

The mechanical properties of bettong and potoroo foods

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Handling Editor:

Bronwyn McAllan

Received: 27 February 2024

Accepted: 28 May 2024

Published: 19 June 2024

Cite this: Mitchell DR *et al.* (2024) The mechanical properties of bettong and potoroo foods. *Australian Mammalogy* 46, AM24006. doi:10.1071/AM24006

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ABSTRACT

Potoroid marsupials (bettongs and potoroos of the family Potoroidae) are considered ecosystem engineers because of the roles they play in maintaining biodiversity. However, severe declines since European arrival have necessitated intense conservation efforts. Vital to these efforts is an understanding of the physical challenges that define their niches. The mechanical properties of their foods, such as toughness and stiffness, represent a physical interface with the environment that can contribute to quantitatively defining their niches. Here, we provide mechanical property data from wild bettong and potoroo foods, such as roots and tubers, fruit, fungi, invertebrates, seeds, and leaves. Toughness ranged from approximately 56.58 J/m² (fungal sporocarp of *Descolea* sp.) to 2568.15 J/m² (tubers of the blue yam, *Brunoniella australis*). Similarly, stiffness of the wild foods ranged from 1.15 MPa for *Descolea* sp. to 30.4 MPa for *B. australis*. However, the mechanical demands of accessing the kernels from within the shells (testae) of sandalwood and quandong (*Santalum* spp.) seeds far exceed measurements of any foods tested. We also tested some farmed foods, alongside inclusion of data from previous studies. Taken together, these data can also improve selection of comparable foods in designing diets for potoroids, and other species, in captivity.

Keywords: captive management, conservation, diet, elastic modulus, fracture toughness, habitat use, mastication, Potoroidae.

Introduction

Bettongs and potoroos are considered ecosystem engineers (Jones *et al.* 1994; Neilly and Schwarzkopf 2018; Davies *et al.* 2019; Decker *et al.* 2019; Ross *et al.* 2020) because their habitual digging and burrowing behaviours used in foraging (Garkaklis *et al.* 2004; Vernes and Jarman 2014), seed caching (Murphy *et al.* 2005; Chapman 2015), and refuge (Sander *et al.* 1997) are obvious examples of autogenic environmental change (Jones *et al.* 1994). These disturbances lead to bioturbation and aeration of soil, creating litter traps and facilitating incorporation of nutrients. This can in turn alter vegetation compositions and nutrient cycling (Neilly and Schwarzkopf 2018; Ross *et al.* 2019, 2020). Furthermore, potoroids are known dispersers of seeds and fungal spores through their specialised diets (Claridge *et al.* 1992; Vernes *et al.* 2002; Eldridge and James 2009; Palmer *et al.* 2021). Yet potoroid distribution and diversity has been greatly affected by European settlement (Short 1998; Westerman *et al.* 2004), with many species now extinct and others suffering niche contractions (Short 1998). Revitalising populations and distributions of remaining species is an essential consideration for maintaining biodiversity and ecosystem health in Australia. Resolution of this goal has been approached through translocations (Christensen and Burrows 1994; Short and Turner 2000; Priddel and Wheeler 2004) and the establishment of reserves (Bice and Moseby 2008).

Important to these conservation efforts is a clearer understanding of the niche parameters of potoroids because an awareness of abiotic and biotic limitations helps to inform decisions of locality and habitat choice for future populations. Different species of bettongs and potoroos have evolved from various environments with historic distributions across much of Australia; and from contrasting environments come contrasting

resources. The mechanical properties of food are quantifiable metrics that can delineate fundamental niche limits. Studies involving potoroid feeding ecology mention contrasts in food hardness or resistance between species (e.g. Mitchell *et al.* 2018); however, these assumptions remain unqualified in the literature. Most research into the properties of different foods has been limited to primate diets (Agrawal *et al.* 1997; Williams *et al.* 2005; Coiner-Collier *et al.* 2016; Laird *et al.* 2020), or plant materials usually in the context of browsing and grazing herbivores (Sanson *et al.* 2001; Read and Sanson 2003; Caldwell *et al.* 2016). Here, we provide food mechanical property data for food groups known to be dominant components of potoroid diets.

