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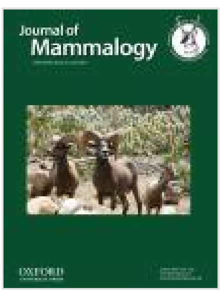

Editor
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IMPACT FACTOR	1.840
5 YEAR IMPACT FACTOR	2.247
SI: ZOOLOGY	38 out of 153

Published on behalf of

American Society of Mammalogists
www.mammalogy.org

Activity patterns of the giant panda (*Ailuropoda melanoleuca*)

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DOI: http://dx.doi.org/10.1093/jmammal/gyv118 First published online: 25 July 2015

One of the most fundamental questions in animal ecology concerns the activity patterns of animals and the environmental and intrinsic factors that influence such dynamics. Activity patterns of the elusive and endangered giant panda (*Ailuropoda melanoleuca*) are not well understood. Using GPS collars equipped with dual-axis accelerometers on captive and wild giant pandas for the first time, we investigated the impact of day, season, and weather on wild panda activity in Wolong Nature Reserve, Sichuan, China. Most pandas were not crepuscular as previously reported but had 3 apparent activity peaks, in the morning, afternoon, and around midnight. We found a peak in panda activity in June, then an apparent decrease in August and September, followed by an increase again from November to March of the following year. Activity patterns roughly corresponded to mean daily movement distances across seasons and movement behavior in a GPS-collared captive panda (studied to establish a baseline for interpreting collar-recorded activity of wild pandas). There was greater activity in times of higher solar radiation throughout every season, especially under cold conditions. This result suggests the potential for climate change to impact panda behavior in ways not previously reported. Our analysis also suggests that pandas may be constrained by tight energy budgets from their low-nutrient diet and may adjust their energy budgets by modifying their activity time and level across seasons. Our study has implications for understanding animal activity patterns across species, particularly relationships among forage, weather, and energy expenditure over time.
Key words:

activity pattern conservation giant panda GPS collar weather

Activity patterns of animals are important because they reveal key information about an animal's biology, such as bioenergetics, foraging strategy, evolutionary adaptations, and physiological responses to environmental cues. Activity patterns of animals may vary with temporal and spatial characteristics (**Beier and McCullough 1990**) and physiological factors including sex and reproductive status (**Schmidt 1999**; **Kolbe and Squires 2007**). Environmental factors such as weather and forage quantity and quality also have an impact on activity patterns (**Garshelis and Michael 1980**; **Beier and McCullough 1990**; **Beltrán and Delibes 1994**), in addition to other factors such as prey availability and predation pressure (**Podolski et al. 2013**). However, activity patterns are poorly understood in many species due to the logistical constraints involved in measuring activity when animals are elusive, constraints which limit the accuracy and resolution of activity data across space and time.

Such constraints have limited the knowledge available on the activity patterns of one of the world's recognizable endangered species—the giant panda (*Ailuropoda melanoleuca*). Endemic to southwestern China, giant pandas are known for being specialized bamboo foragers, despite retaining the simple stomach and short intestines of a carnivore (**Schaller et al. 1985**; **Liu and Viña 2014**). As a result, giant pandas are limited by a tight energy budget, digesting less than 20% of what they eat, a constraint that requires them to forage for up to 14h a day and sleep for much of the remainder (**Schaller et al. 1985**). A key theme recurring throughout giant panda research involves investigating how this particular foraging strategy of giant pandas has evolved and more broadly how pandas have adapted to the environmental constraints in their limited mountainous forest habitat (**Schaller et al. 1985**). Activity patterns are an important piece to this puzzle, since pandas need to carefully allocate their limited energy for daily and seasonal activities, particularly when future availability of bamboo may be uncertain due to climate change (**Tuanmu et al. 2013**). Activity patterns may in turn reveal key information about how pandas adjust their limited energy budgets in response to local weather conditions across seasons, according to their individual physiological state.

