

Review

# Understanding Species–Habitat Associations: A Case Study with the World’s Bears

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**Abstract:** Habitat modeling is one of the most common practices in ecology today, aimed at understanding complex associations between species and an array of environmental, bioclimatic, and anthropogenic factors. This review of studies of seven species of terrestrial bears (Ursidae) occupying four continents examines how habitat models have been employed, and the functionality of their predictions for management and conservation. Bear occurrence data have been obtained at the population level, as presence points (e.g., sign surveys or camera trapping), or as locations of individual radio-collared animals. Radio-collars provide greater insights into how bears interact with their environment and variability within populations; they are more commonly used in North America and Europe than in South America and Asia. Salient problematic issues apparent from this review included: biases in presence data; predictor variables being poor surrogates of actual behavioral drivers; predictor variables applied at a biologically inappropriate scale; and over-use of data repositories that tend to detach investigators from the species. In several cases, multiple models in the same area yielded different predictions; new presence data occurred outside the range of predicted suitable habitat; and future range projections, based on where bears presently exist, underestimated their adaptability. Findings here are likely relevant to other taxa.

**Keywords:** habitat adaptability; habitat model; habitat selection; habitat suitability; use versus availability; Maxent; presence points; GPS radio-collars; anthropogenic variables; species distribution models



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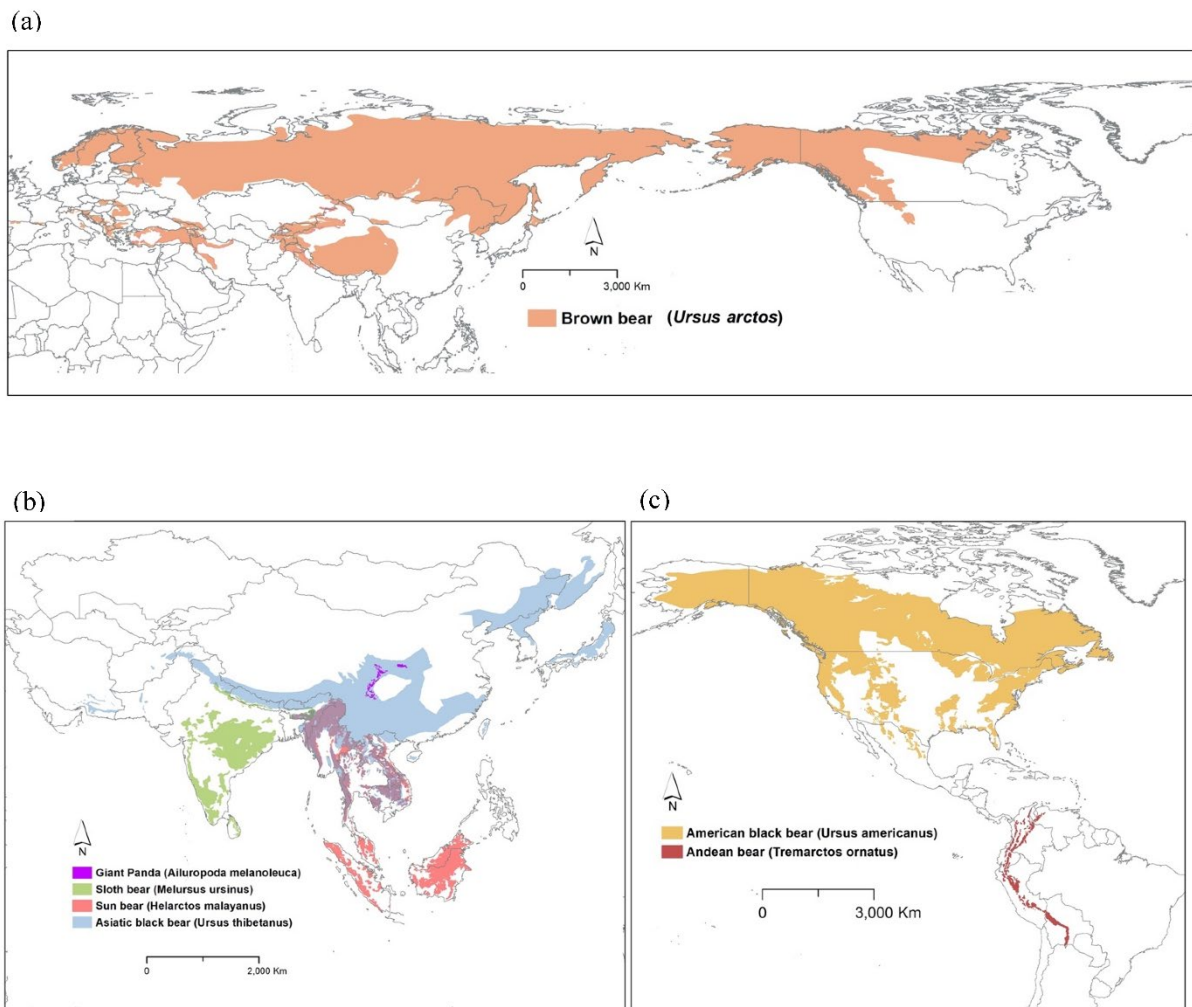
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## 1. Introduction

An intriguing product of evolution is that some species within a given taxonomic family have wide niches, whereas others have much narrower niches, and likewise some species are distributed much more broadly than others. A particularly striking example of this variation in niche and range is the bear family Ursidae [1]. This family consists of only eight species, one of the smallest among the Order Carnivora. Of those eight species, only one, the brown bear (*Ursus arctos*), ranges across multiple continents: North America, Europe, and Asia (Figure 1a). Four species are endemic to Asia (Figure 1b), one endemic to North America (American black bear, *U. americanus*), one endemic to the Andes mountains of South America (Andean bear, *Tremarctos ornatus*) (Figure 1c), and one endemic to the Arctic (polar bear, *U. maritimus*). Among the Asian endemics, the Asiatic black bear (*U. thibetanus*) is wide-ranging across a diverse array of habitats from the Russian Far East to Southeast Asia and westward to Iran. Conversely, sun bears (*Helarctos malayanus*) are restricted to Southeast Asia, and sloth bears (*Melursus ursinus*) are confined to the Indian subcontinent. Giant pandas (*Ailuropoda melanoleuca*) once ranged across a large portion of China but are now limited to a small mountainous area that was once the western edge of their historic range. This paper investigates habitats used by the seven species of terrestrial bears, which excludes the polar bear, or “sea bear” from its Latin name.



**Figure 1.** (a) The brown bear ranges across three continents (and once ranged into North Africa). (b) The Asiatic black bear, sun bear, sloth bear, and giant panda are all endemic to Asia, and their ranges at least partially overlap on a broad scale. (c) The American black bear is endemic to North America (3 countries), and the Andean bear is endemic to South America (5 countries). Depicted here is the maximum present range, combining categories for extant and possibly extant range from the IUCN (International Union for Conservation of Nature) Red List.

The aim here is not to define what constitutes suitable habitats for these seven species, but rather to demonstrate the extraordinary diversity, complexity, and adaptability in their use of habitats. Moreover, a co-equal aim is to show that our perceptions of how bears use and select habitats, and thus our perception of what is most suitable, is partially a construct of the methods employed. Habitat is multi-faceted and not static. In its simplest form, bear habitat is the dominant cover type (usually forest). However, to a bear, the value of a habitat lies in the types and quantity of foods produced, safety, and in some places, escape from the heat. Matthiopoulos et al. refer to these three habitat components as resources, risks, and conditions, respectively [2]. Most bears do not have significant non-human predators, aside from other bears, but tigers (*Panthera tigris*) pose a threat to sloth bears, sun bears, Asiatic black bears, and brown bears in parts of their range. Humans, though, are a potential or perceived significant threat in most places. Thus habitat may be judged from a bear's perspective by a combination of the proximity of humans and infrastructure, such as roads and dwellings, plus the availability of concealment. However, humans also may provide bears a source of concentrated food in the form of crops, livestock, beehives, and garbage. All of the bears use these to various degrees (although least for giant pandas,

and to a very minor degree for sloth bears). In human-dominated landscapes, it is often difficult to extract the human factor, and typically a goal of habitat studies is to understand how the human factor interplays with habitat selection.

This paper has six main sections. It begins with a definition of habitat, then follows with a general overview of the diets and broad habitats used by the seven terrestrial bears. Next is a review of methods and their corresponding assumptions to examine finer-scale habitat associations. The Section 4 is a summary of papers examining habitat use, selection, or suitability for individual species. The Section 5 draws some conclusions about the adaptability of bears, limitations of the methodologies, and implications for using modeling results in management and conservation. The Section 7 is a list of recommendations for future studies of bear–habitat associations, aimed at reducing biases and misinterpretations, and leading to more reliable real-world applications. The general conclusions and recommendations stemming from this review should apply to other species as well.

## 2. Definitions

The original meaning of *habitat* is the type of place (meaning the collection of resources and conditions) where each particular species can live. The word is derived from Latin, basically meaning the area that a species inhabits (that which is habitable). Some argue that we should only use this original meaning because that is how it was used by several early ecologists [3,4], even though most modern authors do not use it this way [5]. That being the case, it makes no sense to refer to habitat suitability, as all of a species' habitat is by definition suitable. Likewise, it would make no sense to refer to habitat use; instead, one should refer only to use of specific components of habitat.

Through time, however, scientists began referring to those habitat components as habitat types, sometimes with specific names (e.g., forested habitat). Even the seminal paper by Johnson referred to habitat as a vegetative type [6]. Moreover, looking back at early literature, the purported original meaning is not entirely clear. In 1917, Nichols defined habitat as “any unit area in which the combined influence of climatic, edaphic, and biotic factors is essentially uniform throughout” [7], and in 1922, Yapp commented that most authors at that time were using the term to mean “factors or conditions of the environment,” adding that “ecological factors are so numerous and so variable that their possible combinations are bewildering . . . [so] nature draws no hard and fast lines” [8].

It is useful to recognize that there are now two distinct definitions of habitat, one being species-specific, and the more-common usage being a way to define environmental space [9]. Gaillard et al. referred to these as the functional and structural meanings, respectively [10]. Here, I use *habitat* in the structural sense: a spatial unit with definable characteristics in terms of resources or conditions (similar to [2,11]). Hence, rather than “bear habitat” (a very ambiguous term, as this paper will demonstrate), I will refer to different kinds of habitats, characterized by environmental features, such as vegetation, topography, human influences, etc. Accordingly, *habitat use* means the extent to which different definable components of the environment are used. *Habitat selection* refers to the process of choosing different habitat types or components. *Habitat preference* refers to the underlying proclivity for choosing a habitat, but can be measured only in controlled situations where animals are provided a range of choices. *Species–habitat association* (as in the title of this paper) is the connection between habitat features and the occurrence or demographics of the target species. *Habitat suitability* is the extent to which the habitat can sustain the species (i.e., population viability). Often it is equated to selection, assuming animals select habitats that are most suitable, but this is a poor assumption in that animals like bears often select habitats that offer abundant resources (food), but where human-caused mortality may reduce their suitability. Habitat suitability should technically be measured via the population growth rate, but this is rarely done, because it requires distinguishing which specific habitat features contributed to the observed growth rate.

### 3. Broad Differences among Species

#### 3.1. Dietary Patterns

Six of the seven species of terrestrial bears are omnivores, feeding on plant and animal matter, but to different degrees. The giant panda, conversely, is a true herbivore, specializing in bamboo. It is not only the most divergent from the other bears in terms of diet, but also falls within a separate subfamily (Ailuropodinae). Its diet varies mainly in terms of the species (>40) and parts of bamboo consumed ([12,13]).

The Andean bear is the next most vegetarian bear, with over 300 plant species identified in its diet [14]. Like the giant panda, it is in a separate subfamily (Tremarctinae). Members of this nearly extinct subfamily of so-called short-faced bears once ranged widely across North and South America and included species that were far more carnivorous than the sole extant survivor from this line [15,16]. Andean bears also consume some small mammals, and occasionally prey upon or scavenge larger mammals, including some wild ungulates and domestic cattle, where available. However, their main foods are plant meristematic tissues (bromeliads, palms, bamboo, cacti) and fleshy fruits [17,18].

