



Annual Review of Animal Biosciences

The Distinctive Biology and
Characteristics of the
Bare-Nosed Wombat
(*Vombatus ursinus*)

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Annu. Rev. Anim. Biosci. 2024. 12:1.1–1.26

The *Annual Review of Animal Biosciences* is online at
animal.annualreviews.org

<https://doi.org/10.1146/annurev-animal-021022-042133>

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Keywords

Diprotodontia, Vombatidae, common wombat, digging, cube-shaped scat, Australia

Abstract

The bare-nosed wombat is an iconic Australian fauna with remarkable biological characteristics and mythology. This solitary, muscular, fossorial, herbivorous marsupial from southeast Australia has continent and continental island subspeciation. Vombatiformes also contains hairy-nosed wombats (*Lasiorbatus* spp.); koala (*Phascolarctos cinereus*); and extinct megafauna, *Phascolonus gigas* (giant wombat), *Diprotodon*, and *Thylacoleo* (marsupial lion). Culturally important to Aboriginal people, bare-nosed wombats engineer ecosystems through digging, grazing, and defecation. Olfaction and cubic fecal aggregations appear critical for communication, including identity, courtship, and mating. Though among the largest fossorial herbivores, they have a nutrient-poor diet, a home range up to an order of magnitude smaller than expected, and a metabolism among the lowest extreme for mammals >10 kg. Metabolic depression may confer advantages over resource competitors and fossorial lifestyle protection from predators, fires, and climatic



extremes. Bare-nosed wombats are loved and persecuted by European colonists. Recent population increases may reflect softening attitudes toward, and greater protections of, bare-nosed wombats.

INTRODUCTION

The bare-nosed wombat (*Vombatus ursinus*, a.k.a. common wombat) is an iconic Australian marsupial. The species is much loved by Australians and internationally, culturally important to Aboriginal peoples, and also derided by sections of Australian society (1). Much knowledge exists about this species, documented in published, cultural, and anecdotal forms (**Table 1**), and the last comprehensive overview was published 15 years ago (2). The last decade in particular has seen a significant expansion of research interest, and here we build upon the important foundation by Triggs (2) and earlier versions of this text. In this review, we synthesize the broad knowledge surrounding bare-nosed wombats and update critical knowledge advances, limitations, and future research directions. Although thorough, we seek not to be encyclopedic but rather to provide a critical repository and promote key resources to guide the reader in navigating the body of literature on bare-nosed wombats.

Although species specific, this review contributes to broader knowledge around key themes of which the biology of bare-nosed wombats is representative. Most notably, bare-nosed wombats are an excellent model for fossorial terrestrial vertebrates, ecosystem engineering, organisms in which olfaction is a dominant means of communication, and digestive and metabolic adaptations to nutrient-poor diets. Additionally, bare-nosed wombats face a range of natural and anthropogenic threats that inform management of geographically widespread species (**Figure 1**). We have attempted to cover as many critical topics as possible, but space constraints mean three themes were not included, and instead we point the reader to key resources in these areas. An expanding body of literature exists on parasitism and disease, including disease management, and References 3–7 represent excellent entry points. Extending logically from parasitism and disease, Bryant & Reiss (6) extensively review veterinary medicine. Finally, the peer-reviewed literature associated with the rescue, rearing, rehabilitation, and release of bare-nosed wombats is sparse, despite extensive sector knowledge, but examples of well-regarded resources include References 2, 8, and 9.

TAXONOMY, PHYLOGENETIC RELATIONSHIPS, AND EVOLUTION

There are three extant species of wombat (**Figure 1**): the bare-nosed wombat (*V. ursinus*) and two species of hairy-nosed wombat (northern hairy-nosed, *Lasiorbini krefftii*; southern hairy-nosed, *Lasiorbini latifrons*) (2). All three belong to Vombatidae, which is one of eight families in the suborder Vombatiformes. Within Vombatiformes, Phascolarctidae is the only other family containing an extant species, the koala (*Phascolarctos cinereus*) (10, 11). Suborder Vombatiformes sits within order Diprotodontia, which is morphologically unique among Australian marsupial orders and speciose, consisting of ~150 extant species including possums (suborder Phalangeriformes) and kangaroos and wallabies (suborder Macropodiformes) (10). Evolutionary relationships among the 11 families within order Diprotodontia have been conflicting, but Vombatiformes is consistently resolved as the sister clade to all other families—supported by multiple genetic analyses ranging in molecular marker type (subsets of specific genes to genome-wide single-nucleotide polymorphisms) (12–15). Across all molecular analyses, Vombatiformes is estimated to have emerged 30–40 million years ago, in the late Eocene or early Oligocene (12, 13, 15).



Table 1 Interesting biological features of bare-nosed wombats that are supported by established evidence, and common myths

Established interesting biological features		
Feature	Details	Literature
Taxonomic relationships within the Vombatiformes	Families Phascolarctidae (containing the koala), Diprotodontoidae (containing the diprotodon), and Thylacoleonidae (containing the marsupial lion)	Johnson (24)
Sought after by Aboriginal hunters	Highly valued for flavor of meat and proportion of fat relative to body size	Bulmer (32), Eyre (33), Morgan (34), Pyke (35), Smyth (36)
Largest burrowing herbivore	The three wombat species represent the largest burrowing herbivores in the world	Johnson (58)
Polyphyodont	Dental arcade is open rooted and continuously growing	Allen et al. (29)
Ancestral marsupial karyotype	Bare-nosed wombats retain the ancestral marsupial $2n = 14$ karyotype ($n = 7$ chromosomes); the bare-nosed wombat genome is ~ 3.5 Gb in length	Deakin & O'Neill (20), Westerman et al. (21), NCBI (22)
Backward-facing pouch	Joey develops in a pouch that, when distended, opens posteriorly	Green & Rainbird (60)
Cube-shaped feces	Feces form a cubic shape in the distal colon owing to rhythmically contracting muscle bands of differing thickness coaxing corners longitudinally as moisture is absorbed and the shape firms, and the extent of water reabsorption causes the fecal material to break at regular transverse intervals	Yang et al. (94), Magondu et al. (95)
Extreme metabolic rates	Field metabolic rates 40–60% that predicted for herbivorous mammals > 10 kg; fecal material retained for long periods in the gastrointestinal tract, where bacterial communities exhibit phenological changes as fermentation and digestion progress	Evans et al. (103), Martin et al. (116), Barboza & Hume (122, 123), Eisenhofer et al. (125), Barboza (120)
Small home range relative to mass	Home range size an order of magnitude smaller than expected for similar-sized mammalian herbivores	Johnson (58)
Brief foraging rhythms	2–6 h/day	McIlroy (71), Simpson et al. (72)
Burrow-switching behaviors	Switch burrows they sleep within every 1–9 days	Skerratt et al. (68), McIlroy (71), Evans (73), Martin et al. (88)
Female bias dispersal	Females disperse further than males, possibly indicated mothers leave burrow to their offspring associated with the energetic cost of burrow acquisition and creation	Banks et al. (51), Tan et al. (52)
Common myths		
Myth	Rationale/Origin	Literature
Square-shaped anus	Suggested cause of square-shaped feces, but demonstrated incorrect by recent research	Yang et al. (94)
Territorial	Suggestion attributed to misused terminology relating to home range and occasional disputes over foraging patches or burrow occupancy	Roger & Ramp (146)

(Continued)



Table 1 (Continued)

Common myths		
Myth	Rationale/Origin	Literature
Social species	Wombats are tolerant of co-occurrence in foraging areas, which may be confused with being social, but act independently; attachment of people to the colloquial collective noun, a wisdom	Evans (73)
Can run up to 40 km/h	Unknown origin, as no literature on running speed exists; observed maximum speeds by researchers suggest it may be closer to 20 km/h	None
Cartilaginous plate on rump	Hardened rump; however, a cartilaginous plate is inapparent in X-rays, and dissections demonstrate that hardening is fascia (fibrous connective tissue)	Vogelnest & Allan (151)
Crush predators within burrows	Anecdotal evidence of other species found dead in wombat burrows; may occur in extremely rare circumstances, but evidence is lacking	None
Backward-facing pouch to avoid soil fowling	When quiescent, the pouch is flattened to the body and is not technically backward facing; it is unclear if females with a distended pouch (containing a large pouch young) engage in digging behaviors frequently	Green & Rainbird (60)

