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Review

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Nest construction in mammals: a review of the patterns of construction and functional roles

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Nesting behaviour in mammals has been investigated in a wide variety of species but to date there has not been any scholarly review of the incidence and roles of these nests. Not all mammals build nests but, while some large species regularly build nests, nest-building behaviour is more commonly associated with small mammals weighing less than a kilogram. Quantitative data for the amounts of different materials used in a nest are rarely reported but mammal nests are typically constructed from fresh (rather than dead) plant materials. Animal-derived materials seem to be rare in nests, but anthropogenic materials are reported. Few studies have examined the roles these different materials play but more physically robust materials provide support for the structure. Many mammal nests have maternity roles, but a variety of other roles were recognized. A wide range of mammalian orders use nests for resting and environmental protection. Less common roles were as sites for torpor or hibernation, or as a refuge from predation, or the materials may have anti-parasite properties. These different roles were often not mutually exclusive. It is hoped that this review will stimulate interest in the functional properties of mammalian nests. It also suggests various themes that would be interesting areas for future research.

This article is part of the theme issue 'The evolutionary ecology of nests: a cross-taxon approach'.

1. Introduction

Animals of a range of taxa regularly produce constructions that extend their phenotype [1]. Many structures are associated with reproduction, for instance wasp nests [2,3] and bird nests [1] are constructed to primarily serve as a location for offspring to develop. However, other structures are built, such as beaver (*Castor* sp.) dams or bowerbird (Ptilonorhynchidae) bowers, which have other functional roles, such as environmental management or mate attraction [1,2]. There has been a recent research focus on avian nests, particularly in recent years, when more functional considerations of the nest, such as insulation or weatherproofing, have come to the fore [4,5]. It seems that fish and mammals are the only other vertebrate groups that have adopted behaviours that allow them to construct complex physical structures [2,6]. Reptiles tend only to dig nests, or at the most pile up plant materials in a mound to serve as a nest [7]. Those amphibians nesting outside of water produce foam that they use to build a relatively simple nest for their eggs [2,8]. By contrast, mammals can construct a range of structures, many (but not all) of which seem to be related to reproduction, especially maintenance of the offspring [2].

Functional properties of bird nests were reviewed recently [5,9] but to date a review of mammalian nests, and their functional significance, has been lacking. A mammalian nest was defined by Hediger [10, p. 174] as 'a rather loose construction of plant material—never a goal of flight, rarely for sleeping but mainly for support of offspring'. This definition implies that, like in birds [5], mammal nests are also mainly used for rearing of the offspring but to date this idea has not been tested. However, it is known that mammals construct a variety of structures many of which involve burrowing into the ground to form a network of

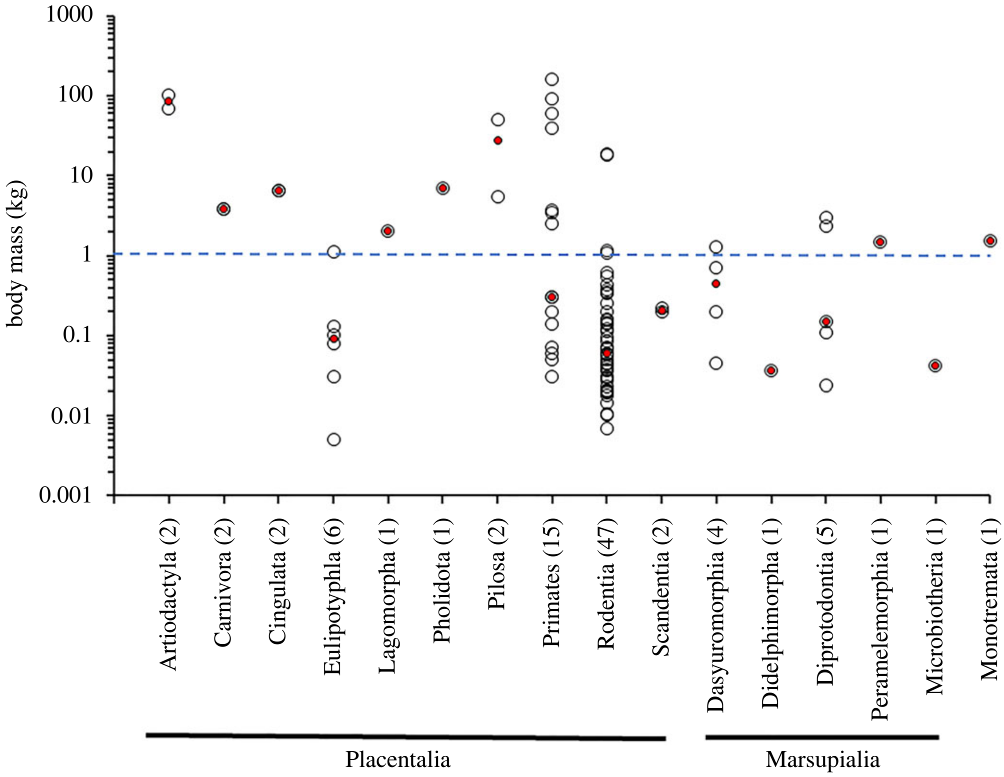

Figure 1. Values for body mass (kilogram) for the individual species represented in an assessment of nest building in each mammalian order shown. Numbers in parentheses indicate species represented in each order (see electronic supplementary material). White circles indicate actual values and filled (red) symbols indicate the median value. Note the $\log_{10}$-scale on the *y*-axis and dashed line indicates a mass of 1 kg. Data collected from the original reports or from Alhajeri *et al*. [13]. (Online version in colour.)

tunnels, described by Hancocks [11] as 'construction by subtraction'. These burrows may be lined with plant materials simply piled up in chambers, which may provide physical comfort or affect the microenvironment in the burrow (e.g. [12]), but often such structures are resting sites. This review is not, however, concerned with the organization of these relatively simple nest structures but rather it focuses on 'construction by addition' [11], where the nest involves production of a structure following some form of construction behaviour by the individual. For example, arboreal nests on branches may require an organized structure to support them or nests may also have a complex structure of layers of different materials, as is often seen in bird nests [5].

This is the first comprehensive (but by necessity not exhaustive) review of the literature to collate information about those mammalian taxa that construct nests by addition, and then to attempt to identify key roles that the nest may play in a species' biology. The review firstly identifies those mammals that are reported to build nests before exploring the types and possible roles of the materials that are used in construction. The following sections explore what we know of nest construction behaviour and describe the roles that mammalian nests are reported to play and explore whether all mammalian nests are simply maternity units [10]. This analysis will help us to develop an understanding of those factors that influence nest construction in mammals, which will hopefully stimulate further research into the functional properties of their nests.

2. Mammals that build nests

This review has identified 93 different species from 16 orders of mammals that use 'construction by addition' in their nest-building activities (figure 1). The following section reviews the patterns of nest building observed in various mammalian orders.

While monotremes construct burrows, evidence that they contain well-constructed nests has only recently come to light [14]. Captive platypuses (*Ornithorhynchus anatinus*) selected mat-rush (*Lomandra longifolia*) leaves and tussock grasses (*Poa ensiformis*) to weave their breeding nests within a burrow but they ignored eucalyptus bark and leaves [14].

