



## The role of den quality in giant panda conservation

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### ABSTRACT

Small features in ecological systems are often underrepresented in conservation monitoring, management and policy. Tree cavities and other forms of refuge play disproportionately large ecological roles due to their importance for shelter and rearing vulnerable offspring. Giant panda (*Ailuropoda melanoleuca*) cubs are highly altricial, and dependent on dens. In Fengtongzai—a reserve with cavity-containing old growth forest—we measured 19 structural and microhabitat variables in potential tree dens. We also established data loggers in rock cavities in Foping Nature Reserve (which due to logging does not contain old growth) and tree cavities in Fengtongzai to monitor temperature and humidity inside and outside dens to evaluate microclimatic buffering. Fengtongzai pandas selected tree dens that were better concealed, with large interiors and entrances but smaller entrance to interior ratios. Microclimate inside dens differed dramatically from ambient conditions outside: in cold weather dens were warmer, in hot weather dens were cooler, dens were less humid and dens had more stable microclimates. Dens used by maternal pandas were warmer, drier and less variable than tree and rock cavities that were not used. Tree dens showed better capacity to buffer against extremes of temperature and humidity than did cave dens. Our findings have important conservation implications, including the value of den sites and the need for better monitoring and management. Specifically, management practices that preserve large old trees may increase carrying capacity and any experimentation with artificial dens as a conservation intervention should reference our findings on structural and microclimatic characteristics of preferred den sites.

### 1. Introduction

Habitat conservation for at-risk species is a cornerstone of conservation strategies, but often broad-scale habitat assessments are done with less regard for key ecological features that have substantive effects on carrying capacity. Some of these “small natural features” (SNFs) play important and disproportionate roles in maintaining ecological processes and supporting individual species that depend upon them and thus may be considered keystone structures (Lindenmayer, 2017). Large old trees are iconic ecological structures laden with human values associated with “pristine” nature that have been shown to perform many diverse and irreplaceable ecological roles, yet continue to decline to the detriment of ecosystem function and biodiversity preservation (Lindenmayer and Laurance, 2017). Large old trees are especially vulnerable to anthropogenic disturbance, including altered fire regimes, harvest, edge effects and invasive pests (Cockle et al., 2011;

Lindenmayer et al., 2012). In part due to their prominent ecological role for cavity-dependent species, large old trees constitute one of the most important SNFs in forested ecosystems (Lindenmayer, 2017), providing cavities used for shelter or nesting for 30% of all vertebrate species in some ecosystems (Lindenmayer et al., 2012).

Large old trees often are affected by decay, resulting in cavities of sufficient size to afford protection for cavity-using species, especially those that use cavities for rearing offspring. Further, tree cavity availability is an important ecological factor limiting population size in many species (Cockle et al., 2010; Newton, 1994), and the loss of cavity trees is associated with declines in cavity-dependent species and efforts to replace this ecological role with artificial nest boxes and other conservation interventions (Bolton et al., 2004; Manning et al., 2013; Ruegger, 2017), although these efforts have met with varying success (Le Roux et al., 2016b; Maziarz et al., 2017; Rowland et al., 2017). Thus, the ecological value of large cavity-containing trees may not

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always be easily replaced, indicating that preservation of old trees should be prioritized.

Cavities—including tree hollows and rock caves—provide areas of security for wildlife, allowing animals to hide from and escape predators, competitors and other threats. They also may provide a more stable microclimate, buffering animals against extremes of temperature and humidity (O’Connell and Keppel, 2016; Rowland et al., 2017; Sedgeley, 2001), which in some cases has been shown experimentally to influence offspring fitness (Dawson et al., 2005). These SNFs therefore are rendered even more important by the effects of climate change which is forecast to produce more extreme weather events. Microhabitats that buffer against climatic extremes may play an important role in the persistence of many species in the face of climate change (Scheffers et al., 2014). A number of features of cavities, such as tree size and cavity depth and opening size, may influence the use of cavities (Fernández and Palomares, 2000; Le Roux et al., 2016a), as well as the effectiveness of microclimatic buffering (Isaac et al., 2008; Sedgeley, 2001).

Here, we investigate the role of tree and rock cavities in giant panda (*Ailuropoda melanoleuca*) denning ecology. Ursid species use tree dens, cave dens, and some dig their own dens in earth or snow, where they rear their cubs for the first two to four months of life (Garshelis, 2004). Pandas are reliant on tree cavities and rock caves for rearing offspring (Pan, 2014; Schaller et al., 1985; Zhang et al., 2007), but do not use dens outside the maternal denning context. Dens are believed to be of vital importance for cub survival, but little is known about their denning ecology and nothing is known about the role that dens play in microclimatic buffering.

Formally iconic for its endangered status, the giant panda has now been downlisted to Vulnerable by the International Union for the Conservation of Nature (Swaigood et al., 2016; Swaigood et al., 2017). Although recently experiencing positive population and habitat trends, the panda will remain conservation-reliant for the foreseeable future (Zhang et al., 2015). What is needed to advance conservation for the species is rigorous ecological knowledge to enhance adaptive management of pandas and their habitat inside and outside protected areas (Swaigood et al., 2016; Swaigood et al., 2017).

