The status of research on the mammals of Sulawesi, Indonesia

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Keywords
conservation, ecology, mammals, Sulawesi, taxonomy

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ABSTRACT

1. The Indonesian island of Sulawesi is widely considered a mammal conservation hotspot, mainly due to the high number of threatened endemic species with limited geographical ranges that are found there, and also due to the biogeographical importance of Sulawesi as the largest island in the Wallacea region.
2. To date, there has been no comprehensive review to evaluate the status of what we know about mammals in Sulawesi. The overarching goal of our review is to contribute towards identifying knowledge gaps in the biology and ecology of mammals in Sulawesi.
3. Our specific aims were to: 1) identify taxonomic and geographic bias in published research; 2) identify biases within existing ecological knowledge; and 3) identify key research priorities for the future.
4. Our review covers a total of 280 articles (published between 1921 and 2017) on 144 species of mammal from Sulawesi.
5. Through our review we found: 1) a strong taxonomic bias, with the majority of studies being conducted on primates (59% of published articles); 2) a geographic bias, where significantly fewer studies took place in the provinces of West Sulawesi and Gorontalo; and 3) a bias in research topics, with most studies (50% of published research) focusing on taxonomy and behaviour.
6. As an outcome of this review, we provide specific recommendations for future researchers, including: 1) a checklist of understudied species, with particular emphasis on understudied species of conservation concern; 2) a checklist of understudied research topics, with an emphasis on the need to conduct detailed auto-ecological studies; and 3) suggestions on how to adjust research methods on population and habitat studies.

INTRODUCTION

Sulawesi, Indonesia, is widely considered to be a biodiversity hotspot (Myers et al. 2000, Wilson et al. 2006). Its geographic position and biogeographical isolation have contributed to its high numbers of endemic mammal species (Whitten et al. 1987, Groves 2001, Cannon et al. 2007), many of which have restricted geographic ranges (98% of all non-volant mammal species in Sulawesi) and are categorised as threatened species by the International Union for Conservation of Nature (IUCN; i.e. they are Critically Endangered, Endangered or Vulnerable; Whitten et al. 1987, Ceballos & Ehrlich 2006, Schipper et al. 2008, Jenkins et al. 2013, IUCN 2017). Consequently, the island of Sulawesi has been recognised as a high priority area for the conservation of mammals (Carwardine et al. 2008, Catullo et al. 2008, Wilson et al. 2016).

The mammals of Sulawesi have been extensively studied; research subjects include taxonomy (Evans et al. 2003, Groves et al. 2008, Maryanto et al. 2012, Rowe et al. 2016), natural history (Sugardjito et al. 1989, Kyes et al. 2000, Merker et al. 2005), behaviour (MacKinnon & MacKinnon 1980, Brien & Kinnaird 1997, Gursky 2000, Grow & Gursky 2010) and conservation (Riley 2002, Merker et al. 2005, Grow et al. 2013, Sheherazade

& Tsang 2015). Several authors have reviewed studies of Sulawesi mammals and have focused on specific taxa or specific topics, including the taxonomy and conservation of the anoa *Bubalus* spp. (Groves 1969, Manansang et al. 1996a, Burton et al. 2005), population dynamics of Sulawesi macaques *Macaca* spp. (Riley 2010, Palacios et al. 2011, Kyes et al. 2013), conservation strategies for the tarsier *Tarsius* spp. (Gursky 1998a,b, Gursky et al. 2002, Shekelle & Leksono 2004, Shekelle & Salim 2009), the taxonomic status of Sulawesi rodents (Musser et al. 2010, Musser 2014) and conservation strategies for the babirousa *Babyrousa* spp. (Manansang et al. 1996b). To date, there has been no comprehensive review evaluating the status of knowledge of the mammals of Sulawesi, although knowledge gaps do exist. The lack of a unified overview may have negative consequences by hampering further scientific progress (if researchers ignore critical research gaps) and conservation efforts (if funding is not directed towards conservation priorities). Our goal here is to contribute towards identifying the knowledge gaps, and so to enhance and refocus research on Sulawesi mammals. Filling the knowledge gaps is particularly important because mammal populations of Sulawesi are heavily impacted by overhunting (between 2002 and 2003, trade of wild mammals for food increased by 30% in north Sulawesi; Lee et al. 2005) and deforestation (there is an ongoing 1.1% yearly decrease in forest cover; Miettinen et al. 2011).

Our specific aims through this review are fourfold: 1) to identify taxonomic and geographic bias in published research (answering the questions: are we focusing our research efforts on a limited number of taxa? Are there understudied taxa and geographic areas, and if so, which are these?) 2) To identify biases in the ecological knowledge provided by Sulawesi mammal studies (are most studies focused on behaviour, taxonomy, or other topics?) 3) To identify key research priorities for the future.

We structured our Results around thematic sections. In the first, 'Taxonomic scope of Sulawesi mammalian studies', we aim to identify taxonomic bias in published research. We identify understudied orders (after accounting for species richness) and speculate on the possible causes of bias. We also identify the most-studied and the least-studied species. In the section 'Research topics on Sulawesi mammals', we investigate biases in research topics both within and between taxa, and speculate on the possible factors driving biases (e.g. importance of research topics, conservation status, species charisma). This section may assist researchers and stakeholders by refocusing future research topics on Sulawesi mammals. In the section 'Conservation status and research efforts', we examine whether research efforts are related to the IUCN Red List categories of the species (e.g. are Endangered species more or less studied than Least Concern species?) This information will help stakeholders to identify understudied species of conservation concern and redirect future research efforts.

In the section 'Research approaches for population and habitat studies', we review progress in population and habitat studies. We focus on the methods used to estimate population size (direct methods vs. indirect methods; Buckland et al. 2004), the type of habitat studies (e.g. habitat use vs. habitat selection) and the scale of habitat selection (Johnson 1980). In the section 'Geographic bias in Sulawesi mammal research', we provide an overview of the geographical distribution of mammal studies throughout Sulawesi. We identify the most-studied and least-studied provinces and evaluate whether studies are typically performed in conservation areas.

