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A synthesis of giant panda habitat selection

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Abstract: The giant panda (*Ailuropoda melanoleuca*) is a global conservation icon, but its habitat selection patterns are poorly understood. We synthesized previous studies on giant panda habitat selection. We confirmed that pandas generally selected forests with moderate to high bamboo densities, mid-elevations, both primary and secondary forests, and areas more distant from human activities. Pandas did not select steep slopes. We also highlighted the interactive effects among different habitat components, such as weaker selection for gentle slope and large patch size in disturbed secondary forests compared with primary forests. Pandas selected for land cover and disturbance at the level of the geographic range and selected for variables such as slope and bamboo density at the level of the home range. Furthermore, selection for higher bamboo cover did not change with bamboo availability, but selection against secondary forest declined as availability of this forest type increased. Our results have implications for the conservation of pandas, particularly the need for inclusion of areas previously seen as less suitable (e.g., moderate slopes and secondary forest) in protected area and habitat restoration planning.

Key words: *Ailuropoda melanoleuca*, bamboo, China, conservation, coupled human and natural system, forest, giant panda, habitat selection, wildlife

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The study of habitat has important implications for understanding resource needs and ongoing threats to the most endangered ursid in the world, the giant panda (*Ailuropoda melanoleuca*). Various habitat factors have been explored, including characteristics of the geophysical environment (e.g., elevation, topographic slope, and aspect; Schaller et al. 1985, Liu et al. 1999), vegetation structure (e.g., bamboo and tree cover; Reid and Hu 1991, Viña et al. 2008, Tuanmu et al. 2011), natural disturbances (Linderman et al. 2006, Viña et al. 2011), and human impacts (e.g., timber harvesting, livestock grazing; Liu et al. 2001, Pan et al. 2001, Hull et al. 2011b). Generally, studies to date have focused on habitat use (i.e., panda occupancy of a given area with certain environmental conditions) and few have explicitly addressed habitat selection (i.e., use as a function of availability). Habitat selection studies are needed to better understand how pandas prioritize where to spend time, given limited available options.

Giant pandas are currently found in the forests of southwestern China. They are part of coupled human and natural systems (Liu et al. 2007, Liu et al. 2013). Human impacts have relegated the remaining 1,600 wild giant pandas to small and fragmented areas totaling roughly 21,300 km^2 (State Forestry Administration 2006, Viña et al. 2010). Pandas were once distributed throughout the lowlands of western China, but today are limited to a fraction of their historical range in 6 fragmented, mountainous regions (Wei et al. 2012). Panda habitat is currently being managed to help sustain the population, including via creation of nature reserves and implementation of payments for ecosystem

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services programs that recruit locals for forest monitoring and re-plantation (Liu et al. 2008, Vina et al. 2010).

The giant panda is a specialist species, with bamboo comprising about 99% of its diet (Schaller et al. 1985). Pandas consume >60 bamboo species across their range (Hu and Wei 2004) and forage for up to 14 hours/day (Schaller et al. 1985). Despite possessing specialized enzymes for digesting cellulose in the gut (Zhu et al. 2011), pandas have a short, carnivorous digestive tract that lacks compartments for rumination, so passage rates are high (Schaller et al. 1985). Nutrient uptake is also low due to the low nutrient quality of bamboo (Schaller et al. 1985). This limitation means that pandas need to be highly selective when choosing habitats to fulfill their foraging needs.

Panda habitat is mixed coniferous–deciduous forest with bamboo dominating the understory (up to 90% of the understory cover) with a varying mid- and overstory tree species mix and structure (Bearer et al. 2008). These assemblages provide opportunities for pandas to use diverse bamboo species, ages, and plant parts as environmental conditions change (Reid et al. 1989). The high availability of bamboo throughout the mountain ranges in southwestern China allows pandas to occur at higher densities than many other bear species throughout the world (Garshelis 2004).

Whereas giant panda reliance on bamboo is well-documented, other elements of panda habitat selection are not well-understood (Liu et al. 2005, Hull et al. 2011a). Pandas occupy remote, inaccessible areas with thick vegetation, making research logistically difficult. Additionally, the Chinese government imposed an 11-year ban (1995–2006) on telemetry-based tracking of giant pandas for animal safety reasons (Durnin et al. 2004). Yang et al. (2006) has summarized panda habitat-selection patterns from published studies, but the authors did not present a quantitative analysis and also did not differentiate habitat selection and use, thus confounding the 2 concepts and obscuring the effect of habitat availability. In addition, the paper was published before many recent contributions to the habitat selection literature (i.e., before 10 studies included in the current review). Habitat selection is important because it represents an expression of animal behavior (i.e., a choice) that is presumably linked to how animals respond to different habitat availability (Manly et al. 2002, Nielsen et al. 2010).

Habitat availability characterized by variables such as slope, aspect, elevation, and forest disturbance varies considerably across the geographic range of pandas (Zhang and Hu 2000, Hu and Wei 2004, Yang et al. 2006). Panda habitats tend to occur as multiple insular areas associated with different mountain ranges. For instance, panda habitat in the Qinling mountain range tends to occur at lower elevations and is flatter when compared with the rest of panda range due to both natural and human factors (Hu and Wei 2004, Tuanmu et al. 2012). Hu and Wei (2004) and Wang et al. (2010) also noted that the available habitat in the Xiangling mountain ranges was more fragmented than habitats in the rest of panda range. Although several authors have identified differences in habitat availability throughout the range of pandas, quantitative studies on selection of those habitats are lacking (but see Zhang and Hu 2000 for a comparison between Dafengding and Yele reserves).