Potoroids are known specialists of nutrient-rich, highly digestible foods. The diets of the seven extant species of potoroids include high proportions of such disparate food groups as hypogeous fungal sporocarps (i.e. truffles), fibrous roots, tubers, bulbs, the stems and leaves of plants and grasses, fruits, flowers, and insects (Seebeck *et al.* 1989). Fig. 1 illustrates dietary variation across extant species of potoroos and bettongs. Some species, such as members of the genus *Potorous*, have diets dominated by truffles, while the rufous bettong (*Aepyprymnus rufescens*) has a diet dominated by fibrous roots and tubers. We predicted these food groups would be discrete in toughness and stiffness. However, of additional interest was the particularly durable shells (testae) of *Santalum* spp., which some bettongs are known to crack open to extract the nutritious kernels within (McNamara 2014; Chapman 2015). We expected these shells to represent a maximum extreme of biting capacity that these species would encounter, so the testae of these seeds were also tested.

Foods consumed by animals in the wild are often described in terms of their puncture and crushing resistance, which have been collectively described as mechanical

properties (Lambert *et al.* 2004; Wieczkowski 2009). Although informative, these terms do not fully describe the mechanical properties of food breakdown in the oral cavity. Measures that more meaningfully describe a food’s resistance to fragmentation include the Young’s modulus (E) – a measure of material stiffness or resistance to crack formation – and fracture toughness R – a measure of resistance to fracture propagation (Lucas 2004). When a force is applied to an object, some force is dispersed throughout the structure of the object. This force per unit of area is stress (σ), measured in newton per metre square (N/m^2). When stress within the object reaches a magnitude greater than a critical yield point, it can cause deformation of the object’s structure (Fig. 2a). This deformation, calculated by dividing the change in length of the material by its initial length, is called strain (ϵ). Young’s modulus (E), calculated by dividing stress by strain, offers an estimation of how much force is required to instigate a degree of deformation in the material (Lucas *et al.* 2001; Lucas 2004). The greater the value of E , the stiffer the material, and the more force is needed to deform it. Fracture toughness (R) represents the energy required to propagate a crack in a material of a given area and is represented by joules per metre squared (J/m^2) (Fig. 2b). These data obtained from potoroid food groups will not only benefit conservation initiatives of these important species through better understanding their physical limitations in their respective environments, but will also help identification of suitable dietary substitutes in captivity (Williams *et al.* 2005).

Methods

Field collections and the majority of mechanical property sampling took place in August 2023 in the New England

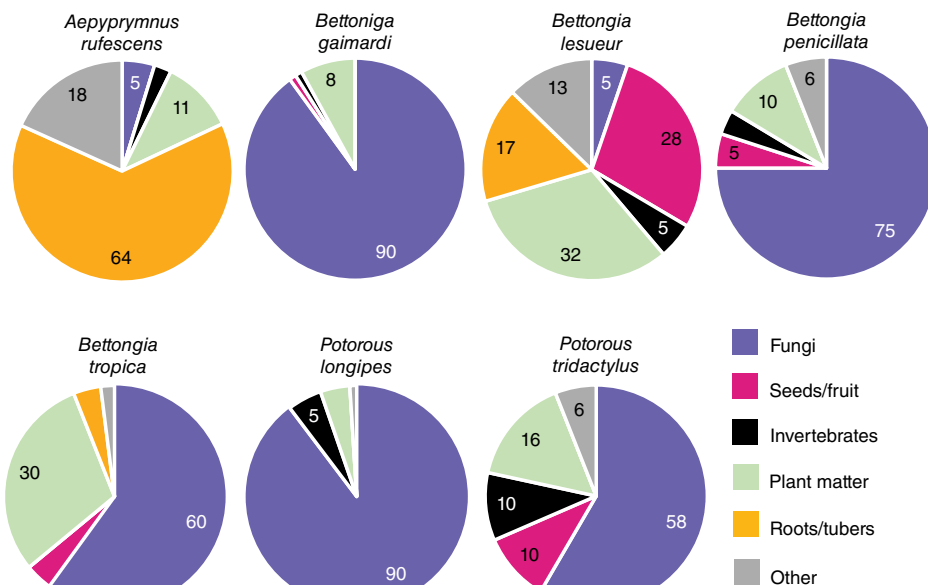


Fig. 1. Proportions of different food groups in the diets of all extant species of the Potoroidae. Proportions are averaged across seasons and publications when applicable (Guiler 1971; Bennett and Baxter 1989; Taylor 1992; Claridge *et al.* 1993; Green *et al.* 1999; McIlwee and Johnson 2002; Vernes *et al.* 2002; Bice and Moseby 2008; Robley *et al.* 2008; Zosky *et al.* 2017). Note: grass material identified in McIlwee and Johnson (2002) as the dominant component of the *Aepyprymnus rufescens* diet has been confirmed to be tuber and stem-base material (Christopher Johnson, pers. comm.). Numbers indicate rounded proportions greater than 5%.