In the section 'Patterns in Sulawesi mammal research', we provide an overview of the taxonomic scope of mammalian research in Sulawesi (single-species studies vs. multiple-species studies), and also assess trajectories in the number of articles on each research topic over time.

METHODS

Taxonomic and geographic scope of the review

Our review is focused on all terrestrial mammals living in the Sulawesi mainland and on its satellite islands (Fig. 1; Talaud and Sangihe Islands; Togian Islands; Banggai Islands; Tukangbesi Islands; and Salayar Islands). We adopted the checklist of Sulawesi mammals (Suyanto et al. 2002) and updated it using recent publications (Kitchener et al. 1995, Ruedi et al. 1998, Merker & Groves 2006, Bates et al. 2007, Groves & Shekelle 2010, Merker et al. 2010, Musser et al. 2010, Maryanto et al. 2012, Mortelliti et al. 2012, Musser 2014, Rowe et al. 2016, Shekelle et al. 2017).

Literature search

The literature search was conducted using two main search engines: Web of Science and Google Scholar. Articles were searched for during March–May 2017 using the scientific name of each species in combination with the key words: 'mammals', 'population', 'habitat', 'ecology', 'evolution', 'distribution', 'behaviour', 'Celebes', 'Sulawesi'. To maximise completeness, we also searched for key authors who have published extensively on Sulawesi mammals (including, for example, S. Gursky, G. Musser, M. Shekelle, and C. P. Groves) and references cited in the selected articles.

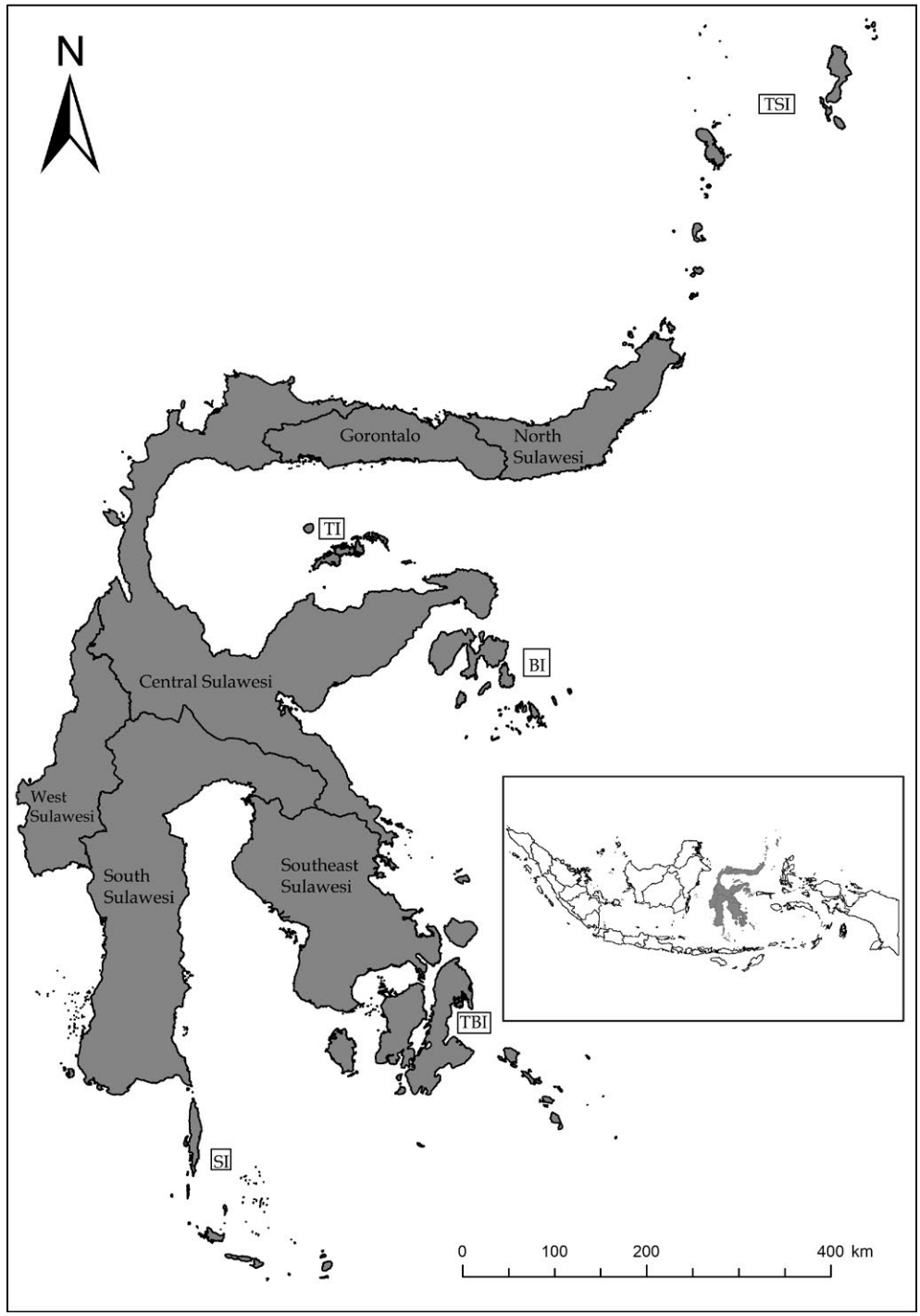

Fig. 1. Map of Sulawesi showing the six Sulawesi Provinces and the satellite islands: the Selayar Islands (SI) are part of the South Sulawesi province, the Tukangbesi Islands (TBI) are part of the Southeast Sulawesi province, the Banggai Islands (BI) and Togian Islands (TI) are part of the Central Sulawesi province, and the Talaud and Sangihe Islands (TSI) belong to the North Sulawesi province. Inset, map of Indonesia, showing the location of Sulawesi.