We sought to better understand panda–habitat relationships by synthesizing existing studies, emphasizing habitat selection. To our knowledge, this is the first effort at quantitatively analyzing findings across the available panda habitat-selection studies. In doing so, we characterized selection by giant pandas with respect to available geophysical, vegetation, and disturbance conditions. We also synthesized the complexities of the habitat selection process for pandas: (1) multivariate effects, (2) interactions among different habitat factors, and (3) variation in selection across habitat selection levels (from geographic range to within-home range; Johnson 1980). Exploration of habitat selection complexities is needed because most previous panda research focused on single-variable relationships at one selection level, thus potentially oversimplifying the habitat selection process for this species. We conclude with a discussion of current weaknesses and future directions for research on giant panda habitat selection that could facilitate conservation planning for this species.

Methods

We performed literature searches in English (ISI Web of Science and Google Scholar) and Chinese (Wangfang Data and the Chinese National Science Digital Library) to find publications that described giant panda habitat. We sought references in refereed journals, university theses and dissertations, books, government documents, and edited book chapters. We used the key words "giant panda" and

Table 1. Summary of studies on giant panda habitat selection reviewed from the English and Chinese language literature.

Study	Location[a]	Area (km^2)[b]	Sampling date	Data type[c]	Use vs. availability[d]	Plot size (m^2)
1. Bearer 2005, Bearer et al. 2008	Wolong NR	2,000	2001–2003	F, G	feces vs. no feces	30 x 30
2. Feng et al. 2009	Part of Qinling Mountains	5,700	2006–2007	G	sign vs. GIS	85 x 85
3. GPFDWC[e] 2004	Gansu Province	4,000	1999–2001	F	sign vs. no sign	20 x 20
4. Kang et al. 2011a, b	Wanglang NR	460	1997–2009	F	sign vs. no sign	20 x 20
5. Kang et al. 2013	Wanglang NR	320	2012	F	feces vs. no feces	20 x 20
6. Liu 2001, Liu et al. 2005, Liu et al. 2011	Foping NR	290	1991–1995	F, G	collar vs. GIS	10 x 10, 30 x 30
7. Pan et al. 2001	Part of Qinling Mountains	15	spring 1987	F	sign vs. no sign	variable[f]
8. Qi et al. 2009, 2011, 2012	Liangshan Mountains	10,067	2005–2007	G	sign vs. GIS	30 x 30
9. Ran et al. 2003	Yele NR	200	Jun 2001	F	sign vs. no sign	20 x 20
10. Ran et al. 2004a	Xiaoxiangling Mountains	400	2001	F	sign vs. no sign	20 x 20
11. Ran et al. 2004b	Baoxing County	1,700	2001	F	sign vs. no sign	20 x 20
12. Reid and Hu 1991	Wolong NR	25	1986–1987	F	feces vs. no feces	20 x 2
13. Tang and Hu 1998	Yele NR	24	Apr 1994	F	sign vs. no sign	10 x 4
14. Wang et al. 2006	Baishuijiang NR	77	Jun 2005	F	sign vs. no sign	20 x 20
15. Wang 2003	Liaoxiancheng NR	126	autumn 2002	F	sign vs. no sign	20 x 20
16. Wang et al. 2010, Ye 2008	Entire panda range	160,000	2000–2001	G	sign vs. GIS	250 x 250
17. Wang et al. 2008	Pingwu County	5,959	1998	F, G	sign vs. GIS	20 x 20, 30 x 30
18. Wang 2008, Wang et al. 2009	Minshan Mountains	9,569	1999–2007	F, G	sign vs. GIS	20 x 20, 30 x 30
19. Wei et al. 1996	Mabian Dafengding NR	25	1991–1992	F	feces vs. no feces	20 x 2
20. Wei et al. 1999, 2000	Yele NR	25	1994–1996	F	feces vs. no feces	20 x 2
21. Zeng et al. 2002, Guo 2003	Wanglang NR	300	Apr 1998	F	sign vs. no sign	unknown
22. Zhang et al. 2006, 2009	Fengtongzhai NR	20	2002–2003	F	feces vs. no feces	20 x 2
23. Zhang et al. 2011	Sichuan Province	~110,000	1999–2003	F	sign vs. no sign	20 x 20

[a]Locations of the study are expressed in terms of the most specific place identifier and include names of nature reserves (NR), counties, mountain ranges, or provinces.
[b]Size of study area corresponds with only the area sampled.
[c]Habitat data were obtained from field survey (F) or a GIS (G).
[d]Sign means all animal sign including feces, foraging site, footprint, hair, animal sighting; feces means feces only.
[e]Gansu Provincial Forestry Department of Wildlife Conservation.
[f]Large quadrats that were searched for signs; quadrats ranged from 5 to 29 ha.

"habitat selection" and "giant panda" and "habitat." We filtered individual references to determine relevancy to our study. The inclusion criterion was that the study provided data or results on habitat selection (i.e., compared the environmental conditions of areas used by pandas with conditions available [or not used] in the landscape). Many references (n >40) solely analyzed habitat use, some of which incorrectly (n = 10) adopted the term habitat selection in the title or abstract. Three references satisfied the habitat selection criterion but were excluded from our synthesis because of low sample sizes (i.e., <50 used or available data points), which were further reduced when the authors of those studies divided the data into ≥4 habitat classes (e.g., types of forest, magnitudes of slope). We summarized studies with respect to design and implementation and identified 3 categories of habitat factors that affect pandas: geophysical, vegetation, and disturbances (Table 1). We chose these categories based on previous panda research (Liu et al. 1999). We noted which measured habitat components were found to significantly relate to panda habitat selection for each study (Table 2). We also explored interactive effects among different habitat components.