The high degree of altriciality characterizing giant pandas—they are the most altricial of all eutherian mammals (Gittleman, 1994)—makes panda cubs extremely vulnerable to both predators and climatic extremes. Cubs are born almost naked and therefore have little thermal insulation until approximately one month of age when the pelage grows in (Zhu et al., 2001). Pandas do not hibernate, but mothers with cubs make use of available dens to rear cubs for at least 3–4 months following birth of the cub (Schaller et al., 1985; Zhu et al., 2001). Previous research in a reserve with virtually no old growth trees (and therefore no documented tree dens) demonstrated that pandas select cave dens based on den structural characteristics such as den entrance and chamber size, as well as external features such as distance to water and slope (Zhang et al., 2007). Further, habitat-use patterns indicate that pandas sometimes have a strong preference to occupy old-growth forests more than secondary forests (Hull et al., 2014; Wei et al., 2018; Zhang et al., 2011). Thus, we hypothesize that large old trees are important resources for giant panda denning and that they may be influential in limiting population size. Indeed cavity availability is a factor limiting population size in approximately 40% of cavity-dependent mammal and bird species (Cockle et al., 2011).

Our research addressed several important topics in the denning ecology of giant pandas needed to understand habitat requirements and inform management decisions. Our specific objectives included: (1) understand the factors predicting tree cavity use by comparing for the first time characteristics of used dens versus unused cavities in a reserve containing old-growth trees with natural cavities sufficiently large for panda denning; (2) conduct the first study on the capacity of panda dens to buffer against external climatic extremes by (a) compare microclimatic buffering by used versus unused tree and rock dens and (b)

compare the buffering capacity of tree versus rock dens. These data allow us to understand the characteristics of dens pandas use in den selection, guiding decisions to protect and manage for naturally occurring den sites and defining the optimal properties of den sites in proposed interventions, such as construction of artificial dens. If the quality or quantity of den sites is a limiting factor regulation population size in pandas, then these data can be used to develop management strategies to enhance population size in this at-risk species and increase the carrying capacity of their protected and unprotected habitat.

## 2. Material and methods

### 2.1. Study area

To examine cavity and site characteristics for giant panda maternal dens found in old-growth trees, we collected data in the Fengtongzhai Nature Reserve (hereafter “Fengtongzhai” or FTZ). We compared these findings with those presented in Zhang et al. (2007) describing the characteristics of rock cavities that best predict use by giant pandas in Foping Nature Reserve (hereafter “Foping” or FP). In both locations and for both den types, we also examined microclimatic characteristics of used and unused dens.

Fengtongzhai (102°48′–103°00′E, 30°19′–30°47′N) is located in Baoxing County, Sichuan Province, China, covering 390 km<sup>2</sup> and ranging between 1000 and 4896 masl. Fieldwork in Fengtongzai focused in the core region of the reserve where the highest density of giant pandas were found (Fig. 1; Zhang et al., 2009). The annual range of temperature, humidity, and rainfall are 5.9–7.2 °C, 79%–83% and 730–1300 mm, respectively. Vegetation varies with elevation, but in panda habitat is mixed deciduous broadleaf forest transitioning to coniferous forest with elevation. Although there is some history of logging in this reserve, there still remain many stands of old growth forest with trees large enough to contain suitable cavities for denning. Foping, located in the Qinling Mountains, holds an estimated population of 67 adult giant pandas. Foping also is characterized by mixed deciduous broadleaf forest at lower elevations and coniferous forest at higher elevations (see Zhang et al., 2007 for details). Historically, this reserve has been almost completely clearcut and few trees suitable for denning remain, although the secondary forest is matured to the point that habitat is otherwise highly suitable for pandas.

For the purposes of our comparisons of tree versus rock dens, implications of habitat differences between reserves should be considered. All tree cavities were found in one reserve and all rock cavities in the other. Our analyses make direct comparisons only with regard to microclimate and control for climatic differences between reserves by analyzing the capacity of cavities to buffer against ambient conditions outside the cavity (see below). With regard microhabitat surrounding cavities, there are numerous additional habitat differences beyond reserve differences involved in the typical location of caves on steep slopes and large old trees on gentle slopes and ridges, thus making any statistical comparisons unmeaningful. Similarly, size and shape of rock and tree cavities are substantively different from tree dens, so direct statistical comparison is not warranted.

### 2.2. Microhabitat data collection and analysis

We conducted surveys on foot for tree dens Fengtongzhai from April to December 2010. To identify cavities that could be potential panda maternal dens, we used the parameters described by Zhang et al. (2007), requiring that an adult giant panda could enter and stand quadrupedally within the den. Used dens were identified by presence of a panda mother and cub during monthly monitoring surveys during the cub-rearing season (July to December) from 2005 to 2010, and/or presence of panda sign (fur, scratch marks, and bedding materials). Since pandas do not hibernate and are only known to use dens for rearing cubs, we consider the presence of spoor a reliable indication of a