The sloth bear is the most insectivorous bear, with specialized morphological adaptations for myrmecophagy (ant and termite feeding). There are no known places where this species exists without termites or ants as a dietary mainstay, although the extent of ants and termites in the diet can vary significantly by location and season [19]. There are very few places where termites are not a major portion of the diet (i.e., where ants totally replace termites), meaning that the geographic and elevational range of this species within the Indian subcontinent is largely constrained by the distribution of termites [20]. Sloth bears also consume a variety of fruits, but not much vegetative matter [21,22].

The sun bear is second in terms of the extent of insect feeding. This species seems to prefer fruits, and across its range in Southeast Asia, it eats a very wide diversity, depending on what is seasonally available. In one small study site in Borneo, sun bears consumed 115 species of fruits in 30 families [23]. Most of the fruits in Southeast Asia are tree-borne, so these bears spend much time in trees feeding; if they waited for the fruits to fall, many would disappear from competitors or rapid decomposition in the tropical environment. However, in some seasons or years when fruits are lacking, the sun bear's diet is composed largely of insects [24]. They are especially noted for excavating stingless bees from their nests inside hollow trees [25]. While this species is sympatric with Asiatic black bears across most of mainland Southeast Asia, and the two share a diet of the same fruits, sun bears rely more on insects, and this slight difference in diet may allow the two species to coexist [26,27].

Asiatic black bears consume a variety of fruits and nuts, green vegetation, ants and other insects, and prey on some small mammals and small-sized ungulates [28]; their predation on ungulates may be high in some areas [29,30]. Although it is somewhat coincidental that there is another species with the common name "black bear", the American black bear is also quite similar to the Asian counterpart in terms of its general reliance on fruits and nuts, green vegetation, varied dependence on insects, and occasional predation on ungulates, primarily neonates [31]. Unlike the Asiatic black bear, the American black bear may rely heavily on fish in some areas, both coastal and inland [32,33].

The brown bear, having the largest distribution encompassing an enormous range of habitats, exhibits the greatest dietary plasticity, from nearly entirely herbivorous to near-obligate carnivory [34,35]. On the Tibetan steppe, it subsists on marmots (*Marmota himalayana*) and pikas (*Ochotona curzoniae*) because fruits are nearly absent [36,37]. In coastal North America and east Asia, seasonally abundant salmon (*Oncorhynchus* spp.) are an important food, but not the only food. In interior parts of North America, the brown bear (called grizzly bear) preys on burrowing rodents and neonatal ungulates, but also relies heavily on forbs, roots, and fruits. In Eurasia, they also prey on neonatal ungulates and consume vegetable matter and a variety of fruits, but consume more hard mast (nuts) than in North America [38]. Additionally, in Europe, supplemental feeding is common in some countries,

providing a reliable, concentrated food source that can constitute an appreciable portion of their diet [39].

### 3.2. General Patterns of Habitat Use

Whereas bears are normally thought of as forest-dwelling animals, most of the species also occupy treeless environments. Brown bears live in the northern treeless tundra, where their diet is largely vertebrates and green vegetation [38]. One unique population of American black bears occupies treeless tundra of northeastern Canada, where they prey on caribou (*Rangifer tarandus caribou*) [40]; climate change is also enabling northward expansion of American black bears into more treeless environments, where fruits and insects are scarce, so they have adapted by feeding largely on meat [41]. Grizzly bears historically existed in grassland prairies of North America, but were extirpated there, and protected remnant populations are now expanding out of their core forested range into some of these vacant areas [42,43]. A population of Asiatic black bears in Japan lives in a primarily grassland habitat where ants are a major dietary component [44]. Both brown bears and Andean bears inhabit grasslands at high elevations above treeline in their respective ranges; in the Andes, these habitats are referred to either as puna or páramo. In the Himalayas, brown bears have been recorded at >5000 m, and Andean bears recorded above 4000 m. Asiatic black bears match or exceed Andean bears in maximum elevation, but only due to a higher treeline [14,28,35]. However, Asiatic black bears make seasonal forays into treeless alpine areas [45]. Sloth bears use lowland, grasslands with scattered trees in parks in Nepal and India; these areas have a high density of termite mounds, but may flood seasonally pushing the bears to higher elevations [46].

Several bear species also occur in arid regions. A small brown bear population exists in the Gobi desert of Mongolia, where they are dependent on scattered oases [47]. Andean bears occur in a low elevation arid region of Peru, where they depend on waterholes and during some periods of the year must subsist on the woody parts of pasallo trees (*Eriotheca ruizii*) [48]. Asiatic black bears in the western-most part of their geographic range in southern Iran live in a sparsely vegetated area where they are highly dependent on abandoned fruit orchards [49].

All of the terrestrial bear species occupy various kinds of forests. In northern latitudes, brown bears, American black bears, and Asiatic black bears inhabit boreal forests. There they consume fruits when seasonally available, but often just a few species of berries due to low diversity. Otherwise, they consume green vegetation and a large proportion of ants [38,45,50,51]. Brown bears are more predatory on vertebrates than either of the black bear species, although vertebrate consumption varies with ungulate abundance, including domestic species [52].

Temperate forests tend to have a greater diversity and abundance of fruits, especially nuts, than boreal forests, providing each bear species with a richer diet and thus a better buffer from year to year variations in productivity of any single fruiting species [53]. In North America, temperate forests in the eastern half of the continent tend to have richer supplies of fruits and more nuts than in the west, so American black bears tend to be larger and more prolific in the east [54].

Asiatic black bears, sun bears, sloth bears, and Andean bears all occupy tropical and subtropical forests. Andean bears regularly use montane humid forests, elfin, and cloud forests [14]. Asiatic black bears and sun bears co-occur in mixed deciduous and semi-evergreen forests across Southeast Asia, although there is evidence that in montane forests, with rich supplies of oaks, Asiatic black bears exclude sun bears [26]. Sun bears use higher elevations where Asiatic black bears are absent, reaching 2000 m on Borneo [55]. A particularly interesting dichotomy occurs with sun bears in that about half their range falls within seasonal tropical forests north of the Isthmus of Kra on Peninsular Malaysia (10°30' N), and half in the aseasonal dipterocarp rain forests of the Sundaic region to the south, including the islands of Sumatra and Borneo [56]. The Sundaic region experiences highly synchronized masting events followed by inter-mast periods of 2–9 years when



fruits are much less abundant, greatly influencing sun bear diet and health [57]. Sloth bears are the most lowland-dwelling tropical species, generally occurring below 1000 m in Nepal and India (although reaching 2000 m in the Western Ghats) and below 300 m in Sri Lanka [19,58,59]. During the 1990s they were extirpated from Bangladesh, due to the conversion of lowland forests to agriculture, whereas Asiatic black bears and some sun bears continue to persist there [60].

#### 4. Methods of Studying Fine-Grained Habitat Use, Selection, and Suitability

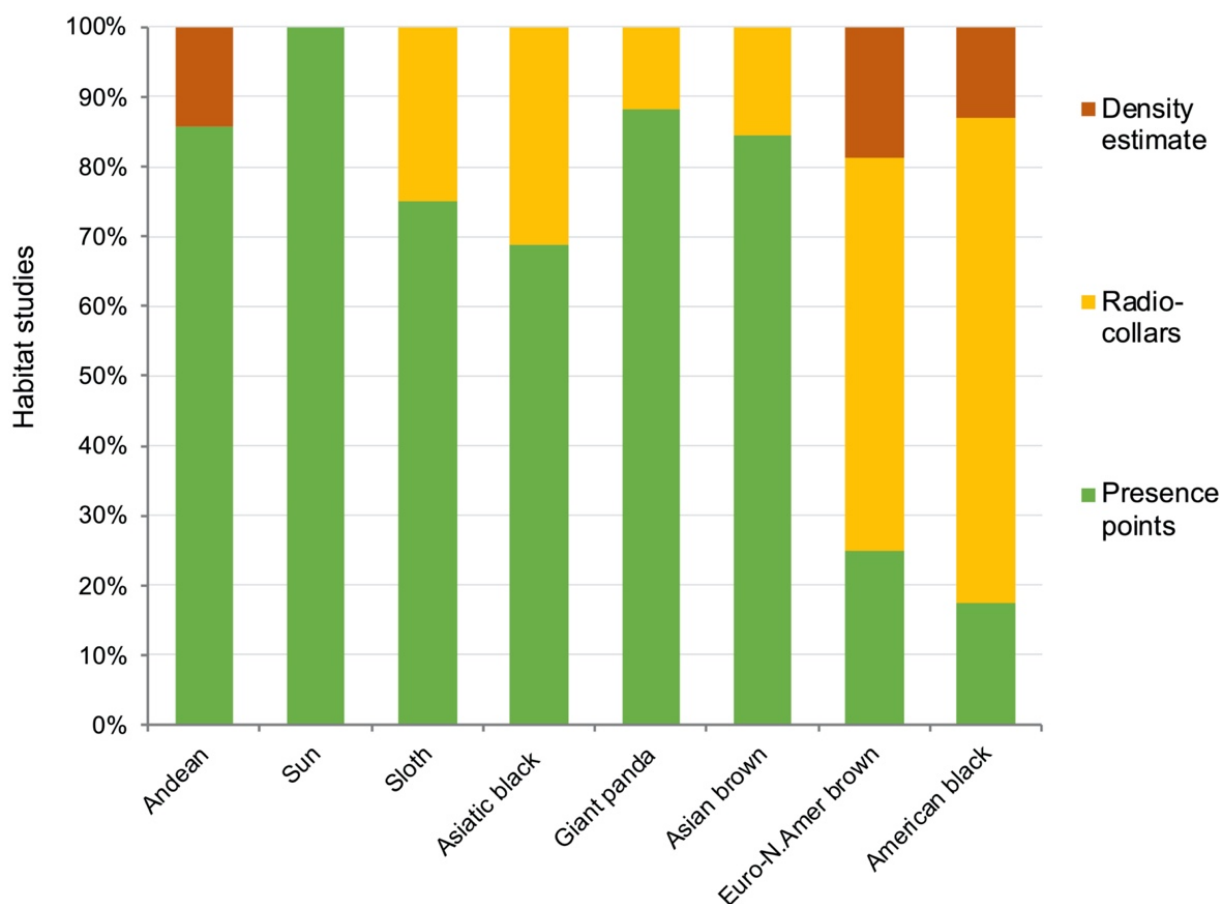
Quantification of habitat use, selection, and suitability occur as a stepwise conceptual process by which ecologists try to understand species–habitat associations. Ecologists may aim to (1) understand why animals (or plants) occur where they do, (2) create maps of their distribution or potential distribution, and (3) make predictions about how the distribution may change in the future [2]. Investigators generally begin by examining environmental and anthropogenic variables (resources, conditions, and risks) around sites that were known to be used, then compare that to random (available) sites in the landscape to gauge selection; scaled selection indices may be used to assess relative habitat suitabilities, which assumes that the animals are making choices that, on whole, maximize their fitness [9].

In a highly influential paper, Johnson proposed four hierarchical orders of habitat selection, where at each level, the animal chooses from within a different window of available resources: the first order determines where the species exists (presumably all suitable habitat); the second order determines the placement of home ranges; the third order pertains to site use within home ranges; and the fourth order regards selection of specific foods or other resources at each site [6]. Often researchers are unclear about which level they are investigating, or employ use at one spatial scale and availability on a different scale, and fail to recognize that animals make choices at multiple scales [61,62]. Furthermore, strict adherence to use–availability comparisons leads to the mistaken assumption that increased availability of preferred habitats should always motivate increased use; i.e., that there is never enough, or even too much of a good thing [9]. This assumption clearly does not fit species like bears, which use many types of foods in different habitats, and where conditions change seasonally, and even week to week [63]. An ironic consequence of measuring selection via a comparison of use to availability is that selection may seem low for frequently used but very common habitats, and high for occasionally used habitats that are rare, just opposite of how it would be perceived from use alone.