In some instances, we used additional analyses to compare habitat selection across studies. One analysis that was used in many studies was the Vanderploeg and Scavia relativized electivity index (VS relativized index; Vanderploeg and Scavia 1979). This index is robust and stable across varying magnitudes of resource availabilities (Lechowicz 1982, Manly et al. 2002). The index ranges from −1 (strong selection against) to 1 (strong selection for), with values around 0 indicating that habitats are being used in proportion to their availability (i.e., no selection). We calculated this index on topographic slope, bamboo cover, and forest age for studies that provided adequate data (Ran et al. 2003, Kang et al. 2011b). We also constructed plots that portrayed habitat use versus availability for these same 3 variables. These habitat characteristics were chosen because of a combination of available data and known importance to panda habitat selection. We divided slope into 5 discrete categories (<5°, 6–20°, 21–30°, 31–40°, and >40°) and bamboo cover into 4 discrete categories (0–25%, 25–50%, 50–75%, and 75–100% cover) based on the most common delineations used in the studies. We also performed a χ^2 goodness-of-fit test (Neu et al. 1974) to evaluate panda selection of primary versus secondary forest. We also classified habitat selection according to level. Selection levels consisted of first order (i.e., factors influencing occurrence across the species' range), second order (i.e., factors influencing selection of the home range), third order (i.e., factors influencing selection of habitats within the home range), and fourth order (i.e., micro-site features such as food items or shelters selected within the home range; sensu Johnson 1980).

Results

Scope of habitat selection studies on the giant panda

We located 23 studies (Table 1) and deemed those conducted within the same reserve as separate observations if the researchers, time frames, or spatial extents differed. In 9 instances, we found 2 or 3 references that used the same data set and we counted these as a single study (Table 1). Most studies (52%) were conducted in areas of 20–500 km^2. The remaining studies with the largest areas included the panda range-wide data set (Ye 2008, Wang et al. 2010), 2 province-wide data sets (GPFDWC 2004, Zhang et al. 2011), and 2 mountain range-wide data sets (Qi et al. 2009, 2011, 2012; Wang 2008; Wang et al. 2009; Table 1). All studies except one were conducted at the population level (i.e., individual pandas were not identified). Most studies (74%) documented panda occurrence via indirect evidence (e.g., feces, tree marks, partially eaten food) and paired these used locations with available locations sampled nearby. Of these, most (76%) located sample plots along transects but few (35%) provided detailed information on how availability plots were located (e.g., min. distance to used plots, choice of location), which hindered our ability to draw inference. Survey transects and corresponding plots tended to be opportunistically located along established human and animal travel routes, potentially introducing bias (see Discussion section for further discussion on methodological issues). For those studies not relying on field plots to characterize availability (26%), some selected random locations across the study area (8%) or the entire study area (17%) using a geographic information system (GIS).

Panda habitat-selection studies have analyzed 46 habitat factors—including 8 geophysical, 30 vegetation, and 8 disturbance factors (Table 2). Approximately 52% of the studies included geophysical, vegetation, and disturbance factors simultaneously. The most frequently studied factor was vegetation (91% of studies), followed by geophysical (87%) and disturbance (61%). The most common methods used for data analysis were the VS relativized index (35% of studies) and the χ^2 test (35%). Other types of analyses included Mahalanobis distance, regression, discriminate function analysis, and ecological niche factor analysis.

Single geophysical factors

Pandas selected for gentle and moderate slopes with abundant solar radiation and mid-elevations. Of the 18 studies that considered slope, 78% found significant effects of slope on giant panda habitat selection (Table 2), with 56% documenting a negative relationship. We summarized the VS relativized index from the slope data from 10 studies with available raw data and found that 70% showed positive selection for gentle to moderate slopes with 30% showing a quadratic relationship (i.e., peak in selection at moderate slopes; Fig. 1). Steep slopes (>40°) represented <20% of available panda habitat and pandas selected <6% of these steeper areas (Fig. 2a). We found the greatest variation in available habitat for moderate slopes (5°–20° and 21–30°), which made up between 19–41% and 20–54% of the landscape, respectively. Availability of these slope classes did not appear to consistently influence selection.

Of the 16 studies that analyzed panda habitat selection with respect to aspect, 69% found a significant result (Table 2), but selected aspects varied by study area. Liu et al. (2011) found that solar radiation was a positive predictor of panda habitat selection and suggested that solar radiation may be a more direct indicator of selection than

Table 2. Summary of giant panda habitat selection with respect to various geophysical, vegetation, and disturbance factors from 23 studies reviewed in the English and Chinese language literature (listed by mountain range). An "x" indicates the factor was a significant correlate of habitat selection, an "o" indicates the factor was not significant, and a blank space means that the factor was not considered in the study.

Study	*Geophysical*	Elevation	Slope	Aspect	Slope shape	Hillside position	Distance to water	Moisture index	Solar radiation index	*Vegetation*	Forest type	Landscape metrics	Basal area	Canopy cover	Tree ht	Tree density	Tree dispersion	Tree DBH	Tree stump density	Fallen log density	Fallen log dispersion	Shrub ht	Shrub cover	Shrub density	Shrub dispersion	Shrub DBH	Understory ht	Bamboo presence	Bamboo species	Bamboo cover	Bamboo ht	Bamboo density	Bamboo diam	Proportion old shoot	Proportion young stem	Proportion old stem	Proportion stems broken	Proportion dead bamboo	Bamboo growth type	Bamboo condition	*Disturbance*	Forest disturbance	Farmland	Livestock grazing	Herb collection	Poaching	Severity of disturbance	Distance to road	Distance to village
Liangshan																																																	
Qi et al. 2009, 2011, 2012[a]		x	x	x							x																															x						x	x
Wei et al. 1996			x	x										x																		x	x		x														
Minshan																																																	
Kang et al. 2011a, b		x	x	x	x	x	x				x			o	x			o				o	x						x	x	x								x	x		x							
Kang et al. 2013[a]			o	x[b]										o		o	x[b]	o	x[b]	x			x[b]	x	o	x[b]				x	x	x	x	x															
Zeng et al. 2002; Guo 2003		x				o					x																	x												x		x		x	o	o	x		
Wang et al. 2006		x	x	x		x	o				x			o				x												x	x								x	x		x							
Wang et al. 2008[a]		x	o	o			x				x																	x															x					x	x
Wang 2008; Wang et al. 2009[a]		x	o	o			o				x																	x	x														x					x	x
Qionglai																																																	
Bearer 2005; Bearer et al. 2008[a]		o	x	x								x	o	x	x								o				x			x	x	x	x									x						x	
Ran et al. 2004b			x	o		x					x			o	x			x				x	x							x	x									x									
Reid and Hu 1991			x																												x	x	x	x			x												
Zhang et al. 2006, 2009[a]			x	o										o		o	o	x[b]	o	o				o	o	x[b]					x[b]	x[b]		x															
Qinling																																																	
Feng et al. 2009[a]		x	x	o	o	x	o	x			x																	o																				x	x
Liu 2001; Liu et al. 2005, 2011									x		x			o	o	o		o												x	x	x	x	o	x	x		x					x						
Pan et al. 2001																																										o							
Wang 2003		x	x	x		x					x			o																x																			
Lesser Xiangling																																																	
Ran et al. 2003			o	x	x	x					x			o	o							o	x							x												x							
Ran et al. 2004a																																										x		x	o	o		o	
Tang and Hu 1998			x	x										x																		x																	