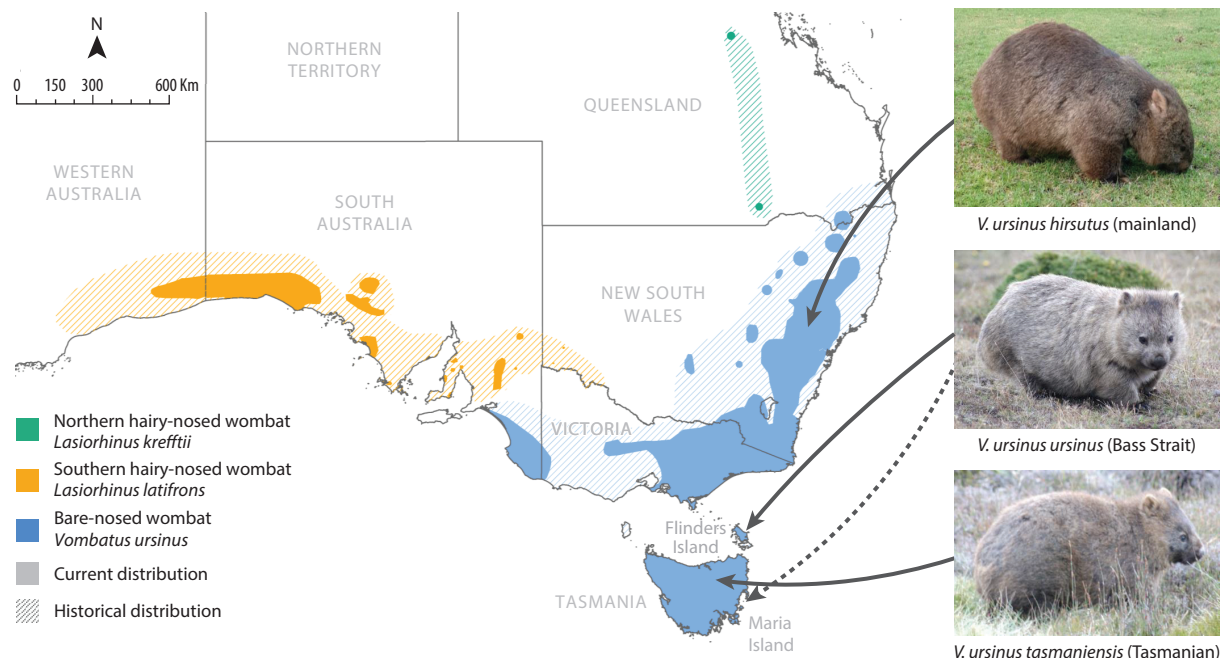


Figure 1

The current and historical distributional range of the three extant wombat species, with representative images of each bare-nosed wombat subspecies. The dotted arrow associated with *Vombatus ursinus ursinus* designates the translocated Maria Island population. Current distributions were sourced from the IUCN Red List of Threatened Species.

Bare-nosed wombats (described by George Shaw, 1800) were historically assigned to subspecies based on morphometric data (see the section titled Morphological Description) and geographic isolation (**Figure 1**). Three allopatric subspecies are recognized: south-eastern mainland (*Vombatus ursinus hirsutus*; Perry 1810), Bass Strait islands (*Vombatus ursinus ursinus*; Shaw 1800), and Tasmanian (*Vombatus ursinus tasmaniensis*; Spencer & Kershaw, 1910) (16, 17). Geographic isolation likely occurred owing to sea-level rise with the end of the Last Glacial Maximum (18). Recent genomic assessments of *Vombatus ursinus* subsp. from these three regions confirm a genetic distinction among mainland, Bass Strait, and Tasmanian individuals (19).

Marsupial genomes are unique in that they have relatively few chromosomes that are larger in size than those of other mammals (20). Bare-nosed wombats have a $2n = 14$ karyotype ($n = 7$ chromosomes), with all members of family Vombatidae retaining the ancestral marsupial karyotype (20, 21). The bare-nosed wombat genome was recently sequenced and assembled and is ~ 3.5 Gb in length with approximately 22,000 protein-coding genes (22).

THE FOSSIL RECORD

The marsupial fossil record within Australia is sparse. Fossil wombats had developed large forms by the middle Pleistocene. *Phascolonus gigas* was up to twice the size of modern bare-nosed wombats, weighing up to 100 kg, distributed across the Australian mainland. Although *Phascolonus* resembled modern wombats, its paws were not adapted to digging, suggesting it did not dig huge burrows. A new species of primitive wombat (*Nimbavombatus boodjamullensis*) was recovered from the Riversleigh World Heritage Area, Queensland, Australia (23), and represents the most complete early wombat. Two partially preserved maxillae that were recovered, including dental arcades and isolated loose teeth, suggest *N. boodjamullensis* had developed a mastication process similar to that of modern wombats. Giant wombats, such as *P. gigas*, as well as other Australian megafauna species, declined significantly 50,000–46,000 BP (24). The archaeological faunal remains found across southeast Australia (e.g., 25–28) suggest no significant morphological differences between the bare-nosed wombats of the late Pleistocene and modern populations.

CULTURAL IMPORTANCE TO AUSTRALIAN FIRST NATIONS PEOPLES

Prior to European invasion, bare-nosed wombats were widely utilized by First Nations people, and this tradition continues in many parts of southeast Australia today (**Figure 2**). Zooarchaeological assemblages containing wombat remains have been excavated on the Australian mainland (25–27) and Tasmania (e.g., 28–31). The species is ethnographically recorded as being highly valued for the flavor of its meat (32) and high proportion of fat relative to body size (32–36).

There are many detailed accounts of Aboriginal hunting practices for bare-nosed wombats. On the mainland, several ethnographic accounts describe wombats being dug from (34–37) (**Figure 2**) or suffocated within (33) burrows. In Gippsland in Victoria, Gunaikurnai would take wombats sunning themselves at the entrance of burrows or drive wombats from burrows using dogs (32). The use of the bare-nosed wombat within Tasmania appears to have been widespread, with written accounts from all parts of the island except the southeast (38). Plomley (39) notes few Tasmanian word groups for the wombat, suggesting that this species held special significance among Palawa communities. George Augustus Robinson, who undertook extensive expeditions throughout Tasmania between 1829 and 1834, produced many written accounts of Palawa hunting strategies (38). Robinson described how wombats occurred in such numbers that they could be driven through the brush by torchlight and then speared or clubbed (38). The Wombat Plains, near present-day Scottsdale, is one such example.



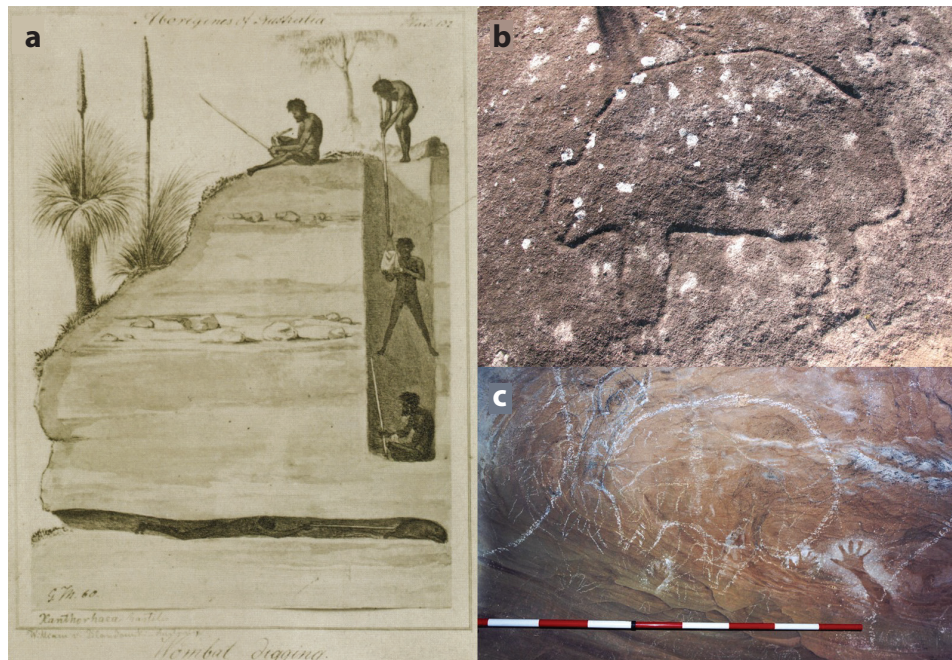


Figure 2

Cultural depictions of the bare-nosed wombat within the ethnographic and archaeological record are not common in southeastern Australia. (a) *Wombat Digging*, an illustration by Gustav Mützel (1855, Plate 132 *Aborigines of Australia: Wombat Digging*) inspired by Blandowski's (37) description of a multiday expedition to excavate a wombat from its burrow in central Victoria. The length and complexity of this process support interpretations of the high cultural significance of wombats in this region. Wombats feature as rock art motifs in limited locations in southeastern Australia, with only two regional sites having published records. Panel *b* (an engraved wombat on a rock platform) and panel *c* (an art motif) show two examples from Wollemi National Park, located in Wiradjuri country approximately 100 km northwest of Sydney. Both representations were found to be at higher elevations than other motifs in the park, interpreted to reflect the geographic distribution of the species (120).

