

PREDICTIVE REVIEW

A global analysis of ecological and evolutionary drivers of the use of wild mammals in traditional medicine

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ABSTRACT

1. Ingredients derived from wild mammals are widely used in traditional remedies. Large datasets of traits, geographic ranges, and phylogeny are also available for mammals. Therefore, mammals are an ideal group in which to explore the ecological (e.g. range size, body mass) and evolutionary (i.e. shared ancestry) correlates of the use of animal-derived products in traditional medicine.
2. In a global analysis of correlates of the use of wild mammals in traditional medicine, we tested how life-history traits relate to the use of mammal products to treat disease. We compiled data from the primary literature about folk remedies based on mammals via a literature search using ISI Web of Knowledge, Scopus, and Google Scholar. Then, we used modern phylogenetic comparative methods to estimate phylogenetic signals in the diseases that mammal body parts are used to treat and to test whether geographic range size and body mass are related to medicinal use. We tested whether mammalian species that are used more in medicine are also those that are more threatened by extinction.

3. Our results show that 521 mammalian species are used to source products to treat 371 ailments. We found support for the hypothesis that phylogenetic relatedness correlates with the use of mammal-derived remedies in traditional medicines. Specifically, we confirm our hypotheses that closely related species are more similar in terms of their perceived medical versatility than distantly related species and are used to treat similar diseases. Furthermore, we demonstrated that large marsupials are more versatile and are used to treat more diseases than smaller marsupials.
4. In our database, 155 mammalian species are considered threatened (Vulnerable, Endangered, or Critically Endangered), and a further 46 are Near Threatened, suggesting that overexploitation for medicinal use could be an overlooked source of threat that should be considered in mammal species conservation assessments. We demonstrate that phylogenetic relatedness correlates with the use of mammalian species as remedies in traditional medicine, and urge future researchers to evaluate the negative effects of overexploitation of mammals for medical purposes. Such overexploitation could cause non-random extinction patterns in the mammalian tree of life.

Palavras-chave

animais medicinais, caça, conservação de mamíferos, etnozootologia, medicina tradicional, revisão mundial, zooterapia

RESUMO EM PORTUGUÊS

1. Produtos derivados de mamíferos silvestres são amplamente utilizados em remédios tradicionais. Para esses animais, também há disponibilidade de ampla base de dados que inclui os atributos, áreas geográficas e filogenia. Portanto, os mamíferos são considerados um grupo ideal para explorar os aspectos da ecologia (e.g. porte, massa corporal) e evolução (ou seja, ancestralidade compartilhada) e correlacioná-los ao uso de produtos derivados de animais na medicina tradicional.
2. Em uma análise global dos usos de mamíferos silvestres correlacionados a medicina tradicional, testamos como os atributos da história da vida se relacionam com os padrões de uso atual de produtos de mamíferos para o tratamento de doenças. Compilamos dados da literatura sobre remédios populares derivados de mamíferos por meio de pesquisa bibliográfica usando os portais: ISI Web of Knowledge, Scopus e Google Scholar. Em seguida, usamos métodos comparativos filogenéticos para estimar o sinal filogenético no tratamento de doenças com produtos derivados de mamíferos e para testar se o tamanho da área geográfica e a massa corporal estão relacionados ao uso medicinal. Também testamos se as espécies de mamíferos mais utilizadas na medicina tradicional são também aquelas que estão mais ameaçadas de extinção.
3. Nossos resultados mostram que 521 espécies de mamíferos são usadas como fonte de produtos para tratar 371 doenças. Encontramos suporte para a hipótese de que a relação filogenética se correlaciona com o uso de remédios derivados de mamíferos na medicina tradicional. Especificamente, confirmamos nossas hipóteses de que espécies próximas filogeneticamente são mais semelhantes em termos de sua versatilidade medicinal percebida do que espécies distantemente relacionadas; espécies com parentesco comum são usadas para tratar doenças semelhantes. Além disso, demonstramos que grandes marsupiais são mais versáteis e são utilizados para tratar mais doenças quando comparados com marsupiais menores.
4. Em nossa base de dados, 155 espécies de mamíferos são consideradas ameaçadas (Vulnerável, Ameaçada ou Criticamente Ameaçada), e 46 quase ameaçadas, sugerindo que a exploração excessiva para uso medicinal pode ser uma fonte de impacto negligenciada e que deve ser considerada em avaliações sobre conservação de espécies de mamíferos. Demonstramos que a relação

filogenética se correlaciona com o uso de espécies de mamíferos para os remédios na medicina tradicional, além disso estimulamos os futuros pesquisadores a avaliar os efeitos negativos da superexploração de mamíferos para fins medicinais. Essa superexploração pode causar padrões de extinção não aleatórios na árvore da vida dos mamíferos.

INTRODUCTION

Animals are common sources of ingredients of remedies for treating human diseases (Mahawar & Jaroli 2008, Ferreira et al. 2012, Alves & Rosa 2013a, Martinez 2013, Castillo & Ladio 2019) in several traditional medical systems, mainly in Latin America, Africa, and Asia (Alves & Rosa 2013a, Alonso-Castro 2014, Vijayakumar et al. 2015, Yeshi et al. 2017, Janssen & Gomez 2019, Albuquerque et al. 2020). Animals can also be used in combination with medicinal plants. Their body parts are commonly sold in public markets and fairs around the world in both rural and urban communities (Alves et al. 2013a).