Table 2. Continued.

Study	*Geophysical*	Elevation	Slope	Aspect	Slope shape	Hillside position	Distance to water	Moisture index	Solar radiation index	*Vegetation*	Forest type	Landscape metrics	Basal area	Canopy cover	Tree ht	Tree density	Tree dispersion	Tree DBH	Tree stump density	Fallen log density	Fallen log dispersion	Shrub ht	Shrub cover	Shrub density	Shrub dispersion	Shrub DBH	Understory ht	Bamboo presence	Bamboo species	Bamboo cover	Bamboo ht	Bamboo density	Bamboo diam	Proportion old shoot	Proportion young stem	Proportion old stem	Proportion stems broken	Proportion dead bamboo	Bamboo growth type	Bamboo condition	*Disturbance*	Forest disturbance	Farmland	Livestock grazing	Herb collection	Poaching	Severity of disturbance	Distance to road	Distance to village
Wei et al. 1999, 2000			x	x										x																	x	x	x	o															
Multiple mountains																																																	
GPFDWC 2004[c]		x	x	x	x	x					x			o	x			x				x							x	x	x	o								x		x							
Zhang et al. 2011[a]		o	x											o				x					o				x	x														x							
Wang et al. 2010; Ye 2008[a]											x	x																																					

[a]Multivariate study.
[b]Significant in univariate analysis only.
[c]Gansu Provincial Forestry Department of Wildlife Conservation.

aspect alone. Elevation was significant in 9 of 11 studies, because pandas selected mid-elevations where palatable bamboo was typically found (2,000–3,000 m), a pattern that likely reflects both biogeophysical limitations that prevent bamboo growth at extreme high and low elevations and human impacts at low elevations. In one study (Qi et al. 2011), elevation (and slope) was more important to habitat selection for females than for males. Hillside position was analyzed in 8 studies and pandas generally selected ridges (63% of the studies), upper slopes (50%), and mid-slopes (50%) over valley basins (Table 2).

Single vegetation factors

Pandas selected forest areas with larger patch sizes, but individual structural components of those forests were not consistently important (Table 2). Selection for specific forest types varied across 13 studies, with some (46%) showing selection for both coniferous and mixed coniferous–deciduous forest and others for 1 of those 2 types (15% each). Landscape metrics were evaluated in 2 studies, which showed that pandas tended to select larger, more connected patches (Bearer et al. 2008, Wang et al. 2010).

The structural attributes of forests were quantified using various tree-, shrub-, and bamboo-based vegetation metrics (Table 2). Selection of tree and shrub structural attributes was not consistent among studies. For example, only 29% of the studies (n = 14) that evaluated canopy cover found a significant effect on panda habitat selection, 63% (of 8 studies) found that tree diameter was important, and 67% (of 6 studies) found that tree height was important (Table 2). Similarly mixed results were found for shrub-related metrics (Table 2). For example, 67% (of 6 studies) found that shrub cover was significant, and 50% (of 4 studies) found that shrub height was significant (Table 2). Collectively, our results indicate that tree and shrub attributes are inconsistent determinants of panda habitat selection.

Pandas consistently selected areas with higher bamboo cover. Of the 9 studies that examined this variable, all demonstrated significant positive effects (Table 2). We summarized the VS relativized index for 6 studies and found that pandas did not select areas with <25% bamboo cover, but selected for areas with 50–100% cover (Fig. 3). A non-linear relationship was identified, with selection reaching an asymptote at 75% for most studies with available

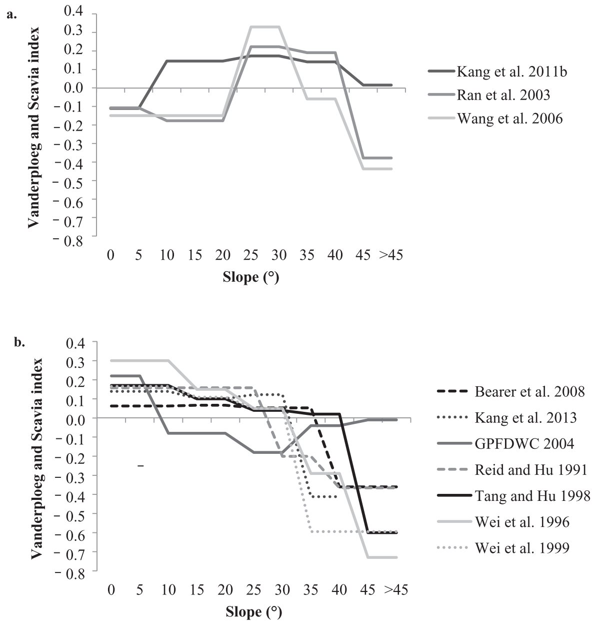

Fig. 1. Giant panda selection for slope by slope class. Values shown are Vanderploeg and Scavia relative electivity indices (Vanderploeg and Scavia 1979) divided into studies showing (a) quadratic and (b) linear and non-linear decreasing trends. Slopes were estimated in mid-sized field plots (10 x 4 m^2, 20 x 2 m^2, 20 x 20 m^2, or 30 x 30 m^2).

