurid species, however, excrete urine of moderately high osmolarities (up to 4000 mosmol/L; Morton 1980b). The capacity to excrete urine of such concentrations may be necessary because of the high protein content of insect prey, despite the presence of 70–80% free water in such food.

Water metabolism is affected markedly by the high proportion of free water present in the food. All species examined show high rates of water turnover relative to herbivorous, granivorous or omnivorous marsupial and eutherian mammals (Nicol 1978b; Morton 1980b; Green & Eberhard 1983), suggesting that the ample supply of water in food frees most dasyurids from the necessity to restrict their water usage. Rates of water turnover are correlated highly with rates of energy metabolism, both in captive and free-living dasyurids, further indicating that water is metabolised relatively passively with energy (Green & Eberhard 1983). As a consequence, desert-dwelling dasyurids appear to experience little difficulty in obtaining sufficient free water from their food (Morton 1980b).

Reproduction

As in other marsupials, the female reproductive system is characterised by a duplex uterus and a vaginal complex where the ureters pass between the lateral vaginal canals before entering the urinary bladder (Pearson & de Bavay 1953). The two uteri open into the median vagina, which usually has a transverse septum along its length. In non-breeding animals, there is no direct connection between the median vagina and the urogenital sinus. Instead, two lateral vaginae loop out and slightly forwards from the median vagina before passing back to join together at the junction with the urethra to form the urogenital sinus. At parturition, a temporary pseudovaginal canal develops from the median vagina to the urogenital sinus, thereby allowing the fetuses to avoid the lateral vaginae.

The lateral vaginae function principally as storage organs for spermatozoa received during copulation. The ovaries are located along the dorsal surface of the uteri. Before ovulation, the lateral vaginae and uteri increase substantially in size, but the lateral vaginae regress during pregnancy.

The male reproductive system consists of an external pendulous scrotum located in front of the retractable penis. A large segmented prostate gland surrounds the urethra and two or three pairs of Cowper's glands. These glands provide fluid and mucus for the ejaculate, but the details of their functions are unclear (Setchell 1977; Fletcher 1985). Considerable variation occurs in the structure of the penis of dasyurids. Many, but not all, species have a bifid tip to the penis and the two branches are assumed to direct semen into the lateral vaginae of the female. In addition, members of the genera *Dasyurus*, *Myoictis*, *Parantechinus* and *Pseudantechinus* have an unusual penile appendage lying above the penis. The appendage consists of accessory erectile tissue derived from the corpora cavernosa and is attached to the levator muscles by a branch of the tendon which normally runs only to the penis (Woolley & Webb 1977; Woolley 1982a). The function of this appendage remains obscure.

The oestrus cycle of marsupials can be divided into a pre-oestrus or follicular phase and a luteal phase. In the follicular phase, growth and development of the Graafian follicle occur in the ovary and marked changes appear in the genital tract. After the Graafian follicle ruptures and the mature ovum is extruded, the luteal phase is initiated by conversion of the ruptured follicle to a corpus luteum. The luteal phase is terminated by the demise of the corpus luteum and may be followed by lactation, another follicular phase or dioestrus.

Progesterone, the steroid hormone produced by the corpus luteum, has been measured during the oestrus cycle of only two dasyurids, the Kowari, and the Eastern Quoll (Fletcher 1983; Hinds 1983). In the oestrus cycle of both species are two peaks of progesterone. There is a transient pro-oestrus rise in progesterone in all females, followed about two weeks after oestrus by elevated levels which continue for up to three weeks more. After this time, progesterone values fall dramatically indicating the end of the luteal phase and probably the demise of the corpus luteum. In both species, birth occurs about the time of decline in pro-oestrus progesterone secretion by the corpus luteum, so that gestation takes place only during the luteal phase. The source of the progesterone, however, is uncertain. Because some progesterone is produced before oestrus and before the corpus luteum becomes active, the ovarian interstitial tissue may also secrete the hormone (Fletcher 1983). The presence of the pro-oestrus progesterone in both species indicates that it may be important in eliciting oestrus or preparation of the urogenital tract for receiving spermatozoa.

Many dasyurids are polyoestrus, cycling regularly every 20–40 days during the breeding season until pregnancy ensues. Some species, notably *Antechinus* species, *Phascogale* species and the Tasmanian Devil, are monoestrus. Gestation periods vary from 12 to about 35 days (Woolley 1973).

The reproductive physiology of male dasyurids is generally poorly known. Polyoestrus species undergo various degrees of testicular regression after the breeding season, but in the Kowari, blood testosterone levels do not appear to change seasonally (Fletcher 1983). Rather, testosterone peaks at the time females come into oestrus, suggesting that testosterone stimulates production of the seminal fluid in readiness for mating and has little to do with spermatogenesis (Fletcher 1983).

In monoestrus *Antechinus* species, very high levels of testosterone and other androgens occur in August or September, probably to prepare the accessory sex glands for mating. In association with the extreme aggression exhibited by males at this time, however, these high hormonal levels have serious effects on the animals (Fig. 21.1). The rise in plasma androgens is associated with

depression of plasma corticosteroid binding globulin with a concomitant rise in corticosteroid concentration (Bradley, McDonald & Lee 1980; McDonald *et al.* 1981). As there is no high affinity binding protein in the plasma of dasyurids, all the androgens circulating in plasma are biologically active and result in the maximum corticosteroid binding capacity being exceeded quickly. Further, the depression of corticosteroid binding capacity is potentiated by an increase in adrenocortico-trophic hormone as a result of increased aggressive behaviour. The result of these endocrine changes is the induction of a state of stress in the male, causing major ulceration of the gastric mucosa (Barker *et al.* 1978; Bradley *et al.* 1980; McDonald *et al.* 1981). Parasitic and pathogenic organisms invade the animal (Barker *et al.* 1978) and it dies within a few days. These events have substantial ramifications for the life history of *Antechinus* species and *Phascogale* species, which are discussed in later sections.

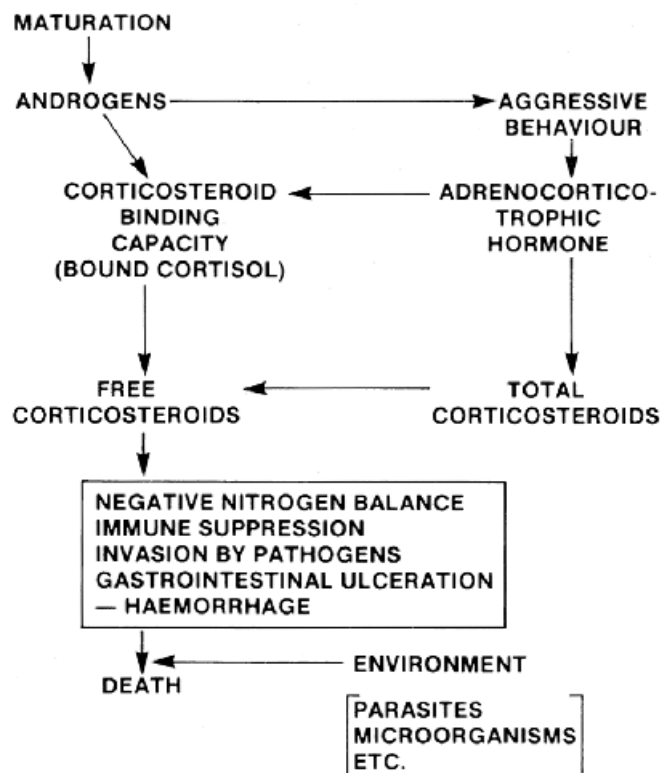


Figure 21.1 Hormonal changes associated with the die-off of male *Antechinus* spp. and *Phascogale* spp. (After Lee & Cockburn, 1985)

Sperm morphology is uniform among the Dasyuridae (Harding *et al.* 1982). The dasyurid spermatozoon is among the largest in mammals and characteristically has a wedge-shaped head with a laterally flattened flagellum. Karyotypes also have proved to be conservative in each species so far examined (Young *et al.* 1982). The autosomes of different species are generally indistinguishable on the basis of gross morphology, chromosomal arm lengths and G-banding pattern, but there are minor differences in the position of the centromere and the size and position of interstitial C-banding heterochromatin on the X chromosome.

Embryology and Development

After its release from the Graafian follicle of the ovary, the unfertilised egg moves into the oviduct, where it is fertilised. Immediately after fertilisation, the ovum becomes surrounded by a mucoid layer and the keratinous shell membrane that is characteristic of all marsupials. Within 24 hours, it moves down into the uterus, along with up to 50 other eggs shed at the same ovulation (Hughes 1982a; Selwood 1982). After entering the uterus, the eggs rapidly undergo the first and second cleavage divisions, but then undergo developmental arrest for several days. The blastocyst expands slowly after cleavage resumes and, in the Brown Antechinus, by about the 16th day the embryo possesses a distinct embryonic area (Selwood 1980). By the 22nd day, the embryo has a notochord and primitive streak. Organogenesis proceeds from this point to birth within seven more days. In species with shorter gestation periods, such as *Sminthopsis* species, the periods of developmental arrest presumably do not occur.

During birth, the female braces her cloaca above the substrate with her tail, which is extended behind the body. The head may be curled under the body, as it often is during sleeping, and the female may lick her cloacal area vigorously. The actual passage of neonates from the cloaca to the pouch has not been observed, but it is clear that the time taken is very short – perhaps only 30 seconds (Hutson 1976). The neonates probably are aided in their journey by the mother's posture, which enables them to crawl downhill (Williams & Williams 1982). The birth posture of dasyurids differs from that of larger marsupials, which sit on their tails or lie on their sides.

As with other marsupial young, the neonates become attached firmly to the teat and do not detach voluntarily for some weeks. Because many more eggs develop in the uterus than can be accommodated in the pouch, supernumerary young frequently are born. When they cannot find a nipple to which to attach, such young are discarded. Growth in the pouch is rapid; as an example, the Wongai Ningau, *Ningau ridei*, is considered (Fig. 21.2). At birth, the young have functional forelegs, nostrils and mouth. Ear buds appear at day 10 and the hindlimbs begin to develop digits at day 13. The head and dorsum begin to turn grey at about day 22 and by day 23 the eye is a large dark spot. At day 27 the ears are flat pads, the digits are well formed and fine hairs appear on the body. By day 38 ears are formed fully and vibrissae are developed. Finally, at day 43, the eyelids are separable, although eyes do not open until day 48. At day 70, the young have adult colouration. The young first detach from the nipple at 43 days. The mother leaves them in the nest at 48 days, although they continue to suckle for a further 40 days (Fanning 1982). Most dasyurids appear to show similar schedules of development; the timing is correlated with maternal body weight (Russell 1982).