Animals used in traditional medicine practices belong to a wide variety of taxonomic groups, including invertebrates and vertebrates (Alves & Rosa 2006). Mammals are among the most frequently used animals in traditional folk medicine (Bourdy et al. 2004, Alves & Rosa 2006, Vázquez et al. 2006, Alves et al. 2007, Mahawar & Jaroli 2008, Mahomoodally et al. 2019). Mammalian species also play key roles in terrestrial and aquatic ecosystems, and overexploitation of their body parts for medicinal uses may represent an additional threat to some species, including tigers *Panthera tigris*, leopards *Panthera pardus*, saiga antelope *Saiga tatarica*, elephants *Elephas maximus* and *Loxodonta africana*, rhinoceros (Rhinocerotidae), pangolins (Manidae), musk deer *Moschus* spp., and bears (Ursidae; Alves & Rosa 2013b). Therefore, the overexploitation of these and other species should be considered in conservation programmes, especially when medicinal products derived from them are sold in great numbers (Lee 1999, Alves et al. 2013b). However, little is known about how ecological and evolutionary processes relate to the use of wild mammals in traditional medicine. Understanding what factors correlate with the use of wild mammals can help future conservation actions and may also direct medical research by orienting screening for substances.

The choice of which animal to use for medicinal purposes is related to the users' beliefs and knowledge (Adeola 1992, Apaza et al. 2003, Alves & Rosa 2006). Vertebrates are the most commonly used animals in folk medicine (Alves & Rosa 2013a), perhaps because of their large body size. In fact, larger animals tend to provide more products that are used as ingredients in traditional remedies than smaller ones (Alves et al. 2008,

Alves et al. 2010, Alves et al. 2011, Alves et al. 2016). The body parts mostly used for therapeutic products include hard parts (e.g. horns, scales, and bones), fat tissues, secretions, and oils. The products from each species are usually employed to treat similar diseases (Alves & Rosa 2006, Mahawar & Jaroli 2008, Castillo & Ladio 2019). As a result, species that have more body parts extracted for medicinal use may be more threatened with extinction (Alves & Rosa 2013a), since there will be more demand for them.

Human populations also select and use mammals as remedies based on the geographic distribution of the species and their occurrence in each environment; resource accessibility allows people to experiment and adapt their uses, increasing the chances of having them incorporated into folk medicine. It is expected that widely distributed species have contact with several human populations, which would have more opportunities to develop therapies with their body parts (Alves & Rosa 2007, Xing et al. 2020).

No study to date has assessed how these factors together relate to patterns of medicinal use of wild mammals by humans. Closely related species tend to have similar morphological and behavioural traits due to common ancestry (Felsenstein 1985, Harvey & Pagel 1991). This pattern may depend on the model of trait evolution, but a simple Brownian Motion model can produce strong phylogenetic signals in morphological traits (Revell et al. 2008), which suggests that species more closely related to each other would have similar morphological traits (Blomberg et al. 2003). If users of traditional medicine target species because they have a given trait (e.g. long horns), it would be plausible to expect a phylogenetic signal in medicinal use, driven by species' traits, which in turn is shaped by their common descent. Therefore, the question that remains is: can we use the phylogenetic position of a given species to predict if another species will be used to treat the same disease? Similarity in medicinal use may occur because close relatives share a common evolutionary history (see Teixidor-Toneu et al. 2018 for an example with medicinal plants), making them more likely to have similar morphological, physiological, and behavioural traits (Blomberg et al. 2003, see also Zhu et al. 2011).

Given the long and intricate relationship between wild mammals and humans (Happold 1995, Mesquita & Barreto

2015, Alves et al. 2016, Barboza et al. 2016, Renoux & de Thoisy 2016), mammals are an ideal group in which to understand the ecological and evolutionary correlates of the use of animal-derived products in traditional medicine. We take advantage of the wealth of high-quality life-history data available for mammals and combine them with an extensive, new database on the use of mammals in traditional folk medicine in several traditional medical systems worldwide, in order to test the following five main hypotheses:

1. Closely related species are used to treat similar diseases. We expect that co-evolution of medicinal properties (be they derived from physiological or morphological traits) determines the pattern of medicinal use.
2. Closely related species that are used in medicine are more similar in terms of their therapeutic versatility than distantly related species. As close relatives tend to share similar therapeutic properties, similar numbers of their body parts will be used to treat different ailments.
3. Therapeutic versatility is correlated with species' geographic range size. We expect small-ranged species to have limited contact with distinct peoples and therefore fewer opportunities to be used for treating multiple diseases.
4. Body mass determines therapeutic versatility. Heavier species, having larger body parts, offer more opportunities for treating multiple diseases.
5. Body mass and therapeutic versatility can be used to predict threat category. We expect that larger species and those used to treat more diseases are more prone to extinction than others.

METHODS

Data compilation and disease categories

We compiled data from the primary literature about folk remedies based on mammals by a literature search using ISI Web of Knowledge, Scopus, and Google Scholar, conducted from January 2017 to December 2018, using the following search terms combined with the word 'mammals': 'medicinal animals' and 'folk medicine' or 'folk remedies' or 'traditional medicine' or 'traditional remedies' or 'ethnozoology'. We searched for the same terms in English, Spanish, and Portuguese, and found studies performed from 1937 to 2018. In addition, we used a snowballing approach to search the reference list of relevant publications to identify additional studies that could indicate mammalian species used for medicinal purposes. We only included in our database publications that provided evidence of at least one mammal species being used for medicinal purposes. Studies that

mentioned common names without scientific names were excluded. Based on these criteria, we compiled 397 publications. Species' nomenclature followed Burgin et al. (2018; available at <https://mammaldiversity.org>). We recorded information on mammal species, family, order, conservation status, body parts used, and the ailment for which remedies were prescribed, for 565 species. There was no information about which specific body part was used to treat ailments for 256 species (45%); these species were only mentioned as being used in traditional medicine in general. We explain below (see Data analyses) how we estimated the use values for these species. We also obtained information about geographic range size, phylogenetic information, and country. After gathering this information, our final dataset contained 521 species.