However, to date, information on activity patterns of the giant panda is limited to a select few radiotelemetry studies conducted in the 1980s to mid 1990s. These earlier studies reported that the panda was crepuscular (most active at dawn and dusk) in Wolong Nature Reserve (**Schaller et al. 1985**), and diurnal (active throughout the day) in the Qinling mountains (**Pan et al. 2014**). Seasonal activity was similar across studies, with the highest activity in spring and the lowest activity in summer–autumn (**Schaller et al. 1985**; **Pan et al. 2014**). However, these studies were constrained by the temporal resolution afforded by radiotelemetry, which limited collection of data to select days throughout the year when weather conditions were favorable. There also have not been any quantitative studies on seasonal and diel activity patterns in pandas, leaving much to be explored on this topic. The panda's allocation of energy toward various activities is not well understood, particularly with respect to how they respond to harsh weather and time periods of poor quality forage.

We were afforded a rare opportunity to begin to fill these gaps by measuring the activity patterns of wild giant pandas using recently developed, advanced GPS collars equipped with dual-axis accelerometers (**Hull et al. 2011**; **Hull et al. 2014**). This study is the first to use this specialized technology on an analysis of activity patterns of wild giant pandas. We set out to more precisely characterize the activity patterns of giant pandas on both a daily and seasonal scale at a fine temporal resolution and their relationships to weather and movement. We also calibrated the data against observed behaviors in GPS-collared captive pandas to link activity levels to classes of behaviors. This study contributes to the understanding of the panda's unique adaptive strategy by illustrating how pandas adapt their activity levels to meet the demands of a tight energy budget in the context of a dynamic environment. Such an analysis has implications for panda conservation and for a broader understanding of energy allocation strategies across different animal species.

MATERIAL AND METHODS

Study area.

Our study area lies in Wolong Nature Reserve (102°52′–103°24′E, 30°45′–31°25′N), Sichuan Province, southwestern China (**Viña et al. 2008**). The reserve was established in 1963 and is one of the earliest protected areas for giant pandas in China, covering an area of about 2,000 km^2 in the Qionglai Mountain range (**Fig. 1**; **Liu et al. 1999**; **Xu et al. 2006**; **Hu et al. 2011**). There are about 150 wild giant pandas in Wolong, which also harbors at least 4,000 species of plants and 300 species of other animals (**State Forestry Administration 2006**; **Chen et al. 2010**). The climate in Wolong is characterized by a cold and dry winter and a warm, humid summer and autumn (**Li et al. 1992**). We built a small meteorological station (HOBO Microstation with RG3 Rain Gauge, Onset Computer Corporation, Pocasset, Massachusetts) at the Hetaoping Research Base just below our study site where the distance to the farthest collared panda activity region was approximately 10 km (**Fig.1**). We recorded weather characteristics including barometric pressure (mm Hg), air temperature (°C), solar radiation (W/m^2), and relative humidity (%) at 5-min intervals from June 2010 to September 2011.