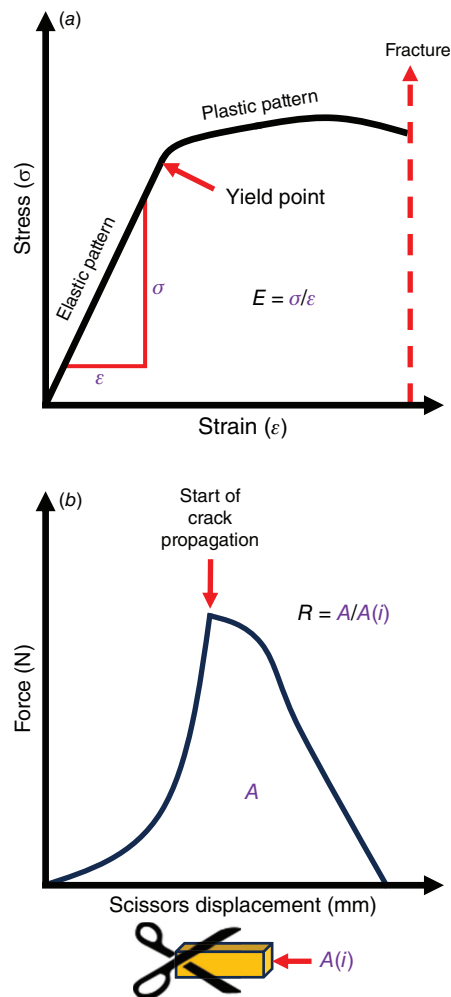


Fig. 2. (a) During the application of forces to a material, stress and strain increase linearly in an elastic pattern until reaching a critical yield point. Stress then exhibits a plastic pattern, being unable to return to its original form, until reaching a final point of fracture. Young's modulus (E) is calculated by dividing the stress (σ) by the strain (ϵ) at the initial, linear portion of the curve. (b) When commencing a cut through a piece of material with a cross-section of $A(i)$, the force increases with the initial resistance until the point of crack propagation, beyond which force steadily decreases until the cut is complete. Toughness (R) is calculated by dividing the area (A) beneath the curve by $A(i)$.

bioregion (Table 1). Targeted species of introduced and native plants with roots and tubers consumed by *A. rufescens* (Schlager 1982) were carefully uprooted. Plant samples were identified using reproductive or vegetative morphological characteristics and compared to vouchers lodged in the N. C. W. Beadle herbarium. Six species of subterranean fungi were raked from the topsoil at the base of *eucalypts* (*Eucalyptus* spp.) and identified to either genus or species based on morphological characters of sporocarps, microscopic examination of spores, and comparisons with collections made during previous studies in this region (Danks et al. 2010, 2013; Nest et al. 2023). Samples of browse and

fruit were also collected from the Simpson Desert and brought to Armidale at time of sampling. Sandalwood seeds and quandong seeds were bought online as dry samples but fresh quandongs were also later collected locally from South Australia to compare the properties of the two food conditions. Fresh samples were stored in zip-lock bags and refrigerated. Measurement of mechanical properties took place within 24 h, with the exception of fresh quandongs, which we obtained on a later date. These were flown to J. A. L.'s lab in Tennessee and tested ~ 1 week after their collection. These were tested by the same researcher (J. A. L.) on the same equipment, but on a date following the sampling period for the other foods. Fungi and plant material in the New England bioregion were collected under Department of Planning and Environment Scientific Licence SL102681.

We also included data from farmed foods, sampled both by ourselves and by others for previous research, as a means of comparison. This information was included as familiar reference points to assist understanding of the dietary delimitations inherent in some potoroid diets, and to identify foods of similar properties for formulating diets of captive animals.

Some measurements were taken to compare the physical dimensions of wild food types. This included the maximum diameter of roots/tubers, and maximum diameters of fungi, fruits, and whole browse, as the most likely maximum axes bitten across by potoroids.

Mechanical tests used to quantify the E and R of foods were performed using a Lucas Scientific FLS-2 portable tester, an updated version of the FLS-1 tester (Darvell et al. 1996; Lucas et al. 2001), fitted with 50, 100, and 1000 N load cells. The tester is similar to Instron materials testing machines used in engineering and materials science laboratories, and has been used to collect the mechanical properties of mammalian foods (mainly primate) in the wild for over 20 years (Wright 2005; McGraw et al. 2016; Talebi et al. 2016; van Casteren et al. 2016, 2019; Paine et al. 2018; Chalk-Wilayto et al. 2022; Laird et al. 2020, 2022). The tester consists of three central components: (1) a stainless-steel test stand that houses interchangeable load cells, (2) a data integration box which records compressive and tensile forces in real time, as well as the displacement of the tester's crosshead, and (3) a computer with software that reads the data output from the integration box. Interchangeable parts allow researchers to perform a wide variety of mechanical tests (Lucas et al. 2001).