We restricted our search to peer-reviewed papers and book chapters published by May 2017 in English or Indonesian. We excluded conference abstracts, theses, and books, and articles on mammals that are not endemic to Sulawesi if the research was undertaken outside Sulawesi and its satellite islands. For each selected article, we summarised and synthesised the main findings, including focal taxa, research findings, and geographic location.

Taxonomic bias, research topics, and IUCN categories

Taxonomic bias was examined by assessing the number of published articles for each taxon (order and species). To avoid misclassification of focal taxa, we adopted the nomenclature used in the IUCN Red List (http://www.iucnredlist.org/) and Integrated Taxonomic Information System (https://www.itis.gov/).

Research findings were classified into nine research topics (adapted from Verde Arregoitia 2016): taxonomy (including evolution and genetics), physiology, population, habitat, distribution, behaviour, food habits, reproduction, and conservation (definitions are provided in Table 1). The total number of articles in each research topic was calculated by summing the number of articles covering each research topic. Articles dealing with multiple research topics (i.e. Grow & Gursky 2010) contributed to the tally count of each research topic.

The most-studied and least-studied species were identified by summing the total number of articles focused on each species; articles dealing with multiple species (e.g. Musser 2014) were counted once for each species. As an example, Shekelle et al. (2017) focused on two species, so we included this entry in our data base twice but considered it as one article where appropriate. We did not include articles in which focal taxa were studied only at the genus level (e.g. *Tarsius* spp.; Groves et al. 2008).

We obtained the IUCN Red List category for each species (http://www.iucnredlist.org/). Species that were recently described or re-classified and did not have a category were classed as 'uncategorised' (e.g. Mortelliti et al. 2012, Rowe et al. 2016, Shekelle et al. 2017).

Population and habitat studies

We extracted detailed information from articles focusing on the topics population and habitat. We placed habitat studies into the following categories: habitat use studies, habitat selection studies, and habitat quality studies (definitions are shown in Table 2). We also identified the scale of habitat selection (Johnson's multi-scale habitat selection; Johnson 1980), and the method used to collect population data (direct, indirect or both methods, as defined in Table 2). We adopted the definition of habitat use proposed by Krausman (1999), habitat selection definitions proposed by Johnson (1980), habitat quality definitions by Johnson (2007), and population methods by Buckland et al. (2004; Table 2).

Table 1. Research topics and definitions used to categorise research findings from published articles on Sulawesi mammals, and examples for each category

Research topic	Definition	Examples
Taxonomy	Classifying species and measuring evolutionary history (Verde Arregoitia 2016)	• Morphology (Juliandi et al. 2009) • Genetics (Kawamoto et al. 1982) • Taxonomy (Groves et al. 2008)
Physiology	Physical and biochemical processes involved in animal functioning (Verde Arregoitia 2016)	• Tissue function (Breed & Musser 1991) • Enzymes (Cinque et al. 2017)
Population	Biological populations of organisms, including population declines, trends, population dynamics, reintroduction of species, rehabilitation of species, relocation, and population genetics (Griffiths & Dos Santos 2012)	• Population density (Yustian et al. 2008) • Monitoring populations (Kyes et al. 2013)
Habitat	Resource use (e.g. shelter) and habitat relationships	• Habitat use (Merker et al. 2005) • Habitat selection (Merker & Yustian 2008) • Habitat quality (Johnson 2007)
Distribution	Spatial occurrence of species (Verde Arregoitia 2016)	• Dispersal (Gursky 2010) • Geographic range (Maryanto et al. 2009)
Behaviour	Spatial and temporal movements, everyday activities, and patterns of interaction with conspecifics (Verde Arregoitia 2016)	• Foraging behaviour (Drapier et al. 1999) • Agonistic behaviour (Macdonald et al. 1993) • Social behaviour (Reed et al. 1997)
Food habits	Food availability, distribution, diet composition, preferences including feeding strategies and nutritional content (Martin et al. 1951)	• Food choice (Riley 2007) • Nutritional content (Flores-Miyamoto et al. 2005)
Reproduction	Production of offspring and its timing (Verde Arregoitia 2016)	• Monitoring pregnancy (Houston et al. 2001) • Fertilisation (Thomson et al. 1992) • Reproductive system (Ziehmer et al. 2010)
Conservation	Effects of anthropogenic activities on communities (Verde Arregoitia 2016)	• Land use change (Merker et al. 2005) • Wildlife trade (Sheherazade & Tsang 2015) • Hunting (Riley 2002)

Table 2. Definitions used to categorise research on the topics habitat and population in published articles on Sulawesi mammals

Term	Definition
Habitat	Resources and conditions in an area that determine presence, survival and reproduction of a population
Habitat use	Estimating habitat of a population using occurrence data as surrogate for suitable habitat (i.e. not taking into account habitat availability)
Habitat selection	Estimating habitat by quantitatively comparing habitat use and habitat availability. Habitat selection may be measured at different scales (spatial or temporal; e.g. Johnson's orders of habitat selection, Johnson 1980)
Habitat quality	Estimating habitat quality of a focal species or population by measuring individual or demographic performance (e.g. body condition, growth rates etc.)
Population: direct methods	Estimating density or abundance of a focal species or population using direct observations (direct counts, camera traps, mark/recapture studies, etc.)
Population: indirect methods	Studies estimating density or abundance of a focal species or population using indirect observations (track surveys, sound recordings etc.)

