

Playing favourites - a review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies

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Abstract. Home range and habitat selection are key subjects when studying animal ecology. Defining the space use and resource management of an animal establishes a solid basis for further behavioural and ecological research, as well as conservation management. Studies focusing on determining home range and habitat selection often include further questions regarding for example conservation, animal movement, population dynamics, and inter- or intraspecific interactions. It is therefore unsurprising that home range and habitat selection have been the focus of numerous studies on different vertebrate taxa over the years. We have reviewed 903 publications, on all extant vertebrate clades focusing on these topics from 1980 to the first quarter of 2018. We have observed that allocation of vertebrate orders are independent of species richness, relatedness, and portion of threatened species within the order. We have highlighted the relation between publication numbers and species richness and offer ideas for future research in proposing possible causes for the observed allocation and in highlighting understudied clades. Furthermore, we have observed that topics often studied in concordance with home range and habitat selection are conservation and human influence, intraspecific differences, and home range shifts/exploratory behaviour. Meanwhile, topics like population density, reproductive behaviour, territoriality/aggressive behaviour, and interspecific interactions seem to be less studied. This review highlights and discusses the current distribution of focal points in studies concerning home range and habitat use while identifying less studied fields and taxa - thereby emphasizing potential opportunities for further research.

Key words: Home range, habitat selection, vertebrate, behavioural ecology, study subject preference, topic preference.

Introduction

The concept of home range was first introduced by Burt in 1943. Burt defined the home range as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young”. He further emphasized that “Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range.” Since then, the definition might have been deemed too imprecise by some, but the core ideas of the definition have never been seriously challenged or altered (Boitani & Fuller 2000). The reasons for animals to have home ranges can be numerous. For example, familiarity increases safety, as escape paths and hideouts become known to the point of automatism (Stamps 1995). In addition, as the location of necessary resources becomes known, staying in the vicinity guarantees the availability of resources, while migrating into new, previously unknown territory lacks this reliability (Boitani & Fuller 2000). There are a multitude of other reasons for animals to establish home ranges, but in the end they all come down to one general reason: the benefits of establishing a home range exceed the associated costs, i.e. remembering the layout and potentially defending the resources. The study of home range is therefore closely associated with the study of habitat selection, as animals’ home ranges reflect their ecological requirements.

The study of home range and habitat selection can reveal important information needed to understand animal space requirements. Since the home range of an animal includes everything it requires to survive on a day-to-day basis, investigating the size of the home range and what habitats and microhabitats it contains gives researchers a solid base for assessing animal ecology. From here, numerous more detailed approaches can be executed. Home range overlap and density can for instance be used to infer population sizes (e.g. Benson et al. 2006, Green et al. 2000) while habitat

structure can be used to study resource requirement (e.g. Murphy & Dowding 1995), identify critical areas (e.g. Ingram and Rogan 2002, Waldron et al. 2006), or quantify effects of anthropogenic influences (e.g. Fahrig & Rytwinski 2009, de Maynadier and Hunter Jr 2000). Even though it is by far not the only way to study a species ecology, it provides a first look on species behaviour and ecology and is an essential requirement for creating a complete image of a species’ ecology.

This review provides a general overview on studied vertebrate clades and the topics included in publications that combined home range analysis and habitat selection. We further give an overview of the amount of attention each order of vertebrates has received since 1980, as well as the foci highlighted in said publications. We expect the amount of attention attributed to the various groups and topics to be very variable, and independent of species richness, relatedness of the orders, and number of threatened species within orders. This review aims to give first insights on the focal points of home range and habitat selection studies and to give a starting point to identify opportunities for new research.

Methods

For every large vertebrate class, a search on Web of Science (Clarivate Analytics 2018) was conducted using the parameters shown in Table 1. The classes were: Non-tetrapod vertebrates (in the following called fish), amphibians, non-avian diapsids (in the following called reptiles), birds and mammals. All searches were conducted in the Web of Science Core Collection within the entire time range from 1980 to the first quarter of 2018.

The abstract of each search result was considered and searched for specific foci (Table 2) in order to later distinguish different home range related topics of research. For studies to be considered in this review, they had to (1) calculate some form of home range and (2) study habitat use or quality meaning to quantify the use or avoidance of biotic and/or abiotic environmental conditions, de-

Table 1. Search terms, refining Web of Science categories and access date of every Web of Science search conducted.

Taxonomic group	Search terms	Web of Science categories	Date accessed
Fish	TOPIC: ("home range*" OR "home-range*") AND TOPIC: ("habitat use" OR "habitat selection") AND TOPIC: (fish)	Marine Freshwater Biology OR Limnology OR Fisheries OR Biodiversity Conservation OR Biology OR Ecology OR Multidisciplinary Sciences OR Oceanography OR Zoology OR Environmental Sciences OR Behavioral Sciences	27.02.2018
Amphibians	TOPIC: (home range* OR home-range*) AND TOPIC: (habitat use OR habitat selection) AND TOPIC: (amphibia* OR anura* OR caudata OR gymnophiona OR frog* OR salamander* OR newt* OR caecilian* OR toad*)		13.03.2018
Reptiles	TOPIC: (home range* OR home-range*) AND TOPIC: (habitat use OR habitat selection) AND TOPIC: (reptile* OR testudines OR sphenodontida OR squamata OR crocodylia OR tortoise* OR turtle* OR tuatara* OR lizard* OR snake* OR crocodile* OR alligator*)	Zoology OR Ecology OR Evolutionary Biology OR Environmental Studies OR Biodiversity Conservation OR Marine Freshwater Biology OR Limnology OR Environmental Sciences OR Biology OR Oceanography OR Forestry OR Multidisciplinary Sciences OR Behavioral Sciences OR Fisheries	19.03.2018
Birds	TOPIC: (home range* OR home-range*) AND TOPIC: (habitat use OR habitat selection) AND TOPIC: (bird* OR aves)	Ecology OR Marine Freshwater Biology OR Veterinary Sciences OR Ornithology OR Oceanography OR Zoology OR Biodiversity Conservation OR Agriculture OR Multidisciplinary OR Environmental Sciences OR Environmental Studies OR Behavioral Sciences OR Evolutionary Biology OR Multidisciplinary Sciences OR Urban Studies OR Biology OR Agriculture Dairy Animal Science OR Forestry	27.03.2018
Mammals	TOPIC: (home range* OR home-range*) AND TOPIC: (habitat use OR habitat selection) AND TOPIC: (mammalia OR mammal*)	Ecology OR Marine Freshwater Biology OR Zoology OR Oceanography OR Biodiversity Conservation OR Agriculture OR Multidisciplinary OR Environmental Sciences OR Environmental Studies OR Multidisciplinary Sciences OR Urban Studies OR Biology OR Behavioral Sciences OR Forestry OR Evolutionary Biology	05.04.2018

Table 2. Evaluation topics looked for in the search results, with explanation.

Topic	Explanation
Habitat use/Quality	The study quantifies the use or avoidance of biotic and/or abiotic environmental conditions, describes the influence of environmental conditions on home range, or evaluates the quality of the environment.
Conservation/Human influence	The study explicitly examines anthropomorphic effects on populations or tests the effectiveness of conservation measures.
Population density	The study measures population density or studies the effects of population density on home ranges.
Reproductive behaviour	The study examines behaviour associated with reproduction such as courting behaviour, mating behaviour, breeding behaviour or raising young.
Territoriality/Aggression	The study examines the effects of territoriality and aggression between individuals.
Hr shifts and temporary leaving of the home range	The study describes shifts in home range, excursions outside the home range, or migratory/sedentary behaviour
Intraspecific differences	The study aims to identify differences between individuals of the same species (e.g. difference between sexes, ontogenetic stages or populations).
Interspecific interactions	The study describes interactions between different species
Review	The study is a review

scribing the influence of environmental conditions on home range, or evaluating the quality of the environment. (as described in Table 2). In the case where the abstract was hinting at a topic but was inconclusive about its inclusion, the main text was analysed. Similarly, whenever it was not apparent from the abstract whether home range had been calculated, the study was scanned for the terms "home range", "home-range", "range", "polygon", and "kernel" in order to

find passages that might describe the home range estimation. "Polygon" and "kernel" were included because minimum convex polygon and kernel density estimation are the most common methods to calculate home range. Search results that did not meet these requirements or did not include the required taxonomic groups were excluded. We recorded overall publications per class and per year as well as counting the number of publications treating a certain focus.