EARLY EUROPEAN ACCOUNTS

The first documented sighting of wombats by European colonists was in February 1797 by the survivors of the wreck of the *Sydney Cove* on Preservation Island in Bass Strait (40). In that same year, escaped convict John Wilson surrendered himself to the settlement authorities in Sydney, having spent many years living among local First Nations communities on the Hawkesbury River. Wilson described in detail a new quadruped in the region matching the then-known description of the wombat (described in 40). These early accounts were followed in 1800 by the first scientific description of the mainland bare-nosed wombat (41). The name wombat derived from Wombach, a name Governor John Hunter noted in a letter to George Shaw in 1798.

DISTRIBUTION AND POPULATION STRUCTURE

Distribution records on the Australian mainland (*V. ursinus hirsutus*) stretch from southeast Queensland through eastern New South Wales, the Australian Capital Territory, Victoria, and southeast South Australia (16, 42) (Figure 1). However, range-restricting factors since European colonization have fragmented populations, and most contemporary observations are latitudinally

south of Newcastle, New South Wales; east of the Great Dividing Range; east of Ballarat, Victoria; and very southeast of South Australia (42). Credible observations still occur within the historic range (2, 43) but are rare and indicate isolated populations. The Bass Strait populations (*V. ursinus ursinus*) formally included King Island and large Furneaux Group islands—Flinders, Cape Barren, Clarke—but are now restricted to Flinders Island and a translocated population on Maria Island (16, 19, 44–46). In contrast, *V. ursinus tasmaniensis* has retained distribution across Tasmania (47, 48). Bare-nosed wombats occur from coastal to alpine/subalpine elevations >1,800 m a.s.l. (above sea level) (49) and across a wide range of habitats. Habitat preferences are indicated by proportional overrepresentation in agricultural, dry woodland and grasslands (native and invasive) and underrepresentation in wet woodlands and rainforest (50). Occurrence is governed by availability of forage and areas to construct burrows (2).

Genetic studies of bare-nosed wombats are few but have yielded valuable insights. Biogeographic isolation from flooding of the Bassian Plain following the Last Glacial Maximum (18) and large spatial clines of isolation by distance have been shown (19). Spatial patterns of genetic differentiation occur across the Australian mainland, especially between the distribution in South Australia and western New South Wales (19, 51), but more continuous sampling is needed to better understand genetic variation. Geographically continuous sampling from Tasmania has also revealed isolation by distance (19) and that large water bodies and large-scale land clearing (or persecution) restrict gene flow (52). The recent finding of genetically distinct *V. ursinus ursinus* on Maria Island (19) is consistent with translocation records from Flinders Island in 1971 (45); subspecies designation for Maria Island wombats was unknown previously (19).

Wombat dispersal behaviors may partially explain isolation-by-distance patterns. Dispersal is generally either natal dispersal, whereby juveniles move from their natal site, or breeding dispersal, whereby adults move among breeding sites (53). Most mammals exhibit male sex-biased natal dispersal (53). Bare-nosed wombats exhibit a rare female-biased dispersal trait, with male relatedness higher when geographically close (51, 52). Departure of females from natal sites may reflect mothers leaving burrows to their offspring.

CONTEMPORARY CONSERVATION STATUS

All bare-nosed wombat subspecies are categorized as Least Concern (IUCN Red List, since 2008) (42). *V. ursinus ursinus* was formally on the Australian Government Environment Protection and Biodiversity Conservation Act 1999 List of Threatened Species, owing to early-nineteenth-century extirpations across Bass Strait islands (King, Cape Barren, Deal, Clarke). However, this was revised on February 22, 2019, due to population stability on Flinders Island and genetic assignment of *V. ursinus ursinus* on Maria Island (19, 47, 50, 54).

Data on population trajectories of bare-nosed wombats are the most comprehensive for *V. ursinus ursinus* and *V. ursinus tasmaniensis*, showing increases over the last three decades (47, 50), but no trajectory information for *V. ursinus hirsutus* exists. Recent efforts to estimate the abundance across large spatial scales suggest population sizes of ~72,000 *V. ursinus ursinus* and ~840,000 *V. ursinus tasmaniensis* across their entire distributions (55) and ~432,000 *V. ursinus hirsutus* in Victoria (56). Collectively, *V. ursinus* subspp. are not currently threatened by widespread decline or extinction, but *V. ursinus hirsutus* is poorly understood, and population trajectories can vary locally and regionally (47, 57).

MORPHOLOGICAL DESCRIPTION

Bare-nosed wombats are thick-set, low-slung, barrel-shaped, quadrupedal marsupials, with a broad head set on a short strong neck, featuring a hairless nose, powerful shoulders, a broad pelvis, and



a vestigial tail (~25 mm) (2, 16, 17). As one of the world's largest burrowing herbivores (58), their short muscular legs are well-suited for burrow construction and subterranean dwelling (2). The front feet are broad and equipped with five spade-like claws, whereas the back feet are narrow with four clawed toes and a clawless thumb (2). The fore- and hind limbs function complementarily for burrow construction (see the section titled Burrows and Fossorial Behaviors). Bare-nosed wombat musculature and bone structure are specialized for burrowing, with a large scapular area for insertion of deltoid and trapezius muscles, facilitating forelimb movement (lifting and protracting and shoulder flexing), and the forearm bone adapted for pronation and supination (59).

Bare-nosed wombats have open-rooted, continuously growing teeth (aradicular hypsodonts; polyphyodonty) that allow consumption of highly fibrous and abrasive diets [morphology present since at least 34,790 ± 510 BP (Beta-42122B, ETH-7665B)]. They are born with a full dental arcade, which erupts by 32 weeks of gestation (60). Enamel is present only on the labial side of the tooth (aplodontia), ranging in thickness from 0.6 to 1 mm (61, 62). Based solely on dentition, Vombatidae are unique among marsupials, having only one pair of upper incisors (63). The size and development of the skull distinguish bare-nosed from hairy-nosed wombats and are likely influenced by diet and environment. Bare-nosed wombat skulls are larger, with longer mandible and nasal lengths and a smaller skull-to-zygomatic arch length ratio (64, 65). The masticatory muscles (masseter, temporalis, and pterygoid muscles) are also heavily developed in *V. ursinus* (66). The masseter muscle, associated with horizontal jaw movement (grinding motion), is larger in bare-nosed than hairy-nosed wombats and other marsupial species (66).

Adults are 77–115 cm in length, ~22–25 cm in height, and 17–39 kg in mass (2, 17, 67). Size and pelage vary among subspecies (**Figure 1**). *V. ursinus ursinus* is the smallest (length of 71–82 cm, mass of 15–22 kg) and often has a blonde or silvery-gray pelage, although darker brown and black color morphs occur (67). *V. ursinus tasmaniensis* is mid-sized (72–90 cm, 15–27 kg), and pelage varies from brown to gray, with gray being more common around coastal areas (2, 60). *V. ursinus hirsutus* is the largest (84–115 cm, 22–39 kg) and predominantly brown in coloration (17, 68). In general, pelage is uniform, and dull-red, black, and albino variations are noted occasionally (2). Texture of the coat is coarse, with long, thick (200-μm) guard hairs, which are shorter (~2 cm) and coarser on the hardened rump.