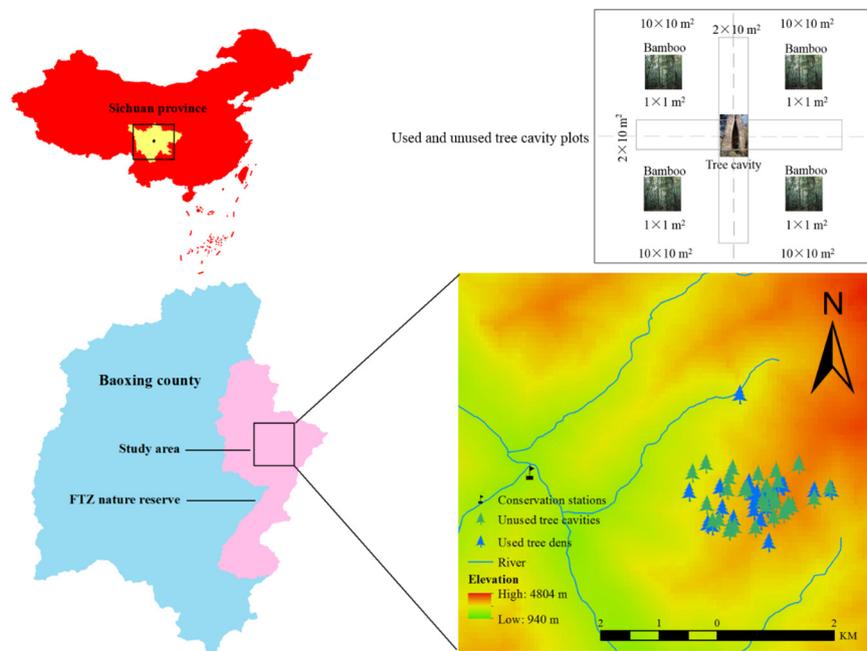


Fig. 1. Distribution of tree cavities in the study area of Fengtongzhai Nature Reserve, China, and study design for deployment of microclimate sensors.

maternal den. We measured 19 microhabitat and physical characteristics of the den and surrounding area (Table S1). We focused our statistical analyses on the comparison of unused cavities with used dens. In addition, we qualitatively compared 11 characteristics with those previously obtained for rock dens in Foping (Table S2; Zhang et al., 2007).

For the tree dens, we assessed data distribution with the Kolmogorov-Smirnov Test to ensure normality. When data met assumptions of normality and homoscedasticity we used independent-samples *t*-tests and when distributional assumptions were not met, we used the Mann–Whitney *U* tests. Further, we examined which of the 19 variables we measured best predicted whether a giant panda would use a tree cavity to den. To eliminate collinearity between variables, we used principal component analysis (PCA) to convert original variables into a set of uncorrelated principal components. To best account for den use, subsets of principal components with the largest explaining variance (i.e., eigenvalue of principal components > 1.00) in all extracted components were transformed as new variables, then were entered into subsequent logistic regression analysis. Finally, we used stepwise discriminant function analysis to further analyze microhabitat and structural characteristics and to test which variables were primarily responsible for separation between used dens and unused cavities.

### 2.3. Microclimatic data collection and analysis

We measured microclimatic characteristics for a subset of ten tree and ten rock cavities that met the criteria for a den. Microclimatic data were recorded in Fengtongzhai and Foping from July 1 to December 31. Cavities were unoccupied during the time of microclimate data collection, so recorded variables were not influenced by occupancy. We measured temperature and humidity by positioning twenty HOBO-H8 hygrothermograph data loggers (i-buttons, Version H08-004-02) 1 m above ground centrally inside each cavity and outside 3–5 m away. Data loggers were programmed to record every 1.5 h, 24 h per day.

Microclimate data was collated into daily data summaries that included the mean, maximum, minimum and range of temperature and humidity recorded both inside and outside the den, for each cavity site across the study period. Because of the altricial nature of giant panda neonates, a critical den characteristic of a maternal den is its capacity to buffer against inclement weather (i.e., the capacity for the den to remain warm and dry). Therefore, we compared the buffering capacity of

used dens versus unused cavities, and between rock and tree dens, by calculating the daily difference between temperature and humidity inside and outside of each cavity, with a larger value indicating greater buffering capacity. We evaluated buffering by examining mean temperature and humidity as well as minimum temperatures and maximum humidity inside and outside cavities. These variables were chosen for their biological salience. Mean temperatures and humidity reflect chronic exposure to potential cold and wet conditions, whereas maximum temperatures and humidity reflect the coldest and wettest condition a cub would experience inside vs. outside the den. We used a paired *t*-test to compare microclimate conditions inside and outside of cavities after these data were logit transformed to meet assumptions of normality.

Data are presented as mean  $\pm$  SE, and all test were conducted using SPSS v21 (SPSS Inc., Chicago, USA), and the significance level was set at 0.05.

## 3. Results

### 3.1. Qualitative comparison of microhabitats between tree dens in Fengtongzhai and rock dens in Foping

Tree dens in Fengtongzhai were found at lower elevation and on steeper slopes than rock dens in Foping (Table S2). Rock den entrances and interiors were wider and shorter than tree dens and tree den interiors were relatively bigger inside compared to the size of their entrances. Tree dens were also farther from water and had more sign of heterospecific use than rock dens. Some of these characteristics might give rise to microclimatic differences between rock and tree dens (see below).