Within each class (fish, amphibians, reptiles, birds, mammals), study subjects were classified into orders. The classification system was chosen according to the ITIS global Catalogue of Life database in order to have one single reference for species numbers (Roskov et al. 2019, Ruggiero et al. 2015). We are aware, that the taxonomic classification used in the data base is controversial but having one single reference for systematics and species numbers brings considerable advantages. For one, combining multiple systematics from different sources is likely to result in counting species multiple times and towards different orders. Furthermore, phylogeny of many clades is unclear and combining them sensibly into a complete vertebrate tree of life would be worthy of an entirely separate review. Lastly, the Catalogue of Life is a publicly accessible data base allowing everyone to quickly assess the order each species is allocated to in this review. Squamates were divided into snakes and lizards and studied separately due to the traditional separation and different ecology. For the same reasons, the Cetartiodactyla were also divided into Cetacea and Artiodactyla. Using the online species databases (Froese & Pauly 2000, Roskov et al. 2019, Uetz P. & Hosek J. 2019), the number of different species in each order was acquired. Then, for each order, two proportions were calculated: The proportion of studies concerning the respective order within the search results of the corresponding class (proportion of publications) and the proportion of species within the class that belong to that order (proportion of species). In the following, these expressions will describe the proportions within the class. Fisher's exact test with a Monte Carlo simulation with 2000 repetitions was used to test whether the distribution of species and publications within orders are the same. The test was limited to orders that had publications allocated to them to avoid having a lot of entries with zero publications and non-zero species numbers. For Amphibia, where only 2 orders were studied, the Monte Carlo simulation was cut since it did not apply to a 2x2 table. Since Fisher's exact test requires mutually exclusive data in every entry to be applicable, we technically cannot apply it to a data set which included publications considering multiple orders. However, the number of publications considering multiple orders was relatively small (22 publications). Therefore, the test was calculated two times: once treating publications considering x orders as x separate publications and once excluding said publications. If both distributions prove to be significantly different from the distribution of species, we assume that the difference, the publications considering multiple orders make is negligible.

A phylogenetic tree was manually build using TreeGraph 2 (Stöver & Müller 2010) after (Betancur-R. et al. 2013, Froese & Pauly 2000, Lapointe & Kirsch 2001, Nelson et al. 2016, Prum et al. 2015, Tarver et al. 2016). Using R (R Core Team 2020) and the R packages: picante (Kembel et al. 2010), ape (Paradis & Schliep 2019), adephylo (Jombart & Dray 2010), ade4 (Bougeard & Dray 2018, Chessel et al. 2004, Dray & Dufour 2007, Dray et al. 2007), phylobase (R Hackathon et al. 2020), Geiger (Pennell et al. 2014), and phytools (Revell 2012), proportion of publications was mapped onto the tree as a continuous variable with the function contMap from the phytools package. Blomberg's K (Blomberg et al. 2003) was calculated to estimate phylogenetic signals with proportion of publications treated as potential signal in order to assess whether closely related orders have received similar attention.

In order to assess whether the portion of threatened species within an order dictates the attention an order was given, data from the IUCN red list of species website was requested (IUCN, 2020). After adapting the phylogeny to the phylogeny used with the rest of the data, the portion of species listed as vulnerable or above within an order were determined. We compared the portion of vulnerable or above species with the portion of publications across all publications (not just within a class) using Fisher's exact test once more in order to determine whether the allocation of attention was similar to the distribution of at risk species.

Finally, orders without any publications were listed as well.

In order to assess which species received the most attention, species with five or more publications were highlighted and discussed

separately. We chose 5 as a cut-off as it constitutes 20 species (approx. 2.5% of all species studied) and the amount is still reasonable to discuss within the page limits of this contribution.

Results

Distribution of Publications within Classes and over Time

In total, the Web of Science searches yielded 1599 results. There were 289 studies found for fish, 85 for amphibians, 337 for reptiles, 474 for birds, and 414 for mammals. Out of all of these, the number of suitable studies was 139 for fish, 39 for amphibians, 207 for reptiles, 300 for birds and 218 for mammals, effectively resulting in 903 relevant publications that studied home range and habitat selection. The full list of considered publications as well as suitable publications is available in the supplementary material under AppendixA_Publications.xls. The proportions of relevant studies are represented in Fig. 1A.

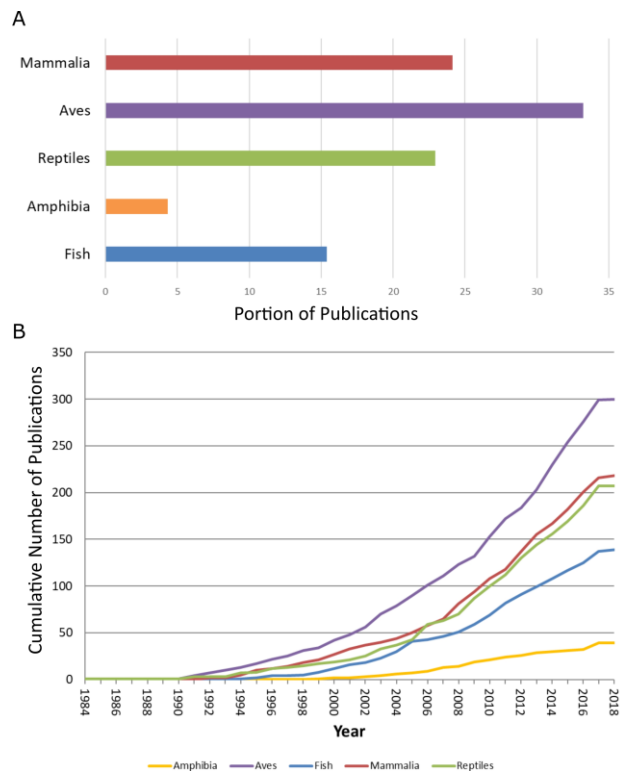


Figure 1. Allocation of suitable papers (A) towards the five major taxonomic groups and (B) over time towards the five taxonomic groups.

As Fig. 1B shows, searches yielded almost no results in the time period from 1980 to the early 90s. The earliest publications in the results were from 1992 for fish, 1994 for amphibians, 1990 for birds and 1993 for mammals. For reptiles, a single paper from 1984 was found, but after that, the next oldest paper was from 1991. Publications per year tended to fluctuate but overall, the number of studies for all taxonomic groups increases over the course of the years as can be seen in Fig. 1B.

Allocation of Orders within Classes

Studied Orders. All comparisons using Fisher's exact test were

significantly different with p -values of $p < 0.001$ for every pair of distributions except for the Amphibia pairs. For Amphibia, in both cases the distributions were also significantly different from each other ($p < 0.001$ for the test including publications considering multiple orders and $p = 0.01581$ for the test excluding publications considering multiple orders). This means that the observed differences between the distribution of studies and species within classes are significant and cannot be explained solely by chance.