Geographical distribution of research in Sulawesi

The geographical distribution of research in Sulawesi was evaluated based on political boundaries (provinces) and on the conservation status of research areas (protected conservation areas such as national parks, and non-protected areas outside these). We used data for political boundaries from the Indonesian Geospatial Information Agency (www.bakosurtanal.go.id), and obtained data on the size of provinces from the Bureau of Statistics of Indonesia (https://www.bps.go.id/; Fig. 1). The distribution of protected and non-protected areas was based on a report of conservation areas in Kalimantan and Sulawesi (Directory of Natural Resources and Ecosystem Conservation 2016) and further updates. The geographical ranges of the Sulawesi mammals were derived from the IUCN Red List Digital Distribution Maps (IUCN 2017). These maps constitute the most up-to-date overview of species distribution in Sulawesi. We emphasise that caution should be exerted when interpreting results because, particularly in the case of poorly known species, the geographical ranges may be biased towards areas of Sulawesi that have been sampled more intensively by researchers. For species not yet listed by the IUCN we used maps from the primary literature (e.g. Shekelle et al. 2017 for *Tarsius spectrumgurskyae*).

Patterns in taxonomic scope of studies and research topics

To assess patterns in research output, each article was assigned to the following non-mutually exclusive categories: single vs. multi-species article, and the nine research topics (Table 1). Each article was then assigned to a time period based on the year of publication (1921–1940, 1941–1960, 1961–1980, 1981–2000, and 2001–2017).

Bias in mammal studies

We used Chi-squared tests to quantify potential bias in the taxonomic scope of published studies, in the research topics and in the geographic distribution of research (including both conservation status and geographic areas). The expected number of articles for the taxonomic scope was based on the number of species in each taxon (we expected the number of articles to be proportional to the number of taxa); for the geographic distribution of research we calculated the expected number of articles based on the area of each province (we expected higher numbers of studies in larger provinces). We calculated the expected number of articles in each conservation status category based on the number of species listed by the IUCN in each category, and we expected equal numbers of articles for each research topic.

RESULTS

Taxonomic scope of Sulawesi mammalian studies

A total of 280 articles on 144 species of Sulawesi mammals were included in this study (time range: 1921–2017, complete list provided in Appendix S1). Research on Sulawesi mammals was not equally distributed among orders ($\chi^2 = 1006.12$, d.f. = 6, $P < 0.001$). Approximately 59% of the articles published on mammals of Sulawesi were focused on Primates (171 articles, number of expected articles based on number of species: 30), followed by Artiodactyla (53 articles, 10 expected articles), Rodentia (31 articless, 113 expected articles), Chiroptera (12 articles, 114 expected articles), Diprotodontia (12 articles, six expected articles), Carnivora (nine articless, five expected articles), and only two articles (11 expected articles) on Eulipotyphla.

The most-studied species was *Macaca tonkeana* (39 articles) followed by *Macaca nigra* (32 articles), *Tarsius spectrumgurskyae* (27 articles), *Babyrousa celebensis* (23 articles) and *Macaca maura* (17 articles). Conversely, we found 27 Chiroptera species, six Rodentia species and one Carnivora species with no coverage in peer-reviewed scientific publications. A total of 60 species was covered by one article only. We found species covered by one article only in all orders: Eulipotyphla (100% of total species within this order), Rodentia (35% of species), Carnivora (33% of species), Chiroptera (32% of species), Diprodontia (25% of species), Artiodactyla (22% of species), and Primates (11% of species). A list of the least-studied and the 10 most-studied mammal species in Sulawesi is provided in Appendix S2.

Research topics on Sulawesi mammals

Numbers of publications assigned to the nine research topics were not distributed randomly among taxa ($\chi^2 = 243.14$, d.f. = 8, $P < 0.001$). Most articles on Sulawesi mammals were focused on taxonomy (105 articles, 27%); the second most-studied research topic was behaviour with 90 articles (23%), followed by habitat with 42 articles (11%), population with 41 articles (11%), distribution with 30 articles (8%) and conservation with 29 articles (7%). The least studied research topics were food habits and reproduction with 21 articles each (7%) and physiology with 16 articles (4%).

Taxonomy was the most common research topic for all taxa (Fig. 2) except Primates for which studies on primate behaviour were most common (76 articles, 44%) and Carnivora for which distribution studies were equal in numbers to taxonomy studies (5 articles, 55%). Within primates, studies on populations and habitat were much more common (32 and 28 articles, respectively) than for other orders (<12 articles in each order). A similar pattern was found for other research topics.

Within the order Artiodactyla, all nine research topics were evenly represented; however, low numbers of articles were focused on distribution and food habits (five articles for each topic). Likewise, within Carnivora, studies were few but evenly distributed between topics (≤ 5 articles in each) with the exception of physiology (no articles). Within Rodentia, we found only one article each focusing on habitat and conservation (3% of articles for each topic) and five articles (16%) on population. Among primates, 76 articles (44%) were focused on behaviour, but few articles were focused on reproduction and physiology (4% of articles in each category). The two articles on Eulipotyphla were on taxonomy. The majority of articles within the Chiroptera focused on taxonomy (87% of articles). Within Diprotodontia, there were few articles (≤ 5 on each topic), and we were not able to find articles focusing on physiology and reproduction (Fig. 2).

Conservation status and research efforts

When comparing the number of publications in each Red List category, we found that these were not as expected based on the number of species ($\chi^2 = 265.91$,