Measuring use is the linchpin for all else. Bears researchers have generally used one of two broad methods: (1) collection of presence points, or (2) locations of animals with radio-collars. These two kinds of data are different in many respects, leading to potential differences in interpretation, as described below. Radio-collars are the primary study method in North America and in some parts of Europe, whereas bear studies in Asia and South America have relied primarily on presence points (Figure 2). A new technique is also emerging whereby the estimated local density of the species of interest is compared to the availability of habitats.

##### 4.1. Presence Points

Presence points can be obtained by a variety of means, including camera traps, sign surveys, sightings, surveys of local people who encounter bears or their sign, or records of dead bears. A fundamental assumption is that any presence point is truly a bear, and if more than one bear species occurs in the area, it is actually the species of interest. Local people's accounts of bear presence should be verified [64]. Even photos can be misidentified as to the species, since some bears look alike [65,66]. Some kinds of bear signs can be confused with that of other species, so to avoid misidentification it may be preferable to only rely on types of signs that are definitive (e.g., claw marks on trees; [67]). However, this can lead to a bias if the more reliably identified sign occurs in certain types of habitats (Figure 3).



**Figure 2.** Relative use of presence points, locations of radio-collared bears, and site-specific density estimates in studies of habitat use, selection, and suitability for the seven species of terrestrial bears. Brown bears are split because of continental differences in the use of these methods. Use of density for Andean bears may be exaggerated by small sample size ( $n = 7$  total studies). Data are from published papers, mainly since 2000, cited in text ( $n = 141$ ), which may not be a perfect representation of all studies.

A complication of presence data is that a lack of detection may signify the absence of use or simply non-detection, and detection can vary by habitat and over time (as sign decays). Lacking true absence data, models are generally fit to the presence-only data to extract covariates that best explain the pattern of use. A fundamental assumption of such models is that the underlying data reflect the true relative use with respect to habitat features. Hence, sampling is a critical component; sampled points that differ in some way from the full inference space would create a potential bias and misinterpretation of habitat selection [68]. It is not the intent here to review the various ecological niche models or species distribution models, or even to comment on general biases and suggested remedies, as there is a vast amount of literature on this [2,69–73]. However, some examples from the bear literature related to these potential issues may be helpful in emphasizing the integrity of the presence points.

Nazeri et al. obtained sun bear presence points (primarily camera trap records) from the Malaysian government, all collected within primary forests and primarily in protected areas in the northern half of Peninsular Malaysia [74]. There is only one bear species in Malaysia, so there is no possibility for species confusion. They used Maxent to extract covariates that best explained where these records occurred, and thereby created a map of suitable habitat. They compared their map to a recent map created via expert opinion. In essence, one map was created by people with little expertise in the species' ecology but having a set of verified presence points and a model, versus another made by a Malaysian field biologist with extensive knowledge of the species ecology but with uncertain presence

records and not applied in a quantifiable way. Comparing the two maps showed significant disparities: the Maxent map predicted habitat to be unsuitable in a number of places where the species expert thought they occurred. Unfortunately, there are currently no data indicating which is more correct. However, it is notable that the Maxent map was based on presence points in the best habitats (primary forests in protected areas), so it is no wonder that the model would predict bears not to occur in other situations.



**Figure 3.** Many habitat studies of bears are based on presence points identified from sign. (a) A sampling problem arises when uncertain sign is either incorrectly counted as a bear, or always discounted. (b) Relying only on definitive sign, such as claw marks on trees prevents identification errors, but may create a bias towards habitats where bears create more of that type of sign (e.g., habitats with many fruit trees that bears climb). Photos: D. Garshelis; R. Steinmetz.

A somewhat tongue-in-cheek niche modeling of Sasquatch sightings makes the point eloquently stated by Baldwin [68]: “just because a model can be built does not mean that it is informative.” Sasquatch is one of a number of crypto-zoological large, bipedal mammals that have purportedly been observed but for which no specimens exist. Sasquatch (or Bigfoot) sightings were collected from across the western U.S. states of Washington, Oregon, and California, and through modeling, a predicted range map was created [75]. Using presence points of American black bears from the same three states produced a very similar predictive map, suggesting either that these two “species” occur in the same habitats, or that many purported Sasquatch sightings were, in fact, bears.

Possibly even more bizarre than the niche modeling of Sasquatch is an example with Asiatic black bears [76]. Presence points were obtained from a database encompassing a wide portion of the known distribution from northeastern China, Japan, and South Korea, to Vietnam and Thailand, and westward to India and Pakistan (Figure 1b). Problems, though, included the fact that the sample size outside Korea was small (22 points), and several points were well beyond the known distribution of the species. That is, the coordinates were certainly incorrect (and in one case, possibly a sloth bear instead). This rather shaky dataset was run in a Maxent model, with 19 bioclimatic variables, 16 landcover variables, plus elevation and distance to the road. The model generated predictions of habitat suitability. Remarkably these areas of purported suitable habitat included a large region where this species has never occurred (i.e., there is no historical or even fossil evidence), including a swath from Mongolia through Siberia and Kazakhstan to Tajikistan (occupied by brown bears), central India (occupied by sloth bears), Malaysia and Indonesia (occupied by sun



bears), and the Philippines (never occupied by any bears). Once again, this illustrates not just the importance of ensuring the accuracy and geographical balance of the presence data, but also recognizing that well-fitting model results do not mean they accurately depict reality.

Large public databases of presence points may foster novel insights about habitat suitability and distribution of species, while at the same time providing a recipe for people with little direct knowledge of the species to publish misleading findings. One recent high-profile paper based on publicly available data and modeling proposed priority “rewilding” sites for bears in places where they never existed historically, including American black bears in Canadian prairies, Asiatic black bears in Malaysia and Tajikistan, and sloth bears in central Bhutan [77]. Knowledge of the species or consultation with experts would have prevented such obvious mistakes.

#### 4.2. Bears with Radio-Collars

Radio-collars provide point locations of known animals, which can be matched to certain habitat variables. In the 1980–1990s, bear biologists obtained locations from VHF radio-collars, generally during the day, and could classify habitat variables in a very broad sense from visual examination. Since then, GPS collars have become the standard, and a large number of habitat variables can be extracted from GIS layers. However, while this new technology avoids many of the sampling pitfalls often encountered with collecting presence points and enables far greater insights, it also highlights the problem of measuring availability. Viewing habitat from the eye of a radio-collared bear, how far away does it consider its available choices?

Judgments about availability can affect our perception of selection as much as the use side of the equation [6,11,78]. Whereas a bear’s home range is technically all “known” to it, and thus available, at each moment in time, it has imperfect knowledge of the exact conditions (e.g., fruit availability) everywhere in its home range, and moreover cannot instantly jump to any other location, but rather must expend time and energy getting there. So, on a short time scale, it makes decisions about habitat use based on what is in proximity. That is, its choices are spatially constrained [79]. Bears are highly mobile, and generally could get to any location within their home range in a day, but that said, even if two different preferred habitats occurred on opposite sides of a bear’s home range, it would not be efficient to continually move between them. This problem regarding availability also pertains to use. With VHF collars, locations were typically obtained at time intervals such that an animal could be virtually anywhere in its home range, but sample sizes were thus relatively small. With GPS collars and points obtained hourly (or even more frequently), each location is partly dependent on the previous one, not just in terms of how far the bear could move, but also by its assessment of its immediate surroundings (i.e., patches of food). This so-called auto-correlation problem is actually an opportunity, as the wealth of points are not only an unbiased representation of the animal’s use of habitat, but also yield information about fine-scale choices in its movements [80].

One recent solution specifically to deal with and appropriately exploit such fine-scale data is the use of step selection functions. These are now commonly used for data collected from GPS radio-collars [81]. Instead of viewing the points as a sample of independent locations, the method examines the choices the animal made when it moved from each point to the next. These movement steps are compared to other random steps that it could have made, but did not, which may have landed the animal potentially in a different habitat or crossing an unproductive or risky habitat feature (like a road). However, mobile animals like bears may be making decisions at multiple scales: both where it wants to be now, and where it wants to be generally heading, all the while gathering more information and modifying decisions. It uses a combination of memory of specific locations, experiences, and current information to assess what is likely to be available where.

## 5. Fine-Scale Habitat Associations within Species

Given that fine-scale habitat use tends to be very specific to the situation at each locale, and because most bears are generalist opportunists, it is difficult to extract general trends by reviewing habitat studies of each species. Moreover, researchers have used somewhat different classification systems of habitat variables. Hence, whereas this section shows the wide variation and also draws out some generalities about the habitat suitability of each species, another prime intent is to highlight inconsistent or suspect results. To gain useful and practical information from habitat suitability studies and thereby inform better management and conservation, we need to be wary of potential methodological and interpretational flaws.

The papers examined here are a nearly complete sample for some species, but represent a selected sample for those species where the number of publications would be too large to completely review (Europe and North America). The intent here is not to cite every applicable paper, but rather to provide a multitude of examples of key aspects of species–habitat associations and the methods used to assess them. The cited papers are mainly limited to those published since 2000 so as to gain an appreciation for kinds of studies occurring recently, although with a few important older papers included. This review excludes a fairly large amount of literature on habitat selection of den sites (brown bears and American black bears hibernate in nearly all of their range; Asiatic black bears hibernate in northern and high elevation parts of their range). The bear species are listed roughly from south (tropics) to north and east to west, corresponding to the increased use of more rigorous methods (Figure 2). This increasing northward gradient in scientific rigor is also evident in the total number of publications (not just habitat studies) on each bear species [82].

### 5.1. Andean Bears

Although this review is mainly limited to papers published in the past 20 years, one cannot discuss the habitat suitability of Andean bears without mentioning the classic field study by Bernard Peyton in 1982 in Machu Pichu, Peru [83,84]. Comparing vegetative and topographic features at sites with bear signs versus random sites without signs, Peyton observed bear sign to be concentrated in certain elevation zones and associated with the availability of bear foods and vegetative hiding cover, and lack of grazing livestock (which trample cover); the only positive association with humans were cornfields in proximity to cover. This study became a model for other sign-based studies of this species.

A field study in Ecuador recorded signs along narrow transects (where detectability was high) and identified montane cloud forests and herbaceous paramo (high altitude grassland) as being the most suitable habitats, the former providing seasonal fruits and the latter year-round terrestrial bromeliads, with surmised seasonal elevational movements by bears between these [85,86]. Oddly, though, a DNA hair-snaring study at the same site captured more individual bears in what was judged as poorer habitats [87].

A sign study in Bolivia also indicated selection of high elevation montane forest, as well as mid-elevation elfin forest, but high elevation paramo was used by bears comparable to its availability [88]. The metric of use in this study was obvious bear trails, so it seems possible that bears used trails more in elfin forests, with high tree density, and were thus more easily detected by investigators than in open grassland where they could walk anywhere and not create a trail.

Velez-Liendo et al. collected bear sign and sighting data (>500 points) across their range in Bolivia, and created two models to predict distribution from suitable habitat: (1) a resource-based model incorporating sources of food, shelter, and water, and (2) a more standard model with assorted variables for topography, forest type associated with major ecoregions, and human features [89]. The two models only agreed on 16% of the predicted range area and 20% of the best-predicted habitat, even though both were based on habitat considerations specific to this species, and both fit the occurrence data well. Differences were in part due to gradients in shelter and key foods (first model) versus abrupt boundaries

between distinct forest types (second model). Later, they used the resource-based model to identify 13 key habitat patches, ranging in size from 400 to 5000 km<sup>2</sup> [90].