Marsupials from the Microbiotheria and Didelphimorphia of South America, and of the Dasyuromorphia, Peramelemorphia and Diprotodontia of Australia, construct nests within natural cavities or nest-boxes [15,16]. Many carnivorous marsupials (e.g. members of the genera *Marmosa*, *Philander*, *Caluromys* and *Didelphis*) commonly build nests of dried leaves or grass stems, transported to the nest site in the mouth or by the prehensile tail [17]. Nests of the brown antechinus (*Antechinus stuartii*) of Australia usually comprise plant materials that are dragged into natural cavities in dead timber and are used for communal roosting [18]. The typical nest of a smaller dasyurid is a dome-shaped structure secured within a burrow, hollow or under a rock overhang. The outer shell of the nest is often formed from leaves to provide some rigidity, but the core may be softer, dried grass [17]. However, in Australia the long-nosed bandicoot (*Perameles nasuta*) and the ringtail possum (*Pseudocheirus peregrinus*) build nests in the branches of trees and bushes rather than in cavities [19,20].

In placental mammals, nests are most commonly constructed by rodents, primates and insectivores of the Eulipotyphla (figure 1). Over half of the mammal species identified are small rodents of the Cricetidae, Gliridae, Muridae, Nesomyidae and Sciuridae. Ross [21] reviewed infant care in placental mammals and suggested that use of nests as maternity sites was common but taxon specific. Ross [21] reported that aardvarks (*Orycteropus afer*, Tubulidenta) leave their offspring in the nest for a couple of weeks but no primary reports were found to corroborate this. However, the use of a nest as a maternity site is reported in almost all mammal orders identified as constructing nests (figure 2). For example, Pereira *et al.* [22] reported that female ruffed lemurs (*Varecia variegata*) constructed nests before parturition and left the offspring there for a few weeks.

Nest building in marsupials, rodents, primates and insectivores is generally associated with body masses below 1 kg (figure 1). Those few nest-building species that are over 10 kg in mass (figure 1) seem to be limited to pigs (Suidae, Artiodactyla), anteaters (Pilosa), great apes (Hominidae, Primates) and beavers (Castoridae, Rodentia). The possible reasons for this size distribution are discussed in the section dealing with functional roles for nests.

3. Materials used in nest construction

Most mammal nests are constructed from plant-derived materials, with leaves and grass being commonly reported, although a range of plant parts and types can be used. The use of animal-derived materials is less prevalent in mammal nests, and anthropogenic materials are increasingly being reported. The following sections explore the types of materials used by various mammals in constructing their nests and the roles these materials may play in nest construction.

(a) Plant-derived materials

Plant-derived materials dominate in mammalian nests and most nest descriptions report that fresh, green plant materials are typically used rather than dried, dead plant parts. For example, nest building in great apes seems to mainly involve bending and weaving of living branches [23–27], and European ground squirrels (*Spermophilus citellus*) prefer to build nests of the grass *Festuca pseudovina* using fresh material rather than dried grass [28].

Reports of nest construction are often qualitative because the nest may be difficult to distinguish from surrounding vegetation, but many reports list the types of plant materials used rather than amounts of each material. For these studies, there is a range of vegetative types used in the nest, including leaves, grass, bark, epiphytes, vines, ferns and mosses, by all of the orders where nest construction is demonstrated (figure 2). For instance, leaves and grasses are often used for nest construction by rodents [29,30] and insectivores [31–34]. By contrast, the Japanese dormouse (*Glirulus japonicus*) uses a high proportion of bryophytes in its nest [29]. The aye-aye (*Duabentonia madagascariensis*), a primate from Madagascar, builds nests high in trees from twigs and leaves [35], whereas bamboo is an important source of nest material and nest sites for the Monito del monte (*Dromiciops gliroides*), a South American marsupial [36]. Willie *et al.* [25] reported that western lowland gorillas (*Gorilla gorilla gorilla*) in Cameroon, had preferences for herbs of the families Marantaceae and Zingiberaceae and woody species of *Manniophyton fulvum* (liana) and *Alchornea floribunda* (shrub). Suitability for nest building, and availability of gorilla food items, were considered the likely determinants of nest material selection. In New Zealand, where the European hedgehog (*Erinaceus europaeus*) is an introduced species, Moors [37] found that nests were constructed on the ground under cover of vegetation

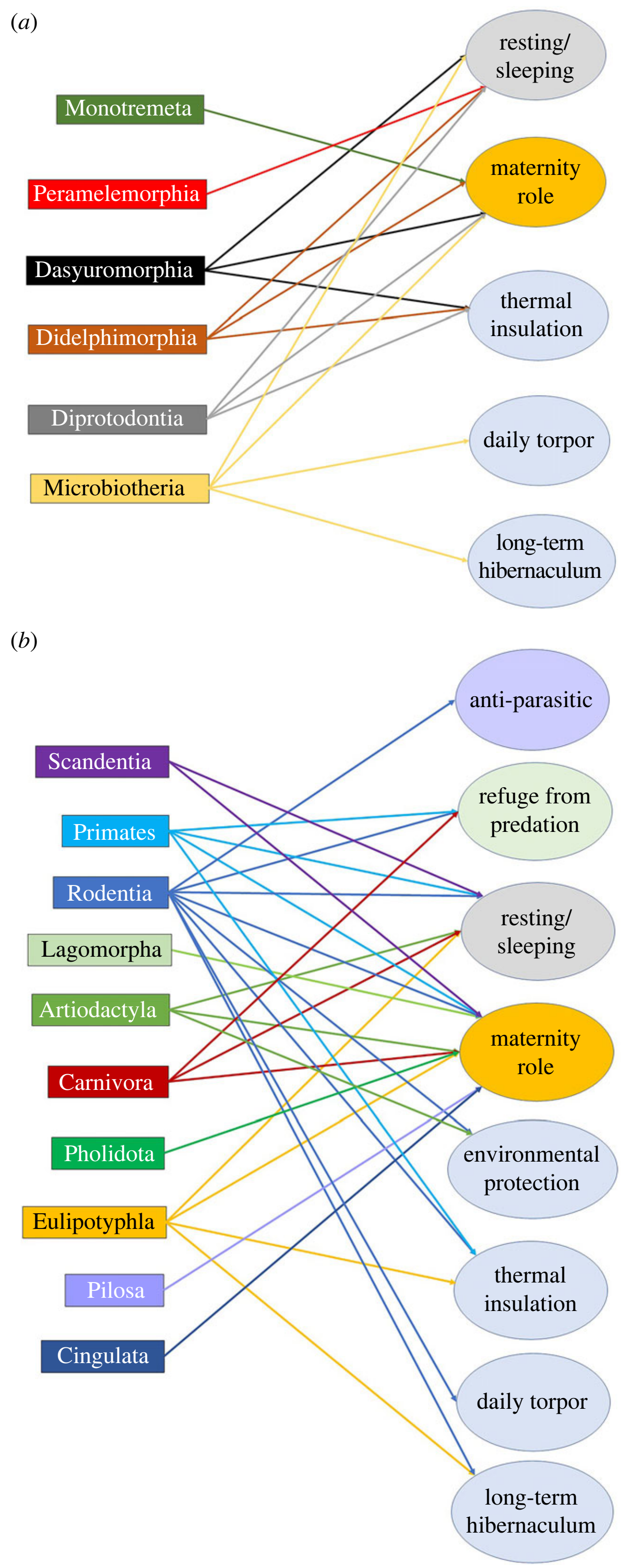

Figure 2. The inter-relationships between order in which nest construction 'by addition' is reported and the roles that such nests are reported to play. (*a*) Orders representing the Monotremata and the Marsupialia and (*b*) orders representing the Placentalia. Orders where nest construction has not been reported are not shown. (Online version in colour.)

using plant materials available at the sites, e.g. marram grass at dune sites, but other sites had dead grass, plant stems and pine needles.