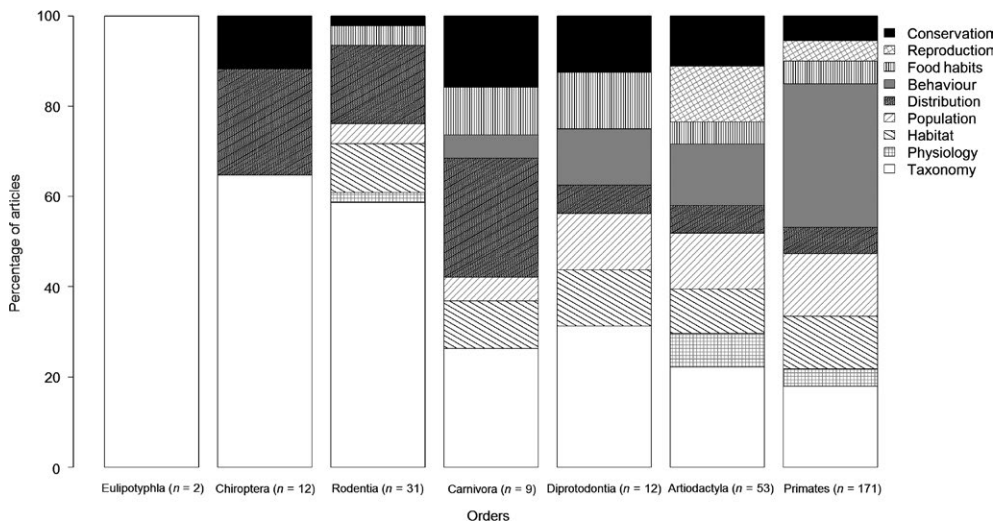

Fig. 2. Percentage of publications within the nine research topics (listed in Table 1) for each order within Mammalia in Sulawesi. From left to right, the graph shows the order and number of articles in each order, from the narrowest distribution of research to the order with the most varied distribution of research.

Table 3. Results for the Chi-squared test comparing the number of published articles with the expected number based on the number of Sulawesi mammal species in each IUCN Red List category. The table shows, for each IUCN Red List category, the total number of species, the number of published articles, and the expected number of articles

IUCN category	Number of species	Number of articles	Expected number of articles	χ^2 value
Critically Endangered	2	33	5.6	134.06
Endangered	14	65	39.2	16.98
Vulnerable	24	129	67.2	56.83
Near Threatened	8	18	22.4	0.86
Least Concern	79	122	221.2	44.49
Data Deficient	29	56	81.2	7.82
Uncategorised	14	53	39.2	4.86
Total	170			265.91***

***$P < 0.001$.

Table 4. The Sulawesi provinces, the total area of each province, the number of species found there, the number of articles, and the Chi-squared test for each of the Sulawesi provinces. For the Chi-squared test we calculated the expected number of publications based on the area of each province and the number of Sulawesi mammal species found in each province

Province	Area (km^2)	Number of species	Number of articles	χ^2_{area}	$\chi^2_{species}$
South Sulawesi	45765	105	33	1.89	0.23
Central Sulawesi	61841	127	51	0.56	4.33
Southeast Sulawesi	38140	90	15	11.36	4.45
West Sulawesi	16937	90	4	8.54	18.45
Gorontalo	12435	87	10	0.50	9.92
North Sulawesi	13846	99	61	184.22	38.03
				207.06***	75.50***

***$P < 0.001$.

d.f. = 6, $P < 0.001$). Specifically, we found that the numbers of articles on threatened and uncategorised species were higher than expected, whereas number of articles on Near Threatened, Least Concern, and Data Deficient species were lower than expected (Table 3).

Research approaches for studies on population and habitat

The majority of habitat studies were focused on habitat use (42 articles), whereas very few articles were on habitat selection (four articles), and no articles were on habitat quality. Within studies focusing on habitat selection, four articles were on second order selection and two were on third order habitat selection. In 72% of the 39 articles on population, the authors used direct methods (see Table 2); in 10%, authors used indirect methods and in 18%, both methods were used. For indirect methods, data were collected using signs such as food remains, footprints and vocalisations; within direct methods 26 articles (90% of articles) used direct counts and in only two articles camera traps were used.

Geographic bias in Sulawesi mammal research

Study sites used for research on mammals were unevenly distributed among Sulawesi provinces (similar results were obtained when calculating expected number of articles based on the size of the province $\chi^2 = 207.06$, d.f. = 5, $P < 0.001$ and on the number of species $\chi^2 = 75.50$, d.f. = 5, $P < 0.001$). Of all studies, 61 (35%) were conducted in North Sulawesi, but only four (2%) in West Sulawesi; other provinces fell between these extremes (Table 4).

The majority of studies on Sulawesi mammals was conducted outside conservation areas: 59% of studies (166 articles), of which 123 articles (74% of the articles describing research conducted outside of conservation areas) reported research conducted outside Sulawesi and its satellite islands. Considering only studies conducted within Sulawesi, we found that the majority (59%) was conducted inside conservation areas, 27% was conducted outside conservation areas and 14% was conducted in both areas. Furthermore, the distribution of studies varied substantially between the different provinces (Fig. 3).

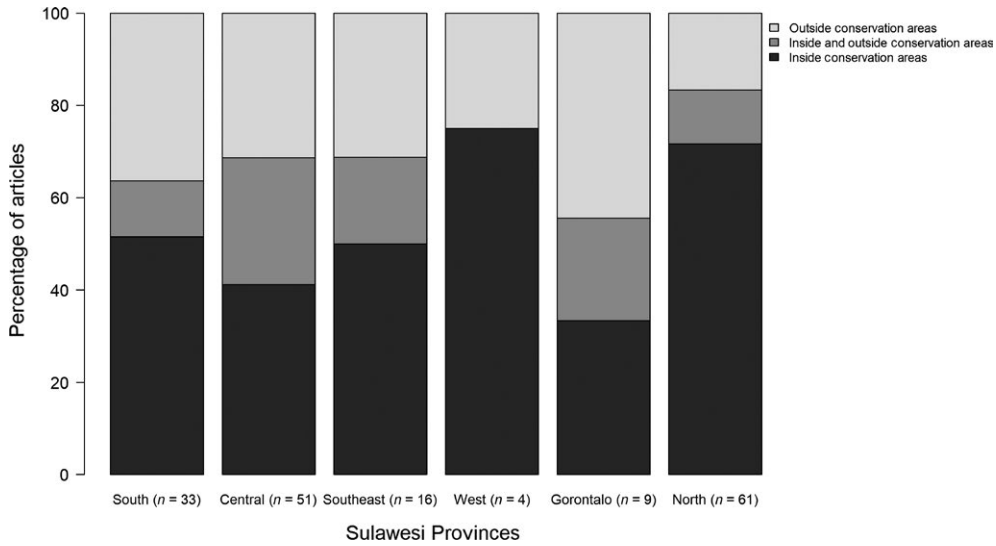

Fig. 3. Percentage of articles conducted inside conservation areas, inside and outside conservation areas, and outside conservation areas for each Sulawesi province. The majority of studies were conducted in conservation areas, except in Central Sulawesi and Gorontalo.