Sexual characteristics are difficult to ascertain by observation unless the female has a large pouch young (2). Females are generally slightly larger than males (0.5–2 kg), although there is much overlap (68). Sexual characteristics are distinct when handling wombats. In males, testes are carried in a small hairless scrotum suspended between the hind legs. The penis is S-shaped and stored internally when not erect, extending 12–15 cm when erect. In females, the pouch, located dorsoventrally, is apparent regardless of reproductive stage. When quiescent, the pouch is flattened to the body, containing two nipples located on each lateral side of the opening. The posterior-facing pouch opening (a distinctive feature of all extant wombat species) may be an adaptation to fossorial behaviors to limit fouling (2, 60). However, pouch development is not entirely consistent with this hypothesis. Pouch development begins opposite to the opening (anterior to posterior) and progresses laterally as breeding approaches (60).

LIFE SPAN AND ACTIVITY PATTERNS

In captivity, bare-nosed wombats have lived >30 years—most notably, Wain, a wombat from Satsukiyama Zoo in Osaka, Japan, lived at least 32 years. However, understanding life span in situ has been challenging. Typical life spans are perceived to be 10–15 years, but this is yet to be demonstrated rigorously. Bare-nosed wombats are difficult to age once they reach adulthood and generally do not have distinctive coloration or markings that permit long-term monitoring. This



challenge is exacerbated by nocturnality and propensity to shift burrows. Bare-nosed wombats also die within burrows, so distinguishing whether an individual has died, moved, or shifted activity patterns is not trivial.

Bare-nosed wombats are predominantly, but not exclusively, nocturnal (69, 70). Healthy wombats forage for 2–6 h (generally achieved by 4 am) before returning to burrows (71–74). Temperature is a major determinant of activity, as bare-nosed wombats struggle to regulate their body temperature above 25°C (70). Most out-of-burrow activity takes place after dusk (65–100% of the active period), but there is much seasonal, age-specific, and individual variation (69, 70, 73, 74). In general, activity periods are shortest in autumn and longest in spring and longer for subadults than for adults, and some individuals can exhibit >50% diurnal activity. Indeed, Plomley (38) and Flinders (75) observed wombats during the day across Tasmania and the Bass Strait islands. The most common behaviors outside burrows are grazing (80–90% of time), walking (10%), and scratching (1–2%) (69, 72).

COURTSHIP AND MATING

Sexual receptivity has been estimated as early as 1.6 years (15.4 kg) but generally occurs at or later than 2 years (60). Signals initiating courtship and mating are not well understood. Olfactory estrus signals from female feces, urine, or cloacal gland pheromones are hypothesized (2, 69). Breeding is year-round but most common in summer (68). Male competition for females has not been documented, raising questions about the nature of pair bonding. Using parentage analysis, Skerratt et al. (68) showed that bare-nosed wombats are polygamous, breeding generally occurs between wombats that share or use burrows in close proximity, and larger males sire more offspring. Detailed descriptions of courtship and mating exist (69, 70, 76–78). Pairing of adults, who would normally be solitary, signals courtship initiation. Pairing may last for more than one day, and individuals involved may traverse a small (~0.25-ha) area repeatedly (>20 times). As copulation approaches, the male closely follows the female, pawing and biting her rear until she lays on her stomach. To copulate, the male lays on his side at a right angle to the female's rump, grasping her rump and hind legs with his fore- and hind limbs. The female may escape, resulting in repeated bouts of chasing and biting until submission to resume copulation. Copulation ceases when the male releases his grip on the female. He may temporarily remain paired and occasionally nudge her rear with his head. Mating appears energetically costly for males, who breathe heavy and rest repeatedly.

DEVELOPMENT AND PARENTAL CARE

Once impregnated, females gestate for ~22 days (2), so births are also concentrated in summer (60, 67, 68). The hairless newborn (~15 mm long, 0.5 g) migrates from the mother's cloaca into the pouch and attaches to a teat. The newborn is first carried on one side of the pouch, and the pouch grows as the joey develops, enlarging in all directions, with the entrance progressively facing posterior (60). Over 6 months, the joey undergoes significant development, becoming fine-furred and reaching 1–1.4 kg; the head emerges from the pouch, and the large pouch young may co-graze with the mother (2). The increasingly distended pouch may eventually drag over the ground. By 8 months, the joey is fully furred, 2.7–3.4 kg, and often out of the pouch grazing, but almost always in physical contact with the mother (2). At 9–10 months (3.6–6.4 kg), the joey leaves the pouch permanently, remaining with the mother, and undertakes mixed grazing and suckling. Weaning occurs at 12–15 months (7.3–19 kg), and the joey becomes independent at 18–24 months (6.8–24 kg). There is no difference in developmental rate or mass of male and female joeys (60). In contrast to many macropods, there does not appear to be embryonic diapause or pregnancy during lactation for bare-nosed wombats (60).



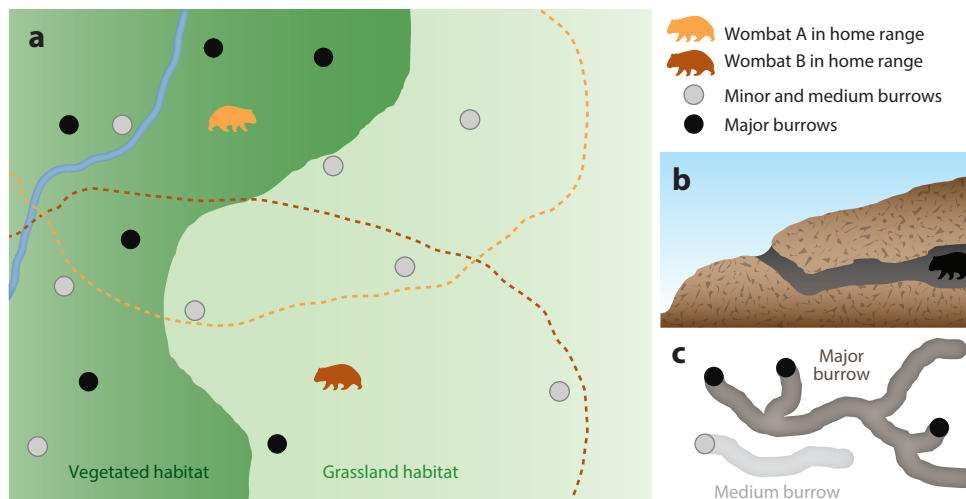


Figure 3

Diagrammatic illustration of bare-nosed wombat home ranges (*dashed lines and light shading*) and burrows (*circles*) in relation to habitat types: dark green vegetated habitat, light green grassland habitat, and blue stream. (a) Two bare-nosed wombats with overlapping home ranges that encompass both vegetated and pasture habitats and contain several major and minor/medium burrows they use for sleeping within and taking temporary refuge, respectively. Note that proportionally more major burrows occur in vegetated habitat, minor/medium burrows are found in both habitat types, burrows may be located in the banks of streams, and burrows are fewer further from vegetated areas. (b) A side-on profile of wombat burrow containing a wombat in a bedding chamber. Note the characteristic spoil mound created by excavation at the entrance of the wombat burrow. (c) The structural differences between major and medium burrows in terms of length, branches, and number of entrances.

BURROWS AND FOSSORIAL BEHAVIORS

One of Australia's great natural history stories features Peter Nicholson, a schoolboy in northeast Victoria, who explored within bare-nosed wombat burrows in 1960. Armed with a torch, spade, and mattock, Peter drew plans of several burrows and made observations of wombats he encountered. The written account was published in the school magazine (79) and remains among the most valuable in-depth studies of burrows (2). Since these formative observations, research on the burrowing ecology of bare-nosed wombats has been led by McIlroy and colleagues (71, 80) and supplemented by other investigations (68, 69, 81–85) (**Figure 3**). The landscape distribution of burrows has been mapped predominantly on foot, with recent studies using drones, noting limitations in heavily vegetated habitats (86). Early research within burrows involved researchers excavating or crawling in them (68, 71, 79, 80); recent research has sought technological solutions, including ground-penetrating radar and robotic vehicles (82, 87).

McIlroy (71) assigned burrows as minor, medium, or major, based on length (ca. 0.3–1.5 m, 1.5–5 m, or >5 m, respectively), entrance size, and extent of soil mound (**Figure 3**). Lengths reflect stages of development and vary in physical and environmental characteristics, patterns of use, and function (71). Minor burrows are often overgrown and in unfavorable habitats (creek beds, under a standing or inside a fallen tree), may be flooded, and are usually too short for wombats to shelter within. Their function is not well understood, but one study reported access to drinking water at dry times of year (83). Medium burrows are used as temporary refuges and diurnal shelters. Major burrows can exceed 20 m in length, are more complex (e.g., different branches, bedding chambers), are more likely to have multiple entrances, and are occupied most frequently (71).