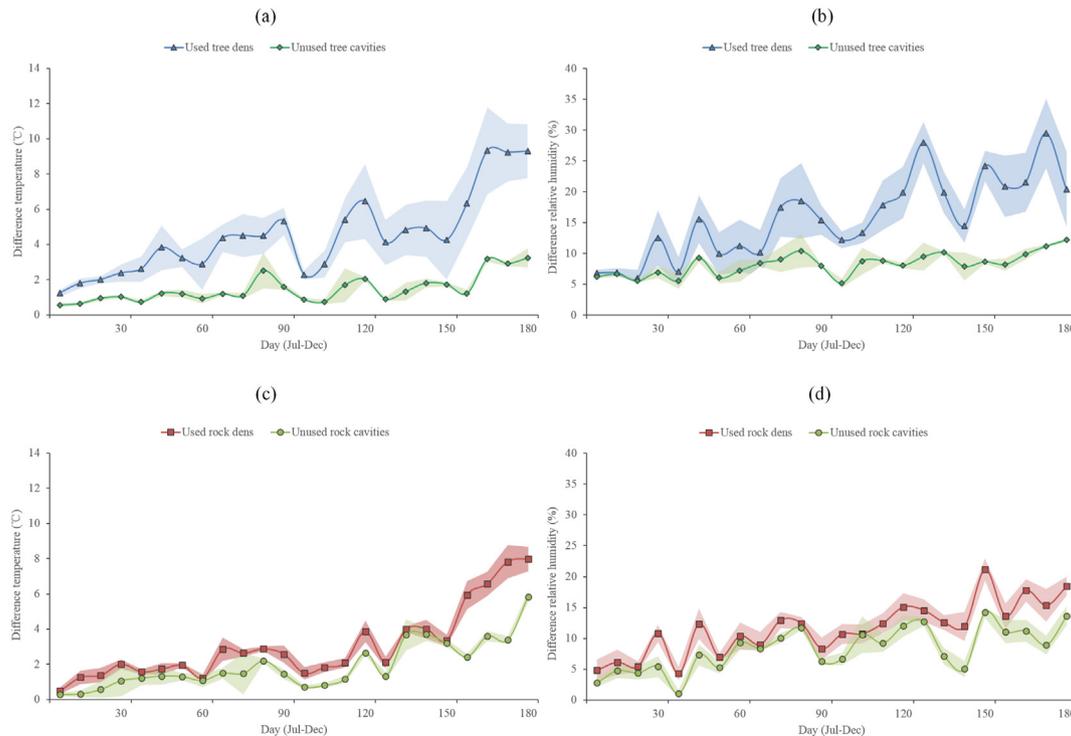
### 3.2. Microhabitat differences: unused tree cavities versus used tree dens in Fengtongzhai

We surveyed 54 tree cavities in Fengtongzhai, 22 of which had been used by giant pandas. Of the 19 variables measured, 9 were significantly different between used dens and unused tree cavities (Table 1). Used tree dens were better concealed (concealment degree < 50 m), and were found on gentler slopes ( $16.32 \pm 1.52^\circ$ ) than unused tree cavities. Very few used dens were found on steep slopes

**Table 1**  
Comparisons of microhabitat and structural characteristics of used tree dens versus unused tree cavities in Fengtongzhai Reserve, China.

Variables	Mean ± SE		t or U	P
	Used cavities (dens)	Unused cavities		
Elevation (m)	2841.91 ± 14.52	2839.13 ± 20.54	0.11	0.92
Slope (°)	16.32 ± 1.52	27.59 ± 1.61	-4.88	0.00
<sup>a</sup> Slope aspect	3.05 ± 0.15	2.88 ± 0.11	306.00	0.36
<sup>a</sup> Tree canopy	2.45 ± 0.18	2.47 ± 0.16	326.50	0.63
Tree height (m)	19.32 ± 1.60	21.17 ± 1.12	-0.98	0.33
Breast height diameter (DBH) (m)	1.24 ± 0.05	1.10 ± 0.03	2.46	0.02
Bamboo density (stems/m <sup>2</sup> )	116.18 ± 9.24	112.09 ± 7.00	0.36	0.72
<sup>a</sup> Bamboo cover	4.41 ± 0.20	4.50 ± 0.14	350.50	0.98
Den entrance distance above ground (cm)	70.55 ± 10.43	113.25 ± 12.75	-2.42	0.02
Distance to water (m)	143.75 ± 13.00	159.09 ± 15.51	-0.41	0.69
The maximum width of the entrance (cm)	56.55 ± 4.76	30.94 ± 2.58	4.73	0.00
The maximum height of the entrance (cm)	213.55 ± 37.93	137.14 ± 19.41	1.95	0.06
The maximum interior width (cm)	93.00 ± 5.13	66.28 ± 3.26	4.62	0.00
The maximum interior length (cm)	108.27 ± 6.60	79.71 ± 4.23	3.82	0.00
The maximum interior height (cm)	473.07 ± 58.31	298.25 ± 38.02	6.84	0.01
<sup>a</sup> Interior/entrance height ratio	2.59 ± 0.43	1.71 ± 0.52	158.50	0.36
Interior/entrance width ratio	1.90 ± 0.18	2.65 ± 0.25	2.64	0.01
<sup>a</sup> Concealment degree	1.09 ± 0.06	2.28 ± 0.23	153.00	0.00
<sup>a</sup> Heterospecific use	1.14 ± 0.08	1.22 ± 0.07	323.00	0.45

<sup>a</sup> Indicates that we used Mann-Whitney U test (df = 52); the remainder were tested with independent-samples t-test.