Figure 2 shows the proportion of publications divided by the portion of species for each order in graph and number as well as the actual proportions. Absolute numbers of species and publications can be found in the Appendix under AppendixA_Publications.xls. In most orders, proportion of publications is higher than proportion of species. In Lepisosteiformes and Esociformes, proportion of publications is over a hundred times higher than proportion of species. In Lepidosireniformes, Acipenseriformes, Hexanchiformes, Lamniformes, Salmoniformes, Microbiotheria, Proboscidea, Sirenia, Testudines, Crocodylia, Orectolobiformes, Otidiformes, Squatiniformes, and Rhinoprismiformes, proportion of publications is over 10 times higher than proportion of species. Meanwhile, proportion of publications is ten times smaller than proportion of species only in Apodiformes and Chiroptera. The proportion of species is only roughly equal to the proportion of publications in snakes. In Caprimulgiformes and Pelecaniformes, proportions are also very similar with factors of 0.95 and 0.94 respectively.

Figure 3 shows the proportional allocation of publications per class over the vertebrate tree of life for orders with at least one publication. The tree is not to be seen as a representative vertebrate tree of life as it is built around the orders used by the ITIS tree of life data base (Roskov et al. 2019; Ruggiero et al. 2015) and some of those orders are controversial. Orders that are used in this review but are not up to date to the used phylogenies are therefore placed where the majority of the species allocated to them would be now. The tree only contains orders represented by at least one publication in the sample. Calculating a Blomberg's K (999 randomizations) with proportion of species as signal reveals that the distribution does not represent a phylogenetic signal ($K = 0.055727$, $p = 0.226226$). Therefore, there is no evidence that suggests that closely related orders receive similar attention.

Table 3 shows the portion of publications and the number of species classified as vulnerable or above by the IUCN red list within each order. The fisher's exact test comparing those distributions states, that the distributions are significantly different from one another ($p < 0.001$) meaning the observed allocation of attention is unrelated to the number of threatened species within an order.

Unstudied Orders. Table 4 contains the unstudied orders as well as their species richness within their respective class. In fish, 39 out of 64 orders containing 15.72% of fish diversity had not been studied. Out of the three amphibian orders, the Gymnophiona containing 2.70% of amphibian diversity had not been studied. In reptiles, only the Rhynchocephalia had not been studied. This order contains only the Tuatara and therefore only contains 0.01% of reptilian diversity. In birds, 17 out of 40 orders containing 1.44% of avian diversity had not been studied and in mammals, 10 out of 29 orders con-

taining 8.77% of mammalian diversity had not been studied. Most unstudied orders were fairly species-poor, containing less than 1% of species diversity (Table 4) within the class but some contained more than 1% of the species richness of their corresponding class. These orders were Atheriniiformes, Clupeiformes, Lophiiformes, Ophidiiformes, Stomiiformes, and Tetradontiformes in fish, the Gymnophiona in Amphibians, and Soricomorpha in mammals.

Most studied species

Table 5 shows the species with 5 or more publications. Most common among the list of species are Testudines and Carnivora. Turtles seem to have a special focus on sea turtles with the green sea turtle (*Chelonia mydas*), hawksbill sea turtle (*Eretmochelys imbricata*), and the loggerhead sea turtle (*Caretta caretta*) holding three of the top 4 most spots in the list. Additionally, two freshwater turtles (*Clemmys guttata* and *Emydoidea blandingii*) and one tortoise (*Testudo hermanni*) are represented. Carnivorans have as many representations as Testudines but the species have lower individual publications. The coyote (*Canis latrans*) has the third most publications out of all animals. Artiodactyla are represented by two species of cervids: the red deer (*Cervus elaphus*) and the white-tailed deer (*Odocoileus virginianus*). In birds, the golden eagle (*Aquila chrysaetos*), the Northern bobwhite (*Colinus virginianus*), and the little bustard (*Tetrax tetrax*) all have 5 publications allocated to them. Rodents are represented by the wood mouse (*Apodemus sylvaticus*) while non-turtle reptiles are the Mississippi alligator (*Alligator mississippiensis*) and the Eastern hognose snake (*Heterodon platirhinos*). No amphibians or fish species have more than 5 publications allocated to them. Fish species with the most publications were largemouth bass (*Micropterus salmoides*), Atlantic salmon (*Salmo salar*), and Lake trout (*Salvelinus namaycush*) with 4 publications each while the European green toad (*Bufo viridis*) and the wood frog (*Lithobates sylvaticus*) were the amphibians with the most publications with 3 each.

Allocation of foci

Figure 4 shows that, in general, conservation and human influence, home range shifts/home range exiting behaviour, and intraspecific differences were the most studied topics while there seemed to be far less studies on population density, reproductive behaviour, territoriality and aggression, or interspecific interactions. A full citation report including an overview which publications were allocated to which topics is found in the appendix under AppendixA_Publications.xls.

Within all classes, at least 10% of publications addressed the issue of conservation and human influence with studies concerning reptiles and birds staying close to 10% while studies concerning fish and mammals neared 20%, and studies concerning amphibians crossed the 20% mark. Population density was generally rarely studied in relation to home range and habitat selection, with birds and mammals being between 5% and 10% while in reptiles and fish, proportion of studies stayed under 5% and no studies were found for amphibians. Reproductive behaviour was studied in around 5% of publications for all classes. Territoriality and aggression were studied similarly as often as population density, while in reptiles, it was studied a little more frequently than population density and there were no cases of it being stud-