Food stiffness was quantified using a compression test. Our study limited stiffness tests to foods that could be cut into either a cube or cylindrical shape for the purposes of crushing. Food samples were crushed between the testing platen and compression jig, and Young's modulus (E) was estimated by taking the slope of the force–displacement curve within its elastic range (i.e. before permanent shape change). The toughness of food tissues was quantified using a scissors-cutting test (Lucas 2004). Most samples were cut into thin matchstick-shaped cuboids or, in the case of leaves and insect cuticle, thin rectangular sheets. Values for

Table 1. Species sampled and sampling locations for wild potoroid foods.

Species	Latitude	Longitude	Locality	Food type
<i>Arthropodium milleflorum</i>	-31.084	150.950	Oxley Scenic Lookout, Tamworth, NSW	Roots/tubers
<i>Hypochaeris radicata</i>	-30.417	151.632	Newholme Field Station, Armidale, NSW	Roots/tubers
<i>Brunoniella australis</i>	-31.084	150.950	Oxley Scenic Lookout, Tamworth, NSW	Roots/tubers
<i>Hydrocotyle laxiflora</i>	-30.418	151.637	Newholme Field Station, Armidale, NSW	Roots/tubers
<i>Taraxacum officinale</i>	-30.480	151.646	University of New England, Armidale, NSW	Roots/tubers
<i>Hysterangium</i> sp.	-30.483	151.640	University of New England, Armidale, NSW	Fungi
<i>Scleroderma verrucosum</i>	-30.483	151.640	University of New England, Armidale, NSW	Fungi
<i>Cortinarius</i> ("Thaxterogaster") sp.	-30.483	151.640	University of New England, Armidale, NSW	Fungi
<i>Labyrinthomyces varius</i>	-30.417	151.636	Newholme Field Station, Armidale, NSW	Fungi
<i>Descolea</i> sp. 1	-30.417	151.637	Newholme Field Station, Armidale, NSW	Fungi
<i>Descolea</i> sp. 2	-30.417	151.637	Newholme Field Station, Armidale, NSW	Fungi
<i>Enchylaena tomentosa</i>	-25.846	139.031	Simpson Desert, Birdsville, Qld	Fruit
<i>Sclerolaena intricata</i>	-25.846	140.031	Simpson Desert, west of Birdsville, Qld	Fruit
<i>Salsola australis</i>	-25.904	139.351	Simpson Desert, Birdsville, Qld	Browse
<i>Maireana coronata</i>	-25.904	140.351	Simpson Desert, west of Birdsville, Qld	Browse
<i>Aristida holathera</i>	-25.846	140.031	Simpson Desert, west of Birdsville, Qld	Nuts/seeds
<i>Santalum spicatum</i>	N/A	N/A	–	Nuts/seeds
<i>S. acuminatum</i> dry	N/A	N/A	–	Nuts/seeds
<i>S. acuminatum</i> fresh	-34.893	137.462	Hardwicke Bay, SA	Nuts/seeds
<i>Panesthia cribrata</i>	-30.417	151.632	Newholme Field Station, Armidale, NSW	Invertebrates
<i>Acrossidium tasmaniae</i> larvae	-30.417	151.632	Newholme Field Station, Armidale, NSW	Invertebrates

fracture toughness (R) were estimated by quantifying the area under a force–displacement curve divided by crack area (Lucas *et al.* 2001; Lucas 2004). To account for anisotropic variation, at least two measurements of E and R per specimen were taken and averaged when possible. Additionally, we calculated the stress- and displacement-limited fragmentation indices ($E.R^{0.5}$ and $R/E^{0.5}$) when both metrics were quantified, as these measures best describe food fragmentation in the oral cavity (Lucas *et al.* 2001). These indices are effectively properties in themselves (Agrawal *et al.* 1997). Lastly, whole *Santalum* spp. (sandalwood and quandong) seeds were loaded until failure using the compression test in order to estimate the maximum force in newtons required to initiate a crack in the outer testae.