Detailed quantitative data for the amounts of different materials used to construct mammal nests are rarely reported and, to the best of my knowledge, are limited to the following examples for rodents. Čanády [30] described four different

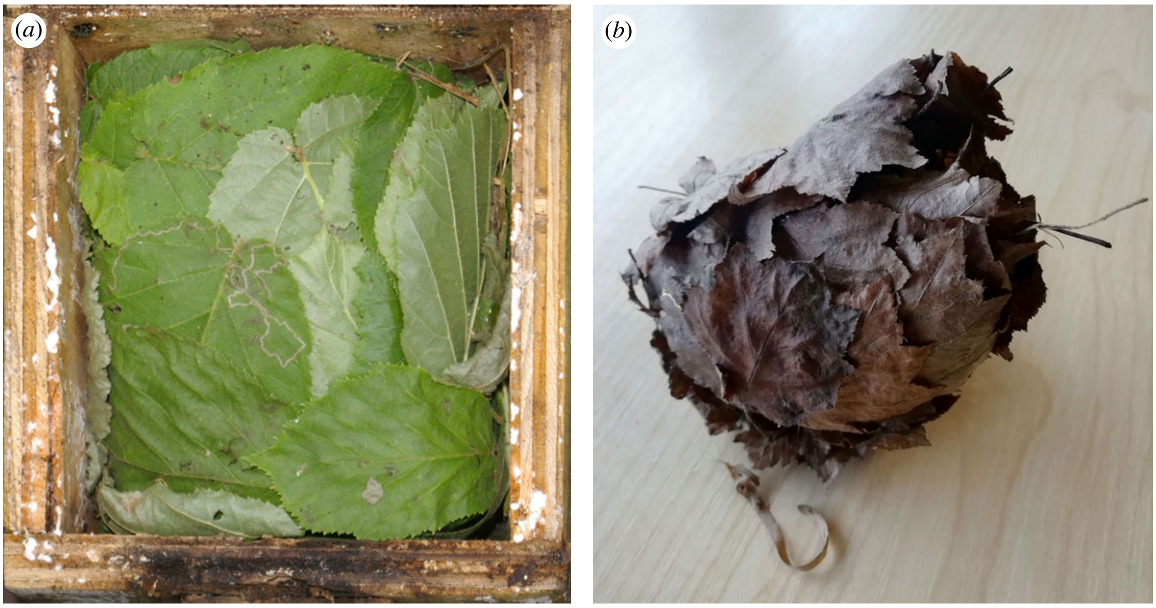

Figure 3. Hazel dormouse (*Muscardinus avellanarius*) layered nests built from leaves *in situ* within a wooden nest-box (*a*) and *ex situ* collected after the breeding season (*b*). Photographs by the author. (Online version in colour.)

types of nests built by the hazel dormouse (*Muscardinus avellanarius*) in Slovakia: foliar (figure 3), layered, mixed and grassy. These types varied in dimensions and volume (although as nests dry out these may change), with foliar being the largest and grassy being the smallest; but nest size did not really differ between plant species in which the nest was built. Leaves from ten different species of plant, and two different types of bark, were used to construct nests, although approximately 75% of foliar nests were built from leaves from only one species. Gubert *et al*. [38] found that 11 different types of plant materials occurred in hazel dormouse nests, but the prevalence of each type of material in the different types of nests was not reported. Bracewell & Downs [39] quantified the materials used in summer nests (types not reported) constructed in nest-boxes by hazel dormice. They identified leaves from 14 species of tree or shrub and bark from honeysuckle (*Lonchera periclymenum*) and wild clematis (*Clematis vitalba*). When combined these two materials accounted for 91.5% of the nest mass (figure 4); leaves formed 47.8% of the nest mass and bark 43.8% of the mass, and 86% of the bark was from honeysuckle. Only grass and moss were materials found in appreciable amounts (5.8% and 2.6%, respectively; figure 4). Hazel (*Corylus avellana*) leaves were the commonest species found in nests together with high masses of English oak (*Quercus ruber*) and field maple (*Acer campestre*) leaves, despite them not being in the immediate proximity of the nest. It was reported that dormice travelled up to 50 m to collect honeysuckle or oak leaves, which may reflect a preference for these materials [39]. A more recent study also demonstrated variety in plant species used in hazel dormice nests and that dormice travelled longer distances for bark and leaves of honeysuckle, oak and beech (*Fagus sylvatica*) than for other species [40].

Plant materials used in mammal nests often appear to be what can be found in the immediate surroundings, and there are only a few reports that species seek out particular types of materials. Whether this conclusion is widely applicable is unclear and further research could focus on developing a better understanding of the factors that determine the variety and amounts of materials used in mammal nests. Such details would help in understanding whether different parts of plants serve particular roles in construction or perhaps have other roles, as yet undiscovered.

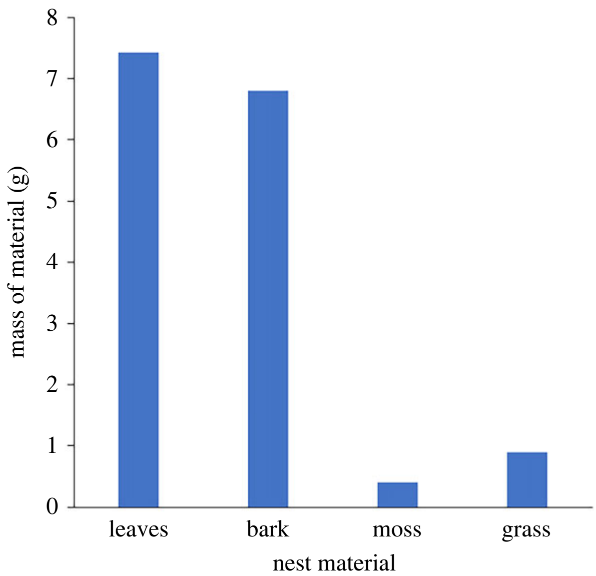

Figure 4. Mean values for the mass of the four different plant materials observed in nests of the hazel dormouse (*Muscardinus avellanarius*) from England. Data adapted from Bracewell & Downs [39]. (Online version in colour.)