Burrow creation/excavation is performed predominantly with the forelimbs, pushing the soil backward or sideways at a 45° angle. The right forelimb is often favored for excavation (71). When excavating walls, bare-nosed wombats may lay on one side to obtain a higher reach. After 2–3 min, accumulated soil is cleared efficiently by fore- and hind limbs (71). A wombat can excavate up to 1.2 m of burrow per night (71), and digging within burrows during diurnal periods has been observed (82). How frequently wombats undertake burrowing activities, and how this relates to life stage and sex, has yet to be investigated. Burrows generally run 1 m below the soil surface (range 0.4–2.8 m), with tunnels <40 cm wide and 30 cm high (68, 71, 80, 82). Burrow terrain is variable, involving sudden changes in incline, particularly near the entrance; sharp corners; the presence of objects; and variable substrate compactness (71, 82). Roots of grasses and other plants can extend through the burrow ceiling (82) and may be foraged upon. Defecation within burrows occurs, although scats are relatively uncommon and insignificant relative to above ground (82).

Major burrows may have supported multiple generations of wombats repeatedly excavating the tunnel network (2). Within these, bedding chambers are a characteristic feature. The term bedding chamber implies preferred sleeping spots, and they are, but wombats are also observed to sleep within tunnels (82). Most major burrows contain more than two bedding chambers along a stretch of tunnel (71, 80). Bedding chambers are up to 60 cm wide, 130 cm long, and 40 cm high (68, 71, 80). Anterior bedding chambers are located 2–6 m from the entrance, with the next 4–10 m from the entrance (68, 71, 80, 82). Chambers commonly contain bedding materials (twigs, bark, leaves, bracken, tussock and other grasses, foliage) (71, 80), with material presence and composition governed by surrounding habitat (80, 82). Burrow maintenance occurs, particularly clearing of mud, rotten vegetation, and bedding material after rainfall (71). Bedding material may then be replaced with new dry stock. Maintenance is also associated with changes in tenancy (71). Deceased and decomposed bare-nosed wombats are not uncommonly excavated by subsequent occupants (2).

Burrows are nonrandomly distributed (**Figure 3**). Inland, burrows cluster under forest cover (94–98% in forest, 2–6% in pasture), in areas where a slope facilitates drainage (68–92% of burrows), and above creeks (37–59% of burrows, particularly medium and major burrows). In coastal areas, burrows cluster in scrub habitats and where vegetation stabilizes sandy soil (69, 82, 88). In subalpine/alpine zones, burrows are located in grass, herb, and heath habitats above the winter water table and in woodland–grassland ecotones (89, 90). Burrows most commonly have a single occupant, but more than one wombat may occur either asynchronously (i.e., on differing days) or simultaneously in different tunnel branches (68, 71, 82). McIlroy (71) estimated occupancy to be 2%, 11%, and 44% for minor, medium, and major burrows, respectively, which is also supported by other studies (68, 81). Burrows are likely a limiting resource, and disputes over occupied burrows are noted (68, 69). In agriculturally fragmented landscapes, burrows can become aggregated in remnant vegetation and riparian areas and into pasture banks and have high occupancy rates (68, 69, 81, 85).

Bare-nosed wombats frequently inspect burrows during foraging (1–4 per night) but prefer 3–4 burrows to reside within, which they switch among every 1–9 days (68, 71, 73, 88). Burrows provide a range of functions, including a location for sleep, avoidance of predators, thermal refuge, and escape from fire (2). Beyond 3 m of the entrance, ambient temperature and humidity are more stable than outside, and notably cooler during summer (82). Wombats may move close to the burrow entrance prior to emerging to determine if outside ambient conditions are sufficiently cool (2, 80), although they have also been found asleep near the entrance early in the day (82), suggesting individual variation. McIlroy (71) reported most wombats emerged from burrows from 4 to 8 pm during winter, whereas emergence times were more dispersed at other times of year, reflecting individual variation to ambient temperature. Seasonality is supported by other studies,



with some identifying earlier activity in winter (72, 73), and adult males may emerge 30 min earlier than females (68).

Other species also exploit burrows for refuge (rest, thermal relief, escape from predators, shelter from fire, access to water). Rabbits frequently use burrows and may excavate smaller tunnels into the walls (80). Other noted species include foxes, cats, bush rats, possums, wallabies, echidnas, snakes, and Tasmanian devils (71, 91). Use of burrows by other species may be either simultaneous to the wombat or after it has vacated (71). Burrow use by other animals is likely much broader, is understudied, and may reflect a mix of entrance explorations and deeper use, probably for multiple purposes (91). Invertebrates have been observed deep within burrows (82), but there is little knowledge of this colonizing fauna.

SOCIALITY, VIGILANCE, AND COMMUNICATION

Outside of courtship and mother–joey associations, bare-nosed wombats exhibit solitary lifestyles (69). There is no evidence of territoriality, as home ranges overlap significantly (69, 73). Although generally tolerant of one another while foraging (92), bare-nosed wombats semi-frequently engage in intraspecific aggressive interactions, including chasing of conspecifics who may encroach upon a foraging spot (5–10 m) (2) and chasing of individuals from occupied burrows (68, 69). Bare-nosed wombats can growl, make high-pitched screeching vocalizations, and will bite the usually smaller subdominant individual being pursued (2, 71). Scars and small patches of fur missing from the rump, flanks, and back, and occasionally damaged ears, are relatively common.

Communication in bare-nosed wombats is understudied, but olfaction is understood to be developed, with visual and auditory signals comparatively less so, though still important (93). Differences in dominance of communication systems are evidenced by responses to other individuals (conspecifics, humans, other animals). Visual and auditory detection of humans is often not made until within 50 m, and commonly less (2). However, when humans are positioned upwind, detection can be rapid and obvious at considerable distances (>100 m) (2). Vigilance behaviors are distinct (92) and can be categorized into two increasing levels. The first involves pausing of foraging and mastication, but otherwise not changing body position, presumably to facilitate auditory vigilance (92). Paused foraging may escalate to an abrupt lifting of the head, the second level, presumably to facilitate visual vigilance, but otherwise remaining unmoved (92). This second level of vigilance may also involve obvious sniffing of the air. Finally, vigilance may escalate to marked behavioral changes, including orienting body position in relation to the signal and retreating to shelter. Whether the dominance of olfactory senses in bare-nosed wombats is associated with any gross anatomical structures, such as vomeronasal organs, is unknown (93).

Perhaps the most distinctive and understudied form of bare-nosed wombat communication involves use of scats. Wombats produce 80–100 scats per night, which are frequently deposited around burrow entrances and on or next to prominent points (e.g., rock, log, slight raise in topography, game trail) (2, 69, 94). Amazingly, the cubes are formed within the distal colon (a soft tube). Research has revealed mechanisms underscoring cube size and corner formation and that cubes aggregate better than if wombats produced spheres (94, 95)—capturing much public attention and garnering the 2019 Ig Nobel Prize for Physics. Aggregations of cubic feces within a wombat's home range are presumably both a visual and olfactory source of communication. The messages delivered are hypothesized to include identity, sex, age, home range, scent trails, burrow use, and estrus (2, 69, 94, 96). Occasional flehmen responses to scat aggregations prior to courtship support a role of olfaction in communicating estrus (2, 78). Additionally, bare-nosed wombats may urinate or create other secretions (a brown, odorous liquid) for communication (2), but this is not well studied.



INTERSPECIFIC INTERACTIONS

Excluding predation, direct interactions between bare-nosed wombats and other species are uncommon. McIlroy (71) documented simultaneous burrow occupancy with European rabbits to be relatively common (29% of major burrows), and occasionally also European foxes (6% of major burrows). However, whether these reflect co-occurrence or direct interactions is unclear.

More evidence shows bare-nosed wombats interact indirectly, through competition over grazing resources. Resource competition research has focused mostly on population-level effects with European rabbits (97–99) and eastern gray kangaroos (100, 101). In both cases, interspecific resource competition reflects dominance of grazing in all three species, whereas no evidence of resource competition with browsing macropods exists (101, 102). Analysis of fecal pellet deposition for grazing and browsing herbivores suggests bare-nosed wombats partition their foraging to avoid habitat overlap and interspecific competition (101). There is less partitioning with invasive, relative to native, species, reflecting evolutionary independence, but fine-scale adaptive niche partitioning to support coexistence does occur (101). Bare-nosed wombats' ability to graze flexibly across habitat types (coastal scrub and grassland, heath, and heathy woodland) provides some advantage over more restricted grazing strategies of eastern gray kangaroos and European rabbits (99, 101). Because bare-nosed wombats have low metabolic requirements (103), they may also be more tolerant to forage scarcity.