Results

All samples were collected from a maximum soil depth of approximately 15 cm. The deepest materials were tuberous roots of the vanilla lily (*Arthropodium milleflorum*). The raw data are presented in Table 2. Some samples, such as pumpkin, which had much higher toughness and stiffness than other fruits, make analysis of food group averages

problematic. However, in general, toughness values for edible materials were higher in seeds, roots/tubers, browse, and insect cuticle. Toughness values generally were lower in fruit, fungi, and some nuts. Similar results were found for stiffness; however, some materials, such as insect cuticle and browse, could not be tested for Young's modulus (E) with the equipment used.

The data are presented graphically in Fig. 3, alongside additional data obtained from other studies of farmed foods. The lowest values of both toughness and stiffness belong to farmed fresh strawberries followed by wild fungal sporocarps of *Descolea* sp. The toughest and stiffest edible material belonged to the tuberous roots of the blue yam (*Brunoniella australis*). However, this species also had smaller tuber diameters as some other species tested (Table 2), which may reduce the challenge of processing them. The upper extremes of both metrics belong to the particularly resistant, inedible testae of sandalwood and quandong seeds (*Santalum* spp.). Interestingly, while we found the testa of quandong seeds (*Santalum acuminatum*) had the highest values for both toughness and stiffness, the testa of a dry quandong seed was lower in toughness and higher in stiffness than that of a fresh quandong seed, indicating a shift in relative properties with drying. Fig. 4a shows a plot of

Table 2. Toughness (J/m^2) and stiffness (elastic modulus) of each species sampled in this study. Maximum diameter (Max \varnothing) was also measured from wild foods, where possible.

Species	Common name	(R)	(E)	Max \varnothing (mm)	Group
<i>Arthropodium milleflorum</i>	Vanilla lily	145.85	8.66	15.4	Roots/tubers
<i>Hypochaeris radicata</i>	Catsear/flatweed	925.55	8.52	6.2	Roots/tubers
<i>Brunoniella australis</i>	Blue trumpet	2568.15	30.40	6.2	Roots/tubers
<i>Hydrocotyle laxiflora</i>	Stinking pennywort	1166.55	23.89	2.3	Roots/tubers
<i>Taraxacum officinale</i>	Common dandelion	727.10	12.00	8.5	Roots/tubers
<i>Ipomoea batatas</i>	Sweet potato	586.80	11.40		Roots/tubers
<i>Daucus carota</i>	Carrot	572.70	7.83		Roots/tubers
<i>Solanum tuberosum</i>	White potato	313.30	6.34		Roots/tubers
<i>Enchylaena tomentosa</i>	Ruby saltbush	518.75	3.54	6.1	Fruits
<i>Sclerolaena intricata</i>	Poverty bush	237.75	NA	1.8	Fruits
<i>Malus domestica</i>	Green apple	233.10	4.56		Fruits
<i>Prunus armeniaca</i>	Apricot – dried	371.80	0.51		Fruits
<i>Fragaria ananassa</i>	Strawberry	10.80	0.23		Fruits
<i>Cucurbita moschata</i>	Butternut pumpkin	939.10	14.14		Fruits
<i>Hysterangium</i> sp.	Native truffle	189.80	3.76	18.1	Fungi
<i>Scleroderma verrucosum</i>	Earthball fungus	557.15	14.18	15.9	Fungi
<i>Cortinarius</i> (' <i>Thaxterogaster</i> ') sp.	Native fungus	201.30	1.70	39.7	Fungi
<i>Labyrinthomyces varius</i>	Native truffle	327.20	5.15	16.8	Fungi
<i>Descolea</i> sp. 1	Native truffle	56.575	1.15	14.6	Fungi
<i>Descolea</i> sp. 2	Native truffle	114.5	1.74	11.4	Fungi
<i>Agaricus bisporus</i>	Button mushroom	316.1	3.15		Fungi
<i>Santalum acuminatum</i>	Dry quandong testa	2675.5	734.00	19.4	Nuts/seeds
<i>Santalum acuminatum</i>	Fresh quandong testa	8050.2	130.67		Nuts/seeds
<i>Santalum acuminatum</i>	Quandong kernel	329.5	23.11		Nuts/seeds
<i>Santalum spicatum</i>	Dry sandalwood testa	4779.3	222.33	21.5	Nuts/seeds
<i>Santalum spicatum</i>	Sandalwood kernel	162.15	15.63		Nuts/seeds
<i>Aristida holathera</i>	Erect kerosene grass	1342.10	NA	1.1	Nuts/seeds
<i>Prunus amygdalus</i>	Almond – raw	733.6	25.19		Nuts/seeds
<i>Cucurbita pepo</i>	Pepita	299.4	20.39		Nuts/seeds
<i>Panesthia cribrata</i>	Wood cockroach	1693.23	N/A		Invertebrates
<i>Acrossidius tasmaniae</i> larva	Tasmanian grass grub	585.2	N/A		Invertebrates
<i>Salsola australis</i>	Buckbush	466.38	N/A	<4.3	Browse
<i>Maireana coronata</i>	Crown fissure-weed	868.28	N/A	2.1	Browse

toughness–stiffness, with both values log-transformed. The pattern shows a general correlation between the two metrics, but there are some deviations. For example, nuts and seeds tend to be higher in stiffness and lower in toughness, while dried fruits and some tubers show the reverse pattern.