To classify the ailments described in the papers, we used the International Statistical Classification of Diseases and Related Health Problems (ICD-10; World Health Organization 2016; <https://icd.who.int/browse10/2010/en>). This classification, used to identify global health trends, is considered the international standard for reporting diseases and health conditions for clinical and research purposes (World Health Organization 2016). The ailments mentioned in the papers we retrieved were placed in 19 disease categories, based on the categories of the ICD-10, as follows: (1) infectious and parasitic diseases; (2) neoplasms; (3) blood diseases and immune disorders; (4) endocrine, nutritional and metabolic diseases; (5) mental and behavioural disorders; (6) diseases of the nervous system; (7) diseases of the eye and attachments; (8) diseases of the ear; (9) diseases of the circulatory system; (10) diseases of the respiratory system; (11) diseases of the digestive system; (12) diseases of the skin; (13) musculoskeletal diseases; (14) diseases of the genito-urinary system; (15) disease of pregnancy, childbirth and puerperium; (16) lesions and poisonings; (17) external causes of mortality; (18) unclassified symptoms and signs; and (19) indeterminate diseases and conditions (Appendix S1).

Traits and phylogenetic data

We used the dated phylogenetic tree by Upham et al. (2019). Specifically, we used the node-dated maximum clade credibility tree built with molecular data only. This phylogeny is the most up-to-date tree for mammals worldwide; it includes 4098 species and was inferred based on a supermatrix of 31 genes (both mitochondrial and nuclear) using maximum likelihood constraints and Bayesian methods to resolve local (lineage) relationships.

We gathered body mass data for the species (PHYLACINE 1.2.1 database; Faubry et al. 2018, 2020). We obtained the geographic range size of each species from the International

Union for Conservation of Nature (IUCN 2019). When range maps were estimated for subspecies (and when maps did not overlap), we summed them to obtain a single value per species, excluding overlapping ranges.

Data analyses

Therapeutic versatility of species was estimated by using the Relative Importance (RI; Bennett & Prance 2000). The RI provides a quantitative method that demonstrates the importance of a given species based on its therapeutic versatility, i.e. the number of medicinal uses (reported specific ailments that are treated with the mammal-derived product) of a species given in the papers (Bennett & Prance 2000). The RI for each species was obtained using the following formula:

$$RI = NUC + NT$$

where NUC = number of disease categories of a given species (NUCS) divided by the total number of disease categories of the most versatile species (NUCVS). NT is given by the number of types of uses attributed to a given species (NTS) divided by the total number of types of uses attributed to the most important taxon (NTMIT). Thus, RI varies from 0 (no medicinal use) to 2 (maximum versatility). Some species ($n = 256$) were considered to be useful for their medicinal properties, but no specific use (relating to any of the 19 disease categories) was determined. For those species, we calculated their RI values by dividing the minimum by the maximum RI value found in all species. Therefore, values close to zero indicate species that are used in traditional medicine, but without any specific disease category.

We assigned a binary trait to each species based on the presence (1) or absence (0) of use to treat ailments in each of the 19 disease categories. To test whether body parts extracted from closely related species were used to treat similar diseases, we tested for phylogenetic signal using Fritz's D (Fritz & Purvis 2010). D is derived from the threshold model of quantitative genetics, and approaches 1 when the phylogenetic structure is random, which means that phylogenetic relatedness does not affect the binary trait state. Conversely, D values approaching zero indicate increasing phylogenetic clumping, which suggests that closely related species share a similar trait state (Fritz & Purvis 2010). Analysis was conducted in the R package 'caper' (Orme et al. 2018).

We used Blomberg's K to calculate the phylogenetic signal in species' therapeutic versatility (RI was treated as a continuous trait). K values > 1 indicate that closely related species are more similar in terms of their therapeutic versatility than expected under a Brownian Motion model of evolution. Conversely, K values < 1 indicate

that closely related species share fewer similar trait values, which suggests that the trait (in this case therapeutic versatility) does not have phylogenetic structure (Blomberg et al. 2003). Analysis was conducted in R package 'phytools' (Revell 2012).

To test whether species' geographic range size and body mass (predictor variables) affected therapeutic versatility (RI; response variable on a log scale), we used a phylogenetic generalised least-squares analysis, which allowed us to account for phylogenetic autocorrelation among sampling units (species) by modelling the variance-covariance matrix of residuals incorporating the phylogenetic relationship of species. We used the 'corPagel' correlation structure, available in the R package 'ape' (Paradis & Schliep 2019), setting the initial Pagel's λ value to 1 (see Revell 2010). Analysis was conducted in the package 'nlme' (Pinheiro et al. 2020) in R v. 4.0.0 (R Core Team 2020). In order to test for non-stationary patterns in the effect of geographic range size on RI, we ran a phylogenetic weighted regression (Davies et al. 2019). This analysis tests if the relationship between range size and therapeutic versatility changes throughout lineages.