Meza Mori et al. used interview surveys to obtain presence points of Andean bears in northern Peru, an area with an altitudinal range of 120–4900 m and a wide range of temperatures and rainfall [91]. They used Maxent and 23 environmental variables (mainly bioclimatic), some of which showed complex relationships with presence data, to predict habitat suitability. Model results were driven by three variables (mean temperature, precipitation in driest month, and forest cover). Although the area of occupied range predicted by this model was similar to that of an IUCN (International Union for Conservation of Nature) map, the spatial overlap between the two maps was poor. The IUCN map was based on the model from Bolivia, mentioned above, and also only mapped patches of a certain size and connectivity [89,90]. Another potential source of discrepancy may be a spatial bias in the interview sampling. On the other hand, only about a third of the presence points in this study fell within the IUCN map, indicating that these new data records should help to better define the range of this species.

Another study in Peru, this one in the equatorial dry forest (a narrow low elevational band along the western Andes) used camera traps to individually identify bears by their facial markings, and thereby estimate density; spatial variation in density was compared to four remotely sensed habitat features [92]. Models for two study sites varied in terms of how many of these variables were included and showed differing effects of elevation and forest cover, apparently related to differences in food availability. Using an estimated density of 4 bears/100 km<sup>2</sup> as representing suitable habitat, they found that only 6% of the predicted range was within the IUCN range map; however, the map predicted by the model was mainly informed by a negative association with roads, rather than a positive association with natural habitat features, whereas the IUCN map was based on other features (but fewer presence points).

## 5.2. Sun Bears

A particularly controversial subject with regard to sun bears is whether they are able to survive in degraded or successional forests, following logging. This species has drawn particular attention in this regard because logging is greatly altering its habitat across much of its range in Southeast Asia. Furthermore, many forests have been converted to agriculture, especially oil palm (*Elaeis guineensis*) in Malaysia and Indonesia, and whereas it is clear that sun bears cannot survive in a monoculture of oil palm, there is mixed information about their use of oil palm plantations.

Scotson et al. accumulated by-catch camera trap photos from across the southern half of the sun bear range and found that a single variable, canopy cover derived from Landsat photos, predicted the rate of photo-capturing sun bears [93]. They did not attempt to include other variables in their model, but considered tree cover a surrogate not only for all other habitat variables, including the availability of food, but also (unexplainably) poaching. An alternate explanation for high rates of photo-capture under a dense canopy could be that bears tended to rest in shady areas to avoid heat stress [94]. Whereas other studies have confirmed that sun bears select for areas with high tree cover, a large number of studies have now demonstrated that sun bears are also widespread in degraded and successional forests in both the mainland and Borneo and Sumatra [67,95–99]. Hwang et al. also pointed to many other camera-trap studies that were not specifically directed at sun bears that have consistently shown high occupancy in forests 6–20 years after logging, and growing evidence that poaching is driving sun bear density more than habitat degradation [67,100].

In an extreme case of habitat alteration, Fredriksson used sign surveys to monitor sun bear use of a large patch of forest that was severely burned, killing most of the understory (and probably most insects) and 80% of fruit trees that bears had used for food [25]. Sun bears were forced to move to an adjacent unburned forest leaving the burned forest virtually vacant. However, within 7 years after the fire, bears began returning to the burned site; in particular, their sign indicated that use of termites steadily increased in the burned area.



This species' reliance on insects is often underappreciated. For example, Hwang et al. found that sun bears used a previously logged forest more than an adjacent primary forest during a poor fruiting year because the logged forest, with more deadwood, provided a greater abundance of termites and bees [67]. Likewise, at a site in Thailand where sun bears and Asiatic black bears occur sympatrically, Steinmetz et al. found that sun bears may be excluded from a habitat that provides high fruit abundance but can coexist with the larger black bears by concentrating on insects [26].

Only one study has so far attempted to determine habitat suitability for sun bears. Nazeri et al., in peninsular Malaysia, used presence records obtained from other sources and a Maxent model with a large number of variables to try to define suitable habitats [74]. This study, mentioned earlier, relied exclusively on presence points from primary forests. A later set of presence points collected by Abidin et al., namely sites of human–sun bear conflicts, which occurred most often on edges of forest-agricultural areas, showed that large areas deemed unsuitable by Nazeri et al. were occupied by sun bears [101].

Abidin et al.'s study is one of several showing that whereas sun bears require forest, they readily exploit oil palm plantations for food [101]. Indeed, sun bears that utilized oil palm fruits are significantly heavier than bears living in forests with no access to oil palm [56]. Normua et al. first showed that radio-collared bears moved back and forth between a forest and an adjacent oil palm plantation [102]. Cheah demonstrated this more conclusively with GPS-collared bears that used oil palm as their main food source, but spent daytime hours secluded in the adjacent forest [103]. Likewise, at other sites, Tee et al. and Guharajan et al. showed with camera traps and sign that sun bears heavily used a forest edge near an oil palm plantation (Figure 4) [98,104]. Large expanses of agriculture are certainly a barrier to sun bears, as evidenced by genetic segregation, but as Kunde et al. showed in Cambodia, a few individuals still manage to cross [105].



**Figure 4.** Sun bear habitat has been severely disrupted by oil palm plantations, but a big question is how much they use the fruits in the plantations. Shown here are oil palm fruits that were cut from trees and piled along a road at the boundary of the plantation and forest (before being picked up), easily accessible to sun bears. Bears thus do not have to climb and damage trees to obtain the fruit, and because they visit plantations at night, they are often not detected by workers [106]. Photo: D. Garshelis.



### 5.3. Sloth Bears

Few studies have been focused specifically on habitat use by sloth bears. In the early 1990s, Joshi et al. monitored radio-collared sloth bears in Chitwan National Park, Nepal and observed seasonal movements mainly by adult male bears between two major habitat types: alluvial tall grasslands in the dry season, and upland sal (*Shorea robusta*) forest in the wet season [46]. Most females and subadult males did not make this shift, and it is not understood why, although social factors were posited. The alluvium became saturated in the wet season, making the excavation of termites more difficult, but those bears that stayed there nevertheless maintained a largely termite-based diet. No other studies of this species reported a seasonal habitat shift.

Twenty years later Ghimire and Thapa conducted a sign survey in this same park, and compared use to availability of four habitat classes, and concluded that bears did not select for either the grasslands or the sal forest, as observed in the study of collared bears, but rather “mixed-forest” [107]. This study, though, highlighted a common problem in relying only on the ratio of use:availability—54% of the sign was found in sal forest, but because this forest was so common (and some was at higher elevations that the bears rarely used), it appeared that this most-used habitat was “selected against”, which of course is illogical [9].

Ratnayeke et al. studied the habitat use of radio-collared sloth bears in Sri Lanka, and compared use to availability of five vegetation types [108]. Tall forests, which were least disturbed by humans and had moister ground conditions with less dense understory, were most selected, although some bears also selected secondary forests. Bears in this study had exceedingly small home ranges, indicating that the available habitat provided a rich supply of food (mainly termites, with some seasonal fruits). It is interesting that whereas the earlier Nepal study found the highest use and density [58] in the grasslands, the shorter grass habitat in Sri Lanka was selected least. A Sri Lanka-wide sloth bear survey based on local interviews also indicated that bears were found mainly in forests with tall trees at elevations below 300 m [59]. However, these authors noted that sloth bears also occurred in forests with sparse tree canopy, but only if human disturbance was low, indicating that concealment is likely important.

In contrast to the situation in Sri Lanka, Akhtar et al. found abundant sloth bear signs in highly degraded areas in central India, but mainly in sal forest [109]. A critical resource in this area, identified in a separate study by the same authors but not in their general sign survey, is boulder fields where the bears can find refuge to rest during the heat of the day and when people in the surrounding area are active (Figure 5) [110]. Two studies in central India, both using DNA in scats to identify individual bears, found that some individuals moved substantial distances through narrow forest corridors between protected areas, while others traveled through human-dominated agricultural areas to get from one protected area to another [111,112], raising the question of what prompted bears to go on such long excursions, through unfavorable habitats, and how they managed to know where they were headed.

Three studies of habitat selection of sloth bears have occurred in the Western Ghats of southwestern India. Puri et al. conducted sign surveys, and using occupancy modeling found that forest cover, terrain ruggedness, dryness (less rainfall), and low human use were positively associated with sloth bear presence [113]. Following on these results, Srivastha et al. used occupancy modeling based on camera trapping (with temporal replicates) and sign (with spatial replicates), with forest cover, terrain ruggedness, and NDVI (Normalized Difference Vegetation Index, which is higher in wetter environments) as ecological variables [114]. However, they found that the two different sources of presence data yielded different results, with accordingly different habitat-based distribution maps. They suggested that micro-habitat features that they could not map, such as the presence of fruiting trees and termites (i.e., main food sources), would be better predictors of sloth bear habitat use. Ramesh et al. used camera trapping in one reserve in the Western Ghats, and measured habitat features at each camera trap station, including the fine scale food-producing factors recommended by Srivastha (although Ramesh et al.’s study came

before). However, they found that all of their covariates were weak predictors of sloth bear occupancy [115].



**Figure 5.** Sloth bears in parts of India regularly use crevices in boulder fields to sleep during the day and come out to feed at dusk. This key habitat offers protection from people and from heat, yet sampling bear sign within this habitat would greatly underestimate its importance. Photo: D. Garshelis.

#### 5.4. Asiatic Black Bears

Studies of habitat use have been conducted in at least 8 of 18 countries occupied by Asiatic black bears. Findings varied tremendously not just across but even within these range countries. Japan has a high population of Asiatic black bears on Honshu Island, which has attracted a number of studies aimed at understanding habitat needs. Three studies were conducted in Nagano Prefecture in central Honshu [116–118]. Early studies (1996–2001) with VHF radio-collars accumulated only ~500 total radio-locations over multiple years; one study had to eliminate 1000 of 1500 radio-locations due to uncertainty about the accuracy with respect to habitat patches [116], raising the possibility that the discarded locations may have been in habitats less accessible to the investigators (i.e., potentially creating a bias). A decade later, GPS collars provided far more locations [118,119]. No consensus pattern of habitat use or selection can be derived from the three studies, possibly because they were conducted in different parts of the prefecture. However, the GPS collar-based studies demonstrated that in summer bears selected early successional forests (after cutting, or natural avalanches) or along forest edges or near roads or rivers because berry production was high due to light penetration [118,119]. Another study in the Japanese Alps showed bears moving to alpine areas in summer and feeding on sprouting herbaceous plants [45]. An interesting takeaway from this telemetry study is that seasonal bear home ranges shifted elevationally, and therefore showed dramatic shifts in vegetational composition; the amount of selection at the scale of the telemetry location thus depended on whether the annual or seasonal home range was considered available habitat.

A study in Taiwan using both VHF and satellite-based radio-collars highlighted potential biases caused by VHF collars being more accessible to investigators in certain locations, associated with certain habitats [120]. These bears also showed significant elevational seasonal shifts, although not the same as reported in the Japanese Alps. Overall, bears selected areas below 2000 m, but it is important to note that this study was in a national park, so these lower elevation areas were not impacted by people. Bear use of habitats judged at the level of individual radio-locations tended to match the seasonally shifting availability.

A recent study in China accumulated and modeled presence data collected over 10 years, from various camera trapping studies, combined with absence data reported in some nature reserves and other surveys [121]. Employing 24 candidate variables, they generated a predicted distribution from maps at two different scales, which were based on different sets of predictor variables. The range area in the final map was 78% less than an IUCN map derived from expert opinion, utilizing some of the same data points. To some extent, this difference arose because the habitat-based map consisted of small, sometimes disjunct pixels, which a person creating a range map would necessarily join together into larger polygons. However, another reason for the discrepancy is that the model was informed by records of no confirmed presence (presumed absence) in broad regions classified as extant in the IUCN map.