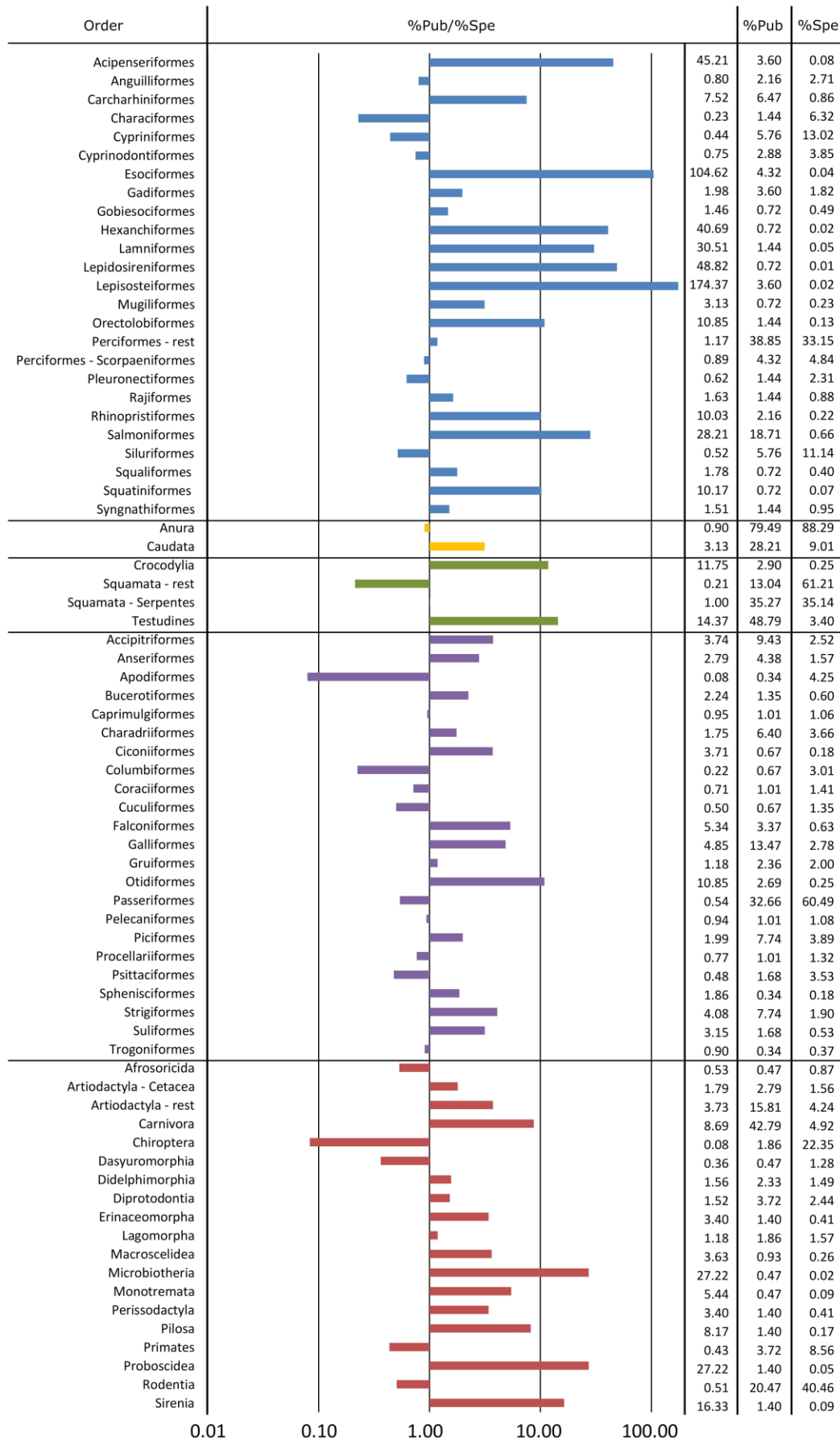


Figure 2. Proportion of publications (%Pub) and proportion of species (%Spe) for all orders containing publications and ratio between them. Orders within classes arranged alphabetically.

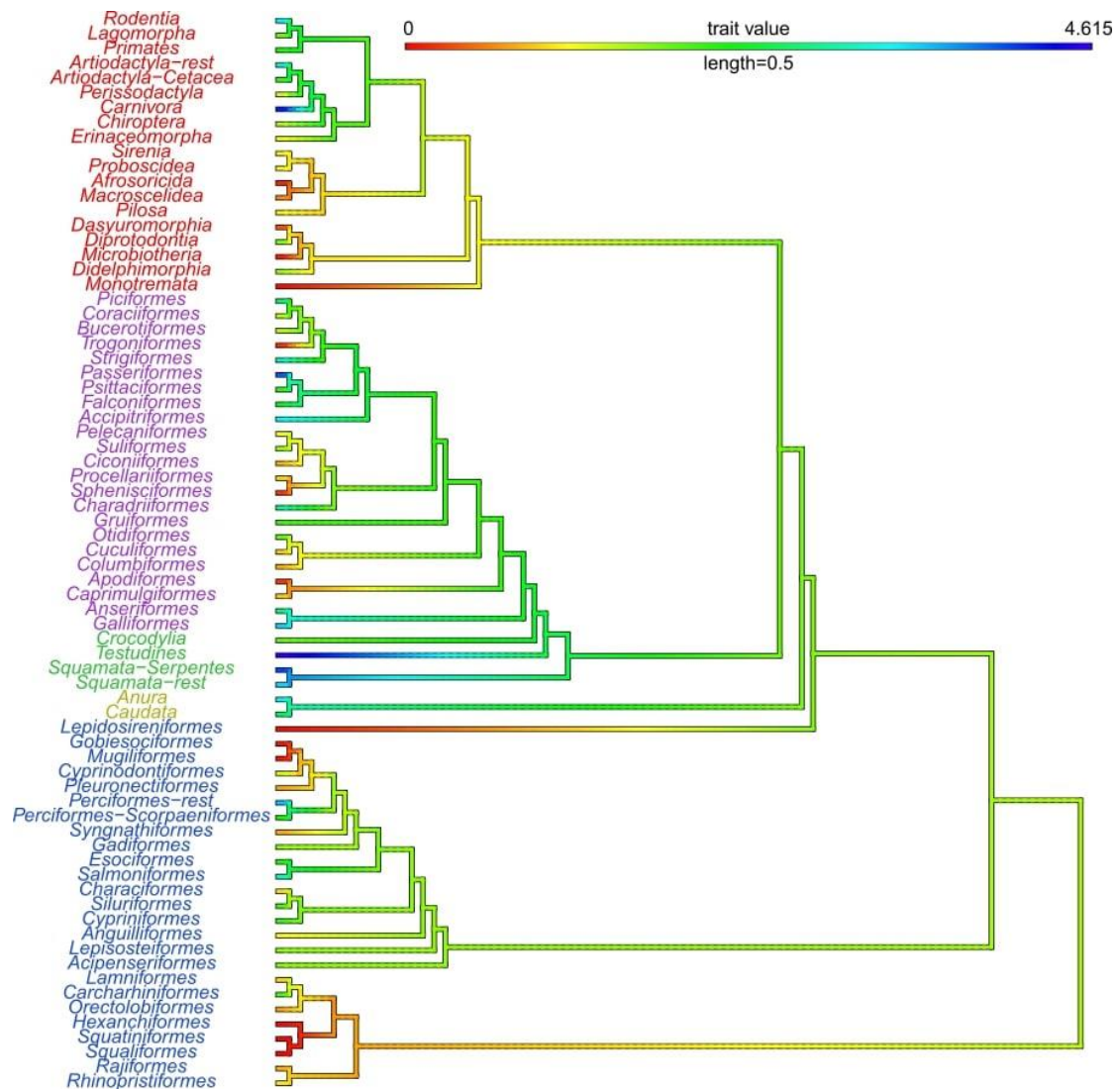


Figure 3. Taxonomic tree of vertebrates showing the Log_{10} (number of publications) mapped as continuous character via the function `contMap` of the `phytools` package. Outdated orders are placed where most representatives of that order are placed today.

ied in amphibians. Home range shifts and exploratory behaviour were highly studied in fish, amphibians and reptiles and not so much in birds and mammals. Intraspecific differences were studied in roughly a third of cases in reptiles, with almost 40% of all studies discussing the topic in some way. In mammals, a little over a quarter of all studies included intraspecific differences. In the remaining clades, around 10%-16% of studies covered the topic. Interspecific interactions were generally not studied much but they were more present in studies about amphibians and mammals. Reviews on the topic remain rare with only three reviews for birds, fish, and mammals respectively, and one for amphibians.

Discussion

Distribution of Publications over Time

The apparent absence of publications before 1990 in the search results is very unlikely to be linked to an absence of interest in home range studies before that time period as ev-

idenced by numerous publications in the field (Cederlund & Okarma 1988, Erikstad 1985, Ernest & Mares 1986, Litvaitis et al. 1986). However, the publication of Worton's kernel density estimation method to calculate home range based on utilization distribution in 1989 immediately precedes the first search results in the web of science search (Worton 1989). As this method not only calculates the area the animal moves in, but also the intensity of utilization within the area (Worton 1989), it is better suited to combine with the study of habitat selection. As searches were conducted for studies encompassing both home range and habitat selection, this could be a reason for the observed bias towards later years. Additionally, although no conscious effort had been made to search for newer studies, searching terms could have somehow favoured newer studies.

The rising numbers of publications in the field of home range assessment and habitat selection is not surprising and follows a much more general trend in the scientific community: Scientific publications generally increased over the course of the last decades (Bjork et al. 2009, Bornmann & Mutz 2015) due to the digitalization and globalization of sci-

Table 3. Portion of publications out of all publications (PoP) and portion of species classified as vulnerable or above (Voa) by the IUCN red list within each order.