data (Fig. 3). This finding was supported by studies that found selection for the most dense patches (Wei et al. 1999, Bearer 2005), and others that revealed no selection for the most dense patches in favor of moderate densities (Wei et al. 1996, Tang and Hu 1998). Selection for bamboo density varied by season (Reid and Hu 1991) and bamboo species (Liu et al. 2005). The structural attributes of bamboo (i.e., ht and diam) were also significant. In most cases, taller and thicker bamboos were positively related to panda selection. Pandas consistently selected areas with higher bamboo cover (i.e., >50% cover) regardless of availability across panda range (Fig. 2b), indicating that bamboo cover is a useful range-wide determinant of panda habitat selection.

Single disturbance factors

Pandas generally avoided areas of persistent human activity (Table 2). All studies ($n = 3$) that evaluated the effects of farmland on panda habitat selection found a negative relationship. In 6 studies that considered distance to human activity (active road or village), pandas selected areas farther from such locations (Bearer et al. 2008, Wang 2008, Wang et al. 2008, Feng et al. 2009, Qi et al. 2012). Qi et al. (2011) found that abandoned logging roads were positively related to pandas' (particularly females') habitat selection, suggesting that human activity is the primary deterrent to road use. Two studies considered livestock grazing and reported that pandas did not select areas used by livestock (Zeng et al. 2002, Ran et al. 2004a). Poaching (mainly of ungulates) or herb collection did not appear to affect panda habitat selection (Zeng et al. 2002, Ran et al. 2004a).

Pandas selected both primary and secondary forests, given that these forests offered a suitable bamboo resource. Most studies that investigated forest disturbance (70%) considered it as a binary variable: primary forest (no timber harvest) or secondary forest (a forest that has re-grown after timber harvest). Forest structure observed across these 2 forest types varied considerably across giant panda range, with some secondary forests supporting bamboo communities similar to what is typically found in primary forests under the appropriate conditions (i.e., a moderate amount of overstory canopy closure [35–70%; Bearer 2005]).

Pandas selected primary forests over secondary forests in 6 of 10 studies (60%) we evaluated (Ran et al. 2003, 2004a; GPFDWC 2004; Wang et al. 2006; Bearer et al. 2008; Zhang et al. 2011). Bearer et al. (2008) suggested that pandas exhibit a non-linear selection for forest age, with selection of primary and secondary (31–100 yr post-harvest) forests over forests cut within the past 30 years. Forests cut within 30 years made up 55% of all available plots, but only 16% of used plots (Bearer et al. 2008). Pan et al. (2001) compared primary and secondary forests that were cut within 6 years where 35–70% crown closure was retained and found no difference in panda habitat selection. The authors also suggested (but did not quantify) that pandas responded negatively to more intensive forest harvesting in the form of clearcutting. Qi et al. (2012) examined selective logging versus clearcuts and reported that pandas were located closer to selectively logged forests (especially for females) and in areas with lower frequency of clearcuts. Studies ($n = 2$) that included intensively managed plantations as another forest type found that pandas did not select plantations (GPFDWC 2004, Bearer et al. 2008).

Availability of secondary forests ranged from 26% to 76% (Fig. 2c). Pandas used secondary forests

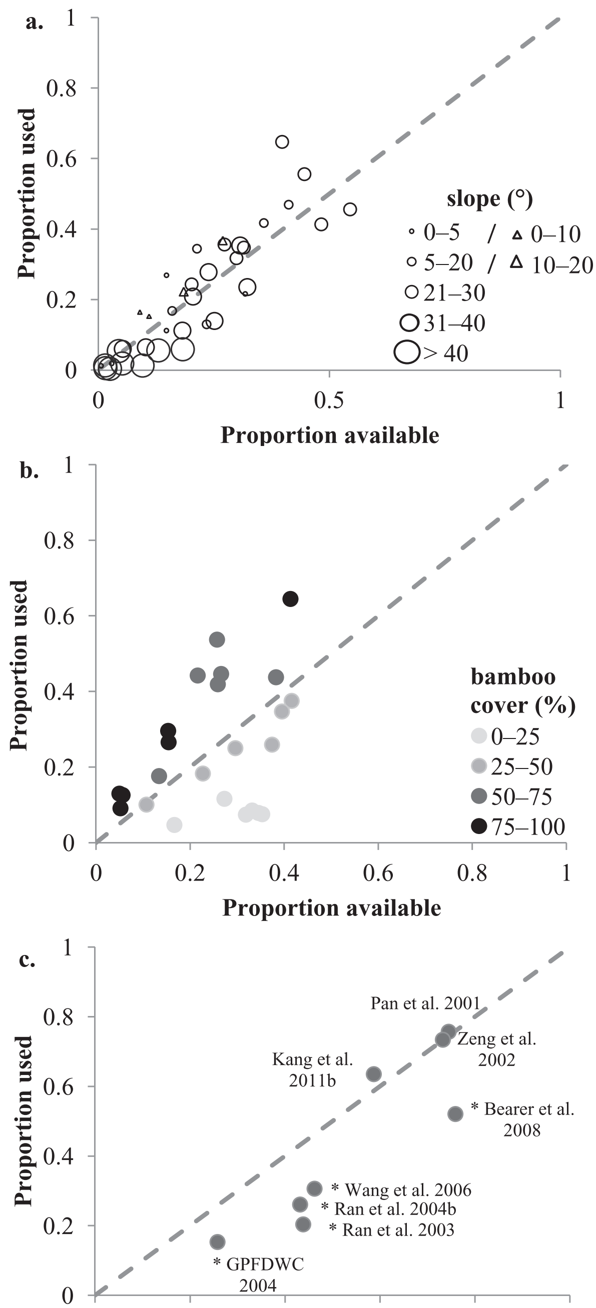

Fig. 2. Giant panda habitat use in relationship to habitat availability for (a) topographic slope, (b) bamboo cover, and (c) secondary forest. Asterisks in (c) represent significant differences at the *P* = 0.050 level (determined via χ^2 goodness-of-fit tests on the distribution of used versus available habitats; Neu et al. 1974).