NATURAL HISTORY

Life History

Dasyurids exhibit at least six different life history strategies distinguished on the frequency of oestrus, the seasonality of breeding, the duration and timing of male reproductive effort and the age at which both sexes achieve sexual maturity (Table 21.1; Lee, Woolley & Braithwaite 1982).

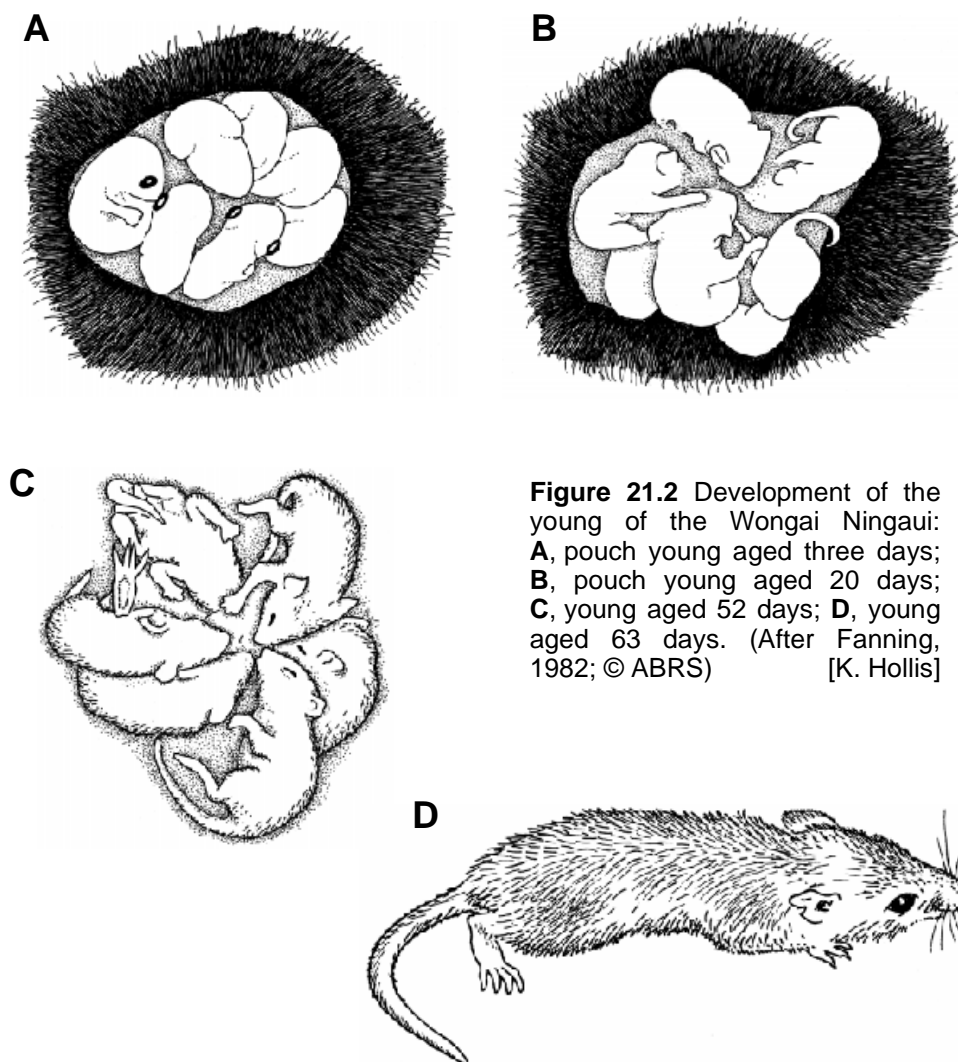


Figure 21.2 Development of the young of the Wongai Ningai: **A**, pouch young aged three days; **B**, pouch young aged 20 days; **C**, young aged 52 days; **D**, young aged 63 days. (After Fanning, 1982; © ABRS) [K. Hollis]

Table 21.1 Classification of dasyurid life histories. (After Lee *et al.*, 1982)

OESTROUS PATTERN	NO. OF SEASONS PER ♂	DURATION OF BREEDING SEASON	SEASONALITY OF BREEDING	AGE OF SEXUAL MATURITY	TYPE OF STRATEGY	NO. OF SPECIES
monoestrus	annual	restricted	seasonal	11 mo.	1	9
	perennial	restricted	seasonal	11 mo.	2	7 or 8
monoestrus or polyoestrus	perennial	restricted	seasonal	11 mo.	3	3 or 4
polyoestrus	annual	extended	seasonal	8–11 mo.	4	4
				6 mo.	5	3
			aseasonal	?	6	3

Strategy 1: In these cases, both sexes achieve sexual maturity at 11 months of age and mate during a short (two to three week) and highly synchronised period each year. All males die within two weeks of mating at the age of 12 months, but females may survive and reproduce in a second season (Wood 1970). All or almost all females breed (Fig. 21.3).

This Strategy is exemplified by the Brown Antechinus. Over the geographical range of this species, matings occur only between late July and late September (Dickman 1982a). In local populations, individual females are in oestrus for about four days (Selwood 1985), but males produce spermatozoa for 6 weeks before matings occur (Woolley 1966). Matings are triggered by rate of change of day length rather than by absolute day length. Reproduction is delayed by both increasing altitude and decreasing latitude (McAllan & Dickman 1986). Young are born after a 27 day gestation (Selwood 1980) and remain in the pouch for 35 days (Wood 1970). Thereafter they are placed in a nest until weaned at approximately 90 days of age.

The death of males after mating and the synchronous appearance of newly weaned young in January and February produce very marked and regular fluctuations in the size and structure of Brown Antechinus populations (Fig. 21.4). Studies of other *Antechinus* species exhibiting Strategy 1 suggest that all will show similar population dynamics (Smith 1984; Friend 1985).

Strategy 2: This differs from the above in that some males survive to breed in a second and possibly a third season. In a population of Dibblers, *Parantechinus bilarni*, (Johnson 1954) studied in the Northern Territory (Begg 1981a), matings occur in late June or early July and young are born in August. About 70% of males mating in their first season survive to their thirteenth month and, of these, 25% survive to a second breeding season. The increased longevity of male Dibblers compared to male Brown Antechinus suggests that the reproductive effort in each breeding season is less intense for Strategy 2 dasyurids. This is supported by Begg's (1981a) observation that only 65–88% of females carry litters each season (Fig. 21.3), whereas at least 92% of female Brown Antechinuses do so (Wood 1970).

Within-year fluctuations in the population size of Dibblers are slightly less marked than in Brown Antechinuses (Fig. 21.4). Densities are lowest between October and December while young are in the maternal nest and highest between February and July due to the influx of young animals. Other species exhibiting a similar life history (for example, the Northern Quoll, *Dasyurus hallucatus*; Begg 1981b) show similar population dynamics.

Strategy 3: This is generally exhibited by larger dasyurids, possibly including the Tasmanian Devil. Mating occurs variably between late autumn and spring. Females are usually monoestrus but, unlike females following Strategies 1 and 2, occasionally enter oestrus a second time if unmated or if the first litter is lost prematurely (Woolley 1971; Settle 1978). Some adults of both sexes may survive three or more breeding seasons, but in the Eastern Quoll most breeding animals are young of the previous season (Godsell 1982). In this species, young are born in June after a gestation period of 19–23 days and remain attached in the pouch for about 7 weeks. They are weaned by the end of October and contribute to marked population peaks in the following summer (Fig. 21.4). Heavy losses of both adults and juveniles reduce the populations to low levels by the next winter breeding season.

Strategy 4: In these dasyurids, sexual maturity is achieved between 8 and 11 months. The breeding season usually extends for 5–6 months between late winter and mid summer (Fig. 21.3), but animals are unlikely to breed in the season of their birth. In some species females probably raise one litter per season such as in the Ooldea Dunnart, *Sminthopsis ooldea* (Troughton 1965; Aslin 1983), but in others two litters may be produced, such as in the Paucident Planigale and the Narrow-nosed Planigale, *P. tenuirostris* (Troughton 1928; Read 1984a). The reason for this difference is unclear: the planigales have gestations of 15.5 and 19 days, respectively, and are weaned at 75 and 95 days,

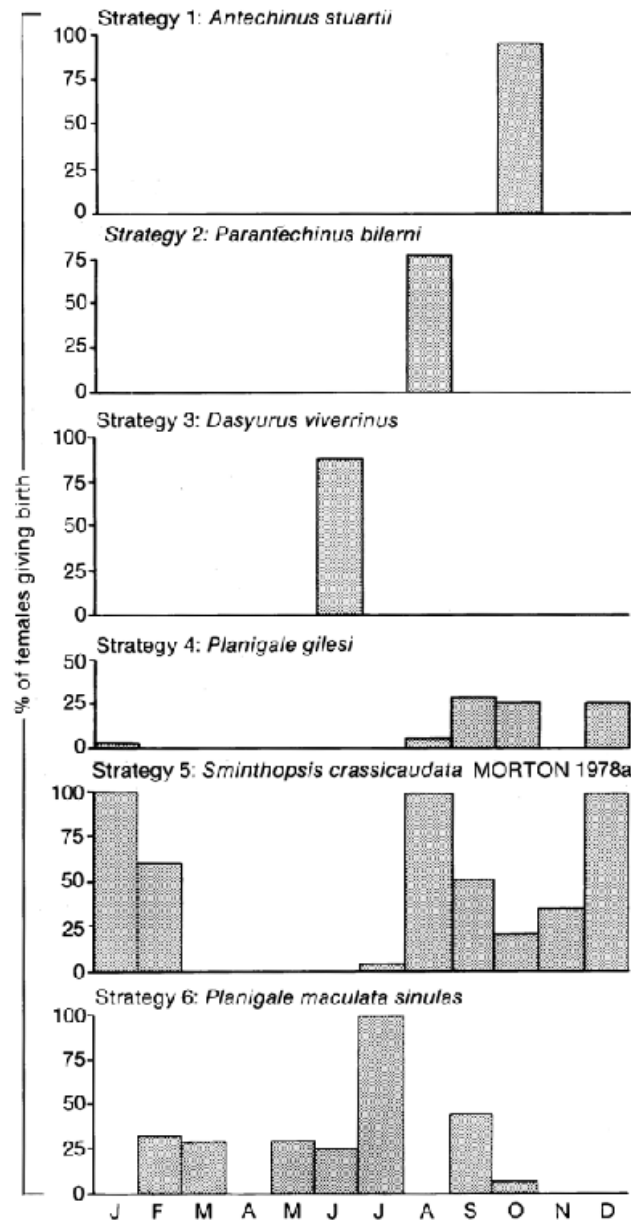


Figure 21.3 Reproductive seasonality and percentage of females giving birth in six categories of life history. (Sources: 1, Wood, 1970; 2, Begg, 1981a; 3, Godsell, 1982; 4, Read, 1984a; 5, Morton, 1978d; 6, Taylor *et al.*, 1982)

whereas the Ooldea Dunnart has a gestation of three weeks and is weaned after only 70 days. Males and females may survive to second and possibly even third breeding seasons in the wild.