We additionally tested the ability of the FLS-2 tester to crush whole *Santalum* spp. seeds. The first sandalwood seed

(*Santalum spicatum*) had a diameter of 20.4 mm and cracked open with 315 N of force. The second, with a diameter of 21.5 mm, was stopped due to slippage at 255 N. However, turning the seed 90° caused this seed to crack open on second attempt at 125 N. An attempt to crack open a dried quandong seed (*Santalum acuminatum*) nearly exceeded the limitations of a 1000 N load cell before

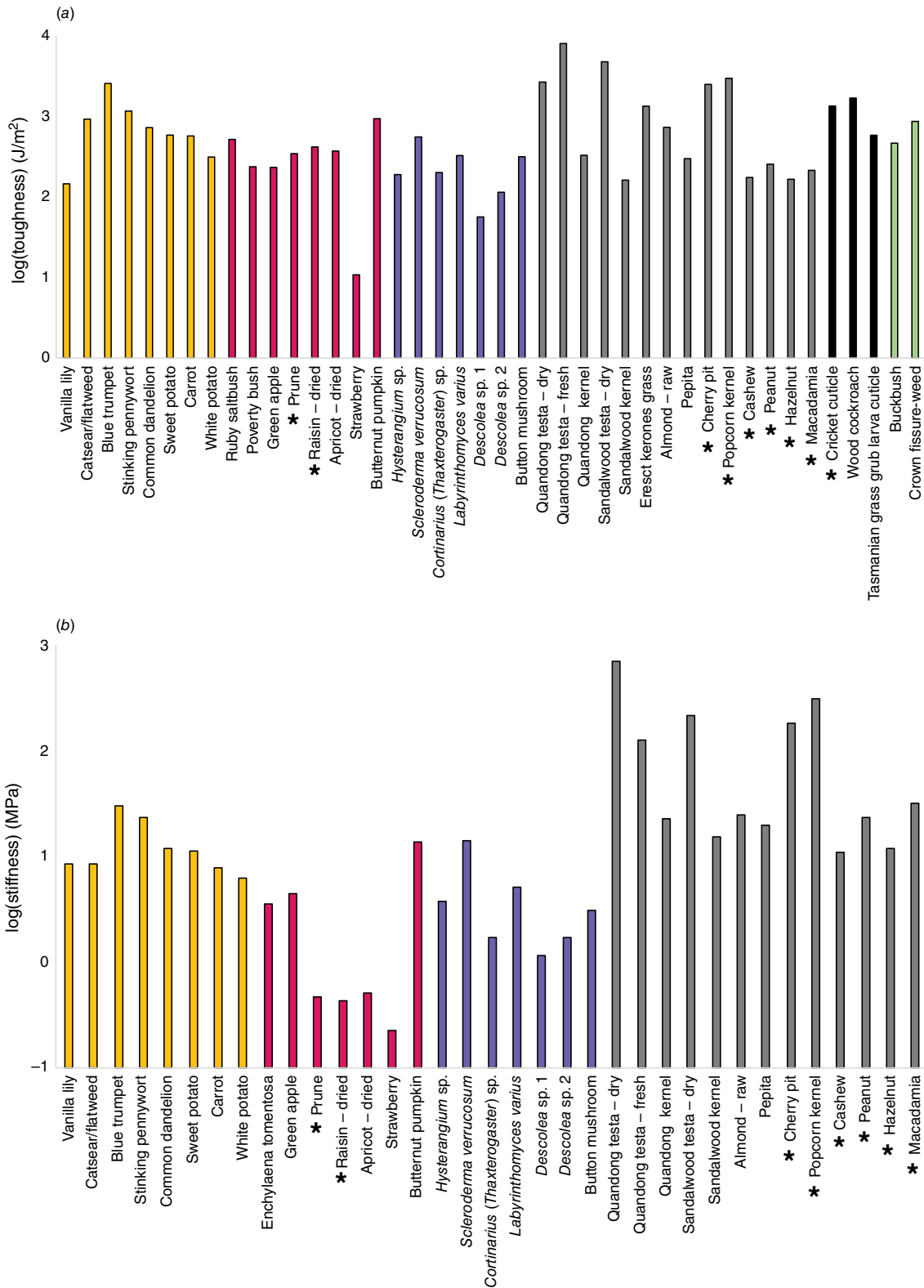


Fig. 3. Food material property data: (a) fracture toughness, (b) material stiffness (Young’s modulus). *Additional data obtained from Agrawal et al. (1997) or Williams et al. (2005). Orange = roots/tubers, red = fruit, blue = fungi, grey = nuts/seeds, black = invertebrates, green = browse.

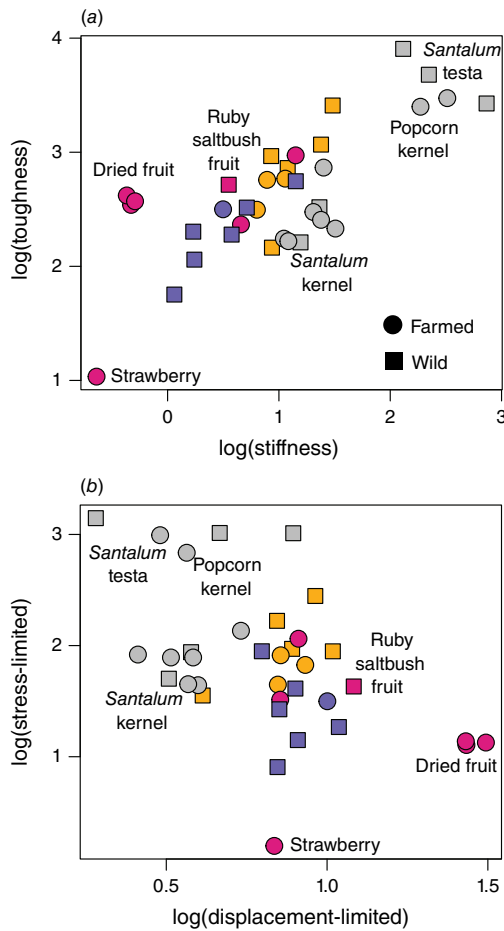


Fig. 4. Plots of foods with measurements of both toughness and stiffness: (a) logarithmic conversions of toughness–stiffness, (b) fragmentation indices – stress-limited ($R/E^{0.5}$) – displacement-limited ($R/E^{0.5}$). Orange = roots/tubers, red = fruit, blue = fungi, grey = nuts/seeds, black = invertebrates, green = browse.

being aborted. This suggests that >100 kg of direct force is required to crack open a quandong seed and indicates quandong testae are not only tougher and stiffer than all other materials tested, but the structure (thickness) of the testae offers additional resistance to cracking.

The fragmentation indices (Fig. 4b) identify a pattern of inverse correlation from high stress-limited foods to high displacement-limited foods. This roughly corresponds to a continuum of brittle foods to chewy foods, from stiff nuts and seeds to highly malleable dried fruits. The only wild fruit sample, from the ruby saltbush (*Enchylaena tomentosa*), represents the highest displacement index