Order	PoP	Voa	Order	PoP	Voa	Order	PoP	Voa	Order	PoP	Voa
Accipitriformes	9.43	21.71	Columbiformes	0.67	19.51	Microbiotheria	0.47	0.00	Psittaciformes	1.68	28.16
Acipenseriformes	3.60	85.19	Coraciiformes	1.01	11.17	Monotremata	0.47	60.00	Pteroclidiformes	0.00	0.00
Afrosoricida	0.47	30.91	Crocodylia	2.90	47.83	Mugiliformes	0.72	2.04	Rajiformes	1.44	11.54
Albuliformes	0.00	10.00	Cuculiformes	0.67	7.28	Musophagiformes	0.00	8.33	Rheiformes	0.00	0.00
Amiiformes	0.00	0.00	Cypriniformes	5.76	26.23	Myctophiformes	0.00	0.00	Rhinopristiformes	2.16	50.85
Anguilliformes	2.16	1.41	Cyprinodontiformes	2.88	40.15	Myliobatiformes	0.00	34.21	Rhynchocephalia	0.00	0.00
Anseriformes	4.38	17.61	Dasyuromorphia	0.47	13.70	Myxiniformes	0.00	11.84	Rodentia	20.47	14.10
Anura	79.49	31.15	Dermoptera	0.00	0.00	Notacanthiformes	0.00	0.00	Saccopharyngiformes	0.00	0.00
Apodiformes	0.34	9.83	Didelphimorphia	2.33	8.70	Notoryctemorphia	0.00	0.00	Salmoniformes	18.71	48.03
Apterygiformes	0.00	80.00	Diprotodontia	3.72	35.37	Ophidiiformes	0.00	2.04	Scandentia	0.00	8.70
Artiodactyla	15.81	41.63	Elopiformes	0.00	11.11	Opisthocomiformes	0.00	0.00	Scorpaeniformes	4.32	2.78
Ateleopodiformes	0.00	0.00	Erinaceomorpha	1.40	12.50	Orectolobiformes	1.44	17.07	Siluriformes	5.76	15.37
Atheriniformes	0.00	38.81	Esociformes	4.32	11.11	Osmeriformes	0.00	30.77	Sirenia	1.40	80.00
Aulopiformes	0.00	0.00	Euryptygiformes	0.00	50.00	Osteoglossiformes	0.00	10.78	Soricomorpha	0.00	15.78
Batrachoidiformes	0.00	19.15	Falconiformes	3.37	11.86	Otidiformes	2.69	30.77	Sphenisciformes	0.34	55.56
Beloniformes	0.00	12.10	Gadiformes	3.60	2.60	Passeriformes	32.66	10.29	Squaliformes	0.72	78.21
Beryciformes	0.00	1.42	Galliformes	13.47	25.40	Paucituberculata	0.00	42.86	Squamata (Lizards)	13.04	18.93
Bucerotiformes	1.35	32.88	Gasterosteiformes	0.00	14.81	Pelecaniformes	1.01	15.52	Squamata (Serpentes)	35.27	11.78
Caprimulgiformes	1.01	7.50	Gaviiformes	0.00	0.00	Peramelemorphia	0.00	40.91	Squatiniformes	0.72	50.00
Carcharhiniformes	6.47	16.18	Gobiiformes	0.72	12.12	Perciformes	38.85	10.18	Stephanoberyciformes	0.00	0.00
Cariamiformes	0.00	0.00	Gonorynchiformes	0.00	14.71	Percopsiformes	0.00	11.11	Stomiiformes	0.00	0.00
Carnivora	42.79	26.35	Gruiformes	2.36	25.91	Perissodactyla	1.40	75.00	Strigiformes	7.74	56.79
Casuariiformes	0.00	0.00	Gymnophiona	0.00	8.20	Petromyzontiformes	0.00	21.62	Struthioniformes	0.00	50.00
Caudata	28.21	51.90	Gymnotiformes	0.00	10.34	Phaethontiformes	0.00	0.00	Suliformes	1.68	27.78
Ceratodontiformes	0.00	100.00	Heterodontiformes	0.00	0.00	Phoenicopteriformes	0.00	16.67	Synbranchiformes	0.00	14.94
Cetacea	2.79	22.22	Hexanchiformes	0.72	0.00	Pholidota	0.00	88.89	Syngnathiformes	1.44	5.96
Cetomimiformes	0.00	0.00	Hyracoidea	0.00	0.00	Piciformes	7.74	7.02	Testudines	48.79	53.81
Characiformes	1.44	10.16	Lagomorpha	1.86	25.00	Pilosa	1.40	30.00	Tetraodontiformes	0.00	4.83
Charadriiformes	6.40	13.28	Lamniformes	1.44	66.67	Pleuronectiformes	1.44	0.93	Tinamiformes	0.00	14.89
Chimaeriformes	0.00	2.13	Lampriformes	0.00	0.00	Podicipediformes	0.00	21.74	Torpediniformes	0.00	45.00
Chiroptera	1.86	15.00	Lepidosireniformes	0.72	0.00	Polymixiiformes	0.00	0.00	Trogoniformes	0.34	2.33
Ciconiiformes	0.67	30.00	Lepisosteiformes	3.60	0.00	Polypteriformes	0.00	0.00	Tubulidentata	0.00	0.00
Cingulata	0.00	10.00	Leptosomiformes	0.00	0.00	Primates	3.72	60.77	Zeiformes	0.00	0.00
Clupeiformes	0.00	6.85	Lophiiformes	0.00	2.06	Pristiophoriformes	0.00	0.00			
Coelacanthiformes	0.00	100.00	Macroscelidea	0.93	10.53	Proboscidea	1.40	100.00			
Coliiformes	0.00	0.00	Mesitornithiformes	0.00	100.00	Procellariiformes	1.01	46.26			

ence. It is easier than ever to access publications from all over the world and to make one's own publications accessible (Bornmann & Mutz 2015). Furthermore, the international competition prompts researchers to publish at higher frequencies (Fire & Guestrin 2019). In future studies, it would be interesting to see whether home range and habitat studies have increased at a different pace than other fields and which factors affect the growth rate of a scientific field. One example of such a factor are advances in technology like telemetry and satellite data, which allow for the acquisition of large data sets with comparatively little effort (Cochran, 1980).

Allocation of Publications within Classes and Orders

The series of Fisher's exact tests suggest that the allocation of publications across orders within a class is significantly different from the distribution of species richness or portion of threatened species. This indicates, that neither the number of species, nor the portion of threatened species is a deciding factor in determining interest in an order. As the calculation of Blomberg's K over the vertebrate tree reveals, closely re-

lated orders also do not receive similar levels of attention. We can therefore conclude that researchers neither concentrate nor avoid particular clusters of closely related orders. This however does not mean it could not be a deciding factor on other phylogenetic levels. There could be a relation between number of studies and relatedness within certain orders on family level. To test this, one would need a much larger sample size so it could be properly resolved on family level or be done in a more focused study.

Considering species richness, one thing has to be kept in mind when doing the calculations this way: orders having exceptionally high or low species richness can show a more extreme relationship between proportion of species and proportion of publications. The large number of species within orders like Cypriniformes, lizards, and Chiroptera (Froese & Pauly 2000, Roskov et al. 2019, Uetz & Hosek 2019) renders achieving equilibrium between publications and species numbers very hard to achieve. To do so would mean, many less species rich clades would have to be ignored or studied very scarcely. This would lead to an overall worse representation of vertebrate biodiversity in the publication

Table 4. Orders without any recorded publication including proportion of species richness (in %) within the class.