(b) Animal-derived materials

Animal-derived materials are typically placed as nest lining in many songbird nests [41] where they confer good insulation [42]. However, compared with reports of plant materials in nests, reports of animal-derived materials within mammal nests are rare. For instance, Northern short-tailed shrews (*Blarina brevicauda*) typically dig extensive burrow systems that contain several nests constructed from grass, sedge and leaves but only one nest contained animal-derived material and that was entirely constructed of vole (*Microtis* sp.) hair [43].

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The few other species where animal-derived material is used in nest building include the European rabbit (*Oryctolagus cuniculus*), which construct blind-ended, isolated burrows to serve as maternity units. A nest is constructed using vegetation collected from outside but is lined with fur plucked from the female's belly [44]. Bilkó *et al.* [45] showed that rabbit nests were 43% fur and 55% plant material, which was almost entirely long dry grass (rather than fresh grass) of various species. In addition, brush-tailed phascogales (*Phascogale tapoatafa*, Dasyuridae) of Australia build elaborate maternity nests in nest-boxes that are made of soft bark strips interwoven with feathers and fur [46]. Inclusion of this good insulating material did not, however, necessarily prevent nest temperatures quickly declining to within 3°C of ambient after a female's departure.

It is not clear why few mammals use animal-derived materials in their nests. Perhaps it reflects under-reporting but more likely it reflects a lack of appropriate materials in the environment or differing roles for the materials used in a nest when compared with birds. The extent to which animal-derived materials are placed in mammalian nests, and the role they may play in thermal insulation, are worthy of further study.

(c) Anthropogenic materials

There is an increasing concern about the presence of plastic and other anthropogenic pollution in the environment that is arising in avian nests [47]. The presence of anthropogenic materials in mammal nests is often reported. In Poland, artificial threads were reported in hazel dormouse nests [48], while in Peru, white-naped squirrels (*Simosciurus nebouxii*) used single-use plastic bags to construct their arboreal nests [49]. Rautio *et al.* [50] also found that plastic bags or wrapping paper were used in 6% of the European hedgehog nests studied in Finland. Likewise, European moles (*Talpa europaea*) typically line nest burrows with dry grass and leaves pulled from the surface but they can also use paper or plastic sheeting. In one instance, where the mole lived adjacent to a bar, the nest was made entirely of crisp packets [33]. Whether anthropogenic materials in mammal nests are in some way deleterious to these animals is not known. Further research is needed urgently into the incidence and consequences of the use of these materials in nest construction.

(d) Roles of materials

Mammalian nests are constructed from a range of materials but do any materials confer any particular function to the nest? Fur and feathers are often used to line nest cups of bird nests and serve as thermal insulation [5]; does the fur in a rabbit nest, for instance [44], serve the same function? The deliberate placement of certain materials in different parts of a nest has been repeatedly reported in songbird nests, with, for instance, the strongest materials being placed in the part of the nest that requires the greatest support [51]. The size of the bird is also important with an increasing body size being related to a greater use of woody stems compared to grass, moss or leaves used by smaller birds [52].

Comparable selection of nest materials for their structural properties has been observed in mammals. For instance, van Casteren *et al.* [53] showed that nest-building behaviour in orangutan (*Pongo pygmaeus*) placed the strongest materials in key supporting roles in the base of the nest; other types of branches and vegetation placed in various parts of the sleeping nest were crucial to develop the comfort of the structure. Similarly, Stewart *et al.* [54] quantified the 'softness' (considered as a measure of 'comfort') of chimpanzee (*Pan troglodytes*) nests as proportion of the leafy, soft area relative to woody area. Greater complexity of the nest was associated with greater softness. Having recorded the force required to bend or break branches used in nests, Stewart *et al.* [54] considered that branch thickness was important in preventing them breaking even after being bent through 90° by the chimpanzees.

Beavers (*Castor* sp., Castoridae, Rodentia) construct both dams and lodges [2,3,11] and are another example of the key placement of plant materials in a construction. Fustec & Cormier [55], studying lodge construction in European beavers, demonstrated a preference for the use of willow (*Salix* sp.) branches of a diameter greater than 4.5 cm to construct the frame for lodge. Thereafter, smaller branches of the predominant local species were used to cover the frame filling the gaps.

Our understanding of the selection and placement of materials in mammalian nests is limited. Some materials may confer good insulation whereas others may provide good structural support. Further research should focus on the physical characteristics of materials exploited by the range of different mammals during nest construction and try to relate this to functional properties.

4. Nest construction behaviour

Detailed descriptions of the construction of nests by birds are relatively rare [5,56], which is frustrating given the diversity in nest morphology and size. For mammals, nest construction behaviour is also described in detail for only a few species, mainly rodents and primates and examples are described below.

Nest building by squirrels (*Sciurus* sp., Sciuridae) has been described in detail [57,58]. The arboreal drey is based on a platform of large (10–15 cm in length) twigs often cut from living trees. Eastern grey squirrels (*Sciurus carolinensis*) in Europe often use twigs covered by leaves but European red squirrels (*Sciurus vulgaris*) strip the leaves off twigs from deciduous trees but not conifers. The structure of bare twigs is then packed out with dead leaves, moss and bark before the completed nest is lined with moss, thistledown, dried grass, feathers or wool, although anthropogenic materials, e.g. paper and woollen thread, can be used. Dreys built in the winter have thicker walls and more lining materials than summer dreys, which often incorporate honeysuckle (*Lonchera* sp.) bark. Most of the building work involves the front feet, mouth and nose but often the cavity is created by the squirrel's body. While some dreys have an entrance hole, in many others the squirrel simply gains entry by pushing through the nest wall. Muul [59] reported that nests built by southern flying squirrels (*Glaucomys volans*) of North America were made from plant fibres, especially stripped bark, usually found in the vicinity of the drey. Arboreal dreys of the Indian giant squirrel (*Ratufa indica*) appear to have a similar structure to nests built by smaller squirrel species but the nests weigh over 1 kg [60].

Another rodent, the harvest mouse (*Micromys minutus*) constructs substantial maternity nests that are larger than non-breeding day nests (figure 5). Breeding nests are built

Figure 5. Examples of harvest mouse (*Micromys minutus*) resting nests *in situ*. Photograph courtesy of Frazer Coomber of the Mammal Society, UK. (Online version in colour.)

suspended in vertical grass stems and have walls constructed with three layers of plant material, mainly derived from grass [61]. The first stage of nest building is the construction of a strong platform of woven grass leaves that are still attached to the stem. More grass is added and woven into a spherical ball. An internal layer of grass is then woven within the nest, which is then lined with cut and shredded grass. In captivity, the nest takes 2–10 days to construct during the night. Non-breeding nests are built more quickly during the day and so are flimsier: with little or no central lining. Most summer nests of harvest mice in Japan were built from grass species, although some herbaceous materials were included, but the species of grass differed between habitats according to availability [62].