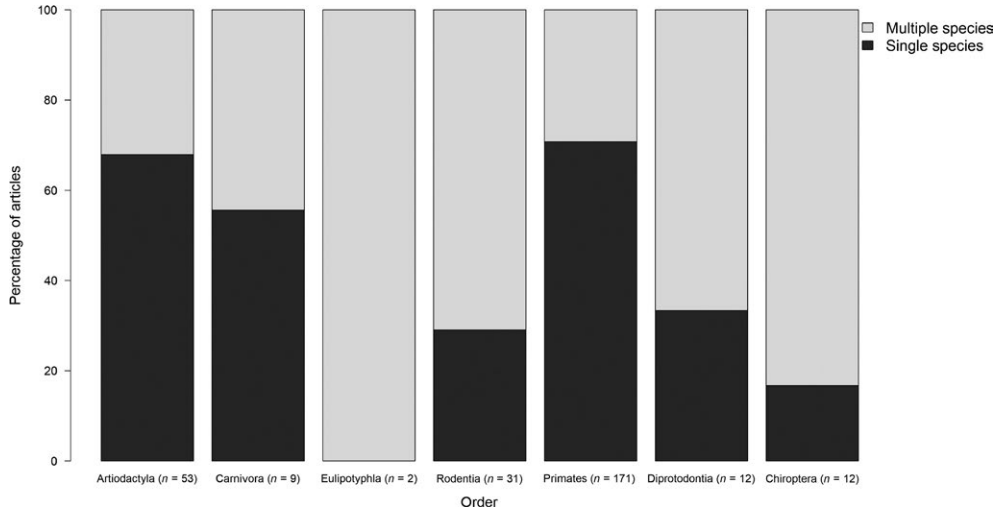

Fig. 4. Percentage of publications on single or multiple species in each order of mammals in Sulawesi. The majority of articles on Artiodactyla (68%), Carnivora (56%), and Primates (71%) were focused on single species. In contrast, all studies on Eulipotyphla were focused on multiple species. Very few articles on Chiroptera and Rodentia were conducted on single species.

Patterns in Sulawesi mammal research

The number of species included in each article varied with order. As an example, within Primates and Artiodactyla, most studies tended to focus on a single species (71% of Primates articles and 68% of Artiodactyla articles), whereas all studies on Eulipotyphla were focused on multiple species (Fig. 4).

Trajectories in the number of articles on each research topic over time are shown in Fig. 5. There was a gradual increase in articles in 1921–1960, followed by a sharp increase in 1961–2017. The strongest increases were observed for the topics taxonomy and behaviour (Fig. 5).

DISCUSSION

Through our review we were able to show clear patterns in the distribution of published articles focusing on the mammals of Sulawesi. In particular we found: 1) a taxonomic bias, with significantly fewer studies focused on Rodentia, Eulipotyphla, Chiroptera, Carnivora and Diprotodontia than

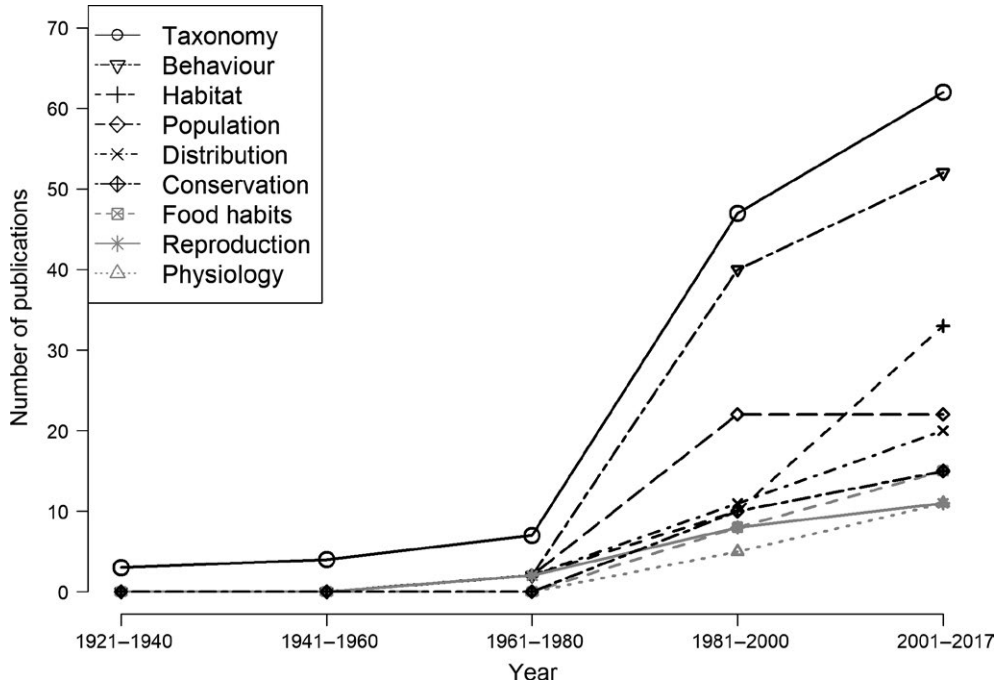

Fig. 5. Trends in research topics on Sulawesi mammal studies from 1921 to 2017. There has been a strong increase in taxonomy and behaviour studies over the last 40 years.

on other orders; 2) a geographic bias, with significantly fewer studies taking place in the provinces West Sulawesi and Gorontalo than in other provinces; 3) a bias in research topics, with most studies focused on taxonomy.