Peaks in populations of Paucident and Narrow-nosed Planigales occur variably between August and January, while troughs occur in June. High numbers captured in early spring perhaps reflect increased mobility, especially of males, but summer peaks are due principally to newly-weaned juveniles (Read 1984a).

Strategy 5: This differs from Strategy 4 in that females achieve sexual maturity at about six months of age and potentially may breed in the season of their birth (Lee *et al.* 1982). In the wild, breeding in the season of birth has not been observed and it is possible that Strategy 5 is therefore ecologically equivalent to Strategy 4. The breeding season is extended. In the Common Dunnart, *Sminthopsis murina*, births occur between September and February (Fox &

Whitford 1982), while in the Fat-tailed Dunnart they occur between July and February (Fig. 21.3; Morton 1978d). In the latter species females may rear two litters per season and, to a greater extent than males, may sometimes survive to breed in two consecutive seasons.

Repeated reproduction in Strategy 5 is possible because gestation is short (11.5–13 days) and weaning occurs at only 60–70 days (Godfrey 1969a; Fox & Whitford 1982). Because litters are produced over an extended period and there is no abrupt seasonal mortality in males or females, Strategy 5 dasyurids are unlikely to exhibit predictable annual population fluctuations (Fig. 21.4).

Strategy 6: This life history strategy is exhibited by the poorly known New Guinean *Antechinus* species and by the Common Planigale, *Planigale maculata* (Gould 1851). Females of these species are probably polyoestrus and produce litters in most months of the year (Fig. 21.3; Taylor, Calaby & Redhead 1982). Males may be reproductive continuously. Unfortunately, the demographic patterns of these dasyurids have not yet been studied.

Ecology

Diet: Small dasyurids of less than 150 g are principally insectivorous, but may supplement their diet with worms, small mammals, lizards, frogs and carrion. At least two species also occasionally eat plant products: the Dusky Antechinus, *Antechinus swainsonii*, eats blackberries and other fruits in summer and autumn (Dickman 1983) and the Brown Antechinus eats the flowers of the epacrid shrub *Acrotriche aggregata* during winter when invertebrates are scarce (Statham 1982). Detailed studies of the diets of six species of small dasyurids suggest that invertebrates generally are eaten in proportion to their availability. Particularly favoured prey include large, soft-bodied larvae, spiders, cockroaches and bugs, whereas apparently unpalatable prey include small springtails, ants, slaters and carabid ground beetles (Hindmarsh & Majer 1977; Hall 1980a; Statham 1982; Fox & Archer 1984; Lunney *et al.* 1986).

The diets of only two large (greater than 500 g) dasyurids have been studied. The Tasmanian Devil eats the carcasses of wombats, red-necked wallabies and sheep (Guiler 1970a), but the bulk of the diet of the Eastern Quoll comprise insects, together with some grass and herbs (Blackhall 1980).

Food and Life History: The duration and predictability of the invertebrate food resource are probably major factors influencing the life histories of dasyurids. Consider first those species exhibiting Strategy 1. All except the Little Red Antechinus, *Dasykaluta rosamondae*, inhabit temperate, forested parts of Australia where peaks in insect abundance arrive reliably each year in spring and summer (Braithwaite & Lee 1979). Mating is timed so that lactation and weaning coincide with these peaks. The probability of reproductive failure due to food shortage at these times is thereby reduced. Two factors ensure that females raise only one litter each year. First, all males die after the first mating period due to the intensity of their reproductive effort. In addition, the time from conception to weaning is relatively long (approximately four months), so that a second litter would be weaned in late autumn when invertebrate food is scarce and the survival rate of young would be low (Lee *et al.* 1982).

Species exhibiting Strategy 2 probably also occur in environments where food is seasonally predictable, but where adult survival is increased relative to species exhibiting Strategy 1. Lee *et al.* (1982) speculate that rock outcrops inhabited by the Dibbler and the Fat-tailed Antechinus, *Pseudantechinus macdonnellensis*, enhance survival by reducing the risk of predation.

Polyoestrus dasyurids inhabit environments where food resources are either seasonal but sometimes in short supply, as in arid Australia (Strategies 4 and 5), or relatively abundant all year, as in New Guinea (Strategy 6) (Lee *et al.* 1982).

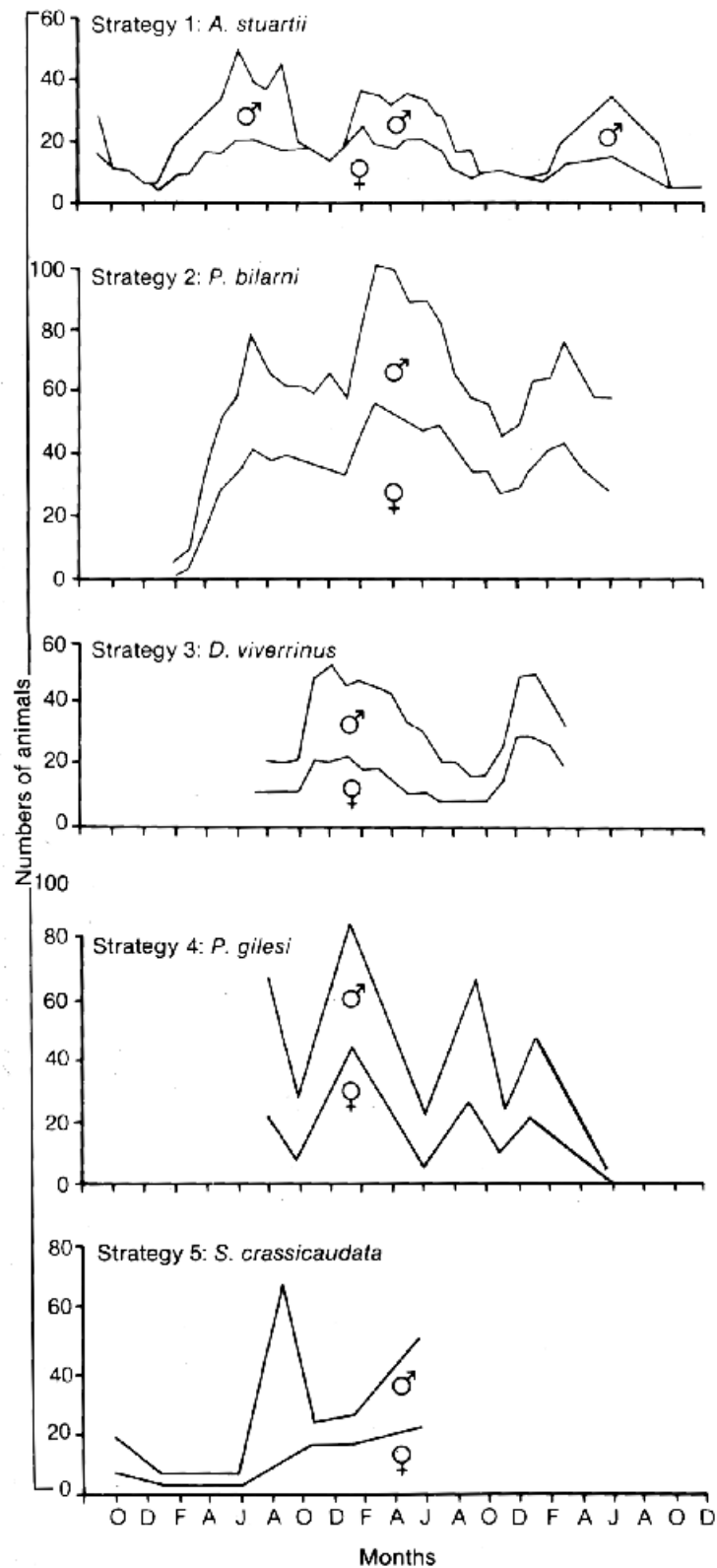


Figure 21.4 Structure and dynamics of populations of dasyurids exhibiting five different life histories. (Sources: 1, 2 and 3, as shown in Fig. 21.3; 4 and 5, Read, 1984b)

In Strategies 4 and 5, the probability of female reproductive failure due to food shortage is higher than in monoestrus species, but the risk of failure can be spread over two litters. Male reproductive effort per breeding season is less than in monoestrus species, so that some survive to breed at least a second time.

Habitat: Dasyurids occupy a broad spectrum of habitats. Most New Guinean dasyurids occur in dense rainforest or moss forest, but three species, *Planigale novaeguineae*, the Red-cheeked Dunnart, *Sminthopsis virginiae* and the Chestnut Dunnart, *S. archeri*, are restricted to coastal savanna and grassland in the plains south of the highlands (Ziegler 1982; Van Dyck 1986).

In temperate Australia, the major habitats occupied by dasyurids are forest, woodland and heath (Fox 1982a). Most studies suggest that dasyurids respond principally to structural components in these habitats such as logs (Dickman 1980), numbers of dwarf shrubs, high stems and vegetation density (Statham & Harden 1982). More subtle floristic attributes also may be important (Fox & Fox 1981). In Victoria, the Brown Antechinus prefers forest patches containing plants with fissured bark, while the Dusky Antechinus prefers patches of ferns with deep leaf litter. These vegetation types harbour insects on which the two species feed (Gullan & Robinson 1980). Up to six species may coexist regionally in forest in south-eastern and south-western Australia, compared with a maximum of four in woodland and savanna (Dickman 1989).