Finally, to test if species' body mass and therapeutic versatility (continuous predictor variables) correlate with their conservation status (ordinal response variable), we built a linear mixed-effects model in 'MCMCglmm' (Hadfield 2015). We treated IUCN conservation category (IUCN 2019) as an ordinal response variable following the levels of threat: Least Concern $<$ Near Threatened $<$ Vulnerable $<$ Endangered $<$ Critically Endangered. For this analysis, we excluded species that were classed as Data Deficient, Extinct in the Wild, and Not Evaluated by the IUCN, retaining 509 of the 521 species. As priors, we specified variance (V) as unit, and $\nu = 0.02$ for both R and G matrices. We controlled for the phylogenetic relationships among species by including the inverse relatedness matrix based on species phylogeny. We ran a single MCMC for 40 million generations, sampling every 80 generations and discarding the first 12 million generations as burn-in. Diagnosis was done by plotting the trace and density of the fixed effects (Alves et al. 2020). Also, Heidelberger and Welch's convergence diagnosis showed that chains converged adequately ($P > 0.05$). The effective sample size for fixed effects and their interactions was 350000. All data and R Markdown dynamic documents describing the analysis are available at FigShare (Alves et al. 2020).

RESULTS

We found 565 mammalian species that are used as sources for medicinal products in traditional folk medicine. Of these, we analysed data from 521 species in

86 families (of the 159 extant families) and 17 orders (of the 27 extant orders) for which we had complete phylogenetic and trait information (Alves et al. 2020). The largest percentages of species belonged to the orders Cetartiodactyla ($n = 130$ species, 25%), Carnivora ($n = 120$ species, 23%), Primates ($n = 72$ species, 14%), Chiroptera ($n = 68$ species, 13%), and Rodentia ($n = 60$ species, 12%).

Almost all of the 521 species (99.4%) had had their conservation status assessed (IUCN 2019): 321 species (62%) were classified as Least Concern, 77 (15%) as Vulnerable, 48 (9.2%) as Endangered, 44 (8.4%) as Near Threatened, 20 (3.8%) as Critically Endangered, 7 (1.3%) as Data Deficient, and 1 (0.1%) as Extinct in the Wild. Two hundred and twenty-two species (43%) were included in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendices: 106 species (48%) in Appendix I, 92 species (41%) in Appendix II, and 24 species (11%) in Appendix III.

We found records of medicinal use of mammals from 131 of the ~ 200 countries in the world, mainly in Asia, Latin America, and Africa (Fig. 1). The five countries with the highest recorded species richness were India ($n = 93$), China ($n = 90$), Nigeria ($n = 83$), Benin ($n = 79$), and Brazil ($n = 65$). Remedies can be

produced with the whole body, but mostly they are made from body parts or animal-derived products, including the following: ankle, anus, bile, blood, bones, bone marrow, brain, cartilage, claws (nails), dung (manure), ears, eye, eyebrow, eye secretion, faeces, fat, foetus, gallbladder, gallbladder stone, gland, hair, hand, head, heart, horn, hoof or foot, intestine, ivory, kidney, leather, legs, ligaments, limbs, liver, meat, milk, musk (from musk deer), oil, placenta, penis, quill, scales, skin, skull, spines, stomach, tail, teeth, testicles, tibia, toe, tongue, urine, vagina, and wings.

Products derived from mammals were used to treat 371 ailments that were included in all of the 19 disease categories. The most common categories were as follows: 'infectious and parasitic diseases' (38 ailments) and 'unclassified symptoms and signs' (32 ailments). Many ailments ($n = 64$) did not have any specific symptoms and were placed in the category 'indeterminate diseases and conditions' (Appendix S1).

In relation to the five hypotheses, we found that closely related species are used to treat similar diseases (Fig. 2). In fact, there was a strong phylogenetic signal in 16 of the 19 disease categories (Table 1). Likewise, closely related species exhibited similar therapeutic versatility ($K = 0.063$, $P = 0.002$). Marsupial species with large

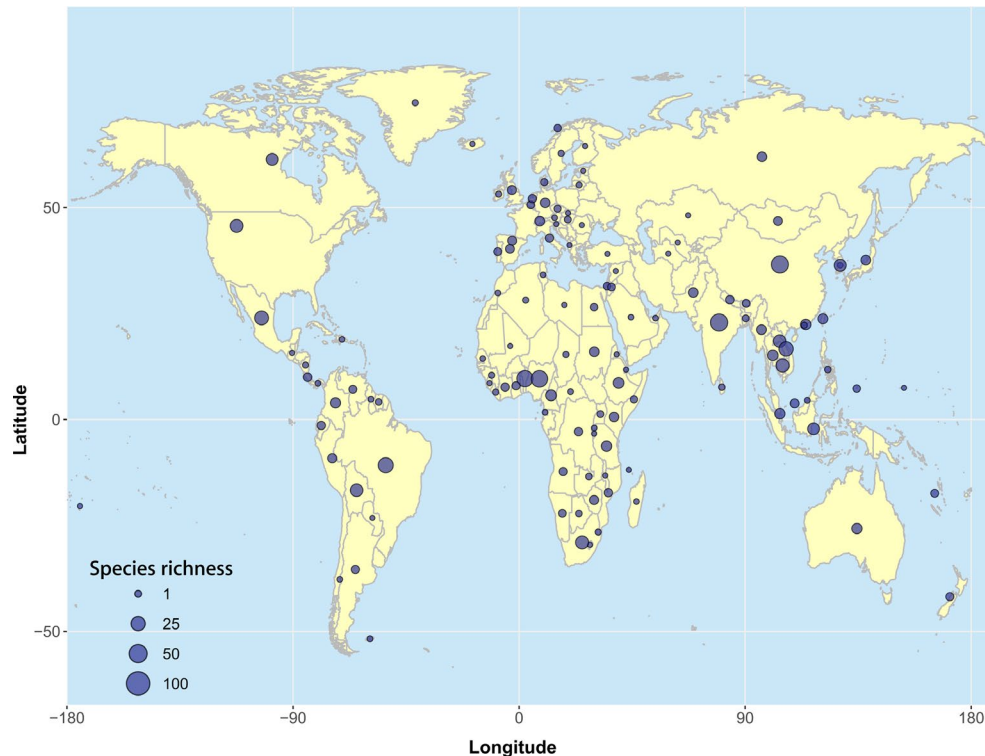


Fig. 1. World map, showing all countries (indicated with circles at country centroids) where at least one species of wild mammal was recorded as being used in medicine. Circle size represents the number of species used per country. [Colour figure can be viewed at wileyonlinelibrary.com]