Taxonomic bias

Through our study we revealed that research on Sulawesi mammals is biased towards certain orders such as Primates (59% of studies). Taxonomic bias is a prominent problem in biodiversity studies (Bonnet et al. 2002, Griffiths & Dos Santos 2012, Donaldson et al. 2016, Fleming & Bateman 2016, Troudet et al. 2017). In line with our results, other studies show that Primates receive disproportionate attention (Trimble & van Aarde 2010), possibly because they are aesthetically appealing, charismatic, and include 'flagship' species (Smith et al. 2012). In addition, the fact that a high number of Primates species are threatened and endemic (Riley 2010, Palacios et al. 2011, Estrada et al. 2017) may make them attractive study animals.

We found that the least-studied taxa were Eulipotyphla, Chiroptera, and Carnivora. These results are in partial agreement with a recent review on Australian mammals, in which the authors found that Rodentia and Chiroptera were the least-studied taxa (Fleming & Bateman 2016). Reasons for this inequality might be that these species are less charismatic, exhibit cryptic behaviour, and are relatively difficult to study (Fleming & Bateman 2016). We also found that some species from these poorly-studied taxa are not covered in any publication or are only included in a single publication (Appendix S2). For example, *Pteropus caniceps* and *Taeromys taerae*, two endemic species classed as Vulnerable by the IUCN, are not covered by any scientific publication and are only covered in a book (Musser & Carleton 2005). The dramatic lack of knowledge for these orders may be reflected in their low percentage of threatened species (Ceballos & Brown 1995). Several species within these poorly studied taxa have restricted distributions in Sulawesi, and may thus be at risk of extinction due to habitat loss and fragmentation (Cardillo 2005).

Bias in research topics

We found that the most studied research topic in Sulawesi mammals was taxonomy. This is not surprising, because the classification of species is an indispensable condition for ecological research, and because the taxonomic status of Sulawesi mammals is still a subject of debate among scientists (Burton et al. 2005, Groves & Shekelle 2010 Shekelle et al. 2017). Furthermore, several new species of mammals have been discovered in Sulawesi during the last decade (e.g. Merker et al. 2010, Mortelliti et al. 2012, Rowe et al. 2016); this may have contributed to the bias.

Taxonomic research is propaedeutic to in-depth ecological studies (Brito 2004, Wilson 2004, Reeder et al. 2007,

Berger-Tal et al. 2011), but we found that even for Carnivora and Diprotodontia, for which the taxonomic status has been relatively clear for several years, there are few publications on ecological aspects. As an example, we found very few studies (≤5 articles) on populations, habitat, reproduction or food habits of Sulawesi marsupials, which may hamper conservation efforts on this taxa (Rondinini et al. 2011).

Research approaches for population and habitat studies

Most population studies on Sulawesi mammals were conducted using direct methods (e.g. visual census) rather than indirect methods (e.g. surveys for signs of presence) or a combination of direct and indirect methods. This result may be driven by the fact that 79% of the population studies (31 articles) were conducted on Primates, which are relatively easy to detect and thus more amenable to direct methods (Aguiar & Moro-Rios 2009). In orders other than Primates, we found the opposite (in 67% of population studies, indirect approaches only were used). This result is intuitive, because for orders other than Primates, indirect methods are appropriate (Wilson & Delahay 2001, Laing et al. 2003, Lollback et al. 2015).

We found that 79% of habitat studies were focused on habitat use, whereas habitat selection and quality were less well-studied. This is likely to be because estimating habitat selection and quality requires formal statistical testing and thus requires larger sample sizes (Kneib et al. 2009). Conservation actions based on habitat use only, however, may be misleading. Only by quantifying selection can researchers identify habitats and habitat features that maximise fitness (Pulliam 1988, Johnson 2007).

We also found that the majority of habitat studies did not incorporate scale-dependence in habitat selection (Johnson 1980). McGarigal et al. (2016) also found that the majority of wildlife habitat studies do not incorporate multi-scale frameworks. Investigating ecological processes at multiple scales is essential for revealing limiting factors and for understanding the basic ecology of species (Mayor et al. 2009, Fleming et al. 2014, Holbrook et al. 2017, McMahon et al. 2017).

Conservation status and research efforts

We found that a higher percentage of Sulawesi mammal studies were focused on threatened species (i.e. species classed as Critically Endangered, Endangered or Vulnerable by the IUCN) than on species in other categories. Our findings are similar to those of Trimble and van Aarde (2010), who conducted a review of southern African mammals and found that a higher proportion of studies was focused on threatened species. Species within these categories face the greatest risk of extinction (Mace et al. 2008), and our findings support the recommendations made by other researchers (Brooks et al. 2006, Wilson et al. 2011), that research on these species should continue to be prioritised.

However, a research bias towards threatened species, if there are many such species, as is the case in Sulawesi (Table 3), may present significant challenges (Drummond et al. 2010, Morais et al. 2013). Indeed the Red List category of a species is often decided based on scarce or insufficient biological information (Amori & Gippoliti 2001). Consequently, species that are Data Deficient may actually be more threatened than successfully evaluated species (Bland et al. 2015, Jetz & Freckleton 2015, Roberts et al. 2016). Evaluations of Data Deficient amphibians showed they were more vulnerable to extinction than their fully assessed counterparts (Morais et al. 2013, Howard & Bickford 2014).

Geographical distribution of research

We highlight a certain degree of geographic bias in Sulawesi mammal studies: a higher number of studies were conducted in North and Central Sulawesi than in other provinces. Bias in the geographic distribution of research is common in mammal studies (e.g. Stocks et al. 2008, Wilson et al. 2016). The distribution of Sulawesi mammal study sites may be driven not by province area or the number of species, but by the fact that accessibility varies substantially between provinces (North Sulawesi is the most developed), as does the location of field research stations (the Kamarora Field Station is in Central Sulawesi). The existence of long-term projects also contributes to the bias in the distribution of research sites. For instance, a project on *Macaca nigra* populations in the Tankoko Nature Reserve, North Sulawesi, has produced many publications on this species in its natural habitat (74% of articles).