In the Australian arid zone, eight species of dasyurids are more or less confined to hummock grassland, three species occur only in tussock grassland and low shrubland, while two species occur in *Acacia* and/or *Eucalyptus* shrubland. A further five species occur in combinations of these habitats or also in stony desert. One species, the Fat-tailed Antechinus, is restricted to rock outcrops (Morton 1982). There is little information on habitat selection by arid zone dasyurids, but some evidence suggests that it is flexible. For example, the Stripe-faced Dunnart, *Sminthopsis macroura*, and the Fat-tailed Dunnart occur on stony substrates in some localities but on clay or loam soils in others. Flexibility in habitat selection may reflect the high mobility of these species (Morton, Denny & Read 1983).

Natural modification of habitats by fire can have variable effects on dasyurid communities. Low intensity fires temporarily may reduce populations of the Brown Antechinus, the Dusky Antechinus and the Yellow-footed Antechinus, *Antechinus flavipes* (Waterhouse, 1838), but high intensity fires reduce numbers more drastically and may cause local extinction (Christensen & Kimber 1975; Newsome, McIlroy & Catling 1975). The Common Dunnart peaks in abundance four years after fire in forest and heath, apparently due to preferences for reduced leaf litter and regenerating vegetation (Fox 1982b).

Predators: Dasyurids fall prey to a wide range of native predators such as owls, dingos and snakes (Morton & Martin 1979; Tilley 1982; Newsome *et al.* 1983a; Shine & Covacevich 1983; Estbergs & Braithwaite 1985; Robertshaw & Harden 1985a). Introduced predators also capture dasyurids. In the south-eastern highlands, Brown and Dusky Antechinuses have together been found in 30% of the stomach contents of feral cats, *Felis catus*, examined by Jones & Coman (1981). In Kosciusko National Park, New South Wales, the same two species form the major mammalian prey of the Red Fox, *Vulpes vulpes* (Green & Osborne, 1981). Yellow-footed Antechinuses, Dibblers (Gray, 1842), *Planigale* species and *Sminthopsis* species also have been recorded as prey of introduced mammals (Friend 1978; Jones & Coman 1981).

Parasites and Diseases: The principal external parasites of dasyurids are ticks, fleas, mites and lice. Internal parasites are protozoans, cestodes, trematodes and nematodes. Mites are perhaps the most numerous ectoparasites with at least 34 described species. Some appear to be specific to a host or locality, such as *Dasyurochirus tapoatafa* (parasitic on the Brush-tailed Phascogale, *Phascogale*

tapoatafa, in Western Australia), but others are geographically widespread and parasitic on three to four species (Fain & Lukoschus 1981). Fleas (more than 15 species) and ticks (at least 10 species) have been recorded from dasyurids throughout Australia. The tick *Ixodes tasmani*, for example, occurs at least on the Eastern Quoll, the Tasmanian Devil and the Dusky Antechinus in Tasmania (Green 1967, 1972) and on the Brown Antechinus in southern New South Wales (Woolley 1966). The flea, *Acanthopsylla rothschildi*, is probably equally widespread. Parasitic lice have been poorly recorded, but are known from the Brown Antechinus in Victoria (Beveridge & Barker 1976) and from the Sandstone Antechinus, *Parantechinus bilarni*, and the Northern Quoll, *Dasyurus hallucatus*, in northern Australia (Clay 1981). The largest number of ectoparasitic species reported from any local population is 18 for the Brown Antechinus at Powelltown, Victoria, but at least 39 species of ectoparasites are known from this antechinus throughout its geographical range (Beveridge & Barker 1976).

Nematodes are the best-known endoparasites of dasyurids and include at least 33 species. Metastrongylid nematodes (lungworms) occur principally in eastern Australia (Spratt 1984). Six species are parasitic on dasyurids and show variable degrees of host specificity: *Antechinostrongylus disgubernaculus* is known only from the Dusky Antechinus in southern New South Wales, whereas *Marsupostrongylus lanceolatus* is known from three species of *Antechinus* from Tasmania to New South Wales.

Infection rates from 1%–100% have been documented for 15 species of endoparasites in populations of the Brown Antechinus (Beveridge & Barker, 1976). The highest incidence of infection is by *Tetrabothriostongylus mackerrasae*, a nematode which forms clusters of up to 464 individuals in the lower half of the intestine. The lowest known infection rates are by the cestode *Choanotaenia* (?) *ratticola* and the trematode *Plagiorchis* species, recorded from single individuals only.

At least two disease states have been identified in male Brown Antechinuses and may contribute to their post-mating death. These are hepatic necrosis caused in part by the bacterium *Listeria monocytogenes* and anaemia caused in part by *Babesia* species (Arundel, Barker & Beveridge 1977). *Toxoplasma gondii* is the only other pathogen known in wild dasyurids and is probably enzootic in the Kowari, *Dasyuroides byrnei* (Attwood & Woolley 1982).

Competition: Competition has seldom been demonstrated within or between species of dasyurids, but is inferred to exist. Intraspecific competition most likely occurs among breeding males: males invest far less in each offspring than do females (Russell 1982) so that male competition for access to females theoretically should be intense. Competition among Strategy 1 males during the breeding season almost certainly contributes to their subsequent, sudden demise. Males of these species are 1.2–1.7 times heavier than females (Lee *et al.* 1982), presumably as a consequence of sexual selection for large size and, hence, ability to secure matings.

Interspecific competition among dasyurids has been demonstrated conclusively only between the Brown Antechinus and the Common Dunnart in coastal New South Wales and between the Brown and the Dusky Antechinus in the highlands near Canberra, Australian Capital Territory. In the first situation, competitive interactions result in spatial segregation of the two species, or in the exclusion of the smaller Common Dunnart from otherwise suitable forest habitat. The Common Dunnart also reaches greatest population density in mid-seral stages of vegetation regenerating after fire when the numbers of Brown Antechinuses are usually low (Fox 1982b).

In competition with the larger Dusky Antechinus, the Brown Antechinus suffers reduced numbers and survival (Fig. 21.5) and restriction in diet, home range size and habitat use (Dickman 1986a). Competition for food is most intense in winter and coincides both with a change in the organisation of Brown Antechinus populations (from clumped to dispersed) and with a decline in insect abundance. The virtual absence of the Brown Antechinus above the winter snowline in New South Wales also is attributable to competition from the Dusky Antechinus, because alpine insects are seasonally in short supply and the opportunity for the Brown Antechinus to find alternative food sources is limited severely (Dickman *et al.* 1983).

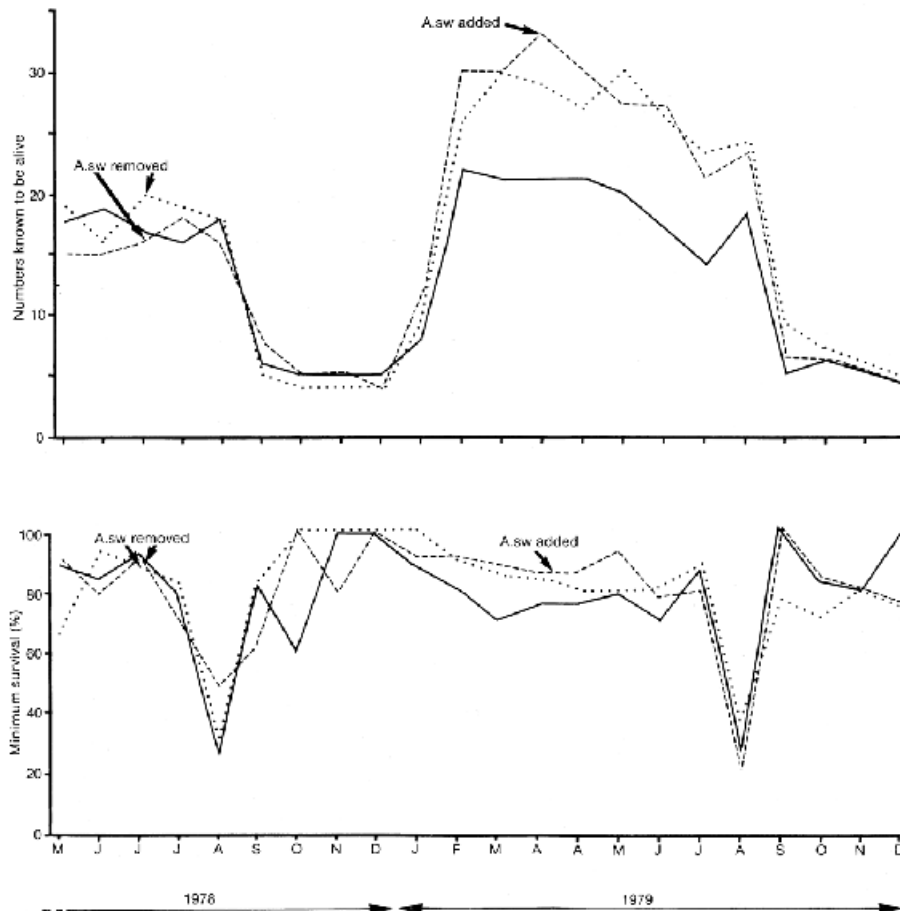


Figure 21.5 Numbers and survival of Brown Antechinuses in three wild populations. Removal of Dusky Antechinuses in 1978 leads to increased numbers and survival of Brown Antechinuses in the following year, thus implicating competition. (After Dickman, 1983)

Social Organisation: Detailed field observations have been made on social organisation in two species of dasyurids. In the Fat-tailed Dunnart males and females occupy large, overlapping home ranges which shift throughout the year (Morton 1978c). During the breeding season (July to February) most individuals nest alone, but in the non-breeding period up to 70% of individuals share nests in groups of two to eight. Nesting groups are probably random, temporary aggregations. Males appear to be non-territorial and move their nest sites more frequently than do females. In contrast, females with advanced young may defend a small area around the nest. Morton (1978c) interpreted this social organisation as a response to unpredictable changes in the abundance and dispersion of invertebrate food.