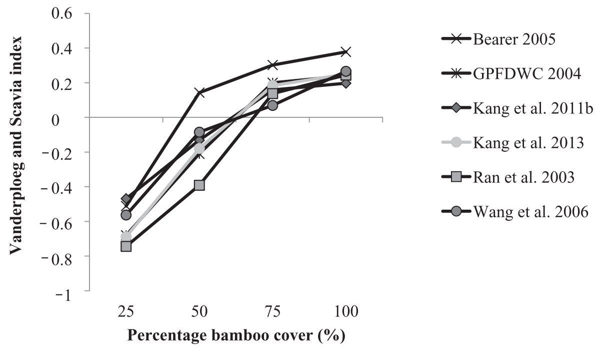

Fig. 3. Giant panda selection for bamboo cover across 6 studies. Bamboo cover was measured using visual estimation in fixed area of 20 x 20-m or 30 x 30-m plots.

significantly less than their availability when these forests made up <60% of available habitat, but used them in proportion to their availability in 2 of 3 studies in which >60% of available habitat was made up of secondary forests.

Multivariate habitat selection factors

Nine studies provided insights into the integrated importance of different variables in habitat selection of giant pandas using multivariate analyses. Bamboo cover and occurrence was consistently important over most other variables analyzed (Bearer et al. 2008, Wang 2008, Wang et al. 2008, Zhang et al. 2011, Kang et al. 2013). Forest attributes (e.g., % canopy cover, canopy ht) were important in some studies (Bearer et al. 2008, Wang 2008, Wang et al. 2008, Qi et al. 2009, Zhang et al. 2011), but not others (e.g., Zhang et al. 2009, Kang et al. 2013). Multivariate studies also identified distance to human disturbances, including active roads (Bearer et al. 2008), villages (Wang et al. 2008, Feng et al. 2009), and crops (Wang 2008), as important positive contributors to panda habitat selection.

Unlike the consistent multivariate selection patterns for bamboo, forest availability, and human disturbance, multivariate selection based on elevation, slope, and aspect varied widely across studies. Slope is often cited as an important predictor of panda habitat selection; however, it was among the most important variables in only 2 of the multivariate studies (Feng et al. 2009, Zhang et al. 2009). Studies that conducted both univariate and multivariate analyses (n = 3) found that some significant single variables were no longer significant when analyzed with other variables (Bearer et al. 2008, Zhang et al. 2009, Kang et al. 2013). These single variables included tree and shrub size and bamboo density and height (after controlling for slope and proportion of old shoots, Zhang et al. 2009), and several tree structural attributes after controlling for bamboo cover, basal area, and overstory height (Bearer et al. 2008). Our findings draw attention to the potential dangers in giant panda habitat-selection studies of analyzing habitat relationships without regard for multiple variables and how they potentially interact.

Interactive habitat selection factors

As suggested by results from multivariate studies, understanding giant panda habitat selection is complicated by interactions among different habitat characteristics. Such interactive effects were only analyzed in 6 studies included in our review. In one study, in areas where human impacts were less prominent, pandas selected lower elevations (Feng et al. 2009).

Bamboo cover and bamboo species composition also interact to influence panda habitat selection. Liu et al. (2005) found that bamboo cover significantly affected habitat selection for *Fargesia qinlingensis* and not *Bashania fargesii*. Similarly, Bearer (2005) found that bamboo cover significantly affected habitat selection for *F. robusta,* but not *B. fabri*. Bearer (2005) also found that selection of slope varied among areas with different bamboo species (at different elevations). Pandas selected for the lowest slopes when foraging on *B. fabri,* but did not select the lowest slopes when foraging on *F. robusta,* potentially reflecting topographic differences in the sites that support each species (i.e., *F. robusta* occurred on slightly steeper slopes [mean $\pm$ SE, 24.5 $\pm$ 0.9°] than did *B. fabri* [19.6 $\pm$ 1.2°]).

Slope also interacted with forest age. Bearer (2005) reported that slope was significant for predicting panda habitat selection in primary and recently cut forests [<10 yr] but not in moderate-aged secondary forests. Mean slope of used plots was significantly greater in the former age classes, but did not differ significantly across ages in the available plots. Similarly, Ran et al. (2004b) noted that pandas selected moderate slopes and avoided the steepest slopes in primary forests, but showed no selection for slope when in secondary forests. Variation existed in slope selection among different seasons in a single study (Reid and Hu 1991). Slope was not the only variable that interacted with forest age, because Bearer et al. (2008) found that distance to road was only a positive correlate of giant panda habitat selection in younger forests (<30 yr) and not older forests.

Of the 2 studies that analyzed landscape metrics (e.g., edge density, patch size; Bearer et al. 2008, Wang et al. 2010), both found that patch size interacted with forest characteristics. When pandas selected dense forests, they chose larger patches that were closer together, and that had more contiguous patches than did unselected habitat (Wang et al. 2010). Similarly, when selecting primary forests, pandas chose larger patches than were present in unselected habitat (Bearer et al. 2008). In contrast, patch size was not important for selection of sparse (forests subjected to intense logging; Wang et al. 2010) or secondary forests (Bearer et al. 2008).