In North America, desert woodrats (*Neotoma lepida*) construct more substantial 'houses' that are a conical or spherical pile of sticks built at the base of trees [63]. The house is well structured with an outer covering of interlaced sticks that is thickest at the apex. The house interior is made from a variety of materials, including animal dung, bones, soil, grass and other plant material, wool and feathers, that form a concrete-like mass that is perforated by passages linking the several entrances to the structure and internal chambers. In western Oklahoma, the southern plains woodrat (*Neotoma micropus*) also builds stick houses, 2 m in diameter and 1 m high, but using cactus pads, sticks and other vegetation found in the vicinity [64]. Cacti represented over half of the material used in construction and sticks approximately one-quarter, with lesser amounts of herbaceous material and cattle dung. However, materials used to build these houses varied between the seasons with more herbaceous plants, sticks and cattle dung added to houses in the autumn as compared to other seasons [65]. Stick-nest rats (*Leporillus conditor*) of Australia build comparable nests where wooden stems of varying thicknesses are woven together to produce a refuge [66].

Nest building for sleeping purposes (see below) is exhibited by all great apes (Hominidae, Primates), which suggests a conserved pattern of construction behaviour [53]. Nests are usually built by the animals pulling and bending live tree branches inward to what will become the centre of the nest and then locking it together under the body. As an example, orangutan nests were built upon a solid base of a large single branch, or a group of stable branches, or a forked branch [53]. Thereafter, several branches were bent and half-broken inward from the surrounding area and woven together to form the structural base of the nest. More branches were bent in or broken off and placed on top of the structure to form a 'mattress' which was covered using leaves and herbaceous ends. Chimpanzees in Uganda select certain trees that adopt a 'lollipop' end shape for nest construction using basketweave methods to create a sleeping platform [26]. For instance, the tree species *Cynometra alexandri* constituted only 9.6% of the trees in the gallery forest but this species was used for 73.8% of nests built. This preference seemed to reflect the stiffness and bending strength of branches commonly found in chimpanzee nests [26].

Curiously, even pigs (Suidae, Artiodactyla) regularly construct nests, which are used for sleeping or for care of the litter post-parturition [67]. Nests constructed by wild boar (*Sus scrofa*) were initiated with a bed of grass, leaves and small sticks in a depression on the ground. More plant materials were piled up until an additional layer of longer, thicker branches were then added and covered with more leaves and grass. Finished nests were up to 1 m high [67].

This section has highlighted that detailed descriptions of nest construction by mammals are lacking so there is a poor understanding of this fascinating process. Further research should focus on describing and quantifying the behaviours required by different species to construct their nests.

5. Functional roles for mammal nests

A number of key roles for mammal nests have been identified during this research. These are: (1) a maternity role (e.g. it is a place for parturition or for tending offspring), (2) a resting or sleeping site during periods of inactivity, (3) providing environmental protection (i.e. providing physical protection from low or high temperatures, wind, rain or snow), (4) a role in daily torpor or hibernation (e.g. it is a place where an individual seeks refuge during periods of reduced metabolism), (5) as a refuge from predation, or (6) having an antiparasitic role (i.e. materials that form the nest offer some chemical defence against parasites). However, it is acknowledged that although these various functions are proposed, for many species the roles will not be mutually exclusive, and it is not possible to distinguish between the relative importance of these roles at present. Those mammal orders that use nests for each of these roles are summarized in figure 2. The following sections explore the various roles using suitable examples for a range of species.

(a) Maternity role

As is the case in birds [5], mammalian nests are commonly associated with a maternity role, which may be a site for parturition, simply a place to raise their offspring, or help in neonatal thermoregulation. Examples are discussed below for the orders of mammals where a maternity role is important.

Kappeler [68] found that nest use was observed in only 11 of 49 species of prosimians, although not all species constructed their own nests, but reused nests constructed by other species. There was general association with the adult leaving dependent offspring in nests while it foraged, often referred to as 'infant parking'. It was suggested that an ancestral primate left its single offspring in a tree hole or nest and selection for larger litters reinforced this nesting behaviour [68]. It is possible that infant parking in a nest may be an advantage if the female holds a feeding territory but is less advantageous if the animal is typically nomadic. Tecot *et al.* [69] showed that use of a nest was limited to a few species of Malagasy lemurs that practised infant parking. Such nests were constructed in the open from leaves, lianas and other materials or were located in tree holes.

A maternity role for a nest may involve being the location for parturition. For instance, site selection for farrowing nests built by wild pigs (*Sus scrofa*) in Spain related to abundant plant cover, proximity to water and a relatively warm location [70]. There was also a need to defend a territory around the nest from other females so that the mother and her offspring can bond before returning to the mixed groups of several females and their piglets of a similar age. Nest construction in Asian wild pigs involved use of an average of 287 young tree samplings that are either bitten off or uprooted [71]. In North America, wild pigs build nests pre-parturition, and the size and complexity are related to the age of the farrowing sow [72]. It was concluded that the function of these nests was more of protection from inclement weather rather than protection from visual predators. Mayer *et al*. [72] compared these nests with resting beds, which were built and used by solitary animals. The construction was similar to farrowing nests but were smaller in relation to the size of the animals. These similarities meant that it was hard to distinguish the role of a nest found in isolation.

Maternity roles for nests have been reported in the coatis (*Nasua* sp., Carnivora), which build semi-spherical arboreal nests of leaves that are used for birth and rearing [73,74]. Nests are also constructed during breeding or lactation by platypus [12] and by many small marsupials [15,16,46]. Tree shrews (Scandentia) build nests in underground cavities but also build open nests of woven plant fibres [75] that Ross [21] suggested are used for maternity purposes. In the Pilosa, anteaters (*Myrmecophaga tridactyla* and *Tamandua mexicana*) and armadillos (*Euphractus sexcinctus* and *Dasypus novemcinctus*) are reported to park their offspring in nests of leaves and grass in a burrow [76,77]. Pangolins (Pholidota) use maternity sites that they line with vegetation both in captivity [78] and in the wild [79].

Nests are intimately associated with reproduction in birds, and this is also the case for a wide range of different mammalian orders. Further research could explore whether other types of mammals are employing nest structures for maternity roles. However, it could be argued that the term 'nest' should be applied to a structure by an animal constructed for the care and safety of its young [80]. However, mammals often build structures that are invariably called 'nests' because they resemble maternity nest structures, but they have differing roles (as explored below). The broader (and common) use of the term 'nest' for such constructions is maintained here because mammals are performing behaviours that involve construction by addition. The result is a structure that very often strongly resembles a maternity nest but was built to have another or multiple roles that do not necessarily involve care of the offspring.

(b) Sleeping or resting site

The use of a nest as a site for resting or sleeping is the second commonest reason attributed for nest use in mammals (figure 2). It is observed in 11 of the 16 orders where nest use is prevalent as illustrated in the following examples, which highlight those factors that seem to be important in the siting of nests.

European moles and golden moles (*Amblysomus* sp.) construct nest burrows that they line with dry grass and leaves pulled from the surface, which are used for sleeping and raising young [33]. Desmans (*Desman* sp.) also construct nests lined with sedges and mosses in burrows for resting [33].

Rodents also construct nests for sleeping. For example, desert woodrats construct stick houses used for resting and sleeping [63]. Harvest mice construct flimsy day nests that are only fit for one individual, in which they rest or sleep during the day [81] and beaver lodges are effectively a refuge for sleeping and resting [55].