The social organisation of the Brown Antechinus appears to vary between populations. In Victoria, animals nest in groups in tree hollows from the time they are weaned in summer until after mating in winter (Scotts 1984). Sons disperse at least 150 metres from the maternal nest soon after weaning and enter the nests of unrelated adult females. Most daughters, in contrast, remain in their natal area (Cockburn, Scott & Scotts 1985). Group membership may be stable until the breeding season, when a maximum of two related females occupy their original nest with a variable number of unrelated males and females (Scotts 1984). Males do not form territories before or after mating, but are highly promiscuous and may mate at least once with up to 16 different females over a period of three weeks (Scott & Tan 1985).

In populations of Brown Antechinuses near Canberra, adult females and up to seven independent young have been observed to nest communally between summer and mid-autumn (Dickman 1982b). Individuals then appear to nest alone, at least for the four months before breeding. Demographic events in Queensland populations of the Brown Antechinus appear similar to those in the southern populations, except that males form a dominance hierarchy in the four months prior to mating (Braithwaite 1979). The extent and causes of geographical variation in the social organisation of this species remain to be explored.

Behaviour

Detailed studies of dasyurid behaviour have been made on only six species. Most species are solitary and, hence, behavioural interactions are limited largely to contacts between littermates, mothers and their young and sexually receptive individuals.

Auditory Communication: Sounds are the best known mode of communication among dasyurids and are usually given as vocalisations or, in the Brush-tailed Phascogale, as tail-rattles and foot-taps (Croft 1982). Vocalisations given during agonistic encounters between conspecifics and in defence of the nest or food range from soft grunts and huffs to growls and high pitched screams. The vocalisations of the larger species are very loud: The Tiger Quoll utters “abrupt, piercing ‘circular saw’ screams” (Fleay 1948). The Tasmanian Devil has a repertoire of seven distinct types of vocalisations. Other dasyurids use at least five calls (Croft 1982). Vocalisations often increase in intensity if defence is prolonged or if an individual increasingly is aroused.

Soft hissing or clucking vocalisations are produced by males of five species during courtship for females (Croft 1982). In several small dasyurids, oestrus and post-oestrus females utter calls which elicit similar vocalisations and rapid searching movements from nearby males. As these species are solitary, such calls probably attract mates and facilitate breeding (Van Dyck 1979a).

Young dasyurids displaced from their mother produce a variety of wheezing, squeaking and hissing sounds, which result in the mother replacing them in the pouch. Maternal vocalisations are given usually in response to displaced young, but in the Kultarr may also function to call young from the nest (Happold 1972). Whether any dasyurids use ultrasound is unknown.

Olfactory Communication: Odours are produced from glandular areas or in the urine and faeces of dasyurids. They may advertise the presence of an individual for several hours or days. All dasyurids probably have specialised glandular areas; these may be aural, circumanal, interdigital, sternal, paracloacal or labial glands (Russell 1985). Secretions from external glands usually are rubbed onto a substrate, but odours from anal and paracloacal glands may be deposited passively with waste products. Captive dasyurids mark their immediate environment, including novel objects, with scent. This may convey information on the sex or physiological status of the marker, as in the Common

Planigale (Van Dyck 1979a), or mark the site of an agonistic encounter, as in the Brown Antechinus (Braithwaite 1974). In the wild, male Tasmanian Devils sniff the urine and faeces of females, presumably to assess their sexual condition.

All dasyurids so far studied occasionally sniff the mouth, nasal area, body or cloaca of conspecifics. Mouth sniffing is probably important in individual recognition in the Fat-tailed Dunnart (Ewer 1968a) and, perhaps, in most other species. Cloacal sniffing allows males to assess the sexual state of females. Mothers often sniff the mouth, body and cloaca of their young. This may help maintain the female's maternal state (Croft 1982).

Courtship and Sexual Behaviour: In addition to the mate-attraction calls and olfactory investigation mentioned above, males usually court females by following them and sometimes by biting or pawing their fur. Males of most species bite the female's neck fur before mounting. In the Tiger Quoll and Western Quoll, *Dasyurus geoffroii*, oestrous females develop a swollen neck as protection from injury and perhaps, to stimulate the male (Settle 1978). There is general resistance by females to mating attempts and courtship lasts only a few minutes in most species.

During copulation males may grip the female's neck, but they also may clasp and usually palpate her body (Croft 1982). In some species the male may rub his chin on the female's nape or shake her head; in most he also treads on her flanks. Copulation lasts several hours with active and quiescent phases, but in the Brown Antechinus copulation may proceed for up to 12 hours (Woolley 1966).

Maternal Behaviour: Nests or dens probably are constructed by most species of dasyurids to provide protection from predators and environmental extremes. Nest-building in the Kowari and the Fat-tailed Dunnart increases after the birth of the young, but in the Brown Antechinus activity begins at least 60 days before birth and can continue for three months afterwards (Settle & Croft 1982a). Females, and sometimes males, carry grass and *Eucalyptus* leaves to the nest in their mouths.

Mother-young behaviour is documented best in the Brown Antechinus (Settle & Croft 1982a). After birth, mothers spend an increasing proportion of the time grooming their young in the nest, until the young first detach from the nipples at 35 days. Older young (5–10 weeks) are retrieved within the nest by the mother pulling them under her body. They later ride on the mother's back outside the nest entrance. If disturbed outside the nest, young up to 12 weeks old scramble for the mother's pouch and are carried to safety (Fig. 21.6).

Agonistic Behaviour: Agonistic behaviour is signalled by vocalisations and sometimes by scent marking, but also by visual display and physical contact. All species use an open-mouth display as a threat to an opponent, often accompanied by an upright posture, narrowed eyes and flattened ears (Croft 1982). The Kowari adds to its threat display by raising one forepaw and elevating its conspicuous brushy tail (Hutson 1982). Submissive individuals, in contrast, generally crouch side-on to an opponent, with the head lowered. If a submissive animal fails to retreat, chasing and fighting may ensue. Bites usually are inflicted on the neck, back and flanks of opponents, but in the Tasmanian Devil the animals may lock their jaws with an audible crunch (Buchmann & Guiler 1977).

Agonistic conflicts often arise over sexual partners or food. In the Tasmanian Devil, males aggressively dominate females at the onset of the breeding season and may confine the female to a den for at least a week after mating (Fleay 1935). Dominance is reversed, however, during late pregnancy and after birth, with females showing high levels of aggressive behaviour. Male Brown Antechinuses show a progressive increase in aggressive behaviour before

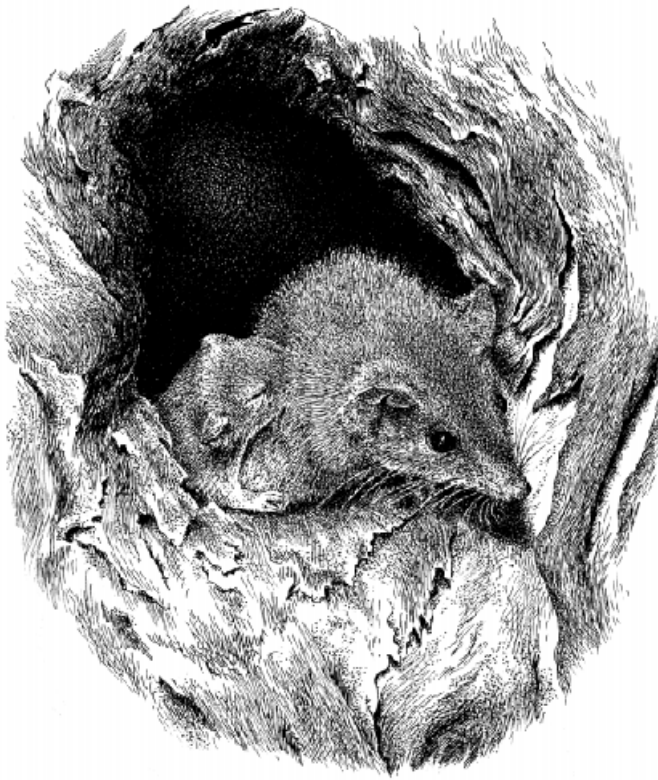
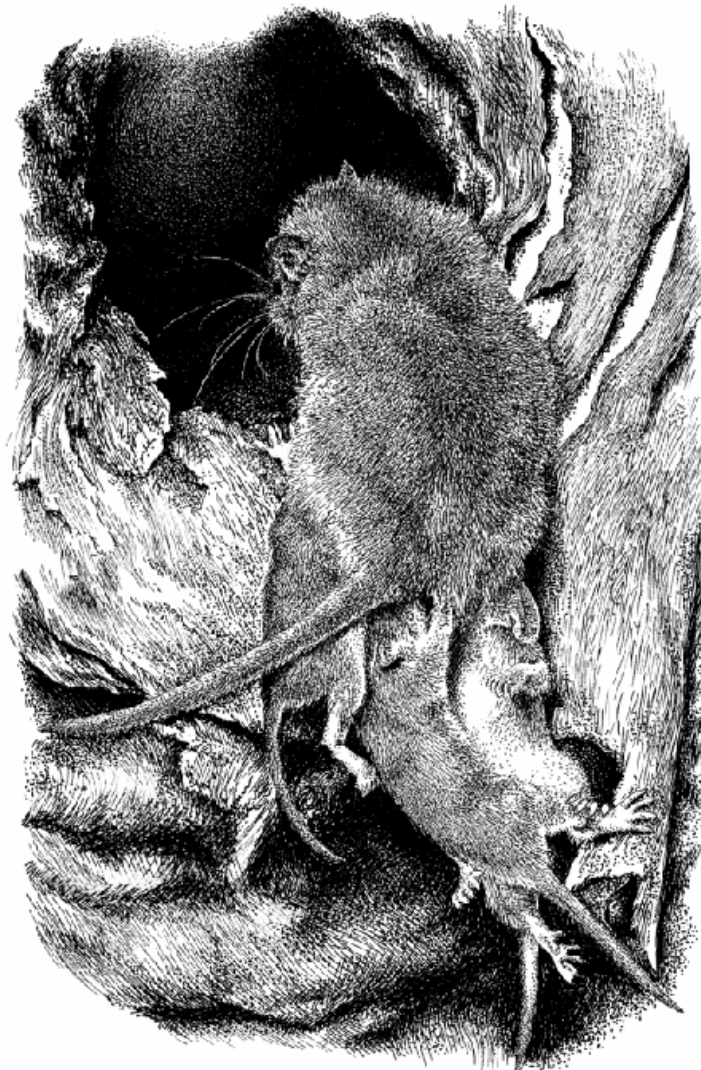


Figure 21.6 Young Brown Antechinuses clinging to their mother while exploring in the vicinity of the nest. Nests are constructed of leaves and grass in tree-hollows.
(After photographs by C.R. Dickman; ©ABRS)
[K. Hollis]



mating, whereas females show no aggression and little defensive behaviour (Fig. 21.7). Cloacal gland marking also increases in breeding males and possibly serves as an additional threat (Braithwaite 1974).