Nevertheless, under certain conditions (e.g., limited grazing habitat, high densities, drought), population-level effects of interspecific resource competition occur. Tamura et al. (100) showed that reduction of bare-nosed wombats or eastern gray kangaroos resulted in population release of the other, tapering to new environmental carrying capacities. Intraspecific resource competition was approximately twice as important as interspecific competition for species' environmental carrying capacities (100), supporting the role of niche partitioning in these coevolved competitors (101). Cooke (97) found European rabbits may have displaced bare-nosed wombats in part of their South Australian range, possibly reflecting the local environment already being marginal for bare-nosed wombats and a greater drought tolerance in rabbits. This interpretation was supported by Tasmanian research (environment not dry and marginal for survival), which found no such evidence of population-level trade-offs between wombats and rabbits (47).

PREDATION

Bare-nosed wombats exhibit a range of traits to avoid or resist potential predators (2). Their relatively large size, rotund shape, hardened rump, and muscular strength make bare-nosed wombats difficult for a potential predator to bite and restrain. Multiple burrows within a home range, and their use as retreat sites, also help resist predation. Wombats are especially protected within burrows, where they occupy tunnel space and block threats with their hardened rump.

Predation research has focused on dingoes, foxes, and Tasmanian devils. On the Australian mainland, Newsome et al. (104) found bare-nosed wombat remains in 2.1% of dingo scats from a coastal area and 51% from a montane site. They concluded that dingoes exhibited greater focus on predation at the montane site, as the dietary frequency was disproportionately greater than the difference in wombat abundance. Dingoes probably learn prey species-specific predation strategies where wombats are more abundant. Whether wombat remains in dingo scats reflected predation of young wombats, diseased individuals, or healthy adults is unknown (104). Nevertheless, there was no indication dingoes were causing wombats to decline, likely owing to abundance of other prey (wallabies and kangaroos) (104). Triggs et al. (105) also investigated wombat remains in dingo, fox, and cat scats in southeast Victoria, finding that 11% of dingo, 1% of fox, and 0% of cat scats contained wombat remains. This was also supported by a study across Victoria, where 12% of



dingo and 1% of fox scats contained bare-nosed wombat remains (106). In both cases, remains in fox scats likely indicated scavenging of carrion or predation of young wombats.

In Tasmania, where dingoes and foxes are absent and *V. ursinus tasmaniensis* is smaller than its mainland counterpart, Rogers et al. (107) found that 6% of Tasmanian devil scats included bare-nosed wombat remains. This frequency increased to 19% in devils translocated to Maria Island, where the even smaller *V. ursinus ursinus* occurs. Whether this difference represents a prey-size effect, the greater density of *V. ursinus ursinus* on Maria Island, or the naivety of *V. ursinus ursinus* to predators—neither dingoes nor Tasmanian devils occur in the natural range of *V. ursinus ursinus*—is unclear. Jones & Barmuta (108) also showed the presence of bare-nosed wombats in the scat of devils (and possibly spotted-tailed quolls) at a montane site, although it is difficult to discern frequency owing to lumping of wombats and wallabies as “large mammals.”

ECOSYSTEM IMPACTS

Digging mammals are important for ecosystem functioning (109). Bare-nosed wombats create new habitats by burrowing, bioturbation around burrow entrances, and shallow bioturbation (grubbing) in grazing areas while consuming grass roots (presumably for carbohydrates) (89, 110, 111). Ecosystem effects also include grazing on vegetation communities, deposition of feces into the environment, and trail creation (89, 110, 111). One recent study estimated that wombats engineer 1.2% of the local landscape, supporting geodiversity and biodiversity (89). Benefits of bioturbation are thought to include changes in chemical and structural properties of turned-over soil; water penetration; reduced surface runoff and erosion; increased soil moisture; organic matter capture; promotion of biodiversity by providing habitat for microscopic and macroscopic organisms; and increased seed capture, germination, and growth. Thus, range contraction of bare-nosed wombats (see the section titled Distribution and Population Structure) has likely contributed to a loss of ecosystem functioning in the Australian landscape (109).

Annual soil turnover from bare-nosed wombats is unknown, but mean excavation volume is estimated at 1.4–2.7 m³ (110, 112, 113). As a relative estimate, assuming bare-nosed wombats excavate one-quarter as much as a northern hairy-nosed wombat (112), a 22-kg individual moving 1.4 m³ of soil once per week would turn over 3.3 tonnes annually. Thus, a population of bare-nosed wombats can have significant ecosystem engineering effects. Research shows burrow mounds promote herb cover (28% cover), and this effect is increased where scats are deposited frequently (52% cover) relative to control areas (14% herb cover), whereas shrubs are reduced on mounds (89). Burrow mounds and other areas where wombats deposit feces have elevated soil nitrogen (89). Within grazing areas, bare-nosed wombats reduce grass biomass, mostly via height reduction rather than percent cover (111). Mechanical disturbance through grubbing may also promote herb dominance (89).

METABOLISM AND WATER TURNOVER

In marsupials, basal metabolic rate (BMR) is strongly positively correlated to body mass (~98% variation explained) (114). Additional BMR variation can be explained by species behavior. For example, burrowing marsupials have lower BMRs than nonburrowing marsupials (114, 115). BMRs summarized across bare-nosed and southern hairy-nosed wombats are only 32% of that estimated for macropods (140 kg^{-0.75} day⁻¹) (115). Low BMRs may be attributed to short foraging bouts, exploitation of stable microclimates (burrows allow less energy expended on thermoregulation), and foraging selectivity (i.e., when ambient temperatures are less extreme) (72, 103, 116, 117).

In contrast to BMRs, field metabolic rates (FMRs) represent the metabolic cost of activities required for survival (e.g., movement, foraging). FMR is also correlated with body size but scales



differently (118) and cannot be derived from BMR. Two studies have estimated FMRs in bare-nosed wombats (103, 116). During the dry season, *V. ursinus hirsutus* using grassy woodlands have FMRs of $155.59 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (54.57 SD), increasing during the wet season to $321.66 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (117.30 SD) (103). Similar FMRs are observed in *V. ursinus tasmaniensis*, with dry-season FMRs of $155.38 \text{ kJ kg}^{-1} \text{ day}^{-1}$ (5.47 SD) (116). FMRs in wombats with sarcoptic mange disease (etiological agent *Sarcoptes scabiei*) can be 40% higher than those observed in healthy individuals ($218.27 \text{ kJ kg}^{-1} \text{ day}^{-1}$, 34.36 SD) (116).

The metabolic process also involves water turnover: the rate of intake (influx) and loss (efflux) from the body (urine, feces, respiration). Bare-nosed wombats have low water-turnover rates relative to other mammals (103, 116). Water influx and efflux in the dry season ($53.13 \text{ mL kg}^{-1} \text{ day}^{-1}$, 12.79 SD; $53.34 \text{ mL kg}^{-1} \text{ day}^{-1}$, 12.70 SD, respectively) are similar, although less variable than in the wet season ($57.37 \text{ mL kg}^{-1} \text{ day}^{-1}$, 21.79 SD; $57.06 \text{ mL kg}^{-1} \text{ day}^{-1}$, 22.93 SD, respectively) (119). In *V. ursinus tasmaniensis*, dry-season water influx and efflux rates ($91.10 \text{ mL kg}^{-1} \text{ day}^{-1}$, 15.75 SD and $90.96 \text{ mL kg}^{-1} \text{ day}^{-1}$, 15.08 SD) are higher than in their mainland counterparts (above values), likely reflecting effects of cooler temperatures. During dry periods, reduced water influx can affect food and nutrient uptake. Water restriction in captive bare-nosed wombats (50% of ad libitum) resulted in 50%-reduced dry matter intake ($\sim 8 \text{ g}$ difference on average, reduced to $24.1 \text{ g kg}^{-0.75} \text{ day}^{-1}$), as well as reduced nitrogen intake and percent of digestible nitrogen (120). Most water efflux was still associated with urinary and fecal loss but reduced by 60% (121).