excluding farmed dried fruits. In addition, the only commercial foods with properties nearing the stress-limited index of *Santalum* testae were the popcorn kernel and cherry pit. With exception to the extremes of toughness, stiffness, and softness, there tends to be a high degree of overlap between farmed and wild samples from each food group.

Discussion

We have provided a collection of food mechanical property data from a range of food groups consumed by bettongs and potoroos. Our results are validated through similar findings for the same farmed foods measured in previous studies (Agrawal *et al.* 1997; Williams *et al.* 2005) and they detail a continuum of food resistance from softer fungi and fruit to more resistant roots and tubers, to the most resistant insect cuticle, browse, nuts, and seeds. These results can help identify some of the challenges species face in selecting food items in the wild, across both native and novel habitats. They can also help explain some of the dietary restructuring observed in potoroids with the arrival of alien resources. For example, the heavy consumption of the introduced flatweed, *Hypochaeris radicata*, by the rufous bettong (Schlager 1982) is aligned with this species' dietary habits, because the mechanical properties of flatweed roots do not exceed the values of the roots from native species in its diet, such as *Brunoniella australis* (Schlager 1982). While there may certainly be chemical and nutritional concerns if potoroids feed on introduced species, having less challenging mechanical properties than typical foods likely eliminates any initial mechanical barrier to the consumption of novel resources. Despite a focus on potoroid diets, many of these food materials are also obviously consumed by other small mammals. Our results are therefore relevant in conservation and management considerations for other species as well.