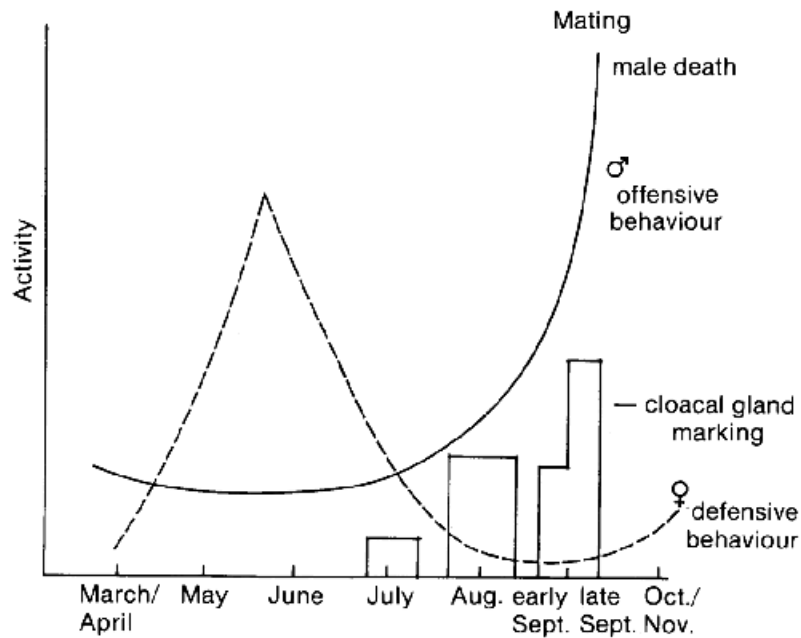


Figure 21.7 Behavioural changes and scent-marking in relation to the life history of the Brown Antechinus. (After Lee *et al.*, 1977)

Play, Exploration and Learning: Social play is evident in the Mulgara, *Dasyurus cristicauda* (Krefft, 1867), the Kowari, the Tasmanian Devil and the five quolls, but not in any of the smaller dasyurids. The predominant form of social play is ‘play-fighting’, where juveniles wrestle, stalk and chase each other. This play may aid the development of social skills and predatory behaviour (Croft 1982).

Active exploration in dasyurids probably begins in the nest when the eyes of the young open and increases as the coordination of the young improves. In captivity, young Brown Antechinuses spend progressively less time exploring familiar areas, even as the total time spent exploring increases (Settle & Croft 1982b). The mother may encourage the exploratory activity of her young and later helps them learn about sources of food (Dickman 1982b). The relative importance of learning versus innate behaviour, however, remains unknown.

Economic Significance

Dasyurids seldom come to public attention and currently are of scant economic importance. On mainland Australia there are reports of Brush-tailed Phascogales and Tiger Quolls attacking poultry (Fleay 1934), but these cases are rare. In Tasmania, observations of Tasmanian Devils feeding on sheep carcasses have given this species a reputation as a sheep-killer. While they may take sick or weakened animals, most meat is probably eaten as carrion (Guiler 1970a).

Small dasyurids may help to control outbreaks of agricultural and forest pests, such as Christmas beetles, by eating both the adults and larvae. The Eastern Quoll is known to take large quantities of corbie grubs and wire worms in Tasmanian pastures and reaches its highest numbers where farmland is interspersed with forest (Godsell 1982).

Dasyurids since European settlement: Early in the twentieth century, mainland populations of Tiger and Eastern Quolls declined drastically in a probable epidemic. The ranges of several other species also have contracted since the advent of European settlement, notably the Western Quoll, the Kowari, the Mulgara, the Dibbler, the Red-tailed Phascogale, *Phascogale calura* and possibly the Brush-tailed Phascogale, the Long-tailed Dunnart, *Sminthopsis longicaudata*, and the Kultarr (Strahan, 1983). The extent of the decline of dasyurids has been documented by comparing the relative abundance of skeletal remains from the surfaces of cave deposits (mostly accumulated by owls) with the extant fauna at the same sites. At 26 sites, populations of dasyurid species in arid parts of inland Australia have declined by 59% since the arrival of Europeans (Morton & Baynes 1985). In contrast, the faunas of the extreme south-west and the northern tropics have fared better.

The causes of these reductions in range are not clearly known. Habitat alteration for agriculture, stock, forestry and suburban growth has no doubt had some effects. More serious changes probably have been wrought by introduced mammals: rabbits change the floristic composition of their habitat; hoofed ruminants compact soils, alter vegetation structure and contribute to erosion; foxes, cats and dogs compete with the larger species for food and prey on the smaller dasyurids (Low 1984). Many species which have survived over large parts of their original ranges are small and presumably inconspicuous or live in protected rocky habitats (Morton & Baynes 1985). No dasyurids have become extinct since European settlement, but the demise of the Dibbler is perilously close (Muir 1985).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Dasyurids occur in virtually every terrestrial environment in Australia from the driest, harshest parts to the tropical rain forests of north Queensland. The Dusky Antechinus even occurs on the continent's highest peak, Mount Kosciusko (Dickman *et al.* 1983). Indeed, the Dasyuridae is unusual among Australian vertebrate families in its relatively even species density across the continent (Morton 1982; *cf.* Pianka & Schall 1981). This results from the comparatively large numbers of dasyurid species present in arid Australia. The radiation of dasyurids in the arid zone gives its fauna a uniquely diverse complement of insectivores in comparison with most other deserts of the world. Representatives of the family also occur on many of the offshore islands of the continental shelf. Tasmania has a conspicuous fauna of six dasyurid species. As noted in the previous section, many species of Australian dasyurids have contracted in range since European settlement. All habitats, except intensively cultivated farmland, still retain at least one dasyurid species.

The family also occurs on mainland New Guinea. At least 14 species are distributed from coastal savannas up to the montane rain forests (Ziegler 1982; Van Dyck 1986). Three species, the Western Quoll, the Red-cheeked Dunnart, and the Chestnut Dunnart are common to both Australia and New Guinea. The endemic New Guinean species are mostly in genera that are also confined to that island and are of considerable evolutionary and systematic interest (Archer 1982a, 1984b). Members of the family occur on the Aru Islands which lie on the

Sahul Shelf between Irian Jaya and the Northern Territory and on some islands of the D'Entrecasteaux group at the south-eastern tip of Papua New Guinea. Apart from these occurrences, dasyurids do not occur beyond mainland New Guinea.

Dasyurids have not been introduced outside their original biogeographic range.

Affinities With Other Groups

Dasyurids have been regarded as the Australian group most like the original marsupials because many of their morphological characters appear to have retained the primitive state (for example, they are plesiomorphic). Palaeontologists and systematists agree now that the dasyurids are indeed a monophyletic group (for example modern dasyurids are all descendants of a common dasyurid ancestor), but the Dasyuridae are not thought to constitute the ancestral Australian marsupial group. Detailed comparative research into fossil history (see below; Archer 1984b), dentition (Archer 1976a; Kirsch & Archer 1982), tarsal bone morphology (Szalay 1982a), basicranial morphology (Archer 1976b), sperm morphology (Harding *et al.* 1982), chromosomes (Sharman 1982; Young *et al.* 1982), and serology (Kirsch 1977a; Sarich, Lowenstein & Richardson 1982; Baverstock 1984) gives a blurred picture of familial relationships of marsupials because no phylogenetic arrangement is consistent with the results of all these studies. Nevertheless, a clearer vision of marsupial origins is emerging gradually and the account that follows is based upon Archer's (1984b) attempt to integrate the various conflicting suggestions.

Archer (1984b) concluded that the Myrmecobiidae diverged from the Dasyuridae in the Miocene (10–20 mybp) and that the Thylacinidae diverged from these two combined groups in the Oligocene (about 30 mybp). These three families, constituting the Dasyuroidea, appear to have separated from the syndactylous Australian marsupials at about the time Australia parted from Antarctica and began its northward drift (in the Eocene, some 45 mybp). The closest living relative of the Australian marsupials is almost certainly the South American microbiotheriid, *Dromiciops australis* (Philippi, 1894), whose ancestors seem to have diverged from the ancestors of Australian marsupials in the Palaeocene about 50 mybp. The microbiotheriids, however, are related only distantly to the large American family, the Didelphidae, which often has been seen as the ancestral group from which many marsupials arose. Thus, dasyurids and didelphids are not related closely and the morphological similarities between some of them appear to reflect insectivore convergence.

In summary, the dasyurids have a long evolutionary history as a distinct group, having diverged from the Australian marsupial stock soon after the Australian continent became isolated from Antarctica. Recent fossil discoveries confirm the presence of a broad dasyurid radiation over the past 20 million years and new systematic work demonstrates that the present-day dasyurid fauna is of a more diverse origin than previously thought.

Affinities within the Dasyuridae

Earlier systematists consistently underestimated the evolutionary diversity represented by the dasyurids, simply because the species, broadly, look so similar in body shape. Only two subfamilies, the Dasyurinae and Phascogalinae, have been recognised for most of this century (Iredale & Troughton 1934; Tate 1947b), the distinctions being based principally upon overly simplistic interpretations of dental characteristics. Appreciation of the true diversity hidden within the Dasyuridae sprang principally from work begun in the late 1960s which broadened understanding of the morphology of the group and led to many generic revisions (Archer 1974, 1975, 1976a, 1976b, 1976c, 1977,

1978a, 1981a, 1982a; Kirsch & Archer 1982). In addition, studies of enzymic relationships (Baverstock *et al.* 1982), serology (Kirsch 1977a), characteristics of DNA (Timms, Westerman & During 1982), phallic morphology (Woolley 1982a) and fossil history (see below; Archer 1982a) resulted in a dramatic increase in understanding of affinities within the family. There remains much to learn, but summarised and presented here in Fig. 21.8 is the currently accepted synthesis of Archer (1982a, 1984).