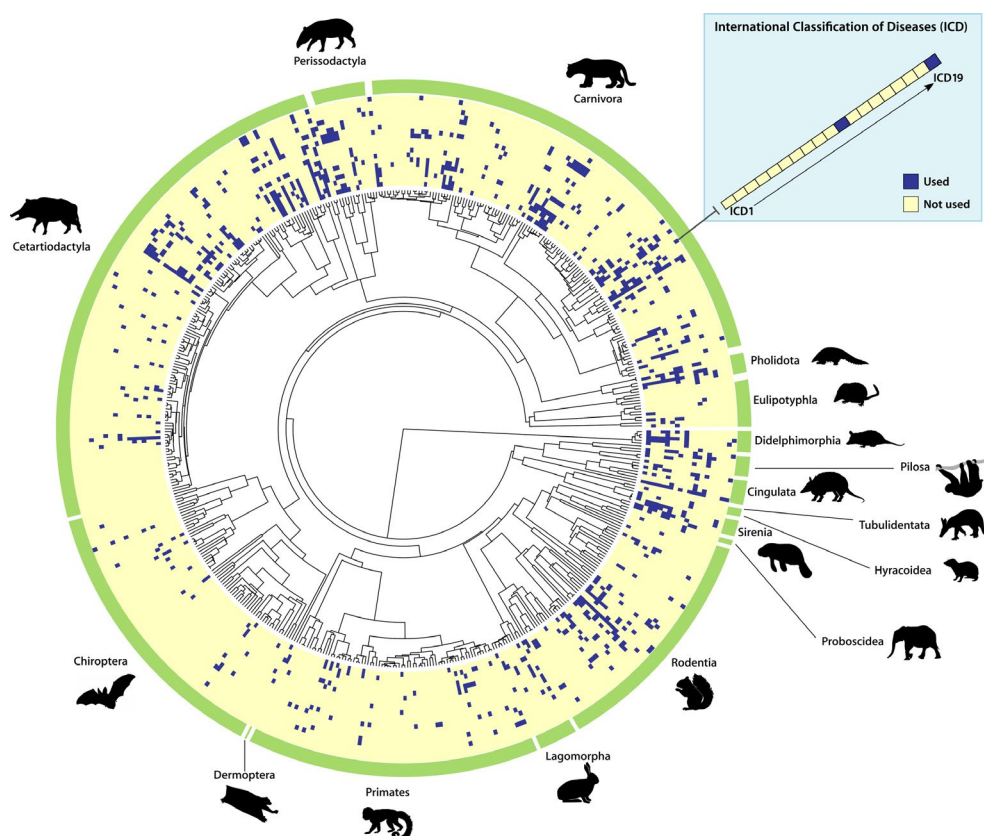


Fig. 2. Phylogenetic tree of mammalian species included in the analysis, in relation to their use to treat diseases in the 19 categories of the World Health Organization's International Classification of Diseases (ICDs). Each species' use to treat ailments in each of the 19 ICDs is shown: each row represents one ICD category ordered from 1 (central ring) to 19 (outer ring; inset, top right of the Figure). Lineages shown as not used to treat any disease category are those described as used to treat an ailment that could not be placed in any of the 19 disease categories. ICD disease categories are numbered as follows: (1) infectious and parasitic diseases; (2) neoplasms; (3) blood diseases and immune disorders; (4) endocrine, nutritional and metabolic diseases; (5) mental and behavioural disorders; (6) diseases of the nervous system; (7) diseases of the eye and attachments; (8) diseases of the ear; (9) diseases of the circulatory system; (10) diseases of the respiratory system; (11) diseases of the digestive system; (12) diseases of the skin; (13) musculoskeletal diseases; (14) diseases of the genito-urinary system; (15) disease of pregnancy, childbirth and puerperium; (16) lesions and poisonings; (17) external causes of mortality; (18) unclassified symptoms and signs; and (19) indeterminate diseases and conditions. [Colour figure can be viewed at wileyonlinelibrary.com]

geographic range sizes had high therapeutic versatility, but range size was not related to therapeutic versatility in placental mammals ($t = 0.701$, $P = 0.483$). Larger mammals had greater therapeutic versatility than smaller ones ($\beta = 0.439 \pm 0.093$, $t = 4.739$, $P < 0.0001$; Fig. 3). For instance, small mammals (body mass < 7.38 kg) had an average RI of 0.055, showing that they are 80% and 88% less versatile than mammals with body mass > 55 kg (RI = 0.272) and > 403 kg (RI = 0.452), respectively (Fig. 3). Neither therapeutic versatility nor body mass was associated with IUCN Red List category (Table 2). Although the mean body mass of a species included as Least Concern in the IUCN Red List is 24 kg, and Critically Endangered species weigh, on average, 112 kg (4.7 times higher; Fig. 4), the Bayesian model produced highly variable estimates

(odds ratio) because of the great difference in the number of species in each IUCN category in our dataset (range: 20 to 321 species).