Like many tree-dwelling marsupials [20,82] many small primates use nests for resting. For example, Nowack *et al.* [83] reported that the African lesser bushbaby (*Galago moholi*) used insulated nests but only in winter months. The Senegal bushbaby (*Galago senegalensis*) uses various sites for sleeping, including nests [84]. The nocturnal golden-brown mouse lemur (*Microcebus ravelobensis*) constructs leaf nests from twigs with leaves attached and uses them for daytime sleeping [85]. The nests were relatively quick to construct, i.e. 46–68 min, and nest use was higher during colder months and during rearing periods [85].

In the Hominoidea, gibbons do not build nests but sleep lying in the open on branches [86,87]. By contrast, all species of great apes construct nests daily for sleeping overnight. Goodall [88] described chimpanzee nests in Tanzania, which were used for sleeping but have also been used to give birth [89]. In Senegal, chimpanzee nests ranged from having no defined shape with few interwoven branches, through to well-defined circular nests with interweaved, well-secured branches [58]. Females seem to invest more time and effort into producing a safe warm nest [27]. Geographical differences in nest-building behaviour in chimpanzees were explained by environmental factors rather than the development of a culture [90].

Like chimpanzees, bonobos (*Pan paniscus*) in the Democratic Republic of the Congo construct nests in trees for resting overnight or during the day [91], preferring to build nests in trees with greater canopy leaf cover [92]. Nests were also used for feeding, social grooming and play, which helped avoid social conflicts within a group. Day nests took on average 2 min to construct but more complicated night nests took an average of 4.7 min. Bonobos seemed to prefer small leaves of *Scorodophloeus zenkeri*, which were chosen more often than other plant species with larger leaves [91].

Gorillas of all species construct sleeping nests every night [23] but construction style varies; Tutin *et al.* [24] defined seven types of gorilla nest in terms of the degree of construction and the raw materials used. The commonest type were nests built on the ground from herbaceous plants closely followed by tree nests (40% and 35% of total nests, respectively). Frequencies of the different nest-types varied significantly between eight habitat types. If there were high densities of understorey herbs, ground nests predominated, but when herbs were rare, most nests were in trees. A general preference for sleeping in herbaceous ground nests was indicated since trees were abundant in all habitat types, except savanna. The frequency of nesting in trees shows a significant positive correlation with rainfall, but effects of climate were confounded by seasonal variation in use of different habitat types. When elephants were attracted to the same localized food sources as gorillas, many tree nests were built even when herbs were available. It was concluded that different nest types reflect a variety of solutions to maximize comfort, depending on available raw materials and the probability of rainfall, or disturbance by elephants, or both [24]. Sanz *et al.* [93] showed that chimpanzees in the Republic of the Congo built nests in trees that were on average over 17 m above the ground. By contrast, gorillas in the same habitat had a wide range of locations—only 26% were arboreal and most nests were on the ground. Most nests (45%) were made of herbaceous plants whereas only 13% were woody and 7% of mixed type. Lowland gorillas in the Central African Republic built nests at various locations ranging from ground level or up to over 12 m high in trees; the height above ground reflected the availability of suitable materials for nest construction [94].

In Sumatra, orangutans generally build their nests in the tree canopy, and may range from around 11 m up in disturbed forest or up to 20 m in primary rainforest [54]. Orangutans built nests in over 30 different species of tree in Borneo and there are age-class differences in the type and reuse of nests [95]. There was a positive relationship between animal size and nest diameter and larger males reused nests more than immature animals. Nests in the open were common but female orangutans with infants preferred more sheltered locations for the nest [95].

The short-term use of nests by mammals for sleeping or resting is very different from nest use in birds, where the primary role is in longer-term reproduction [5]. In mammals, nest construction for resting can be a daily activity and it is often practised by adults and juveniles of both sexes. By contrast, while some bird species may roost in cavities, they do not construct temporary nests for resting. Perhaps this difference reflects the longer time taken to build an avian nest? Further research into the times taken for nest construction in mammals and birds may help answer this question.

(c) Environmental protection

Physiological toleration of low temperatures by individuals may be aided by use of the insulation provided by a nest, which allow for an increase in the range of temperatures at which a species can live within their thermal neutral zone [96]. Nests may also offer protection against wind or rainfall, which has been observed in bird nests [5]. The role a nest may play in environmental protection is discussed below using examples from a variety of mammal species.

A variety of mammal species seem to build nests to provide some form of environmental protection, typically against low temperatures. For example, the western quoll (*Dasyurus geoffroii*) of Australia builds a nest of dry eucalypt leaves in burrows. Both sexes build more substantial nests in cold weather providing thermal insulation between the occupier and the den entrance, whereas in hot weather the nest is simple bedding [97]. Körtner & Geiser [98] suggested that leaves offered good insulation in Australian sugar glider nests (*Petaurus breviceps*). In Australia, female bush-tailed phascogales (*Phascogale tapoatafa*) build a nest chamber variously lined with added bark and feathers. They attempt to balance foraging needs with nest attendance to prevent hypothermia of their litters, by frequently returning during the night [99]. The nest was not, however, considered as providing effective thermal insulation because nestlings rapidly lost heat once the female had left [46].

In chimpanzees, Koops *et al.* [100] tested various hypotheses for nest location in Guinea based on whether selectivity for nest tree characteristics reflected: an antipredator strategy, a response to weather conditions (temperature, humidity, wind), or measured mosquito densities. Chimpanzees nested higher in trees and at higher altitudes during the wet season, which supported the thermoregulation hypothesis and nest-height variation across seasons reflected a humidity-avoidance strategy.

Most research on environmental protection, especially thermal insulation, have been carried out on rodent species. In Alaska, brown lemmings (*Lemmus trimucronatus*) produce both small (approx. 550 cm^3) and large (approx. 2400 cm^3) nests in the low grassy tundra [101]. Large nests seem to be built by reproductively active females and may be used to house offspring; large nests cool more slowly and so may benefit thermoregulation by small offspring. Lemmings have been shown to exhibit reductions in resting metabolic rates when within a nest, a 40–46% reduction in thermal conductance of the lemmings [101]. Insulation may, therefore, be important in minimizing heat loss and making energetic savings.

In the golden mouse (*Ochrotomys nuttalli*) of southern North America, winter nests are around 50% larger than summer nests, presumably to increase insulation during cold periods [102]. The western harvest mouse (*Reithrodontomys megalotis*) in North America had surface nests in the summer constructed in vegetation from woven grasses. The nest was considered to offer insulation from below because the materials used in the nest wall were different from the top and bottom but also there was shade provided by the surrounding vegetation [103].

Hispid cotton rats (*Sigmodon hispidus*) in Costa Rica build domed structures with layered walls with coarser grass in the outer wall and finer grass inside enclosing a depression lined with grasses [104]. The nests are built on the ground at the base of grass clumps, which appear to offer shade and exclude precipitation. Hispid cotton rats from Kansas and Florida were tested in laboratory conditions to determine geographical differences in nest construction under simulated winter conditions [105]. Nests from Kansas were larger and better insulated than those built in warmer Florida. Laboratory-reared cotton rats were able to build nests comparable in characteristics to wild-caught mice despite the lack of experience.