Habitat selection across selection levels

Nearly half (48%) of the reviewed studies were conducted at a first-order selection level. In first-order selection, researchers compared use and availability across large spatial extents (e.g., whole reserves), often with coarse measures of habitat availability (e.g., forest and non-forest land cover types). The variables significant in predicting first-order giant panda habitat selection included distances to human disturbances (e.g., villages, active roads), land cover type (e.g., forest or non-forest), elevation, and the presence of bamboo (Table 3).

To date, no studies have differentiated among second- and third-order habitat selection; hence, we combined these 2 levels for our synthesis (52% of studies). Factors that consistently predicted habitat selection at the second and third levels included slope, position on hillside (e.g., ridge vs. valley), bamboo cover, bamboo density, and distance to human disturbance (Table 3). Fourth-order, or selection of specific resources within a home range, was largely beyond the scope of our paper, but factors looked at have included bamboo and den trees (Table 3; see also Hu and Wei 2004 and Zhang et al. 2007).

No studies effectively compared habitat selection across multiple orders of selection within a single study. Although Qi et al. (2012) looked at multiple selection orders, the analytical approach they used was sensitive to different spatial extents, thereby confounding inference on the behavioral processes of the animals (Hirzel et al. 2002). Kang et al. (2013)

Table 3. Habitat characteristics deemed important for giant panda selection by habitat selection level (sensu Johnson [1980]).

	Habitat characteristics	
Level of selection	**Selection in multiple studies**	**Selection in some but not all studies**
First-order		
Geographic range	Forest land-cover type Bamboo presence Elevation (distribution depends on study area) Far from human disturbance (e.g., village/town/road/cropland)	Gentle slope
Second-order and Third-order		
Home range and Within home range	Gentle/moderate slope Mid-slope/upper mountain High bamboo cover Moderate/high bamboo density Far from human disturbance (e.g., village/town/road/cropland)	Aspect (orientation depends on study area) Mixed forest Coniferous forest Old-growth forest Higher canopy cover Greater tree ht Greater tree DBH High proportion old shoots
Fourth-order		
Resources	Bamboo shoots Younger bamboo culms Bamboo leaves Bamboo species with highest nutrients	Taller bamboo Thicker bamboo Larger diam den trees

investigated selection at 2 spatial scales (both within the third selection order) and found that predictors of habitat selection at the feeding-site scale (1 m^2, bamboo density and diam) differed from predictors at the larger habitat scale (9,000 m^2, proportion of young bamboo and bamboo cover; Kang et al. 2013).

Discussion

Implications for giant panda ecology and management

We synthesized information about habitat selection of the giant panda across a large number of studies throughout panda range. By isolating habitat selection studies from the greater number of studies that described panda habitat use, we characterized choices that pandas make when multiple habitats are available. Our synthesis indicated that giant pandas are more flexible in their habitat selection choices than previously thought, with this flexibility likely related to the availability of preferred habitat components (see Garshelis 2000 for a discussion on habitat selection and preference). First-order habitat selection (i.e., the geographic range; Johnson 1980) by giant pandas provides a perspective on the habitats that are available in their human-influenced landscapes. Habitat variables consistently selected at the geographic range included bamboo presence, forest cover, and areas not in close proximity to human communities. These variables are likely interrelated, with increased human activity corresponding with less bamboo and forest cover. Elevation was another variable that helped define panda habitat selection across their geographic range, but the range of selected elevations was variable and depended on location. In general, pandas have been relegated to steeper mid-elevations in many areas throughout their range because humans occupy the lowlands and in many cases have converted the habitats to development and agriculture. Yet high availability of bamboo throughout the mid-elevations supports them at high densities in a variety of different habitat conditions.

Characteristics of topographic slope, bamboo, and human disturbance influenced habitat selection by pandas at mid-levels (i.e., home range and within home ranges; Johnson 1980). Moderate and steep slopes have frequently been proposed as limiting panda habitat selection because it is energetically costly to traverse steeper mountainsides (Schaller et al. 1985, Liu et al. 1999). However, we found that pandas selected for a broader range of slopes at mid-levels than was previously documented. The importance of slope was reduced in some multivariate models, likely because slope was correlated with other more important variables such as forest type or bamboo cover. Additionally, although the avoidance of steep slopes by pandas was consistent across studies, we also found consistent selection for gentle and moderate slopes that contrasts with how slope is typically represented (i.e., as monotonic and linear) in current habitat suitability models (e.g., Liu et al. 1999). Some studies in our review found stronger selection for moderate slopes over gentle slopes, but we caution that this finding potentially relates to interacting factors such as greater human disturbance on gentle slopes. We also found that selection for slope varied by bamboo species, season, forest type, and study area. In the future, we recommend that habitat suitability models recognize that selected slopes include a wider range than was previously modeled (0–30°), while areas with even steeper slopes might be useable according to conditional criteria (depending on other factors present).

Our results also point to nuances in panda habitat selection for other geophysical variables aside from slope. Slope and aspect relate to the amount of solar radiation striking a surface; this variable was a positive predictor of panda selection in Liu et al. (2011). The authors hypothesized that low amounts of solar radiation could be a limiting factor for plant (specifically bamboo) growth. Selection for ridges, upper slopes, and mid-slopes likely reflects the combined effects of human activity in valley bottoms and preferred scent-marking locations for pandas along easily traversable ridgelines (Schaller et al. 1985).