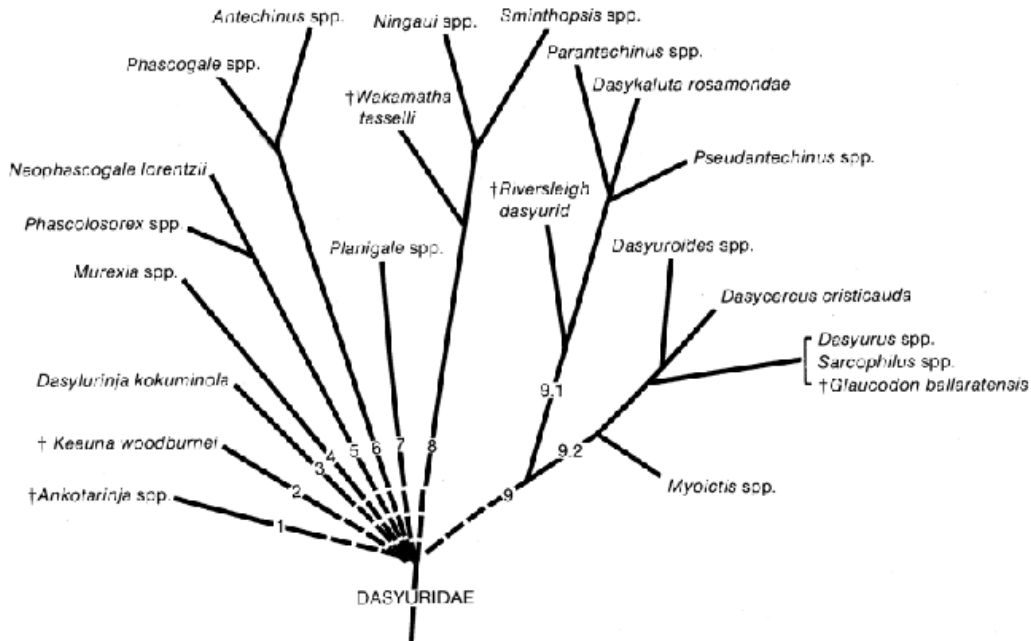


Figure 21.8 A diagram showing the relationships of nine subgroups within the Dasyuridae, considered by Archer (1982a) to represent subfamilies. Daggers indicate extinct forms. (After Archer, 1982a)

Five subfamilies within the living Dasyuridae are now recognised. The first two, the Muricinae and Phascolosoricinae, contain the endemic New Guinean genera *Murexia*, *Phascolosorex* and *Neophascogale*, all of which exhibit strikingly distinctive characteristics and numerous morphological plesiomorphies. None of these species has been the subject of enzymic or serological studies, which would promise to reveal much about the adaptive radiation of the Dasyuridae. The third subfamily, the Phascogalinae, was described originally to accommodate all the smaller dasyurids, but is now restricted to the forest-dwelling *Phascogale* and *Antechinus*. This subfamily contains the most plesiomorphic dasyurids now living in Australia, but their relationships to the Muricinae and Phascolosoricinae are unclear (Fig. 21.8). Fourth, the Sminthopsinae contain the most speciose genus, *Sminthopsis*, together with the other tiny dasyurids, *Planigale*, *Ningau* and the monotypic *Antechinomys*. Finally, the Dasyurinae comprises a diverse range of animals. One grouping within it includes *Parantechinus* Tate, 1947b, *Pseudantechinus* Tate, 1947b and *Dasykaluta* Archer, 1982, genera that mistakenly have been included in *Antechinus*. The other grouping includes the New Guinean *Myoictis* Gray, 1858 together with the largest members of the family, *Dasyocercus* Peters, 1875, *Dasyuroides* Spencer, 1896, *Dasyurus* and *Sarcophilus* Geoffroy & Cuvier, 1837.

As Fig. 21.8 shows, to establish the affinities of the subfamilies is not yet possible, mainly because the fossil record is too sparse. Enzymic data on intra-generic relationships, however, allow some conclusions about the nature of the adaptive radiation leading to the present Australian fauna. For example, about half of the 18 species within *Sminthopsis* are distributed predominantly in the arid zone. Enzymic and anatomical analyses, however, show that the arid-adapted species generally are not related closely to each other, but rather, to other species of the forested fringes. The closest relative of the Stripe-faced Dunnart, a widespread desert dwelling species, is the Red-cheeked Dunnart, an inhabitant of tropical woodlands and forests; that of the Ooldea Dunnart, an inhabitant of arid mulga shrublands, is the Common Dunnart, a species found in open woodlands of the south and east; that of the Sandhill Dunnart, *S. psammophila* Spencer, 1895, a species of inland sandridge country, is the White-tailed Dunnart, *S. granulipes*, which lives in south-western woodlands; and that of *S. youngsoni* and the Hairy-footed Dunnart, *S. hirtipes*, both found in sandplain and sandridge deserts, is the Carpentarian Dunnart, *S. butleri* of tropical woodlands and forests (Archer 1981a, 1982a; Baverstock *et al.* 1982; McKenzie & Archer 1982). Clearly, adaptation to arid environments took place along several lineages within the genus and was not a single event leading to a subsequent radiation. This conclusion, in turn, suggests that the environment in which such speciation took place was the semi-arid belt, for it is there that past climatic fluctuations would have produced numerous fragmentations of habitats, genetic bottlenecks and intense directional selection (Baverstock 1982a). Thus, the contraction and expansion of the arid zone over the past five million years probably resulted in new species of *Sminthopsis* arising at the fringes of the wetter areas. The conclusion also means, finally, that the development of widespread aridity in Australia post-dated the time of divergence of *Sminthopsis* from other dasyurid lineages (Archer 1982a).

The detailed example of *Sminthopsis* presented above reflects general trends, because independent evolution of arid-adapted features can be detected in many dasyurid genera. Such characteristics as evacuated palates, long or incrassated tails, granulated soles on the hindfeet and loss of the first rear digit can be seen among species of *Dasyuroides*, *Ningaui*, *Pseudantechinus* and *Sminthopsis*, indicating that arid-adaptation occurred in independent phylogenetic lineages (Archer 1982a, 1984b). The modern Australian fauna, therefore, is largely a result of a relatively recent burst of adaptive radiation leading to polyphyletic development of arid-adapted species. Several of the lineages converged morphologically, thereby producing the range of superficially similar animals whose true diversity has become apparent only in the past 10 years. The Muricinae and Phascolosoricinae may be most similar to the very early dasyurids, which presumably were adapted to cool, wet conditions. These species now exist in cool, wet forests of New Guinea, a habitat preserved by uplift into high altitudes (Schodde & Calaby 1972; Archer 1981b, 1982a, 1984b), whereas the dasyurids of Australia have evolved in a continent which has experienced prolonged desiccation and the absence of major geological activity.

The distributions of many dasyurids that are confined to Australia also show the effects of past cycles of desiccation and humidification. The Yellow-footed Antechinus is found today in eastern and south-western Australia, but there is a gap of about 1500 km between the south-western population and its conspecifics in the east (Strahan 1983). Fossil deposits in caves of the Nullarbor Plain contain remains of this species (Lundelius & Turnbull 1978), indicating that in wetter periods the environment across the southern portion of Australia was wetter and provided suitable habitat for it. As the country dried over the past 20 000 years, woodland disappeared from the region and the species, along with many other arboreal and semi-arboreal marsupials, retreated to the south-west and south-east. In its place, arid-adapted *Sminthopsis* species occupied the drier areas.

Other responses to cycles of aridity resulted in distributional disjunctions from north to south. The White-footed Dunnart, *Sminthopsis leucopus*, was believed to occur only in Tasmania and the moist areas of south-eastern Australia (Morton, Wainer & Thwaites 1980), but recent collections show that it also occurs in rainforest in north Queensland (Van Dyck 1985). *Sminthopsis leucopus* probably was widespread in eastern Australia during wetter periods in the past, but now has become restricted to cool, wet refuges along the eastern highlands.

The recent evolution of the Dasyuridae clearly has been driven by cycles of aridity, but what of the more distant past? To find out, we must examine the fossil record.

Fossil Record

By 1970, only two fossil dasyurids had been described, *Sarcophilus lanianus* and *Glaucodon ballaratensis* Stirton, 1957. Since that time, rapid growth in palaeontological research has resulted in substantial increases in knowledge, based on a further five extinct genera and at least 18 extinct species (Archer, Clayton & Hand 1984). This fossil record is still meagre compared to that of the diprotodont marsupials and there are more gaps than linkages (Fig. 21.9). The earliest known dasyurids, *Ankotarinja tirarensis* and *Keeuna woodburnei* Archer, 1976, are represented only by maxillary and mandibular fragments recovered from the Ngapakaldi faunal deposits near Etadunna Station in northern South Australia. Both species appear to represent lineages that did not survive to modern times. They retain many plesiomorphic dental characteristics and bear similarity to the most primitive living dasyurids such as *Murexia* species. Other Miocene dasyurids exhibit more derived dental characteristics. *Dasyurina kokuminola* Archer, 1982 (Fig. 21.9) was a more specialised carnivore, but it does not seem to be ancestral to modern carnivorous dasyurids such as *Dasyurus* species. It, too, is presumably a representative of an extinct lineage. *Wakamatha tasselli* Archer & Rich, 1979 also is known from Miocene deposits in northern South Australia and, although it has enigmatic dental characters, it may represent a sister-group to modern *Sminthopsis* and *Ningaui* (Archer 1982a).

Fossils referable to modern genera are not known before the early Pliocene, when species of *Antechinus*, *Planigale* and *Dasyurus* appear in the record (Fig. 21.9). These species do not seem to be related closely to modern members of their genera, with the exception of the Hamilton *Antechinus* species, the latter does appear to be similar to *Antechinus mayeri*, a species found in New Guinean rainforest, and may imply the existence of similar habitat for that area of Victoria in the early Pliocene (Archer 1982a). Overall, however, the Pliocene-Pleistocene fossil assemblages are the first to contain dasyurids that clearly are related to modern species or which show arid-adapted characters (Figs 21.8 and 21.9).