**Fig. 2.** Comparison of buffering capacity for average daily microclimatic variables for cavities that were or were not selected for denning by female pandas (used vs. unused). Data collected over a six-month period in Fengtongzhai (FTZ) and Foping Nature Reserve (FP), China. (a) comparison of temperature buffering in used tree dens versus unused cavities in FTZ, (b) comparison of humidity buffering in used tree dens versus unused cavities in FTZ, (c) comparison of temperature buffering in used rock dens versus unused rock cavities in FP, (d) comparison of humidity buffering in used rock dens versus unused rock cavities in FP.

(i.e., slope > 30°). Used dens were also found in larger trees, and the interior chamber (including the length, width and height) and entrance dimensions were larger than in unused cavities. The interior/entrance width ratio was also smaller for used dens, indicating a preference for an entrance that was narrower compared to interior dimensions. Den entrances were also lower to the ground than in unused cavities.

The results of the principle components analysis supported the univariate findings (Supplemental Information Tables S3–S5; Fig. S1). The most influential variables (i.e., variables with loading coefficients > 0.5) in the first principle component included DBH, den

entrance, distance above ground, den interior width, length and height, and concealment degree (Table S3). The stepwise discriminant function analysis revealed that slope, maximum width of the entrance, and concealment degree have the greatest explanatory power, and, together, correctly classify 86.4% of observations, and significantly discriminated between used and unused dens (Chi-square test,  $\chi^2 = 50.58$ ,  $P < 0.01$ , Fig. S1).

### 3.3. Microclimatic buffering: inside versus outside maternal dens

Dens significantly buffered against outside climate on all variables we evaluated (mean, minimum, maximum, and range of temperature and relative humidity; Table S6; Fig. S2). Mean and minimum temperatures were warmer, maximum temperatures were cooler, and temperature variation was reduced inside versus outside tree and rock dens. Similarly, mean, minimum, and maximum humidity was drier and the daily humidity range was less inside than outside tree and rock dens. During the (colder) nighttime hours, there is a large difference between inside and outside temperatures for both tree and rock dens, whereas during the warming daytime hours, temperature differences inside versus outside dens are less, although mid-day and early afternoon temperatures are somewhat cooler inside than outside dens (Fig. S3a). Humidity follows a similar diurnal pattern, with substantively drier conditions inside dens during the nighttime and more similar levels of humidity inside and outside dens during the daytime (Fig. S3b). Most notable for both temperature and humidity, values remain much more stable across time of day inside dens than outside dens.

### 3.4. Microclimatic buffering: inside used dens versus unused cavities

Several microclimatic variables differed significantly between used and unused cavities. We found that the mean daily temperature differences (buffering) for used tree dens (on average 4.51 °C warmer than outside) were significantly greater than those for unused tree dens (on average 1.47 °C warmer than outside; Fig. 2a;  $U = 1,800,856$ ,  $df = 10,721$ ,  $P < 0.01$ ). The mean daily differences in relative humidity (buffering) for used tree dens were significantly larger (drier compared to outside) than for unused tree dens ( $U = 193,176$ ,  $df = 10,721$ ,  $P < 0.01$ ), with little difference in buffering during the warm summer months and very large differences in buffering during colder winter months (Fig. 2b). Similarly, mean buffering (1.93 °C;  $U = 3,088,717$ ,  $df = 12,909$ ,  $P < 0.05$ ) and humidity (3.30%;  $U = 2,703,758$ ,  $df = 12,435$ ,  $P < 0.01$ ) were significantly greater for used than unused rock dens (Fig. 2c and d), with buffering effects more prominent in winter, albeit less so than for tree dens.

### 3.5. Microclimatic buffering: inside tree dens versus rock dens

Although all tree dens in our sample were in Fengtongzhai and all rock dens were in Foping, we were able to control for potential confounding effects of climatic differences between reserves through analysis of the differential capacity of tree and rock dens to buffer against external ambient temperature. We found the temperature buffering (mean daily difference inside versus outside dens) by tree dens used by giant pandas was greater (1.44 °C) than for rock dens used by giant pandas (Fig. 3a;  $U = 1,826,011$ ,  $df = 9227$ ,  $P < 0.05$ ). Further, tree dens buffered against external relative humidity better (4.24%) than did rock dens (Fig. 3b;  $U = 1,526,646$ ,  $df = 9947$ ,  $P < 0.01$ ). Analyses examining daily minimum temperature and maximum humidity also revealed that tree dens buffered against the coldest temperatures (Fig. 4a;  $U = 241,752$ ,  $df = 959$ ,  $P < 0.01$ ) and most humid conditions (Fig. 4b;  $U = 283,458$ ,  $df = 959$ ,  $P < 0.01$ ) better than rock dens.