DISCUSSION

Our results suggest that many species of wild mammals (at least 565, constituting 9% of the 6399 known species; Burgin et al. 2018) are used by humans to source products used in traditional medicine around the world, especially in Asia, Africa and Latin America. We found support for our expectation that phylogenetic relatedness correlates with the use of mammal-derived remedies in traditional medicines. Specifically, we confirm our first hypothesis, that closely related species are used to treat similar diseases, and our second hypothesis, that close relatives are

Table 1. Phylogenetic signal (Fritz's *D*) of mammals used (binary state: used or not used in a remedy) to treat ailments in the 19 disease categories of the International Statistical Classification of Diseases and Related Health Problems (ICD-10). *P* values lower than 0.05 are in bold

Disease category in ICD-10	<i>D</i>	<i>P</i>
1	0.674	<0.001
2	0.822	0.004
3	0.944	0.194
4	0.597	<0.001
5	0.494	<0.001
6	0.881	0.031
7	0.800	0.007
8	0.654	0.001
9	0.546	0.001
10	0.642	0.009
11	0.682	0.003
12	0.609	<0.001
13	0.645	<0.001
14	0.420	<0.001
15	0.724	0.003
16	0.624	<0.001
17	0.933	0.349
18	0.632	0.026
19	0.913	0.218

more similar in terms of their therapeutic versatility than species in the dataset that are only distantly related. Furthermore, we demonstrated that marsupials (but not other mammals) with large geographic range sizes are more therapeutically versatile than marsupials with smaller range sizes (third hypothesis) and that heavier mammals are more therapeutically versatile than lighter mammals (fourth hypothesis). Contrary to our expectation, body mass and therapeutic versatility were unrelated to IUCN threat category (fifth hypothesis). As far as we know, this is the first study showing that the use of mammals in traditional medicine is related to life-history traits.

The high proportion of known mammal species used as sources of medicines is not surprising, since mammals are common hunting targets (Bodmer et al. 1997, Mesquita & Barreto 2015, Alves et al. 2016, Barboza et al. 2016). Hunted individuals provide not only meat, but also many by-products that can be used as folk remedies. The use of disposable by-products derived from hunting or fishing is a common pattern in the use of animals in traditional medicine (Sodeinde & Soewu 1999, Kakati et al. 2006, Moura & Marques 2008, Alves & Alves 2011, Ferreira et al. 2013, Castillo & Ladio 2019). As a result of this practice, people optimise the exploitation of available animal resources by using all possible by-products (Moura & Marques 2008, Alves & Rosa 2013a).

Products derived from mammals are prescribed for the treatment of several ailments ($n = 371$), with products

derived from the same species being used to treat multiple diseases. Our results demonstrate that species' therapeutic versatility is correlated with their phylogenetic relatedness. Previous studies testing phylogenetic signals in mammals have found that closely related species share high trait similarity, such as body mass and brain size in primates (Kamilar & Cooper 2013), and diet in Didelphimorphia, Lagomorpha, and Rodentia (Olalla-Tárraga et al. 2016). We argue that mammalian evolutionary history is an essential tool that can be used to improve our understanding of the use of animal-derived remedies in folk medicine. For instance, we might speculate that if geographically separated human populations use two congeneric species to treat the same ailment, this will facilitate the identification and isolation of bioactive constituents for pharmacological research. In addition, closely related species seem to provide similar products that are used to treat ailments in the same disease category. For example, aquatic mammals have substantial amounts of fatty tissue, which is widely used in folk medicine worldwide (Alves & Alves 2011, Ferreira et al. 2013, Hajdari et al. 2018) and is usually prescribed for the treatment of musculoskeletal diseases (Ferreira et al. 2009, Alves & Alves 2011, Alves et al. 2013, Ferreira et al. 2016). Similarly, the horns of bovids are used to source medicinal products commonly used to treat diseases in the same category (Alves et al. 2011).

Morphological and ecological traits may also affect the medicinal use of some species. For instance, products from marsupials are commonly used to treat health issues related to childbirth, because people believe that these animals do not feel pain during delivery (Alves & Rosa 2007, Barros & Aguiar Azevedo 2014). The penis of coatimundi (*Nasua narica* or *Nasua nasua* in México, and *Nasua nasua* in Brazil) is considered the most potent remedy for male impotence in Brazil and México (Groark 1997, Alves et al. 2007). Descola (1997) provides an account for the probable origin of this use: "The penis of the coati rejoices in a long fine bone that keeps it constantly rigid. This anatomical peculiarity has made a forceful impression upon the imagination of the Indians, and the men make the most of it, grating the bone into a decoction of green tobacco to make a love philter. Quaffed at the right moment, it is reputed to prevent any flagging of the male member".

Users seem to look for other closely related species when animals with high medicinal utility are not available, suggesting that they believe morphologically similar species might be useful to treat similar diseases. Accordingly, ethnobiological theory predicts that human populations maximise their return (e.g. for feeding, medicine, etc.) by selecting a non-random subset of closely related species sharing similar traits (Zhu et al. 2011, Albuquerque et al.