The least-studied province is West Sulawesi, with only four studies (including one conducted prior to the establishment of the province). West Sulawesi is the most recently established province in Sulawesi; it was separated from South Sulawesi in 2004 (http://sulbarprov.go.id/). In this new province, there is limited financial allocation for research and for developing the research facilities (e.g. field stations, transportation) that are essential for establishing research programmes, particularly in less-studied areas (Gálvez et al. 2000).

The majority of research on Sulawesi mammals was conducted outside conservation areas. However, this was largely driven by research conducted outside Sulawesi (74% of studies outside conservation areas). Considering only studies inside Sulawesi, more studies (59%) are

conducted within conservation areas than outside conservation areas (27%), and only 14% of articles describe studies that were conducted in both areas. It seems likely that, in the future, conservation areas will play an increasingly important role in mammal research, because conservation areas may host the only remaining suitable habitats in Sulawesi (O'Brien & Kinnaird 1996, Lee et al. 2007).

KNOWLEDGE GAPS AND PRIORITIES FOR FUTURE RESEARCH

Our study clearly shows that there are extensive biases in how research has been conducted in Sulawesi. We have shown that mammalian research in Sulawesi has been focused on charismatic and threatened species (with hardly any research on Data Deficient species), that there was a bias towards taxonomic and behavioural studies, and that most of the work has been conducted in well-known provinces. Our study also highlights some methodological biases (a lack of studies focusing on habitat selection rather than use, a lack of studies focusing on habitat quality, and a lack of population studies using indirect methods and combination methods). Below we provide a prospectus of research priorities for future mammalian research in Sulawesi.

Prioritising research on understudied and threatened species

We encourage researchers to focus on endemic species and on species that are classed as threatened by the IUCN but have received relatively little attention (Appendix S2). Among Artiodactyla, we strongly encourage research on the endangered *Babyrousa togeanensis*, because this species is covered in only one article and has a limited geographical range (Malenge, Togian Islands). Among Rodentia, we found: one Critically Endangered species (*Bunomys coelestis*), which is covered in only two publications, four Endangered species (*Echiothrix leucura*, *Maxomys wattsi*, *Melomys caurinus*, and *Melomys talaudium*) and six Vulnerable species (*Echiothrix centrosa*, *Eropeplus canus*, *Haeromys minahassae*, *Hyosciurus ileile*, *Margaretamys beccarii*, *Rattus mollicomulus*) that are covered in fewer than five publications; one Vulnerable species (*Taeromys taerae*) is not mentioned in any publication. Among Chiroptera, we suggest a focus on *Pteropus caniceps* (Vulnerable, no publication), *Neopteryx frosti*, *Acerodon humilis* (Endangered, <3 articles), and *Acerodon celebensis*, *Harpyionycteris celebensis*, *Pteropus chrysoproctus* (Vulnerable, one article each). Even within the order Primates (the most-studied order in Sulawesi, accounting for 59% of articles), we found that *Macaca brunnescens*, *Macaca nigrescens*, *Macaca ochreata* (Vulnerable species) are covered in fewer than four articles each. We also discovered that two tarsier species, *Tarsius pelengensis* and *Tarsius tumpara*, have been the subject of only one article each, despite being classed as Endangered and Critically Endangered by the IUCN.

Increasing basic ecological research

Our findings reveal a lack of basic ecological data on the mammals of Sulawesi (except for several well-known Primates species which have >10 articles each). Detailed auto-ecological studies should be given priority in future research. In particular, we have shown that more research effort should be allocated to studies on the topics population, habitat, and distribution, since these topics are fundamental for defining conservation status and for identifying appropriate conservation actions (Margules & Pressey 2000, Brooks et al. 2006). Furthermore, information on these topics is needed to parameterise predictive models to forecast, for example, the effects of climate change (Clark 2007).

Adjusting research methods on population and habitat studies

Accurate assessments of populations and habitats of wildlife populations are crucial for the implementation of conservation actions (Noon et al. 2012). We were surprised to find that only two studies on mammals in Sulawesi had been conducted using camera traps. Considering that camera trapping is an extremely cost-effective method that has been applied with success in tropical environments (Tobler et al. 2008, Samejima et al. 2012, Bowler et al. 2017) and that can be used to conduct demographic studies (Ahumada et al. 2011, O'Connell et al. 2011, Rovero et al. 2014) at relatively low cost (Welbourne et al. 2015), we strongly encourage researchers to expand the use of this technique in Sulawesi. Camera trapping can be used to estimate occupancy over a large scale (a useful proxy for population abundance), while dealing with the major issue of false absences (MacKenzie et al. 2002, Mackenzie 2005).

Conducting research in less well-known areas

Future research should be targeted towards less well-known areas such as the understudied provinces of West Sulawesi, Gorontalo and Southeast Sulawesi (as well as understudied areas within the other provinces). In particular, research in West Sulawesi has provided outstanding results, such as the discovery of a new species of Rodentia (Rowe et al. 2016) and new distribution records for two endemic Rodentia

species (Achmadi et al. 2014). We emphasise that the provinces of Gorontalo and Southeast Sulawesi have been understudied (10 articles and 15 articles, respectively) and are at risk from high anthropogenic pressures due to mining and agriculture (Sau 2013, Casson et al. 2014).

ACKNOWLEDGEMENTS

We are grateful to Allison Brehm, Anna Buckardt, Malcolm Hunter, Danielle Levesque and Sarah Vogel for discussing and reviewing this paper. We are also thankful to Nancy Jennings for her comments and language editing. BB's graduate research assistantship was funded by the United States Agency for International Development's Prestasi scholarship program, whereas AM's work was supported by the USDA National Institute of Food and Agriculture McIntire-Stennis projects (numbers ME041620 and ME041913) through the Maine Agriculture & Forest Experiment Station.

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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. List of the articles included in this review.

Appendix S2. List of the least-studied and the 10 most-studied species in Sulawesi, Indonesia.