Southern flying squirrels nest in tree hollows but will build nests among tree branches [106]. Stapp *et al.* [107] demonstrated that nests provided southern flying squirrels with a 37% reduction in energy requirements for single squirrels compared to having no nest. This species is a late winter breeder so nests may also be used for maternity care. North American fox squirrels (*Sciurus niger*) take advantage of secondary cavities and nest-boxes but will also use twig and leaf nests when such shelters are not available [108]. The leaf nests seem to confer some thermal advantage to animals during winter because their body condition was as good as those animals sheltering in nest-boxes. Fresh leaves of the grass *Festuca pseudovina* were preferred by European ground squirrels (*Spermophilus citellus*) to build their nests because of its higher insulative property compared with leaves that had dried out [28].

The bush vlei rat (*Otomys unisulcatus*) of southern Africa builds a nest of sticks under shrubs and it contains nest chambers lined with grass [109]. Winter temperatures in the nest exhibit less variation and summer temperatures are lower than the ambient air and have lower water vapour pressures than warrens of Brant's whistling rat (*Parotomys brantsii*). In Ethiopia, giant root rats (*Tachyoryctes macrocephalus*) burrow but line their nests with plant material. Šumbera *et al.* [110] showed that even when burrows were temporarily blocked, the presence of decaying plants did not adversely increase CO_2 levels.

The role of nest insulation in the energetics of mammals has only been tested on captive animals because it is easier to experimentally manipulate environmental conditions, compared with animals in their natural habitat. Although Dryden *et al.* [111] showed that the presence of a nest reduced the oxygen demand of adult male musk shrews by around 20%, most studies involve rodents. As the examples below show, in general, the presence of a nest confers the opportunity to save energy in small rodents.

Bult & Lynch [112] selected strains of house mice (*Mus domesticus*) for nest-building behaviours using cotton and then exposed the mice to prolonged air temperatures of 22°C or 4°C. Mice selected to build nests had higher reproductive fitness (i.e. produced more and better-quality offspring), even at the low ambient temperature. By contrast, Gaskill *et al.* [113] found that the presence of a nest did not affect body temperature in house mice. When captive Norway rats (*Rattus norvegicus*) were exposed to progressively cold temperatures, nest-building activity increased although cold-acclimated animals spent less time nest building than control animals when exposed to an acute reduction in temperature [114].

The presence of a nest prolonged survival time of captive northern white-footed mice (*Peromyscus leucopus*) of North America subjected to low temperatures in the absence of food and water, and the nest-building response was dependent on acclimation [96]. Nest building was better developed in mice collected during the winter than mice collected in the summer. Winter animals provided with the same sort of nesting materials were far more resistant to low temperature, and natural grass and fibre nests placed in a simulated nest cavity provided better protection than exposed nests made of cotton or containing sawdust alone [96]. Glaser & Lustick [115] also showed that the presence of a nest reduced considerably the oxygen consumption of northern white-footed mice and that larger nests had a greater effect.

Most studies investigate the effect of the nest on the animals rather than the characteristics of the nest itself. Male short-tailed voles (*Microtis agrestis*) kept under cold conditions produced nests with better insulation than females. Nest insulation was positively related to both nest mass and wall thickness [116]. Prolonged access to a nest allowed a 28% saving on food intake for a 22 g vole, although this was lower (18%) for a 40 g vole. Gębczyńska & Gębczyński [117] studied the effects of nesting in the bank vole (*Clethrionomys glareolus*) on food consumption. The presence of a nest reduced energy intake although group size had no effect on energy consumed. In the control group with no nest, food intake was three times greater but larger group sizes in the absence of a nest led to lower energy intake due to huddling.

Interestingly, van der Vinne *et al.* [118] found that, in the laboratory, lactating common voles (*Microtus arvalis*) ran the risk of hyperthermia if they stayed in the nest with the offspring. Guillemette *et al.* [119] suggested that in the wild, American red squirrels (*Tamiasciurus hudsonicus*) also ran the risk of overheating in some nests. Nest insulation was negatively correlated with mass of the offspring in each litter but this depended on whether the offspring were furred. The negative correlation with ambient temperature (range of mean temperature 9–13°C) was only observed when offspring were well-developed, which may reflect change in nest materials or, more likely, the adults moving offspring between nests [119].

In the much larger babirusa (*Babyrousa celebensis*, Suidae), both sexes constructed nests using plant material available in their enclosures [120]. These structures were used for sleeping and were more common in the dry season than the wet season [121]. Increased nest construction was considered a response to decreased ambient temperature and increased wind speed, so the nest was thought to impart some thermal benefit to the individuals [121], although this was not measured.

The role of the nest as a means of offering environmental protection seems to be widespread in mammals, particularly smaller rodents. Although nests may provide physical protection from rain or wind, the main benefit seems to be from improved thermal insulation. Further research should explore the functional properties of the nest materials using methods employed to investigate thermal insulation or weather-proofing of bird nests [5].

(d) Role in hibernation or daily torpor

The energetic benefits of a nest discussed above have also been explored in terms of short-term torpor and long-term hibernation in mammals. As explained below, a range of species have been studied to ascertain whether a nest is involved in saving metabolic energy.

The monito del monte (*Dromiciops gliroides*; Microbiotheriidae), a marsupial from South America, uses nests during winter torpor [122]. The number of materials used in nests decreased, but the mass increased by 68%, with increasing altitude. Bryophytes were more likely to be used in low altitude forests while high altitude nests were built more of leaves, twigs and vines. Presumably, this reflected differences in insulation but this was not tested. In Australia, eastern pygmy possums (*Cercartetus nanus*, Burramyidae) build cup-shaped nests of leaves in nest-boxes, which were used for daily torpor [123]. Compared to normothermic resting animals at the same ambient temperature, nest use by pygmy possums reduced energy expenditure on average by approximately 17%, huddling as a pair in a nest by approximately 50%, whereas torpor lowered energy expenditure by greater than 95%.

The European hedgehog is a species that is commonly associated with hibernation in nests. In Finland, Rautio *et al.* [50] identified four different nest types—day, breeding, pre-hibernation and hibernation. In Britain, summer nests are typically hummocks of naturally fallen leaves collected together under brambles, rocks or logs [124]. By contrast, winter nests are constructed, compact structures some 30–60 cm in diameter with walls of dead leaves closely packed to form a laminated mass up to 20 cm thick [125]. Small to medium sized leaves are collected under a bramble and a rotary movement of the hedgehog within the leaves causes them to become tightly packed and regularly orientated [126,127].

Several species of dormice (Gliridae, Rodentia) also use nests for hibernation, including the hazel dormouse, which have woven nests on the ground [38,127–129]. The hazel dormouse also uses its summer nests for daily bouts of torpor during summer months [130]. Other European species, however, such as the larger edible dormouse (*Glis glis*), do not use nests in their hibernacula despite using leaf nests in the summer [131]. Pretzlaff *et al.* [132] suggested that nest temperatures can be higher than ambient temperatures close to freezing because of the presence of the nest. However, the role that the nest plays in maintaining hibernation or minimizing energy expenditure has not been investigated in detail for all dormice (Gliridae) and is worthy of further investigation.