Order	Species Richness	Order	Species Richness	Order	Species Richness
Albuliformes	0.04	Polypteriformes	0.04	Gaviiformes	0.05
Amiiformes	0.00	Saccopharyngiformes	0.08	Leptosomiformes	0.01
Ateleopodiformes	0.04	Stephanoberyciformes	0.21	Mesitornithiformes	0.03
Atheriniformes	1.05	Stomiiformes	1.22	Musophagiformes	0.22
Aulopiformes	0.78	Synbranchiformes	0.35	Opisthocomiformes	0.01
Batrachoidiformes	0.24	Tetraodontiformes	1.29	Phaethontiformes	0.03
Beloniformes	0.80	Zeiformes	0.10	Phoenicopteriformes	0.06
Beryciformes	0.48	Petromyzontiformes	0.14	Podicipediformes	0.22
Cetomimiformes	0.10	Heterodontiformes	0.03	Pteroclidiformes	0.15
Clupeiformes	1.16	Myliobatiformes	0.72	Rheiformes	0.02
Elopiformes	0.03	Pristiophoriformes	0.02	Struthioniformes	0.02
Gasterosteiformes	0.09	Torpediniformes	0.21	Tinamiformes	0.45
Gonorynchiformes	0.11	Chimaeriformes	0.17	Cingulata	0.36
Gymnotiformes	0.69	Myxiniformes	0.24	Dermoptera	0.03
Lampriformes	0.07	Ceratodontiformes	0.00	Hyracoidea	0.07
Lophiiformes	1.06	Coelacanthiformes	0.01	Pholidota	0.14
Myctophiformes	0.75	Gymnophiona	2.70	Scandentia	0.34
Notacanthiformes	0.08	Rhynchocephalia	0.01	Soricomorpha	7.31
Ophidiiformes	1.57	Apterygiformes	0.05	Tubulidentata	0.02
Osmeriformes	0.96	Cariamiformes	0.02	Notoryctemorphia	0.03
Osteoglossiformes	0.75	Casuariiformes	0.04	Paucituberculata	0.10
Percopsiformes	0.03	Coliiformes	0.06	Peramelemorphia	0.36
Polymixiiformes	0.03	Eurypygiformes	0.02		

Table 5. List of most all species with more than 4 publications allocated to them in the data set used for this study.

Class	Order	Species	Publications
Reptilia	Testudines	<i>Chelonia mydas</i>	14
Reptilia	Testudines	<i>Eretmochelys imbricata</i>	13
Mammalia	Carnivora	<i>Canis latrans</i>	11
Reptilia	Testudines	<i>Caretta caretta</i>	9
Mammalia	Carnivora	<i>Vulpes vulpes</i>	8
Reptilia	Testudines	<i>Clemmys guttata</i>	7
Mammalia	Artiodactyla	<i>Cervus elaphus</i>	6
Mammalia	Carnivora	<i>Felis catus</i>	6
Mammalia	Carnivora	<i>Lynx rufus</i>	6
Mammalia	Carnivora	<i>Ursus americanus</i>	6
Aves	Accipitriformes	<i>Aquila chrysaetos</i>	5
Aves	Calliformes	<i>Colinus virginianus</i>	5
Aves	Otidiformes	<i>Tetrax tetrax</i>	5
Mammalia	Rodentia	<i>Apodemus sylvaticus</i>	5
Mammalia	Carnivora	<i>Martes americana</i>	5
Mammalia	Artiodactyla - rest	<i>Odocoileus virginianus</i>	5
Reptilia	Crocodylia	<i>Alligator mississippiensis</i>	5
Reptilia	Testudines	<i>Emydoidea blandingii</i>	5
Reptilia	Squamata - Serpentes	<i>Heterodon platirhinos</i>	5
Reptilia	Testudines	<i>Testudo hermanni</i>	5

history.

Extremely species poor orders, on the other hand, do easily seem overrepresented because number of species within these orders can be so small, that even very few studies within the 289 publications considered can lead to an overrepresentation. Rhinopristiformes, Orectolobiformes, Lamniformes, Lepidosireniformes, Lepisosteiformes, Acipenseriformes, Hexanchiformes, Squatiniformes, Microbiotheria, Proboscidea and Sirenia are only represented in five papers or less but still show a publication to species

number ratio above 10 because of their low number of species compared to other orders within their classes. Low species richness can also cause orders to remain completely unrepresented within the considered publications as orders poor in species are less likely to be prioritized by publications. As Table 4 reveals, most of the unstudied orders than 1% of species diversity within their major classes. While the portion of threatened species within an order can be considered a good criteria for studies on habitat use and home range, it alone can not explain the overall distribution we

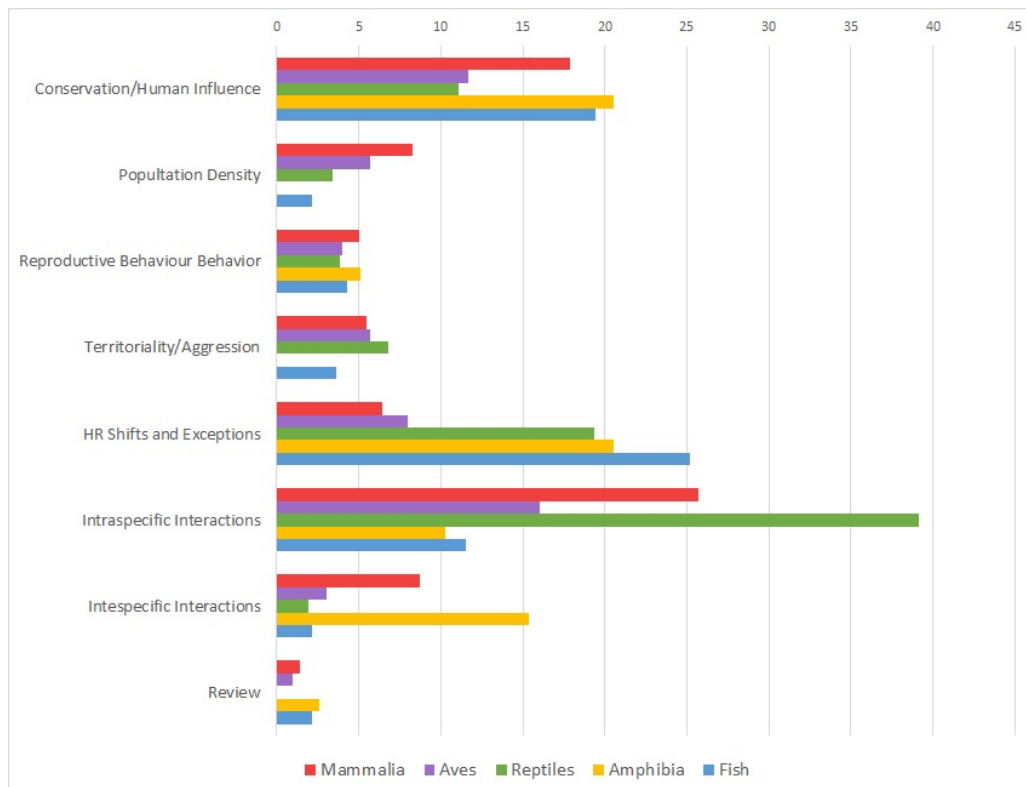


Figure 4. Percentage of publications covering different topics in different classes. 2

observed either as represented in the fishers' exact tests made with the data from Table 3.

It is likely, that here are other attributes allocated towards animals, that could explain the amount of attention a taxon receives. Attributes like animal size (Cochran 1980, Kenward 2000), and mobility (Mayor et al. 2009), that influence the difficulty of applying radio telemetry could play a role in the attractiveness of species and even populations. Many small lizards for instance have small home ranges and hence habitat often needs to be quantified at extremely fine resolutions - up to the point where individual rocks and bushes can be distinguished (e.g. Baltosser & Best 1990, Diego-Rasilla & Perez-Mellado 2003). This could lead to favouring of larger and/or more mobile taxa like Carnivora, Crocodylia, Testudines or sharks and the avoidance or omission of for example Apodiformes, Soricomorpha, or Atheriniformes. We suggest comparing size and/or mobility to number of publications would be a good way to test this hypothesis. We feel however, that this has to be done on a much finer resolution than order level as some orders contain species varying greatly in size.

Animal accessibility is also an explanation worth considering as it can be assumed that deep sea animals for instance (like Coelacanthiformes, Lophiiformes and Stomiiformes (Burton & Burton 2017, Long 1995, Nelson et al. 2016)) or primarily fossorial animals like Gymnophiona (Wells 2010) are hard to track reliably.