The fossil record, although poor, shows two interesting aspects. First, it is consistent with evidence from other fossil mammals in suggesting that much of inland Australia changed from a well-vegetated environment in the Middle Miocene to grasslands in the Pliocene and to arid conditions in the Late Pliocene and Pleistocene (Archer 1981b, 1982a). Second, the Miocene fossils show a previously unrecognised breadth of radiation within the Dasyuridae. These other fossils do not provide ancestors for known groups; rather not until the appearance of the threads of the lineages of modern dasyurids in the Pliocene (Archer 1982a). The phylogeny and systematics of the Dasyuridae are, therefore, more complex than modern species would lead us to expect (Fig. 21.8). Archer (1982a) proposed that three additional fossil subfamilies are

Age	Epoch	South and Western Australia	Victoria	New South Wales	Queensland	Papua
10,000	Recent					
1 my	Pleistocene	Western Australia Maduro Fauna	Cave and Lake Deposits	Cave and Lake Deposits	Russenden Cave Fauna <i>Antechinus</i> sp.	Cave Deposits
2 my	1.8 my	South Australia Kerunja Fauna (Various? Recent Species)	Smeaton Fauna <i>Glauzodon ballaratensis</i>	Fisherian's Cliff Fauna <i>Sarcophilus mcormacensis</i> <i>Antechinus</i> sp. <i>Dasyurus haughtoni</i> <i>D. sp.</i> <i>Smilthopsis</i> sp. <i>Dasyurides achipana</i>	Floraville Fauna <i>Smilthopsis floravillensis</i> <i>Antechinus</i> sp. <i>Dasyurus</i> sp.	Awe Fauna <i>Mylotis</i> sp.
3 my	3.0 my					
4 my	Pliocene		Hamilton Fauna <i>Antechinus</i> sp.	Bow Fauna <i>Dasyurus dunmaili</i>	Chinchilla Fauna <i>Dasyurus dunmaili</i> Bluff Downs Fauna <i>Flanigale</i> sp.	
5 my						
6 my	Miocene	South Australia Horizon & Fauna Unknown <i>Wakamatha tasmani</i>				
10 my						
13 my		South Australia Kuljamerpu Fauna <i>Ankotarinja</i> sp. Other unnamed forms				
16 my		South Australia Ngapakaki Fauna <i>Ankotarinja traversii</i> <i>Reurus woodburni</i> Other Unnamed Fauna			Riversleigh Fauna <i>Antechinus</i> -like Form	
To 23.5 my						

Figure 21.9 Fossil dasyurids, their ages and the faunas in which they occur.
(After Archer, 1982a)

required to incorporate the Miocene fossils in the Dasyuridae. These subfamilies have not been named formally, but all appear to represent different lineages of dasyurid evolution.

The late Pleistocene and Holocene fossil record provides evidence consistent with the interpretations presented above, but also shows the rapidity with which change can occur within dasyurid faunas. Numerous studies of mammalian remains in caves indicate that the ranges of many living species have changed dramatically over the past 20 000 years (Smith 1972; Wakefield 1972; Archer & Baynes 1973; Lundelius & Turnbull 1973, 1975; Baynes, Merrilees & Porter 1976; Hope *et al.* 1977; Archer 1978b; Balme, Merrilees & Porter 1978; Baynes 1982; Lundelius 1983). One of the most striking examples is the Tasmanian Devil, which today is found only in Tasmania. Remains of this species are known from Pleistocene and Holocene deposits in every Australian State (Dawson 1982a); they have been dated as recently as 3120 ± 100 ybp in the Northern Territory (Calaby & White 1967) and 430 ± 160 ybp in south-western Australia (Archer & Baynes 1973). Thus, the Tasmanian Devil occurred comparatively recently over much of the continent, but retreated to survive only on Tasmania as the continent became drier and as Aboriginal people and dingoes altered their environment. Older fossil remains demonstrate the existence of at least two other species of 'devils', *Sarcophilus* in the Pleistocene (Crabb 1982; Dawson 1982a).

The environmental causes of changing dasyurid distributions during the Pleistocene and Holocene are not difficult to envisage in broad outline. Oscillations of the glacial period almost certainly caused climatic instability and rapid alterations in the distributions of suitable habitats for various dasyurid species. The arid zone underwent substantial contraction and expansion (Bowler 1982), probably resulting in similar changes in ranges of dasyurids and the extinction of many species inhabiting wet forests. Baynes' (1982) careful analysis of a late Quaternary small mammal fauna in south-western Australia

shows how the proportions of different species changed through time, probably in direct relationship to climate and the associated vegetational and edaphic changes. The dasyurid fauna inhabiting Australia today is the end-product of an intense period of sorting and sifting over the past half a million years.

COLLECTION AND MAINTENANCE

Dasyurids are best captured in cage traps, folding aluminium traps or pit-traps. Cage traps baited with meat or rolled oats are most suitable for larger dasyurids such as the Tasmanian Devil, *Dasyurus* species and the Brush-tailed Phascogale (Guiler 1970a; Cuttle 1982b; Godsell 1982). Forest dwelling and rock dwelling species, particularly *Antechinus* species, have been studied by capturing them in folding aluminium traps baited with rolled oats and peanut butter (for example Wainer 1976; Stewart 1979; Hall 1980a; Fox & McKay 1981). Studies of other genera, particularly inhabitants of grasslands and arid habitats, have lagged behind those of forest dwelling species largely because of the difficulties of capturing them. Initially, spotlighting at night in open country was used to capture species of *Sminthopsis*, *Antechinomys* and *Dasyuroides* (Philpott & Smyth 1967; Watts & Aslin 1974; Morton 1978b). Aitken (1972), however, demonstrated the efficacy of pit-trapping with drift-fences for capturing small dasyurids in the arid zone. Plastic or metal cylinders are buried so that their upper edges are flush with the ground and a low fence of fly-wire or similar material is pegged upright along the line of pit-traps to guide animals into the pits. The technique has led to an increase in knowledge of the taxonomy and ecology of species of *Ningauia*, *Planigale* and *Sminthopsis* (Cockburn, Fleming & Wainer 1979; Dunlop & Sawle 1982; McKenzie & Archer 1982; Read 1982, 1984b; Kitchener, Stoddart & Henry 1983; How, Humphreys & Dell 1984).

Dasyurids are most commonly preserved as specimens in alcohol after being injected with formalin, or as skins rolled onto cardboard or cotton wool padding. For taxonomic work, the skull is removed and cleaned and kept in a protective container.

Maintenance of dasyurids in captivity is well understood, however, it is time consuming since most species need to be fed carefully each day. Cages need to be floored with sand or wood-shavings and cleaned out every week. Small nestboxes should be provided. It is difficult to provide a diet made up exclusively of insects. Various combinations of minced meat, dog foods, baby foods and vitamin and calcium additives are recommended (Aslin 1982a; Bennett *et al.* 1982; Woolley 1982b). Disease and infertility in laboratory animals are serious problems (Attwood & Woolley 1982) and diet, therefore, needs to be managed carefully.

CLASSIFICATION

Family Dasyuridae Goldfuss, 1820

Subfamily Muricinae Archer, 1982

Murexia Tate & Archbold, 1937 (two species)

Subfamily Phascosoricinae Archer, 1982

Phascosorex Matschie, 1916 (two species)

Neophascogale Stein, 1933 (one species)

Subfamily Phascogalinae Gill, 1872

Phascogale Temminck, 1824 (two species)

Antechinus Macleay, 1841 (11 species)

Subfamily Sminthopsinae Archer, 1982

Sminthopsis Thomas, 1888 (18 species)

Antechinomys Krefft, 1867 (one species)

Ningaui Archer, 1975 (three species)

Planigale Troughton, 1928 (five species)

Subfamily Dasyurinae Goldfuss, 1820

Dasyurus Geoffroy, 1796 (five species)

Dasycercus Peters, 1875 (one species)

Dasyuroides Spencer, 1896 (one species)

Myoictis Gray, 1858 (two species)

Sarcophilus Geoffroy & Cuvier, 1837 (one species)

Dasykaluta Archer, 1982 (one species)

Parantechinus Tate, 1947 (two species)

Pseudantechinus Tate, 1947 (one species)

Generic Descriptions

Members of the Muricinae and Phascolosoricinae and of the genus *Myoictis* (Dasyurinae) are confined to New Guinea.

The Phascogalinae consists of medium-sized dasyurids, 50–200 g in weight, which are found in woodland and forest of northern, eastern and south-western Australia. In addition, four species of *Antechinus* are confined to New Guinea. Apart from grouping on the basis of serology, enzymology and cranial and dental morphology, the phascogalines share the unusual semelparous reproductive pattern. One species of *Phascogale* did occur in inland Australia, but has contracted in distribution and is now found only in south-western Australia. The other member of the genus and all species of *Antechinus* are confined to the forested fringe.

The Sminthopsinae comprises the small dasyurids, ranging from a mere 4 g up to about 40 grams. *Sminthopsis* is the largest genus of Australian marsupials; in addition, suspected new taxa are held in collections. Its species may be found in virtually all terrestrial Australian environments. Two species extend into lowland New Guinea. *Antechinomys* is specialised for life in open country and is confined to inland Australia. Archer (1981a) suggested that the genus be reduced to subgeneric rank within *Sminthopsis*, but most authorities still prefer to consider it separate (Strahan 1983). *Ningaui* contains three species, all from arid habitats dominated by spinifex (*Triodia* and *Plectrachne* species). *Planigale* comprises five species, one confined to lowland New Guinea. The Australian species occur in forests, woodlands and arid grasslands in the east and north of the continent.

The Dasyurinae contains larger species of up to 7–8 kg, but includes some small forms such as *Dasykaluta* which weigh about 40 g. Archer (1982a) believes that the two northern species of *Dasyurus* warrant generic status as *Satanellus* Pocock, 1926. These cat-sized dasyurids occur all over Australia, but most species are found in forests. *Dasycercus* and *Dasyuroides* may best be considered congeneric (Archer 1982a); both are medium-sized inhabitants of arid, inland Australia. The single species of *Sarcophilus* is confined to Tasmania. *Dasykaluta* has a single species in spinifex country of the Pilbara. *Parantechinus* and *Pseudantechinus* have been resurrected only recently as a result of increased understanding about dasyurid relationships (Archer 1982a). The former contains two species with very limited distributions, one in south-

western Australia and the other in the top end of the Northern Territory. Currently, *Pseudantechinus* consists of one species from rocky ranges in inland Australia, but another undescribed species is known from the Kimberley.

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