## 4. Discussion

Our findings significantly advance our understanding of denning ecology in the giant panda and demonstrate how both den site availability and the structure, microhabitat and microclimate of dens selected by maternal females will determine the quality of the den in which offspring are raised. Previous research on dens selected by giant pandas conducted in Foping (Zhang et al., 2007) limited our understanding of this important life-history stage because this site lacked old-growth forests containing tree hollow dens. Our findings in Fengtongzhai show that pandas selected tree cavities based on characteristics that are

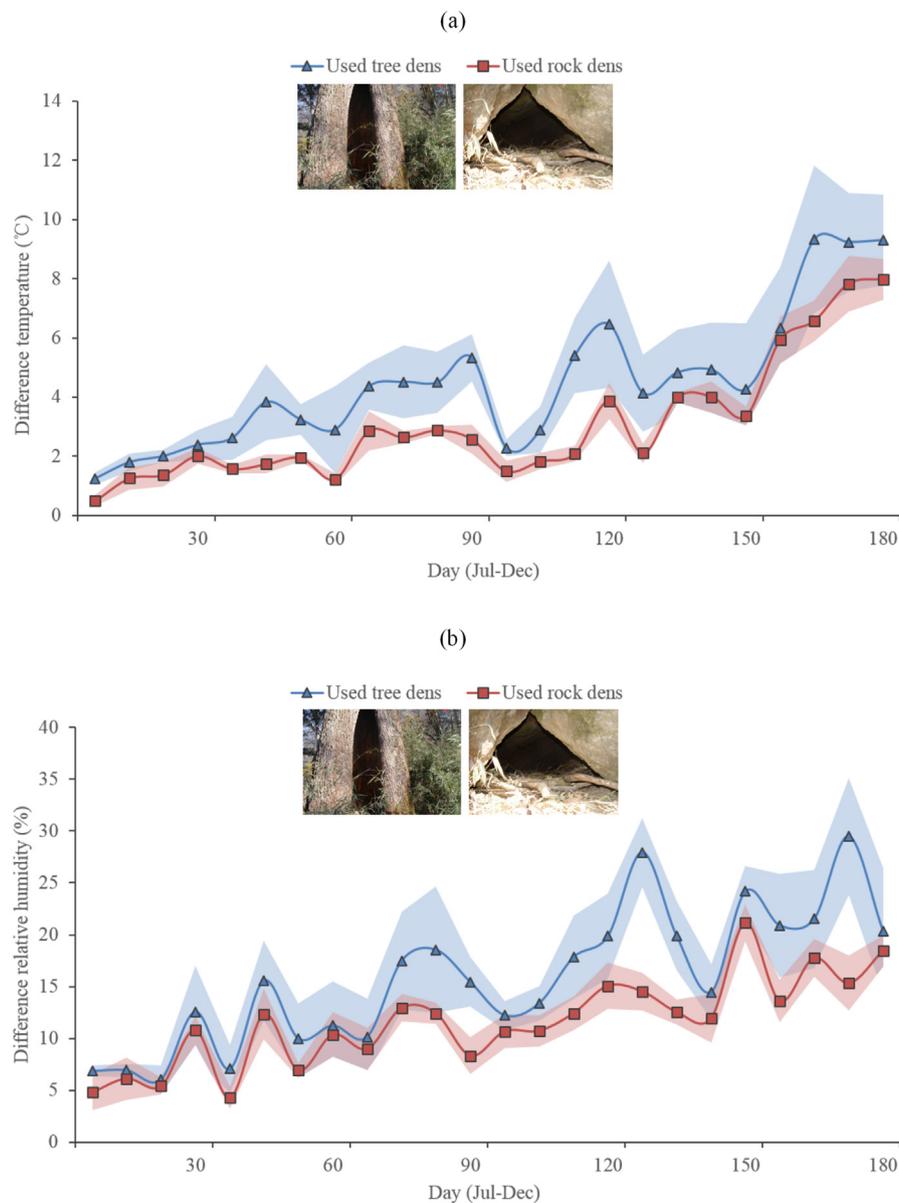
likely to enhance their function in protecting cubs against predators and inclement weather. For example, the combination of small entrance and large roomy interior preferred by maternal pandas likely provides better protection from predators and the weather, while the preference for visually concealed dens offers protection against predators and human disturbance. Our findings in Fengtongzhai are similar to but not identical to the findings for Foping (Zhang et al., 2007); one divergent finding is that in Foping pandas selected for steep slopes but in Fengtongzhai pandas selected gentle slopes. This is likely a byproduct of large old trees finding more favorable growing conditions on gentler slopes and rock caves being more prevalent in steep topographic relief. Together, these findings provide managers with important guidance for the structural characteristics required for the species, thus guiding preservation and conservation intervention strategies.

Many of these structural characteristics affecting use by maternal pandas, such as small entrances and comparatively larger interior cavities, are similar to findings for quite different species, ranging from birds (Le Roux et al., 2016a) to large carnivores (Fernández and Palomares, 2000), including other bear species (Petram et al., 2004); in some cases these structural variables predict survival of offspring (Cockle et al., 2015). Black bears (*Ursus americanus*) similarly require access to large, old trees, where they den in elevated cavities, providing an impetus for preservation of these habitat features (Oli et al., 1997). Den selection behavior in ursids can influence cub survival; for example, black bears selecting dens at lower elevations were more prone to flooding and offspring mortality (White Jr. et al., 2001).