Certain ecological features may make taxa more interesting to study in terms of home range behaviour and habitat selection. The high number of studies concerning Otidiformes could be due to their predominantly terrestrial lifestyle (Stead 1965) which might make their home range and

habitat selection behaviour different from other birds and make them easier to study with radio telemetry. Furthermore, predators like elasmobranchs, crocodiles, mammalian carnivores, raptors, and maybe Esociformes and Lepisosteriiformes could be more interesting as they may potentially serve as indicators of the state of local ecosystems (wee e.g. Carroll et al. 2001, van Franeker 1992).

The possibility of certain taxa being more or less popular or recognizable in the general eye and the scientific community also possibly plays an important role. General appeal of animals and public opinion might influence the intensity with which orders might be studied. As discussed by Rosenthal et al. in 2017, there is a bias towards large, perceived charismatic animals within the general public and the scientific community. The seeming popularity of orders such as sharks (Charcarhiniformes, Orectolobiformes, Lamniformes), turtles and tortoises (Testudines), crocodiles and alligators (Crocodylia), raptors (Accipitriformes, Strigiformes and Falconiformes), mammalian carnivores (Carnivora), elephants (Proboscidea) and sirens and dugongs (Sirenia) could be explained by their appeal. It has also been shown, that there is a positive correlation between popularity of an animal and its relatedness to humans (Batt 2009, Borgi & Cirulli 2015, Rosenthal et al. 2017, Ward et al. 1998). Similarly, aversion to more distantly related taxa is present from early youth in humans (Borgi and Cirulli, 2015; Kubiato, 2012). In their 2017 publication Rosenthal et al. showed that this bias was also present in ecological studies. This is reminiscent of the concept of flagship species which describes "a species used as the focus of a broader conservation marketing campaign based on its possession of one or more traits that appeal to the target audience." (Verissimo et al. 2011). Aside

from appealing species getting more attention, researchers could also strategically favour the study of charismatic species to raise interest in their publications and make them more relevant for conservation purposes. However, the lack of a statistical ranking of animal popularity makes this hypothesis difficult to verify.

Another valid consideration is the direct impact species have on human society as well as public interest in protecting certain species. Some fish species may be of commercial interest for fisheries, such as Salmoniformes (Food and Agriculture Organization of the United Nations 2005, Matthews et al. 1994, Scruton et al. 2005, Young 1996), Acipenseriformes (Acolas et al. 2017, Barth et al. 2011, Food and Agriculture Organization of the United Nations 2005, Gerrity et al. 2008) or Esociformes (Food and Agriculture Organization of the United Nations 2005). Additionally, the study of mammals could also be favoured since large or potentially dangerous animals like wild boars (*Sus scrofa*), coyote (*Canis latrans*), foxes (e.g. *Vulpes vulpes*) or wolves (*Canis lupus*) can enter human settlements motivating studies quantifying contact or assessing damage and risks (e.g. Cahill et al. 2012, Gehrt et al. 2013, Poessel et al. 2016, Treves et al. 2004, Walton et al. 2017). Also, feral cats are considered to be amongst the most destructive invasive species (Lowe et al. 2000), which highlights the necessity to understand their spatial and habitat uses in many ecosystems for appropriate management as evidenced by several publications (e.g. Doherty et al. 2015, Gehrt et al. 2013, Harper 2007).

Testing these factors would be an important next step in unearthing the reasons for the observed taxonomic bias. We suggest doing this on smaller scales at first as it would be easier to identify small scale causes and testing their applicability at larger scales than vice versa. It is important to find the correct scale to test hypotheses. Most of these factors work on species level and any statements on higher classifications are just generalizations of the taxa within just as the observed allocation in Fig 1A. is a further generalization of the observed allocation of orders. By choosing to investigate above species level, we trade precision for a larger sample size per taxonomic unit per workload. We expect no single factor to be solely responsible for the amount of interest in a taxon but rather expect there to be a complex web of factors individually raising or lowering the specific attractiveness of a taxon to researchers.

Most Studied Species

When looking at the list of most studied species, one striking observation is, that apart from sea turtles and house cats, every species occurs in North America and/or Europe (IUCN, 2020). It could be, that many of these species are more intensely studied due to the overall high number of scientific publications in these regions. This could contribute to the popularity of some species as easily accessible model species or species of local conservation interest. *Heterodon platirhinos*, *Alligator mississippiensis*, *Aquila chrysaetos*, *Colinus virginianus*, *Tetrax tetrax*, *Clemmys guttata*, and *Emydoidea blandingii* do not have any special reasons listed within their publications that would not also apply to numerous other species. Their geographical range could therefore make them convenient study subjects.

As for sea turtles, all sea turtles are at least vulnerable (IUCN, 2020). They have a complex life history with migratory stages and periods of site fidelity (Blumenthal et al. 2009, Godley et al. 2003, Hart et al. 2012). Most publications state that understanding their space use is especially important for the identification and protection of crucial areas (Blumenthal et al. 2009, Gaos et al. 2012, Hawkes et al. 2011, Makowski et al. 2006, Seminoff et al. 2002). Modern technology like satellite telemetry allows the reliable tracking over marine megafauna like sea turtles (Christiansen et al. 2017, Hawkes et al. 2011, Hoenner et al. 2012, Makowski et al. 2006).

Spotted turtles (*Clemmys guttata*), Blanding's turtles (*Emydoidea blandingii*) and Hermann's tortoises (*Testudo hermanni*) are declining in numbers (Edge et al. 2010, Innes et al. 2008, Litzgus and Mousseau, 2004, Milam and Melvin, 2001, Rozyłowicz & Popescu 2013). However, this applies to many turtle species. Reasons for these species to be preferred could be tied to their geographic distribution as both species occur in more northern clines where they have to deal with seasonal weather shifts that could influence space use in these ectothermic animals (see e.g. Luiselli et al. 2009).

All but one of the carnivorans studied are mesocarnivores. A reoccurring topic among the mesocarnivore studies is interspecific interactions more specifically intraguild competition and how it affects habitat use (Arjo & Peltscher 2004, Gehrt & Prange 2007, Gehrt et al. 2013, Molsher et al. 2017). Additionally, the habitat use of those animals in proximity to human settlements or otherwise disturbed areas is often studied (Fuller & Harrison 2005, Goad et al. 2014, Godbout & Ouellet 2008, Pandolfi et al. 1997, Poessel et al. 2016). Animals like coyotes and foxes are stated as highly adaptable (Gosselink et al. 2003, Pandolfi et al. 1997) which could make them more attractive to localized habitat utilization studies. Feral cats on the other hand are stated as a big conservation concern (Ferreira et al. 2011, Hall et al. 2000). The only non-mesopredator on the list, the black bear might get attention due to a close proximity to humans and willingness to exploit their food resources (Beckmann & Berger 2003, Manen et al. 2012).

The red deer (*Cervus elaphus*) and the white tailed deer (*Odocoileus virginianus*) are studied for a multitude of reasons like quantifying human influence (Dechen Quinn et al. 2013, Drolet et al. 2016) or the effects of climate change (Rivrud et al. 2010). These problems are however not restricted to those species. It could be that the cervids are used as a readily available model species for large herbivores in general (Rivrud et al. 2010).

Wood mice (*Apodemus sylvaticus*) are studied as they inhabit agricultural land (Rosolino et al. 2011, Tattersall et al. 2001, Tew et al. 2000) Their influence on pastures and their possible role as indicator species for habitat quality therefore has to be studied (Tattersall et al. 2001).

While fish and amphibians did not have a species with five or more publications, the species with the highest numbers of publications (*Micropterus salmoides*, *Salmo salar*, and *Salvelinus namaycush* for fish and *Bufo viridis* and *Lithobates sylvaticus* for amphibians) are also species widely found in Europe and North America (IUCN, 2020). The aforementioned fish species are also commercially important fish,

which might further contribute to the interest in them (Food and Agriculture Organization of the United Nations, 2005).