Small lemurs of Madagascar also hibernate. Grey mouse lemurs (*Microcebus murinus*) hibernate in tree holes which may contain leaf nests [133]. Tree holes offer some insulation from fluctuations in ambient temperature and Schmidt [134] suggested that this improved the torpid state of gray mouse lemurs and so added to the energetic savings. Madame Berthe's mouse lemurs (*Microcebus berthae*) often hibernate together in large leaf nests built by a sympatric cheirogaleid, Coquerel's giant mouse lemur (*Mirza coquereli* [135]). Dwarf lemurs (*Cheirogaleus* sp.) in Madagascar hibernate in tropical environments and the pattern of control of body temperature during hibernation was affected by the size of the tree in which the hibernaculum was sited; larger trees provided better insulation despite nest materials not commonly being used [136].

With respect to hibernation, the use of nest materials in a hibernaculum seems to be species-specific, which may reflect small sample size, and little is known about the insulation provided by nest materials, if they are present. Future research could explore whether factors like body mass or geographical location influence the incidence of nesting material during hibernation in the Gliridae or in lemurs.

(e) Less common roles suggested for nests

Other roles have been suggested for mammal nests in a range of species (figure 2). For instance, nests may have a key role as a refuge from predation, particularly when the individual is sleeping or has a litter of offspring, and the location of a nest may help limit predation in a variety of species. Alternatively, the nest materials may have chemical properties that are antiparasitic.

Vasey *et al.* [137] suggested that red-ruffed lemur (*Varecia rubra*) built nests in trees covered by lianas as a response at least in part to potential predation pressure; the foliage above shielded the nest from aerial predators. Pressure from disturbance by humans led chimpanzees to build sleeping nests in trees at two study sites, but at the second study site, where potential human predation on chimps was lower, nests were also built on the ground [138]. In Central and South America, coatis (*Nasua nasua* and *Nasua narica*) build arboreal nests that are used for birth and resting but may also offer some protection from predation of nestlings by monkeys [74]. Although not explicitly stated many rodent nests may simply offer a place to hide from predators. Harvest mice construct flimsy day nests that are only fit for one individual, in which they rest or sleep during the day [81]. These nests may offer protection from the prevailing weather, but they may simply be somewhere to hide from predators. Investigation of the potential thermal and hydrological characteristics of such nests is needed before it is possible to determine what extent their role is protection from predators. It is unclear whether using a nest as a refuge from predation reflects its primary purpose for construction and further research is needed to better understand the importance of a nest in this role.

Bird species often include green plant materials in their nests that are seen as having an antiparasitic [139] role but whether green plant materials have similar roles in mammal nests is not well reported. Patterson *et al.* [140] reported that nests constructed during spring and summer in Canada by northern flying squirrels (*Glaucomys sabrinus*) and American red squirrels were predominately built from shredded bark of the Eastern white cedar (*Thuja occidentalis*). It was suggested, but not experimentally tested, that this bark had an antiparasitic role in the nests because nest cavities harbour parasites from nesting during previous years. By contrast, Hayward & Rosentreter [141] reported that in Idaho flying squirrels used three species of lichens that formed over 90% of the nest mass and these may deter nest parasites. In the same location, American red squirrels used less than 30% of lichen in the nest, which was mainly built of grass and stripped bark. No other reports have suggested such an antiparasitic role for materials in mammal nests but future research should explicitly test the idea that nest materials limit the abundance of ectoparasites in the nests.

6. Conclusion

This review has highlighted that relatively little is known about the functionality of mammal nests, but it has shown that Hediger's definition of a mammal nest as a place to support the offspring [10] is largely incorrect. Unlike in birds where nests are a key part of reproduction [5], many but not all mammal species use nests for maternity roles. Generally, mammal nests serve a wider range of functions. Some roles, such as environmental protection, are also seen in birds, but others, like serving as a sleeping or resting place, are not. Certainly, for a particular mammal species a nest may serve many roles, which are not mutually exclusive. For instance, in Australia, numbats (*Myrmecobius fasciatus*) spend the night in nests within burrows or cavities that offer not only protection from predators but also confer thermal insulation [142]. I hope that this review will allow us to consider the role of mammal nests in a variety of situations and stimulate researchers to reconsider the roles of nests built by their focal species.

Many types of mammals do not seem to engage with nest building, which seems to be more frequently observed for smaller species. This may reflect a true situation where nest building is favoured by small mammals, but I suspect that for some taxa it may reflect a lack of data. Another reason for the lower incidence of nest building in mammals may reflect a weaker link with reproduction compared with birds. Contact incubation of eggs by birds must take place within some form of nest [5] but while small mammals may park their offspring in nests while foraging [21], many mammals have precocial offspring that can follow their parents soon after birth, or the offspring is simply carried around, which means a nest may be less important in reproduction for larger species.

Nest construction by small mammals provides external insulation which often seems to be associated with a degree of energetic saving under normal metabolism circumstances or during torpor or hibernation. This would make physiological sense because energetic savings would have fitness benefits to animals with a high metabolic rate because they could reduce their food intake. Thus, while nest construction can confer benefits the potential costs to a nest-building individual have received little attention. In particular, nest construction requires energy to seek out, collect and transport the appropriate amounts of nesting materials, which has to be considered in the overall energy budget of the individual. Few studies have considered the energetic costs of nest building [143] but in captive golden hamsters (*Mesocricetus auratus*) distance between a nest chamber and nesting material affected nest construction. As distance from the nest chamber increased, the number of trips to collect materials decreased; the amount of material increased but ultimately a smaller nest was built than when the nesting material was closer [144]. As further research into nest building improves our understanding of nest function, then we will be better placed to consider the cost–benefit trade-off associated with construction behaviour in mammals.

Avian nests can be architecturally very complex [1,5] and mammalian nests do seem to be relatively simple in structure and in some instances can be quickly made; e.g. nests for sleeping made by great apes or the simple day nests of harvest mice, can be built in a few minutes. The use of burrows as dens by mammals allows physical and environmental protection but such structures reflect construction by subtraction rather than construction by addition [3,10,11,28]. A chamber in a burrow may not need additional lining to serve its purpose. However, other nests, e.g. beaver lodges and desert woodrat houses, can be architecturally complex. Further research could pay more attention to patterns of nest construction by mammals to perhaps identify other complex structures and more insight into the evolutionary and ecological drivers for nest architecture.

It is possible that our poor understanding of mammalian nests is masking our appreciation of other functional roles that have yet to be considered. Avian nests may have a primary role in incubation and chick rearing but they have also been attributed roles in sexual selection or control of parasites [145]. While this review has highlighted that there is a maternity role for nests in many species, nests have a greater range of roles in a variety of mammals. Our understanding of nest construction in this class is very much in its infancy and I hope that this overview will stimulate research into nest construction and its functional significance in mammals.

Data accessibility. The data are provided in electronic supplementary material [146].

Authors' contributions. D.C.D.: conceptualization, data curation, formal analysis, investigation, writing—original draft, writing—review and editing.

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