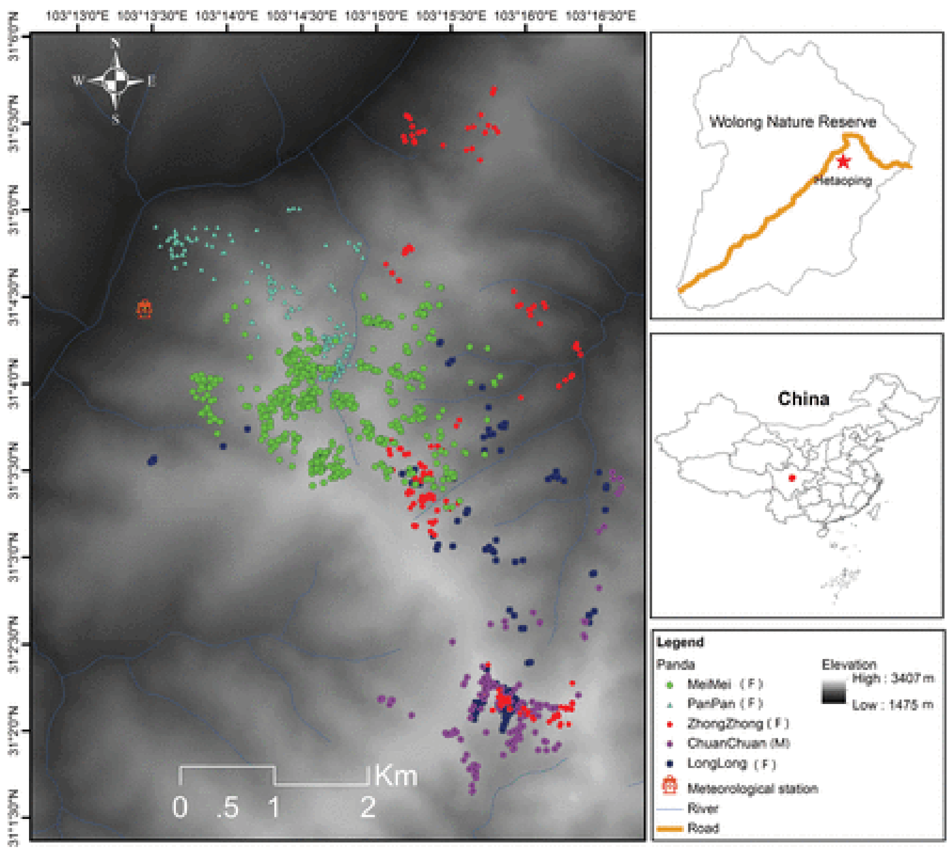

Fig. 1.
Study area for GPS collar tracking of wild giant pandas (*Ailuropoda melanoleuca*) at Hetaoping Research Base in Wolong Nature Reserve, China.

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The area where we tracked the wild pandas is located in close proximity to the Hetaoping Research Base in the northeastern portion of the reserve. The area encompasses 40 km^2, with an elevational range of approximately 1,800–3,400 m, with slopes ranging from 20° to over 50° (**Fig. 1**). There are approximately 22 giant pandas in the study area, an estimate obtained using infrared camera trapping and DNA testing of panda feces collected in the region (**Huang et al. 2015**). There are 4 forest types: evergreen broad-leaved forest, deciduous broad-leaved forest, mixed coniferous and deciduous broad-leaved forest, and subalpine coniferous forest, while arrow (*Sinarundinaria fangiana*), umbrella (*Fargesia robusta*), and Yushan (*Yushania bravipaniculata*) bamboo are found in the understory (**Hull et al. 2010**; **Tuanmu et al. 2010**).

GPS collars and giant pandas.

We captured and fitted GPS collars on 5 giant pandas (4 females and 1 male, 4 adults and 1 subadult) from 2010 to 2012 (**Table 1**). Pandas were anesthetized for brief periods using a compressed-air gun containing approximately 5mg ketamine per kg of animal. After recording basic information on the animals, pandas were left in the same location to recover and resume their normal activities undisturbed. Data were downloaded from collars every few months using a remote receiver. Licensed veterinarians from the China Conservation and Research Center for the Giant Panda (CCRCGP) were responsible for animal safety for the duration of the study. These methods followed American Society of Mammalogists (ASM) guidelines (**Sikes et al. 2011**) and were approved by the institutional animal use and care committee of Michigan State University.

Table 1.
Summary of GPS-collared pandas (*Ailuropoda melanoleuca*) in Wolong Nature Reserve, China.

Panda	Age	Sex	Deployment date	Duration of tracking	Tracking days
Mei Mei	Adult	F	29 March 2010	4 April 4 2010–29 March 2012	726
Pan Pan	Adult	F	11 April 2010	17 April 2010–26 November 2010	224
Zhong Zhong	Adult	F	16 March 2011	23 March 2011–3 April 2012	377
Chuan Chuan	Adult	M	31 March 2011	6 April 2011–27 March 2012	357
Long Long	Subadult	F	04 April 2011	10 April 2011–11 October 2011	185

Enlarge table

The collars were 12-channel Lotek GPS_4400M GPS Collars (Lotek Engineering Inc., Newmarket, Ontario, Canada). The collars contained dual-axis accelerometers operating in vertical and horizontal directions, each consisting of a cylinder containing a small sphere. An integrated data logger registered the number of times that the spheres hit the edges of the cylinders in each 5-min time interval throughout the study period. This information was converted into a unitless scale ranging from 0 (no activity) to 255 (highest activity). GPS collars also recorded longitude, latitude, and elevation every 4h. Fix acquisition rate ranged from 31% to 54% and predeployment static tests showed that position error of collars relative to a differentially corrected GPS unit averaged 16–23 m (n = 30 locations per collar).