Both rock and tree dens demonstrated strong capacity to buffer against outside conditions, providing a more stable microclimate within which to rear cubs than would be available in the absence of these refuges. Specifically, inside dens were warmer than outside dens during cold weather and cooler than outside dens during warm weather. Inside dens also had significantly lower humidity than outside ambient humidity, an important feature in the notably wet climate throughout the panda's range. These biologically important variables influencing thermoregulation differed inside versus outside dens when we examined mean, maximum, minimum and range, indicating that the microclimate inside dens was profoundly different from that experienced outside.

Our comparisons of used dens versus unused tree and rock cavities confirm pandas' dependence on microclimatic buffering of these cavities. Pandas selected rock and tree dens that provided more stable microclimates, buffering against extremes of temperature and humidity. In particular, preferred tree dens were characterized by large temperature buffering capacity during the colder winter months and during nighttime. This stable microclimate provides much more ideal conditions for rearing cubs that have little capacity to thermoregulate; future research should determine whether microclimate influences panda offspring fitness, as has been demonstrated in some other species (Isaac et al., 2008). Even with behavioral adjustments to accommodate cub fragility (Zhu et al., 2001), the high degree of altriciality of pandas will undoubtedly make the microclimate for developing offspring more important than for species with offspring that more rapidly gain thermoregulatory competence.

Perhaps most important for conservation, our findings demonstrate substantive differences in buffering capacity of tree versus rock dens. Although tree and rock dens were studied in two different reserves with somewhat different climates, by comparing the relative difference between inside and outside conditions we were able to show that tree dens have more favorable buffering capacity than rock dens. Compared to ambient conditions outside the dens, average temperatures were higher and average humidity was lower in tree dens than rock dens, and tree dens were also better at buffering against the coldest temperatures and most humid conditions. Thus, tree dens provide more stable and favorable conditions for pandas to rear offspring than do rock dens. In addition to direct effects of thermal challenge from extremes of temperature and humidity, unstable or unfavorable microclimatic



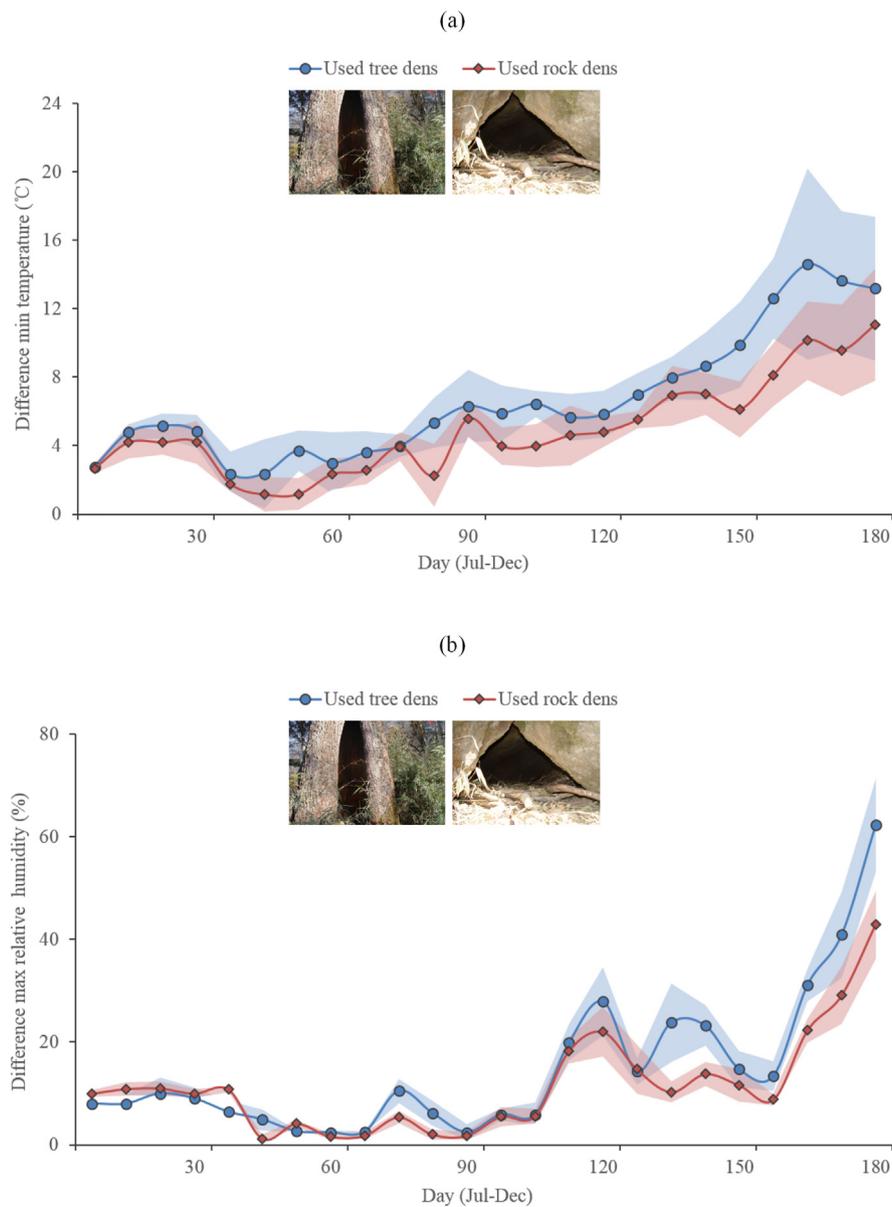
**Fig. 3.** Comparison of average daily microclimatic buffering efficacy as a function of den type (rock vs. tree den). Data collected for used dens only, over a six-month period in Fengtongzhai and Foping Nature Reserve. Difference (a) daily average temperature, (b) daily average relative humidity, with larger values indicating a better buffer capacity relative to exterior conditions.