The new knowledge of food mechanical properties we have presented alongside comparable farmed foods can be informative for developing captive diet regimes and feed formulations. Food mechanical properties can influence skull structure at both developmental and evolutionary scales in mammals (Weisbecker *et al.* 2019; Mitchell *et al.* 2020, 2021), such that softer, structurally weaker foods in captive diets might not lead to adequate skull development needed for tasks expected to be undertaken in the wild. This might affect the ability of captive-reared animals to establish and persist during rapid environmental change, such as brought about by human disturbance and translocations. Appropriate substitutions in captive diets should not only seek to emulate nutritional content of wild diets, but also mechanical properties (Hartstone-Rose *et al.* 2014). For example, our results show that the fruits of wild ruby saltbush are highest of all wild foods on the displacement-limited index. These properties might be best substituted with dried or semi-dried fruits to match this condition. However, some materials regularly interacted with, such as some native seeds with especially resistant casings, may have no obvious substitutes.

An important observation of some potoroid species, such as the woylie (*Bettongia penicillata*) and burrowing bettong (*Bettongia lesueur*), is their ability to crack open the exceedingly resistant shells of sandalwood and quandong seeds to access the kernel inside (Murphy *et al.* 2005, 2015;

McNamara 2014; Chapman 2015). The toughness and stiffness of *Santalum* spp. testae are higher than the highest values found for other foods in previous studies (e.g. cherry pit; Williams *et al.* 2005) and far exceeded any edible materials measured in this study. An attempt to crack open a quandong seed with our tester failed upon approaching the maximum 1000 N limits of the machinery, suggesting at least ~100 kg of direct force in one place is needed to manage the task. The fact that woylies can regularly crack these open, alongside other examples of the hardest nuts known, including macadamias (*Macadamia tetraphylla*) and Brazil nuts (*Bertholletia excelsa*) (McNamara 2014), with skulls typically measuring less than 90 mm long (McDowell *et al.* 2015) is impressive. This is compounded by the fact that the mechanical properties are determined for the material itself, having been standardised for thickness. All else being equal, two foods might differ in accessibility based on thickness alone (Sanson *et al.* 2001), and quandongs have especially thick testae, measuring 2.2–2.4 mm across (Pardoe *et al.* 2019). In fact, the properties of quandong shells might even prevent germination of their own contents (Loveys and Jusaitis 1994), often only made possible with intervention either from cracking or passage through the digestive system of megafauna and resultant softening of the testa (Pardoe *et al.* 2019). Our results identify a potential behavioural attribute that might assist bettongs with the task of cracking open *Santalum* seeds. We found that a fresh quandong testa was extremely tough (8050.2 J/m²) but less stiff (130.67 MPa) compared to a dried testa (2675.5 J/m², 734 MPa), which suggests that the regular, yet seemingly haphazard caching ('scatter-hoarding') of these seeds (Murphy *et al.* 2005; Chapman 2015), might serve to dry out the testae in order to crack them open more easily. Rotating a sandalwood seed 90° seemed to weaken the testa in our cracking tests as well, suggesting that multiple bites from different angles could incrementally weaken its structure.

Potoroids typically use their large sectorial premolars to cut through most foods and crack open hard nut casings (Schlager 1982; Sanson 1989; McNamara 2014). For cracking open nuts and seeds, bettongs tend to repeatedly bite hard with their premolars onto the testa, while manipulating its position in the oral cavity with their forelimbs (McNamara 2014). Considerable effort is reportedly applied to cracking the hardest nuts, however, the exact way this is ultimately achieved is not clear. The biomechanics of cracking open exceedingly resistant *Santalum* seeds by bettongs warrant more extensive study.

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Data availability. All relevant data is contained within this manuscript.

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. D. R. M. and V. W. were supported by the Australian Research Council Centre of Excellence for Australian Biodiversity and Heritage grant (CE170100015). J. A. L. was funded by Leakey Foundation grant (40463).

Acknowledgements. We thank Sofie Costin for access to fresh quandongs and Jen Silcock from the Queensland Herbarium for collecting and identifying plant material from the Simpson Desert. We also thank Andrew Harper and Max Tischler from Australian Desert Expeditions who organised and led the camel trek which allowed us to gather material from the Simpson Desert. This work was conducted on the unceded traditional lands of the Kurna (Adelaide) and Anaiwan and Kamilaroi (New England Bioregion) people and the Wangkangurru and Yarluyandi people (Simpson Desert).

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