Our results on selection for bamboo across all levels of habitat selection confirm its importance for pandas. Our novel contribution to this previously well-documented relationship is that pandas selected for higher bamboo cover regardless of its availability across the landscape. Other habitat factors we investigated may only be important with respect to how they correlate with conditions suitable for bamboo occurrence, growth, and diversity. Wang et al. (2010) found that bamboo cover varied significantly with elevation and aspect but not slope, canopy cover, or position on the mountainside. Bearer at al. (2008) also found that bamboo cover was related to other habitat characteristics (e.g., elevation, overstory cover, slope), but the effects varied by bamboo species. Bamboo density is another related but significant variable, but pandas selected moderate densities in some areas and high densities in other areas. The former finding may reflect the fact that extremely high-density bamboo patches can be more difficult to traverse and also may contain less palatable food for pandas (Schaller et al. 1985). We caution that bamboo density and cover are likely confounded by bamboo age and diameter and suggest further exploration of these relationships.

Beyond consistent selection for bamboo, our findings indicate that broad generalizations on panda habitat selection are likely inappropriate and that researchers and managers should cautiously transfer findings from one study area to another. We found that pandas do not consistently select for specific tree structures at mid-levels, likely because bamboo occurs in forests with many different configurations of middle and overstory vegetation structure. In particular, canopy cover was a poor determinant of panda habitat selection according to our review, suggesting that suitable forest attributes cannot be detected using simple percentage cover measurements. Indeed, our results suggest that panda habitat selection for tree-related characteristics is likely context-dependent and related to complex interactions between tree- and bamboo-related variables (Taylor et al. 2004).

Our findings suggest that habitat selection results should be cautiously applied to management of giant pandas and their habitat. Current management can potentially benefit from improved prioritization of important habitat areas. For example, the creation of nature reserves, delineation of zoning schemes within nature reserves, population monitoring, and planning for potential future habitat restoration can all be improved through better understanding of panda habitat selection. However, habitat selection results alone should not cause managers to discount habitats that are being used less than their availability (Garshelis 2000). For example, our review suggests that areas with steep slopes (>40°) and low bamboo cover (<50%) should be ranked lower but not excluded from panda conservation activities; that is, these areas can be used by pandas and thus may contribute toward conservation.

Similarly, although some have recently advocated for an increased management focus on primary forests (e.g., Zhang et al. 2011), our results suggest that secondary forests in some locations play an important habitat role, particularly in landscapes where secondary forests are a dominant forest type. Although more study is needed to link the population demographics of pandas to primary and secondary forests, habitat restoration to connect fragmented patches of habitat using secondary forests may be worthwhile. In addition to our evidence that pandas select secondary forests in some study areas, other studies conducted on habitat use alone also demonstrate that pandas use secondary forests after sufficient time has passed (Pan et al. 2001, Yang et al. 2006). The value of secondary forests for pandas likely depends on a complex combination of bamboo occurrence and growth, historical and current land-use practices, and proximity to chronic human disturbances. Our finding that pandas did not select replanted forests is not surprising, considering that many replanted forests in the panda range are plantations of dense, exotic monocultures that do not support bamboo growth (Bearer 2005, Lu et al. 2007). Whether selective logging in such plantations can open up the overstory to potentially allow for bamboo growth and support pandas requires further study.

Undoubtedly, the studies we reviewed have added considerably to the understanding of panda ecology. We note that our findings are influenced by differences and biases in sampling designs across studies and hence, generalizations on panda habitat selection should be cautiously used. The biggest shortcoming of studies surveyed in our review was that survey plots were often opportunistically located along pre-selected transects and that these transects served as established human and animal travel routes for monitoring. Such routes do not represent randomly available habitats, and potentially bias data collection to areas that are accessible and easy to traverse. Additionally, few studies spatially or temporally replicated sampling for pandas, and hence detection probability could not be estimated (McDonald 2004). These issues can be better addressed in the future by using rigorous design-based approaches that explicitly produce data that can be used to estimate detection probability. An effective design-based sampling strategy might involve systematically sampling among different strata of high and low panda density (as in Qi et al. 2009). Probability of detection can be estimated a variety of ways including multiple survey methods on the same area (such as pairing telemetry with field surveys), mark–recapture methods, spatially replicated surveys in the same sampling area, or by double-sampling the same area using the same method but with different observers (McDonald 2004). We caution that areas of panda range that are difficult to access are under-sampled in the current literature because most studies are based on researchers encountering sign. Hence, the scope of inference for most studies does not apply to a random sample of panda habitats.

Future directions

Future work should more closely examine different types of human impacts on panda habitat selection, because only about 60% of the studies we reviewed looked at these effects. Many of these studies used distance-based GIS measures rather than more detailed field observations, and hence the magnitude of human activity was potentially lost. Livestock grazing and tourism are 2 examples of emerging threats to the giant panda that specifically warrant future research. We also recommend that future work should better understand how habitat selection varies across mountain ranges; this is a topic better explored using a single, consistent data set with a standard way of defining habitat availability (e.g., used plots paired with an equal no. of available plots located a set distance away).

We recommend that future panda habitat work use multivariate approaches that examine interactions among variables. One area of inquiry that warrants exploration is how giant panda habitat selection is affected by the interaction between distance to human communities and forest disturbances, because most forest disturbances occur closer to roads and villages. Also, the effect of spatial structure of habitat components on panda selection continues to be understudied. For example, the differences we noted between selection for cover in *Fargesia* and *Bashania* bamboo could be related to *Fargesia* growing in clumps that exhibit wide variation in cover across space, while *Bashania* is more uniformly distributed (making bamboo cover in an individual plot less important). Spatial structure of habitat components also differentiates habitat selection between the second- and third-order levels, which we aggregated in our review due to the limited amount of telemetry data that were available.

Lastly, we recommend that future panda habitat-selection research incorporates density-dependent effects. It is unknown how density affects giant panda habitat selection across space. Density-dependent effects are important for determining the extent to which pandas adapt to fewer available resources in competitive environments by altering their selection patterns. Ultimately, the research community should work toward formulating an understanding of how habitat characteristics relate to panda fitness (Garshelis 2000). A better understanding of panda habitat-selection processes is crucial for maintaining provision of panda habitats in the future.

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