Some of the reasons stated within the publications coincide with our assumptions on what could make an order interesting to study, but it also further proves that assessments like these are best done on species level.

Allocation of Topics within Publications

The main topics of home range and habitat selection studies over all classes are conservation/human influence, intraspecific differences, and home range shifts and exploratory behaviour while population density, reproductive behaviour, territoriality/aggression and interspecific interactions are studied less.

Across all taxa, conservation and human influence are always important study subjects, as they constitute the bridge between theoretical interest in these animals and applications important to economy, politics, and other branches outside science. These studies focus on the evaluation and development of concrete conservation applications. In turn, these studies can have access to more funding possibilities than purely theoretical studies (Laudel 2006) further contributing to their popularity. This hypothesis is further supported by the fact that even publications without specific goals in that regard often argue for the importance of their data in developing future conservation plans.

The concern with home range shifts and temporary leaving of the home range is also important when studying conservation efforts, because they can give insights on habitat requirements, dispersal capabilities and home range fidelity. Northern watersnakes (*Nerodia sipedon*), for example, have been reported to increase site fidelity in urban areas, presumably because exploratory behaviour is discouraged by human-related hazards (Pattishall & Cundall 2008). Home range shifts and temporary leaving of the home range also stand in direct relation to conservation efforts because of the way that animals translocated or released due to conservation efforts have to go through a phase of dispersal in which finding a new home range is at risk of failing (Knox et al. 2017). In 2017, Knox et al. for example studied the effects of translocation techniques on post-release dispersal of jeweled geckos (*Naultinus gemmeus*) and highlighted the importance of knowing and optimizing species dispersal capabilities for the successful translocation of populations. Furthermore, studying causes not directly related to active conservation measures or human influence assessment can also give valuable insights on animal habitat requirements and willingness to take risks. Female roe deer (*Capreolus capreolus*), for instance, have been shown to temporarily leave their home range in search for new mating opportunities (Debeffe et al. 2014). It is noteworthy that interest is reduced in birds and mammals when compared to lower vertebrates. One possible reason being that terrestrial lower vertebrates usually have more limited home ranges and are less mobile than birds and mammals. Therefore, habitat shifts are often more prominent and easier to study in these clades. In the case of birds, seasonal habitat shifts like overwintering migrations can span several continents. Even though migrations are in a strict sense home range shifts, causes and effects of migrations are usually considered far above home range scale (Guan et al. 2013).

Intraspecific differences are also often considered. The simplest forms of studying intraspecific differences, to compare males and females, or adults and juveniles, are also most common in the list of publications. Sex and age determination can be achieved rather easily in many species by identifying sexual dimorphism or examining genitalia when marking the animals for relocations or applying transmitters. As long as the sample sizes for the different intraspecific groups are large enough, splitting the data set into subsets and comparing them is usually not an issue and easily done. In mammals, differences between males and females can be interesting for numerous reasons. On one hand, pregnant females or females rearing young could have very different habitat requirements than males in terms of energy intake or safety. This has been shown repeatedly for roe deer (*Capreolus capreolus*) (e.g. Saïd et al. 2009, Tufto et al. 1996). On the other hand, males could show very different behaviour from females when searching or courting for females (Fernando et al. 2008). The number of studies on intraspecific differences is highest in reptiles perhaps because studies focusing on lizards can have larger sample sizes in a set radius, as lizard home ranges tend to be small (as discussed above).

Population density might be less studied because in order to assess population density, there is no need to study home range or habitat selection (see e.g. Gaillard et al. 1993, Krebs 1989, Thomas et al. 2010). Even though space use and population density can be combined, studies focusing mainly on population density might choose those other ways. Reproductive behaviour is also less studied in most clades except in birds, where it is studied more. This can be explained by the fact that bird parents, providing for their offspring, actively forage food and therefore, optimal use of home range and habitat - with possible shifts during nesting and brood care - is critical to species survival (Beltran et al. 2010, Garza et al. 2005, Williams et al. 2016). There is lower interest in mammals in this regard, even though they, too, care for their young, which can be explained due to advantages linked to lactating, saving them the effort of finding suitable food sources for their young.

The publication of studies on interspecific interactions could be hampered by the requirement to study multiple species. This increases the workload because an apparent interaction or influence of one species on the home range and habitat selection behaviour of another must be shown. The most common examples are competition for resources (Bramley, 2014, Indermaur et al. 2009, Molsher et al. 2017, Stakénas et al. 2013) and predation (e.g. Molsher et al. 2017).

The rarity of reviews on the topic can be allocated to two reasons. First of all, reviews are always rare, as it is their aim is to sum up the existing literature on a topic. Therefore, reviews on the same topic are not necessarily needed in quick succession. Reviews on entire clades or communities can be very broad and often focus on specific questions like the ecological effect of roads (Trombulak & Frissell, 2000) or the effectiveness of marine reserves (Kramer & Chapman, 1999). There are, of course, helpful reviews on the subject for specific species as well as for groups of species. Doherty et al. reviewed habitat use of feral cats in 2015, in order to better manage potentially harmful populations. The ecology of mountain gorillas, including their space use has been reviewed by Watts in 1998. Red-cockaded woodpecker forag-

ing habitat has also been reviewed in 2002 by Walters et al. while Clemens et al. reviewed shorebird home range boundaries in 2014.

Conclusion

As suspected, the proportion of home range and habitat selection studies between orders seems to be independent of species richness, relatedness, or amount of threatened species. There are however other reasons for the observed allocation pattern not studied here. We suspect however, that most of these causes act mainly on the level of smaller taxonomic units as orders are too diverse to generalize factors like body size, mobility, ecology or popularity over an entire order. We expect these factors to work mainly on species level. The short list of most studied species we did look at supports this hypothesis in the reasons mentioned by the studies themselves, however it is way to small of a sample to prove it. To properly assess the representation of vertebrate biodiversity within home range studies, multiple reviews executed based on smaller taxonomic units, rather than orders, would be necessary. However, this review might give first insights and clues towards the allocation of publications towards taxonomic groups and might prompt researchers to review certain smaller taxonomic groups in order to more accurately identify groups needing further research. The same can be said about fields of research and foci of home range and habitat use studies. Conservation, intraspecific differences, and home range shifts seem to be the most popular research topics to be studied alongside home range and habitat selection. The applicability of certain foci to certain taxa as well as the benefits drawn from these studies might mostly be assessable on species level, but the review has identified key trend differences between major groups. In both cases, the justification of the allocation of studies should be questioned and possible reasons should be explored to properly identify research gaps on a finer scale. Even though this study does not claim that the Web of Science search it is based on delivers a complete record of home range and habitat studies made in the last 38 years, it assumes the search results to be a fitting approximation.

This review serves as a first broad look across the field of vertebrate space use studies and a first step in assessing the completeness of the field. As research power is limited, there are bound to be gaps in our understanding of these topics but a broad view allows the scientific community to identify potentially interesting and important subjects for further research. We proposed possible reasons why certain clades or topics have received more or less attention. If we were to identify gaps in knowledge and propose taxa to which more attention should be directed, we would suggest to identify gaps not simply by species richness but by richness of at risk species as those taxa are in more immediate need of habitat use assessment studies. Some of them like Proboscidea, Cetartodontiformes, Caudata, Primates, Lamniformes and many more have so far been severely overlooked despite the large portion of endangered species making up these orders. In our opinion, those species are definitely worth considering when choosing a study subject as understanding their spatial use can help to prevent the loss of entire orders currently

threatened to disappear. We acknowledged however, that this study did not explore all the possible reasons for the observed allocation pattern and therefore cannot give a definitive statement on the appropriateness of the distribution. In the end, we see the responsibility in the scientific community itself to decide whether gaps are worth filling.

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