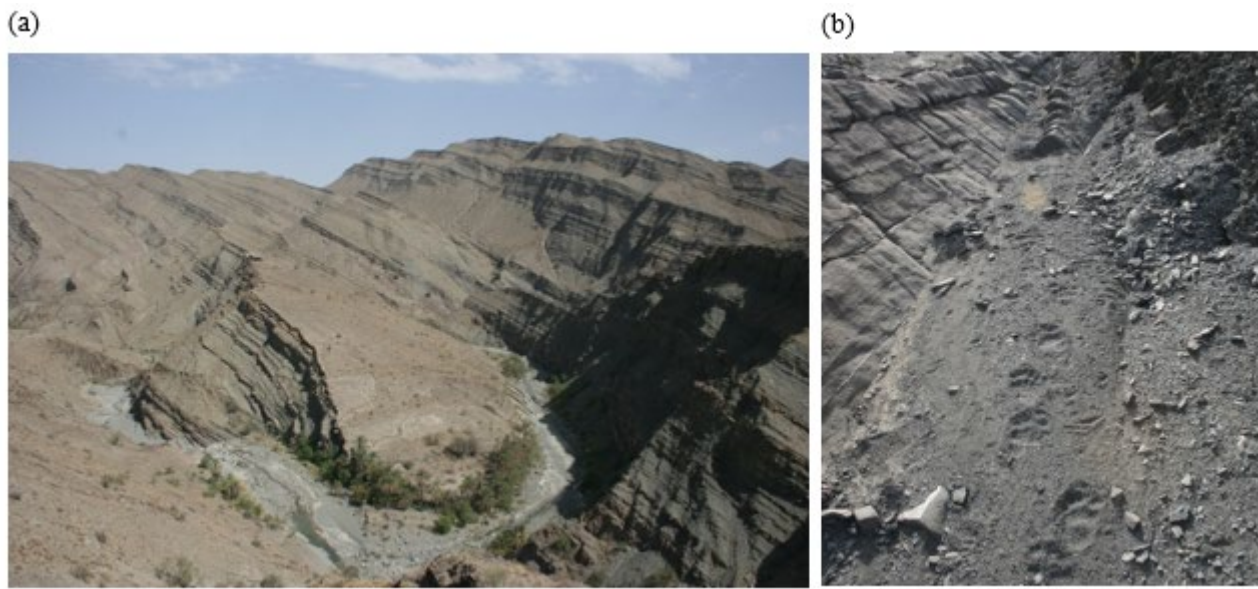
Nepal and Pakistan have similar habitats for Asiatic black bears, and three studies based on the incidence of sign highlighted selections of pine forests above 1600 m (below that was dominated by agriculture) [122–124]. Awan et al. found that different types of sign were associated with different habitats [124], raising the possibility that if detectability or decay rates of different sign types vary (e.g., feces and footprints vs. claw marks on trees), then that could confound the perception of habitat use (Figure 3). A wider landscape study, involving eight countries in the Hindu Kush mountains, employed presence points from multiple sources and explored the effects of 19 bioclimatic variables and 5 topographic or land use variables in a Maxent model; this study mapped the region of suitable habitat but did not provide specific information about what was considered most suitable, except in terms of elevation (1500–3000 m) [125]. Two Maxent models in a national park in Nepal, using the exact same presence data but employing different variables obtained similar range maps, but one used only variables related to topography and land cover [122], whereas the other used primarily bioclimatic variables and concluded that mean temperature was the strongest predictor of Asiatic black bear presence [126]. Given the wide latitudinal range of Asiatic black bears, from the tropics to the subarctic, it would seem doubtful that temperature per se significantly impacts where they occur, although the temperature was likely coarsely related to habitat features on the ground, especially sources of food.

In tropical Thailand (14° N), Ngoprasert et al. found that fruit abundance was 2.3x higher in the local vicinity of Asiatic black bear sign than where signs were absent [127]. Other measured habitat variables, including elevation, ground cover, human disturbance, and distance to a park boundary had no influence on occurrence. By contrast, in neighboring Laos, Scotson et al. used locally collected data near bear sign plus remotely-sensed predictors, and did not observe a significant relationship with fruit abundance [128]. Poaching influenced the incidence of bear signs probably more than habitat choices by bears, resulting in more signs in areas less accessible to people. Inexplicably, their model based on bear signs of all ages (some >2 years old) predicted higher habitat suitability over a much wider area than a model based only on recent signs (<1 year old).

At the other end of the habitat spectrum, in the arid region at the westernmost extremity of the range in southern Iran, Almasieh et al. obtained 200 existing presence points from other investigations and then added 70 new points [129]. Points were rarefied to exclude those <1 km from each other. These points fell into 31 discrete clusters, which they called habitat cores. They used topographic, elevational, landcover, and climatic variables in Maxent to predict habitat suitability, yielding 45 separate patches and over 50 potential corridors. They reported that canyon bottoms in riparian areas, which provided some food and shade, and steep slopes as security from people, were selected by bears (Figure 6). Farashi and Erfani obtained presence records, all from indirect sources, and created another modeled prediction for this same area, using 32 environmental variables, and a suite of 10 different models, of which Maxent performed the best [130]. Even though they used the same model and apparently many of the same presence points as Almasieh et al., their results were very different, with the predicted distribution being a large continuous region, rather than fragmented small populations. The reason is that this model was most influenced by annual precipitation, which would be more consistent than habitat features



across the region. Morovati et al. assembled another group of presence points through field studies; after rarefaction to reduce autocorrelation, their sample of 95 points was reduced to 53 [131]. Instead of just using presence, they also created pseudo-absence points, and using 15 variables, employed an ensemble of models to assess habitat suitability. This procedure produced a continuous distribution that excluded many of their own data points and which was spatially quite unlike either of the other two model predictions from this region. In this model, presence was positively influenced by increasing altitudes, from 300 to 2500 m, just opposite of Almasieh et al.'s conclusion that these bears seek valley bottoms.



**Figure 6.** Asiatic black bears in an arid environment at the western edge of their geographic range in southeastern Iran rely on date palm (*Phoenix dactylifera*) and other abandoned orchards as primary food sources. (a) They use valleys with water sources as places to obtain foods and as travel corridors. (b) Footprints of a bear in a valley bottom. Photos: A. Ghoddousi; T. Ghadirian.

### 5.5. Giant Pandas

Giant pandas are a conservation success story. Once an endangered species believed to be on the brink of extinction, they have been provided extraordinary protection through a system of nature reserves in combination with conservation measures outside the reserves, which together have served to provide an increasing area of suitable habitat and negligible human-caused mortality, enabling their population to increase [132]. Their total current range is restricted to a 25,800 km<sup>2</sup> area within six mountain ranges in three Chinese provinces. Within this small area, a large number of habitat assessments have been conducted, some within specific nature reserves, some in a specific mountain range, and a few using data from rangewide population surveys (National Surveys) conducted at ~10 year intervals, covering the entire extent of possible panda range. The intense effort at habitat assessment, by far exceeding that of any other bear species, is in accordance with a strategy of understanding and improving the habitat conditions both inside and outside reserves to increase carrying capacity, and to link available habitat so animals can move more freely.

In 2014, Hull et al. synthesized the findings of 23 giant panda habitat assessments conducted from the mid-1980s to 2009 [133]. Of these, 22 relied on signs (mainly feces) to define presence points, and 1 used radio-collars; 46 different habitat components were investigated. On the whole, these studies indicated that giant pandas selected for a high density of bamboo, gentle to moderate slopes with high solar radiation at mid-elevation and little human disturbance. In synthesizing these studies, however, Hull et al. observed that many of the studies may have introduced a bias in their sampling locations where panda sign was absent, namely being close to trails with easier access; moreover, studies



did not account for the variation in sign detection due to habitat (i.e., harder to see in very thick vegetation).

A key study by Zhang et al. in 2011 asked the question: “What happens if [due to issues with sampling or scale] the resulting habitat models are wrong?” [134]. This study, the first of its kind, utilized results of the Third National Panda Survey, conducted during 1999–2003. Field observers hiked transects covering the complete range of the species, located signs (feces, foraging sites, and dens), and collected detailed ecological data at each site plus control sites with no sign. They then constructed and compared models to define those variables that best distinguished a presence point from a control point. They found that the presence of bamboo and forest age (old growth versus secondary growth) were the strongest predictors of panda presence. The novel finding that old-growth was as important a predictor as bamboo was not readily explained. The authors posited that shade may have produced more nutritious bamboo, or tree cavities were needed for den sites. They argued for a revision in previous maps of suitable habitat, giving higher priority to old-growth forests. Ironically, another paper published in 2011, which was unique in examining habitat selection from the perspective of radio-collared giant pandas, found that they only chose areas with relatively low solar radiation (compared to what was available) during the peak of summer, but otherwise sought out sites of high sunlight (i.e., opposite shady old-growth forest), presumably related to ambient temperature [135].

Since the key papers by Hull et al. and Zhang et al., more than a dozen additional panda habitat studies have been conducted. Some of these employed GPS radio-collars, leading to some significant new insights. Prior to that, during 1995–2006, a Chinese government moratorium precluded using radio-collars on giant pandas. Four pandas were tracked for about a year each in 2007–2009 in Foping Nature Reserve and five were tracked for about a year each in 2010–2011 in Wolong Nature Reserve. The Foping data showed extensive individualistic seasonal shifts in elevation [136]. In Wolong, Hull et al. confirmed high use in what previous studies ascertained as suitable habitat: forested, gentle slopes at mid to high elevation with high solar radiation. However, the collared pandas also used non-forested (shrubby) habitats and steep slopes, previously deemed to be unsuitable in sign surveys (possibly because they were undersampled) [137]. Selection of habitats varied among individuals, across seasons, and depended on scale (placement of the home range or choice of habitat within the home range). Bai et al. used these same five collared pandas in Wolong, and compared a host of fine-scale habitat features measured on the ground in core versus secondary (distinguished by the amount of use) parts of the home ranges [138]. One of their new findings was that slope steepness was not a good predictor of core vs. secondary use within home ranges. Previously it was thought that giant pandas avoided steep slopes to save energy. In this study, though, it was found that they selected for areas with animal paths through the thick bamboo, which would help conserve energy.

Other recent papers used presence points from the Third and Fourth (2011–2014) National Surveys. A comparison of the locations of panda sign between these two rangewide surveys revealed that pandas shifted in terms of some key variables [139]. Importantly, the selection for old-growth forest discovered in the Third National Survey disappeared 10 years later in the Fourth Survey because the early successional areas outside the nature reserves had matured somewhat, and surprisingly, pandas were found to be equally likely to use these secondary forests as primary forests; that is, habitat suitability improved significantly outside reserves commensurate with a ban on logging [140]. This positive conservation finding was diminished by a new emerging threat: it was found that elevation of panda use increased, not due to a change in elevation of bamboo, but to increased livestock grazing at some lower elevations.

Livestock grazing deters panda use [141,142], probably owing to their disturbance, and their consumption and trampling of bamboo [143,144]. This problem has been increasing as people switch from farming to livestock [145]. A number of studies have also reported that pandas actively shun human development, including roads [133,146–148], which not only present a hazard but also reduce nearby regeneration of bamboo [149]. It now seems

clear that a reduction in human activities, grazing of livestock, and road building would be a top priority for improving panda habitat and thus benefiting its conservation, at least in the short term [150,151]. Longer term challenges remain insofar as effects of climate change, both on the availability of bamboo and also possibly on temperature effects on pandas directly [152], although model predictions differ greatly [153,154]. However, it must be remembered that just a few centuries ago, giant pandas occupied lowland habitats, where temperatures were higher than in the mountains where they live now, and where they consumed different kinds of bamboo and other plants [155]. Although giant pandas are specialist feeders, the many habitat studies that have been conducted have shown that selection can change with differing availability of resources and changing threats, and also that such changes are perceived by pandas at multiple scales [156].

### 5.6. Brown Bears

Reviewing all of the many habitat studies of brown bears around the world would require a full paper on its own. Here, we take a tour across four countries in Asia, eight in Europe, and two in North America, to get a flavor for the techniques and findings, which sometimes conflict.