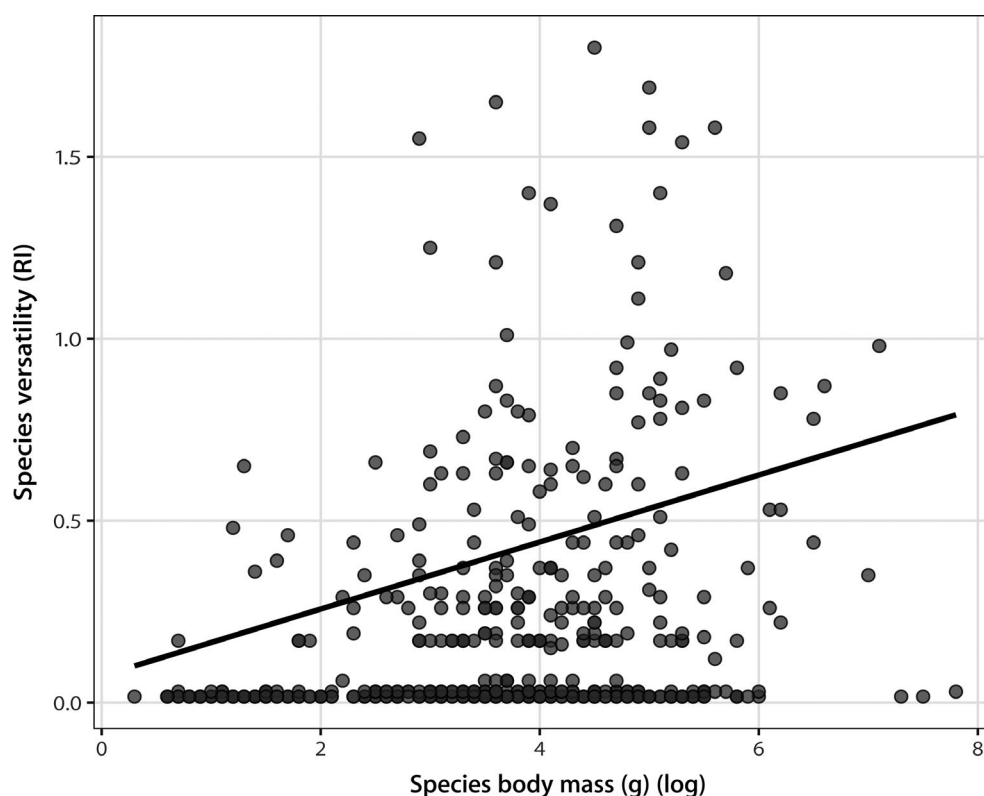


Fig. 3. Scatterplot showing the positive relationship between mammals' body mass (g-log10; range before transformation: 2.1 g-70,000 kg) and species' therapeutic versatility (RI; range: 0.016 - 1.8); sample size = 521. Heavier mammals have greater perceived therapeutic versatility in traditional medicine than lighter ones.

2019, Milla et al. 2018). This can be seen in big cats, which are used frequently in traditional medicine. The big cat most commonly used is the tiger, a species that is Endangered, in part because of its medicinal use (Alves et al. 2009). With tiger populations in decline, people began using other felids as surrogates, such as the snow leopard *Uncia uncia*, and demand for this species increased; leopard bones are used as a substitute for tiger bones in the manufacture of drug wine, which sells far and wide in China and Southeast Asia (Liao & Tan 1988).

Our results suggest that species' therapeutic versatility is related to geographic range size only in marsupials. This partially supports our third hypothesis, because range size was not associated with therapeutic versatility in

placental mammals. This lack of association might be attributed to the huge variability of life and evolutionary history in placental mammals. Conversely, marsupial species with wider distributions tend to be used by several human groups, due to their influence in traditional medical systems. Local human populations could spread the use of certain species in traditional medical systems while migrating to different regions (Belliard & Ramírez-Johnson 2005, Santos et al. 2016).

Body mass is positively related to species' therapeutic versatility, supporting our fourth hypothesis. Larger animals provide more by-products that can be used as remedies than smaller animals, and the products can have diverse chemical compositions, allowing them to be used

Table 2. Results of the Bayesian model (MCMCglmm) for testing the effects of body mass and IR (therapeutic versatility) on threat category of mammalian species; CI = confidence interval, ESS = effective sample size

	Posterior mean	Lower CI	Upper CI	ESS	pMCMC
Intercept	20.92	-195711.34	196618.92	350000	1.000
Body mass (log scale)	-87.21	-194794.19	196109.21	350000	0.999
IR	-90.97	-199550.24	192573.67	350000	0.999
Body mass:IR	-229.30	-194585.99	196352.25	350000	0.998