DIGESTION

The bare-nosed wombat's digestive tract is long relative to its 77–115-cm length (tract-to-body length ratio 9.6) and forms a significant component of body mass (18.5% of wet mass). The stomach is single chambered (monogastric), and the cecum is small. The small intestine is long (35.6% of tract length) but low in capacity (9.3% of content) relative to the proximal colon (42.9% of length, 72% of content), whereas the distal colon is shorter (19.9% of length) and also has low capacity (14.3% of content) (122).

Wombats are hindgut fermenters. Proteins are digested almost exclusively in the stomach and small intestine (122). Saliva composition, stomach pH, and microbial communities demonstrate that fiber digestion occurs in the large intestine to create short-chain fatty acids (123–125). Dry matter is digested primarily in the upper proximal colon (91% of nitrogen, 48% of neutral detergent fiber) through fermentation (122) by bacterial communities composed mainly of Prevotellaceae (carbohydrate/fiber fermentation taxa) (125). Short-chain fatty acid concentrations are highest in the upper proximal colon (87.1 mmol l^{-1}) and decrease as digesta progress to the lower proximal colon (66.6 mmol l^{-1}) (124). Energy generated from short-chain fatty acid fermentation accounts for 61% of the standard metabolic rate of wild bare-nosed wombats (124). Cubic fecal pellets are well developed by the mid-distal colon, forming rectangular prisms $2.3 \pm 0.3 \text{ cm}$ high, $2.5 \pm 0.3 \text{ cm}$ wide, and $4.0 \pm 0.6 \text{ cm}$ long (94).

FORAGING

The bare-nosed wombat diet is dominated by native grasses (71, 99, 119, 126–128), including wiry snow grasses (*Poa labillardieri*, *Poa sieberiana*), wallaby grass (*Danthonia* spp.), kangaroo grass (*Themeda australis*), and weeping grass (*Microlaena stipoides*) (71, 119). Outside of the burrow, wombats spend most of their time feeding, at a rate of 75–100 bites/min, moving slowly within a small area, with purposeful movements between feeding bouts (69, 72, 116). Wombats spend little time drinking while outside the burrow (71, 72), though some burrows may provide water resources and some subterranean drinking may occur (83). Foraging occurs in a range of habitats, including



woodland, pasture, plantation, and subalpine areas (119, 126). Where there is snowpack, wombats will select exposed or shallow snow-depth areas (<35 cm) (49).

Selectivity in dietary choices based on forage availability is observed, independent of habitat type (119, 126), but may shift across elevations. At higher elevations, higher proportions of shrubs (*Olearia phlogopappa*) and herbs (*Dianella tasmanica*) are consumed, possibly reflecting species' accessibility in areas with snowpack (99, 127, 128). Forage selectivity of *M. stipoides* (proportion of fecal pellet) is greater in summer and autumn than in winter, reflecting summer biomass, whereas *Poa* spp. are high in all seasons (119). The grass leaf is the most-consumed plant part (81%, stem and sheath comprising 11%) (119). Bark and roots may also be used when resources are limited (126, 127), and forbs, rushes, and sedges are also occasionally used at low proportions (119). Generally, the proportion of grasses, forbs, and sedges consumed remains consistent across seasons (119), and this diet has been stable for thousands of years, back to the late Pleistocene (129).

Variation in diet leads to differences in dental growth rates at intra-individual and intra- and interpopulation levels (62, 129). Growth rates of mandibular incisors from Australian mainland bare-nosed wombats range from 0.1 to 0.2 mm/day (61, 130). In Tasmania, mandibular incisor growth rates vary between 0.01 and 0.11 mm/day, which is up to 2.5-times faster than other tooth forms (129). These dental growth rates overlap with those from late Pleistocene Tasmania (0.03–0.21 mm/day), with faster Pleistocene growth likely reflecting the more arid environment and coarser plants available (62).

Despite adaptation to low-nutrition diets, bare-nosed wombats are still impacted by shifts in nutrient availability, specifically of nitrogen and fiber. They require $150 \text{ mg kg}^{-0.75} \text{ day}^{-1}$ of dietary nitrogen for maintenance, and diets low in nitrogen result in diminished body mass and nitrogen digestion capacity (115). Nitrogen outflux via urine also diminishes, likely reflecting lower urea influx on reduced-nitrogen diets (115). Increasing fiber availability reduces the digestibility of dry matter and neutral detergent fiber and tends to reduce digesta retention times (115). Diet and dietary variation have also been explored through stable isotopic analyses, which now comprise one of the most comprehensive species-level data sets in the southern hemisphere. Calcium (131) and carbon stable isotopic profiles are consistent with a seasonal diet, and strontium profiles are consistent with the underlying geological substrate (129, 131). No dietary variation between sexes is observed.

MOVEMENT AND SPACE USE/HOME RANGE AND DENSITY

Home range sizes and population densities of bare-nosed wombats are well studied, documented in Tasmania, Victoria, and New South Wales. Bare-nosed wombats are central place foragers, with home ranges centered around resident burrows and high home range fidelity (49, 71, 73) (**Figure 3**). Resident wombats retain up to 99% of their home range throughout the year, but the center may shift seasonally up to 670 m (49, 68, 73), likely reflecting seasonal burrow selection and forage variation. Matthews & Green (49) calculated home range sizes of wombats at higher elevations (1,270–1,800 m a.s.l.) and summarized size estimates across studies. Between 1,550 and 1,800 m a.s.l., altitude positively predicts home range size (49). This relationship extends to lower elevations (49, 68, 69, 71, 73, 81, 127) and is not unduly biased by variation in techniques (e.g., radio collar versus GPS collar, minimum convex polygon versus kernel density, number of fixes), although below 1,200 m a.s.l. there is much overlap. Male bare-nosed wombats generally have larger home range sizes than females (up to 4.4 times larger) and travel faster and further each night. Home range size declines during winter, particularly for males (49, 68), but not in all studies (see 73).

Bare-nosed wombat density estimates range from 0.1 to 1.9 individuals per hectare, with most estimates around 0.1–0.2 (55, 56, 68, 69, 71, 73, 81, 96, 102, 132, 133). Densities are thought to be



lower at higher elevations (49, 127), but research is needed. Recent research has estimated density at large spatial scales (55, 56), facilitating total population estimates for *V. ursinus ursinus*, *V. ursinus tasmaniensis*, and *V. ursinus hirsutus* in Victoria (see the section titled Contemporary Conservation Status). Longitudinal estimates of density change are all from Tasmania and support density increases over the last three decades (55, 69, 133). Although aboveground density estimates are standard practice, ecological relevance should be considered. Expressing densities as a ratio relative to burrows (burrows:wombat) may often be more relevant, as ratios account for the relative availability of refugia, central to wombat life; provide a potentially more accurate indication of environmental carrying capacities; and encompass how site-specific substrate differences influence burrowing and limit abundance and because burrow availability and switching are important in parasite transmission. Burrows:wombat ratios are a relatively straightforward metric to calculate in field surveys, and synthesis from existing research suggests variation from 2 to 20, with an average of ~10 (68, 69, 71, 73, 81, 88, 133).

IMPACTS OF FIRE, FLOOD, DROUGHT, AND OTHER ENVIRONMENTAL FACTORS

Bare-nosed wombats are subject to a range of threatening processes, natural and anthropogenic. The effect of bushfire is surprisingly understudied given its prominence in Australia. What little research exists suggests that bare-nosed wombats have higher survival than many other marsupials, owing to insulation within burrows (2, 134). Newsome et al. (134) studied mammal tracks before and after fire, finding wombats survived fire well relative to wallabies and kangaroos. Fire may lead to collapse of some burrows, particularly when dug under fallen trees that burn (2). Smoke inhalation is likely also important, and wombats may die underground from this, but no research data exist. During bushfire events, other animals have also been reported to use wombat burrows for shelter.

Post fire, there are foraging consequences for surviving wombats. Focusing on scat counts as indicators of habitat use, Heaton et al. (135) found that bare-nosed wombat scats occurred more commonly in unburned heath, sedgeland, dry forest, and highland habitats, suggesting fire was detrimental to forage availability. In contrast, scats were more common in burned grasslands, suggesting fire increases forage in this habitat, likely through palatable new shoots and clearance of ground cover to access roots. No scats were detected in wet forests. In research from highland habitat following fire, bare-nosed wombats increased their home range size to meet dietary requirements and survive the winter (127).