In Asia, studies have been based mainly on presence points (Figure 2). The brown bear population in Iran has been the subject of an inordinate number of habitat studies (at least seven), all using species distribution modeling. One Maxent-based study examined habitat in the lush Hyrcanian forests along the southside of the Caspian Sea along the northern slopes of the Alborz Mountains, and found that bears selected for forested habitats away from human settlements and roads [157]. Another study in the same region using the same model concluded that steeper slopes and higher NDVI were the best positive predictors of habitat suitability, with human disturbance a negligible factor [158]. In the northwestern corner of Iran, in the Caucasus region, investigators ran five different models with presence points and found varying results; the most consistently chosen variable was a positive relationship with shelter afforded by topography (e.g., valleys) [159]. Widely spaced patches of suitable habitat suggested low connectivity. Moving south, into the Zagros Mountain range, two studies found that bears selected for higher elevations (>2000 m), away from people and roads. One of these also indicated that bears preferred areas farther from forest [160]. The other study indicated that the habitat requirements were such that within an area of just 35,000 km<sup>2</sup>, there were 33 distinct patches of suitable habitat with uncertain connectivity among them [161]. In a semi-arid area in the Zagros of Fars Province, marking the southernmost distribution of brown bears worldwide, the overriding factor in habitat selection was availability of water, but staying away from roads was also important [162]. The most recent study obtained 184 independent presence points across the entire range of brown bears in Iran, some collected opportunistically and some from prior research studies [163]. This model chose different principal predictor variables than previous studies, in part because it was a different model (Random Forest vs. Maxent) at a different scale and covering a wider geographic area, and in part because presence points were obtained from opportunistic observations, which could have been biased. The degree of fragmentation of the predicted populations based on habitat suitability depended on how far these bears were likely to disperse. Contrary to some of the findings from the habitat models, a landscape genetics study across the entire brown bear range in Iran showed high genetic variability and interchange within each mountain range (i.e., no obvious fragmentation), but separation between the Alborz-Caucasus bears and the Zagros bears [164].

A consistent finding of the many studies in Iran is that habitats selected by bears were strongly influenced by human development. However, the perceived impact of this factor depended on exactly what parameters were included in the model. For example, in Turkey, elevation and indices of roughness and ruggedness predicted the occurrence of brown bears, but they may have been surrogates for bears avoiding flat places occupied by people, since the investigators did not include anthropogenic variables in the model [165]. Another

investigation in Turkey, employing GPS radio-collars discovered two distinct behavioral types: (1) bears that avoided people and made long-distance seasonal migrations, and (2) more sedentary bears that relied on human sources of food and selected for areas near roads and buildings [166]. This raises the question as to whether investigations that rely solely on presence points would even include observations of bears in and around towns as such areas might not normally be sampled.

Many studies now obtain occurrence data from open access databases, with little understanding as to how they were obtained, and possibly little experience with the species on the ground. For example, a Maxent modeling study covering 11 countries in Central Asia obtained all data from the Global Biodiversity Information Facility (<https://www.gbif.org>, accessed date (20 December 2021)), then selected points within protected areas, and concluded that annual temperatures and precipitation accounted for >90% of the brown bear's predicted distribution, and that landcover, elevation, slope, and aspect mattered little [167]. Likewise, a Maxent-based study on the Tibetan plateau concluded that climatic variables dictated the bears' distribution, whereas 14 different types of landcover had no apparent effect [168]. Seemingly contrary to this finding, a study by the same investigators in the same study site found that landcover, human population density, and NDVI were the three main factors explaining where bears broke into people's houses, a problem that has become extreme in this area [169]. A particularly thorough study in the Himalayas, where investigators collected 720 presence points through their own field sampling, reported that a mixture of climatic, landcover, and human population variables, optimized at a broad scale (generally 64–128 km radius from the bear), were all important, and all relationships were nonlinear; this region has extreme seasonal differences in temperature, rainfall, snowfall, and topography [170].

Brown bears in Europe face different circumstances than in Asia, as nearly every population is heavily impacted by people, and some are small and isolated, although several are expanding [35,171]. Systematic surveys to look for bears and bear signs have been conducted in both the Cantabrian (Spain) and Pyrenees (shared Spain and France) populations, yielding many thousands of data points (one study obtained >3000 separate video recordings of bears) [172]—in fact, far more than all the presence points combined for brown bears in Asia. Using these data, studies found that bears selected for rugged forests with hard mast, and selected against areas close to roads, homes, and agriculture [173,174]. However, since the Pyrenees population is still expanding, it was not possible to differentiate unsuitable habitat from habitat that simply was not yet occupied. Furthermore, as Mateo Sanchez et al. found, bears respond to some factors close by (e.g., food patches) and others more distantly, so habitat suitability models can be quite sensitive to the scale at which each variable is measured [175].

Studies in central Italy were similar to Spain and France: presence data indicated that bears selected for forests with mast, and against sites near people and agriculture [176–178]. Falcucci et al. overlapped habitat suitability model results (from >2500 presence points) for Apennine brown bears with a risk map based on locations of mortalities (mainly anthropogenic), and found that 43% of the area considered highly suitable habitat was close to roads and was a high mortality risk from anthropogenic causes—that is, one cannot tell from presence points alone whether suitable habitat is also a mortality sink [177]. Indeed, Maiorano et al., modeling a compilation of >5000 independent presence points from radio-collared bears, sightings, tracks, hair, and scats in this population learned that there is substantial overlap in the use of mast-rich forests by bears during fall, and by hunters chasing wild boar (*Sus scrofa*) with dogs, which poses a clear risk to bears [178].

In the Italian Alps, investigators preparing to augment a very small, relict population created a habitat suitability map based on presence data. This predicted that bears would use the forests and stay away from human-developed sites with homes or agriculture. Resource Selection Functions generated from collared bears after the augmentation were compared to the former predictions, and found concordance in some respects, but bears actually used orchards and shrublands more than predicted by the initial model, and also

crossed roads more than anticipated [179], again showing that mortality risks may be underestimated in habitat models built from presence points.

In Greece, bears with GPS radio-collars selected for rough terrain away from people, but they came closer to human-related habitat features, such as dwellings, roads, and crops at night [180]. In a number of other European countries, brown bears are attracted to feeding sites with the purpose of either diverting them from using foods in human settlements (diversionary feeding), or congregating bears for hunting or viewing (supplemental feeding). There is now growing evidence that such feeding reduces the size of bear home ranges and likely alters their use of habitats [181,182]. In Slovakia, maize fields have been increasing, and some GPS-collared bears relied on these during fall, whereas other individuals continued to select woodlands and natural foods [183].

In Sweden, bears with GPS radio-collars selected for steep slopes and regenerating forests; those living nearer people selected especially steep slopes, although this selection eased at night when people were not active [184]. The authors explained that regenerating forests had more food (ants, herbaceous plants, berries, and moose [*Alces alces*]). Follow-up studies in the same area showed that bears exhibited consistent individual differences in habitat selection, and moreover that some individual patterns were not apparent at the population level [185,186]. For example, at the population level, bears strongly selected for young forests and against bogs, but on an individual level this dichotomy was not as evident, and may have varied with sex, age, local habitat availability, local population density, learning, and different behavioral responses to the environment.

In North America, a large proportion of habitat selection studies for brown bears/grizzly bears have relied on bears with GPS radio-collars, allowing for investigations of individual, seasonal, and yearly differences. In the Yellowstone Ecosystem, USA, for example, it was well established that grizzly bears were dependent on the seeds of white-barked pine (*Pinus albicaulis*), given that this food factored heavily in their diet and that year-to-year variations in mast crops had significant demographic consequences [187]. However, GPS collar locations showed that about a third of the population made negligible use of white-barked pine, and further, that as availability of this resource declined from trees dying, the bears, unexpectedly, reduced their use of this food, and shifted to alternative foods and habitats [188]. That is, there was a negative trend in the selection for what had been thought to be a preferred habitat.

A big advantage of monitoring individual bears is in being able to decipher different scales, or orders of selection (sensu Johnson [6]), and in understanding mechanisms and motivations for selection and changes in selection. A study in the foothills of Alberta, Canada, found that radio-collared grizzly bears were located in forest clearcuts 23% of the time, and these cuts made up 19% of the landscape, but this broad scale view provided no insights as to their attraction to this habitat: it turned out that they selected it more than expected from availability only during the summer, when feeding largely on ants and ungulate calves [189]. Furthermore, bears selected for certain specific ages and portions of clearcuts (i.e., high light penetration supporting ants on dry warm slopes). Moreover, bears shifted the time of day that they used young clearcuts and more often used older, shadier regenerating cuts, so as to avoid overheating; this result was shown by matching the timing of GPS collar locations in different habitats to temperatures continuously measured there [190]. A follow-up study revealed a high selection for edges between forests of different ages, but this selection was stronger for females than males [191]. Examining data from these collared bears further it was found that their habitat choices were learned over time, and not instinctual [192].

In the same Alberta study site, movements of GPS-collared bears were compared to patches of Canada buffaloberry (*Shepherdia canadensis*), a primary food during late summer and early fall. Bears selected for areas with high contrast in fruiting density between patches of this key food resource [193]. However, their selection for habitat heterogeneity was at a rather small scale, equivalent to their average travel distance within a 5.5 h window (~1900 m).



In neighboring British Columbia, Canada, perceptions of grizzly bear selection varied enormously by the scale of the investigation, suggesting that studies that chose a single scale were prone to misinterpretations. This was demonstrated by several different studies: one used radio-collared bears [194], another used bear visitation at hair snaring sites (visited or not visited during a site check) [195], and yet another used bear densities estimated by DNA from hair-snare sites [196]. To some extent, scale dependency occurs because availability varies by the scale at which it is measured—in other words, the scale issue is a function of the way people examine the selection process that bears make. This causes some habitats to appear to be selected for when viewed at some scales and selected against at other scales. However, additionally, bears may respond differently to habitat variables at different scales. For example, Apps et al. showed that grizzly bears selected for high elevations, steep slopes, and rugged terrain, all to stay away from humans, and at a broad scale, selected for landscapes of higher forest productivity; however, at a finer scale they found a surprising negative association with a “green vegetation index” (from Landsat imagery), because areas of high greenness included both avalanche chutes (which were attractive feeding places) and wetlands (which were avoided) [195].

In another scale-dependency example, a grizzly bear study in a barren-ground environment north of treeline in the Canadian Arctic found that radio-collared bears of both sexes incorporated eskers and tussock/hummock tundra into their home ranges, because these habitats provided the most food in terms of berries, sedges, grasses, and ground squirrels. However, looking at fine scale usage within home ranges revealed that females with young avoided these habitats when males were most likely to be there, indicating that they adjusted their habitat use to avoid infanticide [197].

### 5.7. American Black Bears

American black bears are routinely studied using radio-collared animals, so it is not surprising that this technique is widely employed in habitat studies (Figure 2). In a particularly unique study, Gould et al. used bear detections at hair-sampling sites in an occupancy model to predict the probability of bear use, then tested and verified the results with radio-collared bears and sites where bears were killed in the sport harvest in New Mexico [198]. However, their model was at a coarse scale, including only a positive association with an index of primary productivity (EVI, enhanced vegetation index) and a negative association with roads. Furthermore, their model over-predicted use in an irrigated agricultural area (with high EVI). Some recent innovative studies examined relationships between estimated bear density and habitat, integrating spatial capture–recapture with locations of GPS-collared animals [199,200]. Welfelt et al. discovered that the greater primary productivity in western Washington than in arid eastern Washington did not translate to a higher bear density, due to higher human densities and hence greater human-caused mortality in places where primary productivity was high [200].

Among telemetry studies, sample sizes in terms of the number of individuals and number of locations vary enormously, but GPS collars are now providing massive amounts of data. A recent exemplary study included >86,000 independent locations (reduced from >277,000 in the full dataset) obtained from 236 adult bears over a period of 36 years across the bear range in Florida [201]. Among various studies, analyses have entailed fewer than 10 to more than 20 habitat variables, including vegetation, water, anthropogenic features, and topography. The inclusion of more variables has often revealed that habitat selection or suitability is not easily defined as a certain forest type, but may be a complex array of factors that changes over the course of a year with changing food availability. Moreover, bears may benefit greatly by visiting very small habitat patches with concentrated foods, not easily detected in studies, and for which availability is difficult to quantify (Figure 7).