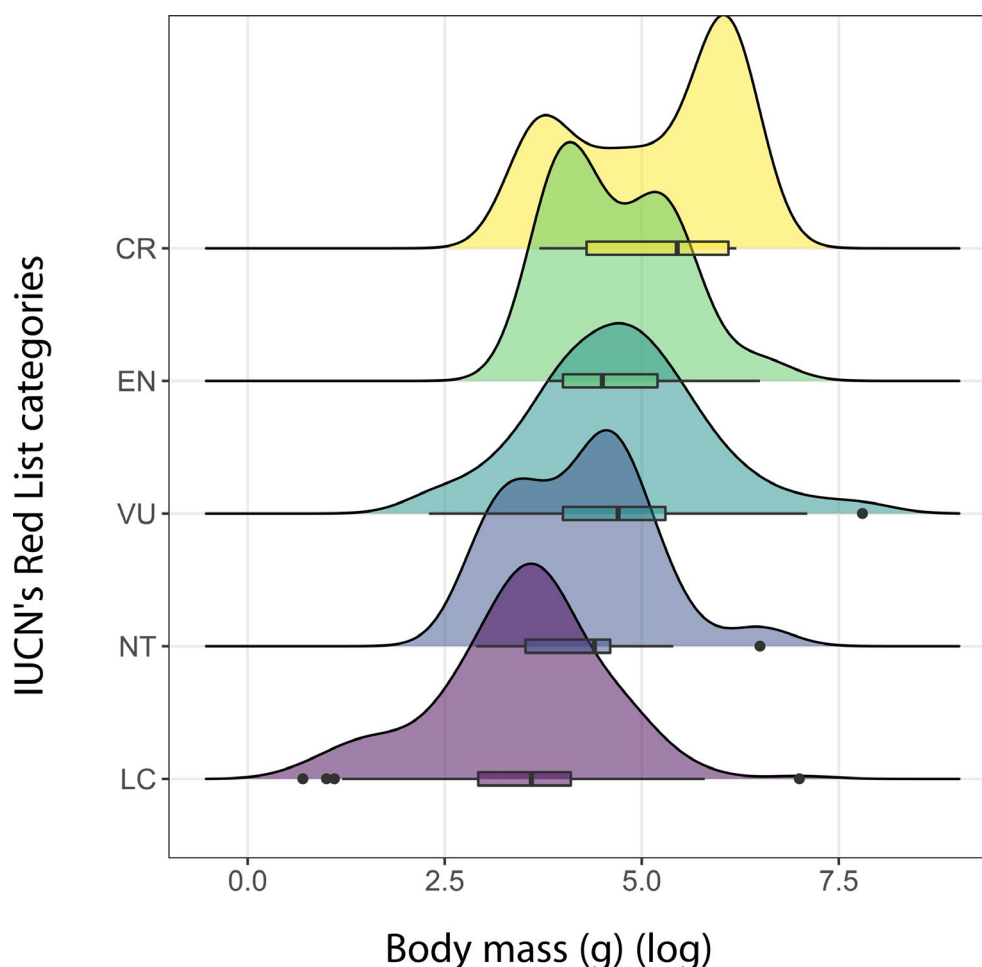


Fig. 4. Density distributions (ridge plots) of mammal body mass (natural log-transformed) within each IUCN Red List category: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). Full details of each category can be found in IUCN (2019). Boxplots show the same data (vertical central line = median, box = limits of the 25% and 75% quartiles, whiskers = 1.5 times the interquartile range; dots = data points beyond the whiskers, i.e. outliers). [Colour figure can be viewed at wileyonlinelibrary.com]

to treat many more diseases than products derived from smaller animals (Alves et al. 2007). Threat category was not directly related to species' therapeutic versatility, but is best predicted by adult body mass (for all species; see, e.g. Cardillo et al. 2008). Thus, any relationship between therapeutic versatility and extinction risk may not be direct, but may be mediated by body mass.

Mammalian species are used in both rural and urban areas for treating diseases in traditional medicine. Overexploitation of mammals for medicinal use could contribute to the decline of already threatened species. In our database, 155 mammalian species are considered threatened (Vulnerable, Endangered or Critically Endangered), and a further 45 are Near Threatened. Although we did not find a clear pattern between therapeutic versatility and threat categories, many previous studies have demonstrated that larger species are under more severe threat

(e.g. tigers, bears, rhinoceroses, pangolins, primates), especially when products made from them are sold, either legally or illegally. There is a pressing need to increase our understanding of the population ecology of these species, in order to assess the impacts of harvesting them (for medicinal or other purposes). The influence of magical and religious beliefs in the use of some animal body parts as medicine is a common characteristic found in various traditional medical systems, evidencing the holistic nature of traditional medicine to address spiritual, physical, and social-psychological problems (Adeola 1992, Alves et al. 2012). In this sense, sociocultural and religious beliefs must be incorporated in conservation programmes if they are to be effective.

Many mammalian species that are used in medicine are included in one or two CITES Appendices, although the reasons for their inclusion are not necessarily related

to medicinal use. The commonality of their use in traditional medicine threatens some mammal species, such as felines, rhinoceroses, and bears (Alves & Rosa 2013a). Along with habitat loss, the exploitation of mammalian species for traditional medicine, and trading of medicinal products derived from them, can be an important source of threat for mammals worldwide, showing the importance of considering this aspect in conservation assessments. We show that phylogenetic relatedness is correlated with species' use as remedies in traditional medicine, and urge future researchers to evaluate the negative effects of over-exploitation of mammals for medical purposes, because such use can cause non-random extinction patterns in the mammalian tree of life. As we highlighted, pressure on medicinal mammals varies among species, and hunting for medicinal use is often not the only pressure on these species, since they are also captured for other purposes, such as for food. Thus, among the many uses of mammals, it is difficult to assess the impact of medicinal use alone on wild populations.

Sanitary aspects of the use of wild mammals by humans, and their implications for public health, are also key aspects to consider (Van Vliet et al. 2017), as illustrated by the recent coronavirus (COVID-19) pandemic. Transmission of COVID-19 to humans is associated with the consumption of wild animals; the Malayan pangolin *Manis javanica* is the prime suspect (Lam et al. 2020), though the route of transmission has not yet been proven. Pangolins are consumed for food and used in medicine, as are other mammals (e.g. bats), which increases the transmission risk of zoonoses, favouring disease outbreaks (e.g. Fan et al. 2019).

CONCLUSION

Our results demonstrate that at least 565 mammalian species worldwide are used as ingredients in traditional folk medicine remedies. We explore how the mammalian tree of life could help to explain how species are chosen for treating human diseases. We found that local people prescribe closely related mammalian species to treat similar diseases, which suggests that the evolution of therapeutic properties derived from morphological or physiological traits may shape patterns in the medicinal use of mammals. We point out novel ways to understand the use of mammals in traditional folk medicine. First, by considering the evolutionary history of species used as remedies, we were able to detect non-random patterns of animal selection in traditional medicine. Second, our results shed light on the use of different mammal species as remedies, and how this use may affect their conservation status. We find that larger medicinal species, which have greater medicinal versatility, were not necessarily more threatened. However,

our study suggests that future conservation initiatives should consider the effects of medicinal use of mammals alongside those of hunting pressure for food.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Categories of diseases treated with zootherapeutic remedies derived from medicinal mammals. Ailments were placed in disease categories following the International Statistical Classification of Diseases and Related Health Problems (ICD-10 Version: 2016). *N* = total number of ailments treated in each category.