Other extreme climatic events impact bare-nosed wombats, including floods and drought. Seasonal flooding does not necessarily present a problem, as wombats can shift burrows to avoid adverse effects (2, 71). However, sudden intense rainfall events may inundate burrows before individuals can move to higher ground. Data on the effects of flooding are scarce, although reports from wildlife carers pumping water out of flooded burrows and finding wombats within suggests drownings may occasionally occur. In the opposite scenario, droughts present a problem to bare-nosed wombats through resource limitation, starvation, and opportunistic infections as a consequence of an immunocompromised state (2), but there is little research on this subject. Wombats can also be exposed to contaminants in the environment, such as those associated with mining (136).

PERSECUTION

Bare-nosed wombats have been the subject of significant persecution from European settlers (2). Introduced rabbits played an important role in the wombat first being perceived as a pest (2). Wells



& Pridmore (137) provide the most extensive description of persecution relevant to bare-nosed wombats. Most persecution has derived from agricultural landholders and is associated with efforts to reduce grazing and damage to infrastructure (wombats pushing under fences, burrowing into farm dams and under building foundations), risks of injury to stock (damaged limbs from stepping into wombat burrows), and facilitation of other unwanted herbivores and predators (wombats creating gaps under fences that macropods and foxes traverse) (138). Other reasons include parasites and disease, erosion, hazards to motorists, complications to rabbit control, sport hunting, property development, and general derision by some sectors of Australian society. Justifications of antipathy are not always supported by evidence (1, 138). However, attitudes toward bare-nosed wombats have become less aversive over time, and this may be a source of population increase in recent decades (47).

Temby (1) provides an excellent summary of state/territory legislative changes through to the 1990s. Overall, legislative changes have moved from antipathy and non-protection to concern and protection. In South Australia, full protection of bare-nosed wombats came through the National Parks & Wildlife Act 1972, with no provision for wombat destruction to control damage. Similarly, there has been full protection without provision for destruction in the Australian Capital Territory since the Animals & Birds Protection Ordinance 1918, with current protections enshrined in the Nature Conservation Act 1980. After a varied protection history, bare-nosed wombats gained full protection in New South Wales through the National Parks & Wildlife Act 1974, with provision for destruction for the purpose of damage control. In Tasmania, wombats are protected with the provision for destruction for damage control and declaration of an open hunting season through the National Parks & Wildlife Act 1970, although a hunting season has never been declared. Owing to public pressure, permits to destroy bare-nosed wombats have decreased greatly in Tasmania (47) and other states where it is allowed.

In contrast, Victorian legislation has been the source of the greatest prejudice against bare-nosed wombats (1). Bare-nosed wombats were gazetted as “vermin” in 1906, and a bounty system was introduced in 1925, which remained until 1966. Wombats were trapped, shot, and poisoned in significant numbers near and distant from agricultural lands (64,000 in the last 16 years of the bounty system) (1, 138). Trapping was undertaken predominantly using jaw traps buried in burrow entrances and on trails (138). Significant time could pass between trapping and trap checking, and captured and injured wombats would often perish (2). Bare-nosed wombats remained classified as vermin under the Vermin & Noxious Weeds (Amendment) Act 1958, requiring destruction by landholders, although many elected to be tolerant. Bare-nosed wombats were declared protected in western Victoria in 1977 but remained classified as vermin in the east until 1984 (1). This system of persecution resulted in the discontinuous distribution between western Victoria and eastern South Australia (**Figure 1**). Although bare-nosed wombats were no longer vermin in Victoria and were protected by the Wildlife Act 1975, lobbying by farmers has meant they have remained unprotected wildlife in 193 parishes (a substantial part of their range) and could be destroyed by use of firearms, fumigants [mostly chloropicrin (tear-gas) or phosphine gas], and traps on private land, and on Crown land within a kilometer of private land (except in National Parks) (1). In 2020, under public pressure, the Victorian Environment Minister announced that the Wildlife Act 1975 would be amended to ensure protection across the state.

Bare-nosed wombats’ impact on fencing infrastructure is an ongoing and understandable challenge for agriculturalists. Bare-nosed wombats tend to push through obstacles in their path, which is particularly problematic when they push under fences intended to exclude predators, such as foxes, and grazing pressure from macropods (2). Efforts to minimize the impact on fence infrastructure include low-level electric fencing (139), exclusion fencing (140), and gates that wombats push through but macropods and foxes do not (140–142). All methods produce desired effects to



varying extents. Wombats become accustomed to gates within a month of installation (if not immediately), and gates and exclusion fencing are effective at excluding or vastly reducing unwanted mammals (140–142).

Forestry presents another form of anthropogenic impact. McIlroy (71) found that densities declined following felling and burning of native forest, particularly owing to burrow destruction by machinery. However, populations rebounded over 3–5 years following pine plantation owing to regrowth of grasses in young plantations with canopy gaps. In contrast, there were fewer canopy gaps, grasses, and wombats in older pine plantations. McIlroy & Rishworth (143) found similar effects of clear-felling and pine forest regrowth, but that more modern thinning techniques support grass regrowth and wombat populations. Thus, pine plantation forestry is not necessarily detrimental for bare-nosed wombats, but native sclerophyll forests are of greater value because they tend to retain grasses regardless of age.

COLLISION WITH VEHICLES

Collisions with motor vehicles are a significant source of mortality for bare-nosed wombats. Several studies have investigated roadkill from the Snowy Mountains Highway in southern New South Wales (144–146). Roger & Ramp (146) explained 62% of model deviance owing to higher mortalities where local forest cover was highest and groundcover greener; when burrows were nearby, but those burrows were inactive (possibly because of the road modalities); and nearer other forms of cover (blackberry bushes). The most important variable was groundcover greenness (45% of model variation), followed by other forms of cover (29%) and amount of nearby inactive burrows (18%). For the 15-km length of highway studied, a mean roadkill number of 27.3 ± 7.12 per year between 2002 and 2005 was recorded (or 0.005 wombat kills per day per km) (146), which was estimated to be 40% of the total roadside population (145). Roadkills were the most important cause of the probability of population decline (145).

Driessen et al. (50) reported that bare-nosed wombat roadkills in Tasmania were widespread along major roads, with the interaction of traffic speed and wombat density likely a main cause of mortality along roads with low traffic volume. Hobday & Minstrell (147) estimated 2,600 wombat roadkills per year in Tasmania, which is likely an underestimate, as these surveys did not include areas with some of the highest roadkill rates in the state (50). Nevertheless, wombat numbers in Tasmania have continued to increase, suggesting roadkills have not been a source of landscape-level population decline (47, 50). Even if roadkill is not causing widespread declines, it should be reduced where possible from an animal welfare and ethical standpoint, as well as to reduce road accidents and associated vehicle damage and occupant injury (50).

Several studies suggest roadkills vary seasonally (43, 145, 148; but not all, see 147). Nguyen et al. (148) found roadkill rates were lower in summer and relatively consistent in other seasons. Analyzing citizen science data, Mayadunnage et al. (43) found bare-nosed wombat roadkills were more common in winter and spring than in summer. Interestingly, most bare-nosed wombat roadkills are healthy individuals (i.e., not suffering from sarcoptic mange) (43). Research on deterrent devices (virtual fences) to reduce roadkills demonstrates they are ineffectual (149, 150). Bare-nosed wombats likely become habituated to deterrent devices. Strategically positioned wildlife underpasses may be more effective in areas of welfare and conservation concern.

CONCLUSIONS

We have built upon Triggs's (2) important foundation to bring together as much knowledge on bare-nosed wombats as possible. Though we could not cover all topics (e.g., parasitism and disease; veterinary medicine; and rescue, rearing, rehabilitation, and release), we hope our synthesis



forms a critical resource to help the reader rapidly assimilate existing information and identify knowledge gaps, limitations, and future directions. Bare-nosed wombats are an excellent model to study fossorial terrestrial vertebrates, ecosystem-engineering organisms, olfactory communication, digestive and metabolic adaptations to nutrient-poor diets, and natural and anthropogenic threats to geographically widespread species. Fruitful opportunities exist to advance fundamental and applied knowledge with bare-nosed wombats, and we are optimistic that recent tremendous knowledge advances will continue.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors acknowledge the Aboriginal custodians on whose traditional lands this review was conducted. S.C. was supported by funds from the Australian Research Council Linkage Program (grant LP180101251) and charitable donations from the Harris Estate.

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