**Figure 7.** American black bears are attracted to concentrated food sources, such as (a) lush sedge along the shoreline of a coastal bay and (b) a small garden of sunflowers. Most habitat use studies are unlikely to be able to measure either use or availability at such a small scale, and moreover, the short time feeding at such places greatly underestimates the attraction to and importance of these food sources. Photos: D. Garshelis.

Several studies have found that American black bears select for habitats known to produce the fruits and nuts that constitute the main portion of their diet, and may avoid some types of anthropogenic features. The actual forest types producing bear foods vary across regions, with deciduous or mixed forests typically used more due to higher food production than pure coniferous forests [202,203], although with some exceptions for those conifer species that produce fruits important to bears [204]. Only a few studies actually measured fruit production in different habitats to inform a habitat model [205]; others attempted to use “greenness” (NDVI) as a surrogate for food production, with mixed results and difficult interpretations [206]. Many fruits that black bears consume are most productive in forest openings or along forest edges; accordingly, some studies found that forest cutting can increase the diversity and abundance of fruits, thus providing better bear habitat [207,208]. Sollmann et al. found that bear density was highest where high forest cover was broken by openings, but were unsure if the openings enhanced fruit production or provided anthropogenic foods [199].

American black bears also may select for habitats where ungulate prey are seasonally available, as for example during moose calving [209,210]. However, studies in both Alberta and Newfoundland, Canada, found that only some individual GPS-collared bears selected for habitats where caribou calved, whereas most of the population did not [211,212]. Furthermore, the traits of individual bears in terms of whether they exploited caribou remained consistent year to year [213].

In some areas, American black bears selected river valleys as corridors for movement through otherwise developed or agricultural landscapes [205,214,215]. Water availability, used for travelways, forage, drinking, and cooling, may be important in some regions but not others [216–218]. In Louisiana, on the landscape scale, bears selected areas with swamps, which comprised just 2% of the landscape, because of an essential tree species that provided elevated cavities for hibernation; however, on a finer scale and during spring-summer months, bears in one study site selected swamps, whereas bears in another site, just 10 km away, had different resources available and did not use swamps [219].

Poor et al. made the important distinction that habitat suitability is not the same as habitat preference: American black bears exhibit high behavioral plasticity and can often adapt to changing conditions related to human development and forest modifications [201]. As an example, the common finding that most bear species avoid roads may be situation-

specific. In Wisconsin, forest roads with little traffic had a positive influence on where radio-collared bears selected their home ranges, although no apparent influence on their habitat use within their home ranges [218], probably indicating that the most roaded portions of the forest were places that happened to offer the best resources for bears, but the roads themselves were not the attraction.

A study of habitat suitability for a group of 18 midwestern U.S. states based on expert opinion highlighted a significant difference of opinion about the effect of roads in particular [220]. Presence points helped validate the model, but 23% of presence locations fell outside the area of most suitable habitat as judged by species experts, suggesting that experts have a narrower sense of what bears need. On the other hand, the expert-based model likely over-estimated the suitability of some portions of as yet unoccupied range due to some fine-scale habitat features that were not included in the broad-scale model.

One purpose for modeling habitat suitability is to predict bear population expansion. This can be particularly difficult because the locations of bears in occupied habitats may not foretell the full suite of habitats that they could potentially occupy; that is, the model may be misinformed by being limited to data from bears inside the current range. Dittmer et al. observed bears at the edge of their range within a sparsely-forested area of Minnesota (considered atypical bear habitat) and used short time windows of habitat use by collared bears to try to predict the minimum amount of forest that they could tolerate; they used this to gauge how far west across a gradient of decreasing forest the population could expand [205]. Gantchoff et al. argued that habitat models could over-estimate the potential range if the sexes are pooled, because females in their expanding population in Missouri were observed to be more constrained to less human-developed areas than males [221]. However, their frame of reference for what females could tolerate was based on where females lived currently. Males are more exploratory and may first venture into novel habitats, but females in more established populations coexist with males in human-developed areas [215].

Population expansion in Mexico offers a particularly intriguing test case for model predictions. Delfín-Alfonso et al. employed a long-term collection of presence points (582 points over 120 years) and examined 19 climatic variables and 4 terrain variables to define a potential distribution, which has been expanding from northern Mexico southward [222]. However, new occurrences of bears have since been reported far south of that model's predicted suitable habitat [223,224]. Another model, restricted to more recent presence points (being more accurately associated with current habitat conditions) and variables related to land cover, elevation and human density, but not climatic variables yielded better predictions relative to these points at the current southern limit of the range (21° N) [225]. On the other hand, the presence of wandering black bears well outside their primary range is not necessarily indicative of a population expansion nor of what constitutes suitable habitat [226]. Only time will tell the difference.

## 6. Conclusions

This review, covering 141 studies of fine-scale habitat use of the seven species of terrestrial bears, yielded three important conclusions: (1) bears use an enormous array of habitats, and adapt to changing conditions in a variety of ways; (2) biases and weaknesses in some of the techniques used to assess habitat selection and suitability have sometimes produced inconsistent or misleading results; and (3) management or conservation recommendations arising from many of these studies have been very limited. This paper concludes by addressing each of these topics.

### 6.1. Adaptability of Bears

One commonality among many of the studies is that human disturbance (e.g., distance to settlements or roads) may strongly affect habitat selection, meaning that what is observed in a human-dominated landscape is different than what would be observed in a landscape without people. Habitats judged to be unsuitable might only be avoided because of people.

For example, bears likely do not avoid roads or habitats along roads, but rather avoid the risk of being hit by a moving vehicle [227]. Indeed, when a COVID-induced lockdown reduced human activity, brown bears in an isolated population in the Italian Alps crossed roads more and used a wider array of habitats [228]. Hence, it is not enough to categorize habitat suitability or barriers simply in terms of human infrastructure, but rather to gauge the effects of human presence. Bears apparently recognize the difference.

Bears also weigh the potential threats of people versus the benefits of foods that humans provide. Thus, whereas some bears might be repelled by human disturbances, other segments of the population are attracted to human-related food sources and may profit nutritionally, even if at more risk. Sun bears exploiting oil palm plantations at night are heavier than those consuming only natural foods. Asiatic black bears in an arid habitat in southern Iran with few natural foods rely extensively on abandoned orchards for subsistence. In the Italian Alps, reintroduced brown bears were predicted not to use orchards, but they did. Some rare, recent sightings of brown bears in Syria occurred in orchards [229]. High densities of American black bears occur near anthropogenic food sources, and population expansion may be facilitated by the availability of edible crops.

Bears are very driven by food. However, whereas many studies have investigated habitat selection, few have investigated food selection in the same way, in part because the availability of different foods is much more difficult to measure. The breadth of the diet varies among areas and species, with the simplest case being the giant panda, which focuses completely on one source of food (although different parts, ages, and species of bamboo). Typically we assume that high use of certain foods is equivalent to selection, and that bears adapt their use of habitat according to the availability of preferred foods that occur there. However, as demonstrated by the case in Yellowstone, where brown bears shifted their focus away from a key declining food [188], our predictions about how they will adapt to changing foods may be wrong. Similarly, brown bears relied heavily on salmon (*Oncorhynchus nerka*) in Kodiak, Alaska, and in normal years adjusted the timing and location of foraging commensurate with the availability of spawning salmon in different streams [230,231]. However, in years when red elderberry (*Sambucus racemosa*) fruited unusually early due to higher than normal spring temperatures, then coinciding with the main salmon run, bears unexpectedly departed the salmon streams to feed on these berries in the hillsides [232]. Likewise, sun bears, which clearly benefit from a bounty of diverse fruits during masting events in primary forests, nevertheless selected for a neighboring secondary forest that produced more insects when fruits were less available [67]. The same seems true for shelter: whereas sun bears often choose resting sites in the canopy of tall trees in primary forests, they use other types of trees to rest in secondary forests [97], and there is no evidence that their health or survival is reduced by doing so. This makes the point that there is a difference between what bears select when offered certain options, and what they need. Most habitat studies (not limited to bears) do not investigate what is truly needed [9]. This may lead to an underappreciation for what bears are capable of adapting to in a changing landscape. That is not to say that we should not be alarmed by trends in declining forest cover in Asia, or by climate change-related projections, but rather to inject some caution on conclusions from habitat suitability modeling.

This review has shown that in a number of cases, bears have been observed in places that models have classified as unsuitable habitat—Andean bears in Peru, sun bears in Malaysia, sloth bears in non-forested areas in India, American black bears in central Mexico. In some cases there may be a distinction between a few wandering individuals and a viable population, but on the other hand, population expansion often begins with the exploratory movements of a few individuals into habitats that differ from where the core population resides [233].

## 6.2. Methodological Shortcomings

The basic method for assessing the suitability of habitats involves measuring use and availability, and comparing the two. Each of these is difficult to measure, and errors or



biases can lead to significant misperceptions. The least biased method for measuring use involves GPS radio-collars. Unlike VHF collars, where locational data were often limited by investigator access and certain times of day, GPS collars provide data wherever the bears go. For 11 years investigators were forbidden from using collars on giant pandas, but when this moratorium was lifted, the new GPS collar data showed that pandas frequently used habitats previously thought to be unsuitable. Radio-collars also provide a view into sex, age, and individual differences. Furthermore, by tracing the routes of bears, one can examine the speed of travel and surmise decisions that bears make with respect to habitats (e.g., clustering of points vs. quick travel through). Moreover, since investigators can obtain locations in near real time via satellite transmission, it is possible to visit points where the bear had just been and examine micro-habitat features that explain why it was there [234].

Sign surveys also can provide information about micro-habitats, but not connected to an individual bear in real time. Furthermore, it is more difficult to ensure unbiased sampling, since the sign is only visible where the investigator looks, and investigators may spend more effort searching in places where they think the bears are likely to be. Further, and importantly, detectability varies by type of sign and by habitat, and different types of signs are apt to be more prevalent in different habitats. Asiatic black bears and sun bears climb more trees and leave easily recognizable claw marks in a forest with many fruiting trees, but in forests where they rely more on insects, signs are harder to detect or to reliably distinguish as being from a bear (Figure 3). Some studies of sloth bears and Asian brown bears have relied on scats, which are easy to distinguish, but scats are more detectable in open habitats.

It is now becoming increasingly common for investigators to obtain data that they did not collect, including camera trapping records from various sources (e.g., so-called by-catch data from studies not focused on bears) and open-access data repositories. These sources provide even less control against sampling biases, and also force the investigator to rely on habitat features obtained from remote sensing rather than on the ground. This limits the scale and nature of the data and also disengages the investigator from the species and conditions on the ground.

Availability is even harder to measure because it involves interjecting a human perception into what the bear perceives as choices. However, the investigator's measure of availability often drives perceived selection. Presence-only models, like Maxent, rely on sampling the background, where the investigator sets the frame of that sampling. Often that sampling is done on a computer, but sometimes investigators have gone to the field to examine "pseudo-absence" points, which are intended to be a random selection of points with no confirmed presence. Even in the best of efforts, though, as shown with giant pandas, investigators may introduce biases by choosing sampling points that are less difficult to get to. Studies have come a long way in recognizing that availability is scale-dependent, and new sophisticated techniques allow for varying the areal window around presence points to try to find the scale at which habitat covariates are most influential.

Availability, and hence selection, changes over time. In the short term, food conditions change within habitats, sometimes week to week. Temperatures within habitats can also change. Hence, certain habitats or portions of habitats are selected only at certain seasons and times of day. If that time frame is short, then on a coarse level it may appear that the habitat is unimportant. Changes also occur over longer time frames. A common example is forest regeneration. When logged forests were newly regenerating outside panda reserves, pandas selected for old-growth forests. However, the perception of old-growth being a key characteristic of habitat suitability turned out to be wrong, as shown by pandas' increasing use of later successional forests that were protected from logging.