conditions will entail energetic costs, especially when maintaining body temperature under colder temperatures. Giant pandas face extreme energetic challenges due their low-energy diet, and energetic constraints thus influence a number of life-history variables (Nie et al., 2015). Pandas thus are predicted to be more vulnerable to challenges to thermoregulation.

We do not fully understand the consequences for pandas living in areas where old growth forest has been logged, but if these differences in microclimatic buffering have fitness consequences, panda habitat with old growth trees may have higher carrying capacity than areas without this important resource for denning. Habitat selection research has shown that pandas sometimes have a strong preference for old-growth over secondary forest (Hull et al., 2014; Hong et al., 2016; Wei et al., 2018; Zhang et al., 2011), a pattern which may be enlightened by our findings. The higher incidence of pandas found in old growth forests may be governed in part by the provision of higher quality dens in these areas. In areas with insufficient numbers of large old trees in panda habitat, our findings provide guidance to managers wishing to

trial the use of artificial dens. Artificial den construction should follow the preferred structural and microhabitat features we documented, and they should be tested for their ability to buffer against inclement weather. If these design criteria are not followed, managers risk the possibility of creating “ecological traps” (Hale and Swearer, 2016), attracting pandas to use them but not providing the required microclimate needed for their offspring to thrive. Experimental trials with artificial dens commencing soon in Liziping Nature Reserve will benefit guidance established by our data.

The microclimatic insulating properties of tree cavities will become even more important under climate change. Microhabitat features that buffer against extremes of temperature will provide important refuges that may allow for the temporary persistence of species under climate change (Scheffers et al., 2014). Further, old-growth forests mitigate against climate change on much broader scales than the microclimate of the cavities they contain, providing landscape level cooling effects equivalent to 50-year forecasts for temperature increase in some cases (Frey et al., 2016). It is thus plausible that preservation of old-growth



**Fig. 4.** The greatest microclimate change during a day over a six-month period between used tree den in the Fengtongzhai and used rock cavity in the Foping Nature Reserve. The difference in (a) the daily minimal temperature over time between used tree dens and used rock cavities, (b) the daily maximal relative humidity over time between used tree dens and used rock cavities. Larger values indicating a better buffer capacity relative to exterior conditions.

forests will mitigate against climate change impacts for giant pandas and other species of wildlife, and thus managers and policy makers are encouraged to prioritize preservation of large old trees in panda habitat (Zhang et al., 2011). Some models have forecast that loss of bamboo habitat for foraging will impact giant panda populations (Li et al., 2015; Tuanmu et al., 2013; Zhang et al., 2017); however, it is possible that climate change-induced distributional shifts in the various species of bamboo adapted to different elevations will result in no net loss to bamboo forage (Wei et al., 2015), since pandas are not specialists on particular species of bamboo (Schaller et al., 1985). Our findings highlight the potential importance of conserving den cavities and large old trees for mitigating against other negative consequences of climate change for pandas.

Many species of birds (Cockle et al., 2015; Cockle et al., 2010; Saunders et al., 2014), marsupials (Isaac et al., 2008; Rowland et al., 2017), and eutherian mammals (Fernández and Palomares, 2000; Sedgely, 2001) depend on tree cavities for rearing offspring and thus widespread logging of old growth forests is having large but often

unknown consequence for wildlife abundance, likely contributing to the defaunation crisis (Dirzo et al., 2014). Although artificial cavities can play a role in limiting the negative impacts of the loss of old growth forests, these interventions are costly, may not be sustainable, and do not always work (Le Roux et al., 2016b; Maziarz et al., 2017), often due to poor microclimatic buffering capacity of artificial cavities (Rowland et al., 2017).

Current monitoring practices for giant pandas and their habitat does not include systematic surveys of large old trees, but our data points to the possibility that these trees are critical limiting resources used by denning maternal females, possibly facilitating offspring survival. Population decline for cavity-dependent species may lag behind declines in tree hollow availability, and other sources of refuge, underscoring the need to develop monitoring plans so that proactive conservation measures can be taken (Manning et al., 2013). Globally, forest management practices de-emphasize preservation of large old trees, favoring instead limits on harvest of younger trees, a practice that is misaligned with the conservation value of older trees (Cockle et al.,

2011). Future monitoring and management plans should emphasize this critical resource so that we can better judge its importance for giant panda conservation. Systematic trials with artificial dens—in the absence of sufficient natural den sites—may be used in an adaptive management context to determine if these management actions lead to population increase.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.12.031>.

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