Threats also can change over time and vary spatially. Whereas panda habitat improved outside reserves, increased livestock grazing inside some reserves affected bamboo and pandas directly. The most obvious threat is direct killing by people, which for many bear populations (except pandas) is a main population driver. Human-caused mortality reduces density and may thereby alter bear distribution relative to habitat. It can thus appear

that habitats subject to the highest levels of human-caused mortality are actively selected against by bears. Conversely, bears may choose habitats that unknown to them have a high mortality risk, and in that sense, these “attractive sinks” may really be viewed as less suitable, even if they provide abundant resources [235]. Ciarniello et al. found that grizzly bears in British Columbia, Canada, existed at one-quarter the density in an area with better food resources than a more mountainous area where foods were poorer because in the food-rich area they foraged close to roads where human-caused mortality was high, whereas in the mountainous area they foraged farther from people [236]. Likewise, in another site in British Columbia, Lamb et al. estimated demographic parameters from DNA mark-recapture information and found that in a local area rich in production of some key berries, grizzly bear survival was low and population growth negative, due to high human-caused mortality, but bears actively moved into the area due to the attractive foods [237].

### 6.3. Implications for Habitat Management

The number of studies employing niche models, habitat suitability models, or species distribution models has been exploding, with over 1000 new papers published yearly on a variety of species [238–240]. In this Section 7, we explore some issues that may limit the implications of models for the management and conservation of bears worldwide.

A basic issue is whether model results are likely to be reliable and useful. For many papers, it is hard to assess the quality of the data, and why certain predictor variables were chosen, due to poor or unclear protocols, and general lack of standardization and documentation [240]. Presence points are often obtained with sampling methods that are not fully described, or retrieved from public databases where multiple sorts of errors may occur [241]. The number of points used in the models reviewed here ranged from several thousand to less than 100. Predictor variables are likewise either collected in the field (micro-habitats near points), or from easily-accessible databases. The number of predictor variables in the models reviewed here ranged from more than 20 to just 1.

Investigators can create models with easy-to-use programs (e.g., Maxent) and high computing power. This has the advantage of allowing investigation of a wide range of potential influences at various scales. It is now increasingly evident that scale optimization is both species and habitat dependent, and essential for creating models that better mimic nature [62,242]. However, this review has also highlighted some associations that are hard to explain. For example, is bioclimatic variability the actual factor driving the distribution of brown bears in Central Asia, or does temperature and precipitation affect local food availability (e.g., [243]), or are they related to other habitat characteristics that were not measured [244]? Models commonly use environmental or bioclimatic surrogates, but biologists should ideally consider the foods that bears rely on in each habitat plus risks they are likely to face. The profusion of available data in the hands of investigators who have limited experience with the species has the danger of creating what Nielsen et al. [245] called a “technology trap”, leading to misinterpretations and misguidance for practitioners. Studies on the ground are still needed to either verify or correct the deductions stemming from models [67].

Some studies, mainly in North America, have linked habitat associations with density, which is ultimately what managers and conservationists are interested in [196,199,200,246–249]. On the other hand, density can be as much a function of human-caused mortality and social factors within bear populations as other components of the landscape [200,236,246,249]. Furthermore, it may be difficult to relate density, which inherently pertains to some larger area, to fine-scale habitat features. In a dry forest in Peru, cliffside travel corridors, waterholes, and patches of fruit were observed to be important for individually identifiable Andean bears, but density was too blunt an instrument to pick these out as crucial habitat features [48,92]. Better than density would be linking habitat to fitness [10]. In a unique such study in the Canadian Rockies of Alberta, Boulanger et al. found that radio-collared

grizzly bears gained weight more quickly if they had access to forests of multiple seral stages, but as a consequence of living in this area suffered higher rates of mortality [250].

Models built from presence points yield a snapshot of how animals are likely to be distributed on the landscape but may not be good at predicting how populations are apt to respond to landscape changes. The concept of a gradient of suitable habitats may lead practitioners to assume that increasing the availability of the most suitable habitats should increase population growth, but for generalist species, this may not hold true. If bears have enough of the preferred habitat, then providing more of it will not necessarily increase use, or population growth [9]. Generalist omnivores are likely to benefit from variety, even if some habitats provide more food or better shelter. Additionally, a number of studies are beginning to show that individual or sex-age related variability plays a part in selection, so what seems best on a population level, might not be best for all. Moreover, it is worth being cautious of results of any single study given the variability and discrepancies among studies.

Discrepancies may arise for a number of reasons. Some datasets may be biased. Equally important, we might expect models supplied with different arrays of predictor variables to gauge habitat suitability differently. These factors may account for the inconsistent results obtained among studies of sloth bears in the Western Ghats of India, Asiatic black bears in central Japan and southern Iran, and brown bears in the Zagros Mountains of Iran. As this review has demonstrated, combinations of variables at different scales can help explain where bears occur on the landscape, but these should be viewed as imperfect surrogates for how bears actually discriminate habitat suitability. Population-level views may inaccurately represent the variation in behavior that exists within populations. Further, being highly adaptable, bears are likely to find ways of coping with site-specific circumstances in different ways. As such, it is not surprising that a model generated from observations in one area may not readily transfer to another. A good example is the rangewide map of Andean bears generated from a Bolivia-based model which poorly matched results of site-based models in Peru.

Scharf and Fernández compiled data from habitat studies of brown bears across Europe, and tested predictions from a composite model against previous individual site models [251]. They found transferability of results to be high among sites close together, but weaker for distant sites, where conditions are more different. In particular, individual models used different surrogates for human impacts; furthermore, the way humans interact with bears varies geographically. The composite model for European brown bears predicted that only 56% of the area actually occupied by bears is suitable habitat, suggesting that the model greatly under-estimated what bears view as suitable (i.e., what they can adapt to). By contrast, a study that compared habitat suitability models for snow leopards (*Panthera uncia*), a more specialist species than brown bears, concluded that despite some differences in sampling and predictor variables, models were in basic agreement about that species' habitat needs [252]. This is also generally true for giant pandas, the most specialist bear; nevertheless, some significant differences exist between panda habitat studies, some of which may be due to ecological differences among the six mountain ranges that they inhabit, some due to changing environmental conditions, and some due to different sampling of points, different variables, and different scales.

A recent review paper by Lee-Yaw et al. investigated 201 studies, spanning a diverse array of animals and plants, that tested the predictions of species distribution models against independent assessments of occurrence, abundance, population performance, and genetic diversity [253]. Of these, predictions of occurrence were by far the simplest, yet only half the model predictions were accurate. The authors emphasized that predictions from these models should be treated as hypotheses in need of testing with other data, rather than informing management and conservation directly.

Many of the bear studies reviewed here made predictions about the future—often dire consequences of habitat alterations from logging or climate change (e.g., [93,167]). What is generally lacking, though, are real tests of these predictions (but for other taxa

see [254,255]). In the particularly unique case of two rangewide giant panda surveys conducted 10 years apart, the first showed a strong reliance on old-growth forest, while the next survey (essentially testing the first survey's prediction) indicated that once early successional forests had a chance to mature, pandas used them to the same extent as old-growth. Even tests of present predicted distributions are uncommon. This review revealed some cases where genetic data indicated that habitats were not as fragmented as models predicted (brown bears in Iran), or where bears were living outside the predicted range (e.g., sun bears in Malaysia, American black bears in Mexico); but often such contrary information is not published. It would be harder yet to demonstrate the absence of bears in places where models predicted that they should occur.

Rarer still are cases where conservation actions stemmed directly from results of habitat suitability studies, even though most modeling papers justify this as the main reason for the study. There tends to be a disconnect between modelers and decision-makers [238], which is evident in general between ecological theory and conservation practice—what Knight et al. called the “research–implementation gap” [256]. Bridging this gap requires that the scientific process yielding the actionable recommendations be understood and considered credible by practitioners. This means that models should be transparent and repeatable (not sensitive to data inputs and methodological decisions), and that they employ knowledge of the biology of the target species and fully consider the inherent complexity of the situation on the ground; further, there needs to be a more active exchange of information between modelers, species experts, conservationists, and decision-makers [257–260]. That is not to say that this has not occurred in a few exemplary cases. For example, some studies predicted and then created habitat corridors to connect bear populations, which have been instrumental in a successful conservation effort [261,262]. However, more work needs to be done to check and verify habitat suitability studies and to ensure that credible results are implemented in management and conservation programs.

## 7. Recommendations

This paper closes with 10 concrete recommendations for future investigations of bear–habitat associations apparent from this review.

1. Ensure that sampling is representative of the available resources and conditions. Generally, this will be the case for data from GPS collars, but biases can arise with point sampling, especially using sign (which is created and decays at different rates in different habitats), and potentially to a large extent in data repositories where the investigator has no control over the data collection. The veracity of the data should be examined, not simply assumed.
2. Choose candidate covariates that have probable biological connections to the species, not just ones that fit a model. The British statistician George Box is famously quoted as saying “all models are wrong, but some are useful.” It is hard to imagine a useful model in which the predictors explained much of the variation in the model, but did not actually relate biologically to the target species.
3. Test habitat availability at multiple scales. Human investigators cannot know how a bear perceives its world—what specific resources it seeks, what threats it is trying to avoid, what it knows or remembers as to where resources and threats are located, and how it weighs these various factors. The best we can do is test various spatial windows.
4. Employ both ground-based and remote-sensing-based variables. Ground-based variables bring the investigator closer to what the bear perceives in its environment, especially the foods. Investigators should have a connection with their target species. One way of doing that is to examine sites used by GPS-collared bears. Remote-sensing variables enable investigators to have a wider view of environmental variables and measure things that cannot be measured at ground level.
5. Search for variables that meaningfully measure risks, and distinguish selection from suitability. Human-related factors are commonly included in models, but they may



be difficult to interpret. Investigators commonly measure distances to roads or settlements, and assume that negative associations imply bears' perceptions of risk. However, in many cases, bears are attracted to human foods, or to habitats where roads are built, so their selection may be maladaptive. It is important to recognize that selection does not equate to suitability.

6. Be aware that population-level associations may hide important individual-level differences. This review has pointed to a number of cases where individual bears or bears of different sex-age groups in the same area responded to resources differently, including both natural and human-related foods.
7. Compare results of multiple models, explain discrepancies, and build composite models. This review highlighted a number of cases where multiple studies in the same region achieved contradictory results, but authors typically ignored these. Models are one approach for deciphering complex data, but that very complexity means that models do not mimic nature precisely. Increasing knowledge requires not just constructing more models, but understanding why results differ among models. Efforts to systematically compare individual models and build composite models are likely to increase the reliability of outcomes.
8. Test model predictions. Model predictions can be compared to each other, but better yet, compared to actual bear occurrence or demography. This has been accomplished in very few cases, as this review revealed, and often key aspects of model predictions have not been upheld. A concerted effort to test predictions of published models would be highly worthwhile.
9. Increase transparency to enable practitioners to utilize results. Habitat modeling papers are often written with the professed goal of benefitting bear management or conservation, but connections between research papers and actions on the ground are scarce. This disconnect may arise from the practitioners' view that models are unreliable, not understandable, not realistic, or not clear insofar as to what actions should be taken.
10. Look for associations between habitat and demography, not just relative use of different habitats. Habitat use is a potentially misleading parameter by which to judge habitat suitability. Cases were mentioned here where bears were attracted to habitats where survival is poor, or conversely, where habitats used for just a short period of time provided a crucial resource.

A final key point is to appreciate not just the complexity and variability of the environment, but also the adaptability of bears. This makes characterizing the suitability of their habitats very difficult. It also underscores why it is so difficult to explain what "bear habitat" is (at least for most of the species), and why the older, functional definition of habitat as a species-specific collection of resources is not very useful for this taxa. Further, it also means that we should be wary of habitat-based model projections about the future.

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