Captive pilot study.

We conducted a pilot study on 1 captive adult female panda in the Hetaoping research base to establish a baseline for linking specific behaviors to different values obtained from the GPS collar activity sensors. It is extremely difficult for researchers to observe pandas directly in the wild, especially in Wolong where there is complex terrain (**Schaller et al. 1985**). We fitted the same type of GPS collar on 1 captive panda and observed and recorded the behavior of this captive panda using a video monitoring system, the contents of which were later transcribed. We recorded a total of 541h (from 1100 [25 January 2011] to 2355 [6 February 2011] and from 0000 [10 February 2011] to 2355 [19 February 2011]). We recorded the primary behavior being performed during continuous 5-min increments that corresponded to the same 5-min increments measured by the collar. Behaviors were determined based on a well-established ethogram used for captive pandas (**Zhou et al. 2004**). Behaviors included 4 main types: inactive, feeding, moving, and other (**Table 2**). We calculated the mean and range of activity counts for each type of behavior, and compared among them using 1-way analysis of variance (ANOVA).

Table 2.
Ethogram for behaviors observed in the captive panda (*Ailuropoda melanoleuca*) behavioral observation pilot study and proportion of time allotted to each behavior by a captive (adult female) panda.

Behavior	Description	Proportion of time (%)
Inactive	Resting (sleeping, lying, or stationary standing, not moving).	44.6
Feeding	Eating any type of food.	43.07
Moving	Directional walking from one point to another point, fast or slow.	3.31
Other	Drinking water, play fighting among pandas, feeding cubs, etc.	9.02

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Measurement of activity patterns.

The 2 main variables that we were interested in for the analysis of wild panda activity patterns were percentage of active time and activity level. For percentage of active time, we defined inactive behavior as occurring when both the vertical and horizontal sensor values were 0 and active behavior as any instance in which either the vertical or horizontal values (or both) were nonzero. This decision is supported by the pilot study on the captive panda which showed that all inactive behaviors corresponded to 0's in both sensors (**Table 3**). With respect to activity level, we used the activity count (0–255) obtained by the vertical sensor only, since a previous study demonstrated that accuracy was higher from the vertical sensor than the horizontal sensor (**Coulombe et al. 2006**). Collars also recorded temperature every 5min, but we omitted this variable from the analysis (and instead used temperature recorded by the weather station). This is because temperature recorded by the collar was influenced by the research animals' posture, activity and pelage type (**Maier et al. 1996**; **Schwartz et al. 2009**). The collars recorded data over time spans ranging from 6 months to 2 years (see **Table 1**).

Table 3.
Summary of GPS collar-recorded activity levels for each behavior observed in a captive GPS-collared panda (*Ailuropoda melanoleuca*) (X and Y correspond to the horizontal and vertical sensors).

Axis	Behavior	$\overline{X}$	*SE*	Minimum	Maximum
X	Inactive				
	Resting	0.000[a]	0.000	0	0
	Feeding	14.198[b]	0.143	1	44
	Active				
	Moving	27.318[c]	1.191	3	81
	Other	11.982[d]	0.573	1	40
Y	Inactive				
	Resting	0.000[a]	0.000	0	0
	Feeding	15.364[e]	0.131	1	42
	Active				
	Moving	23.576[c]	0.859	4	61
	Other	12.524[b,d]	0.576	1	35

Different superscript letters (a–e) indicate significant differences among different behavioral types for the captive panda according to analysis of variance.

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Individual pandas were used as the sampling unit in all analyses in this study. For each panda, we computed the hourly mean activity count and hourly percentage of active time to describe the diel (daily) activity pattern, and monthly mean activity level to describe the seasonal activity pattern. We conducted *t*-tests to evaluate differences in monthly mean activity of all studied individuals from one month to the next. We also described the activity pattern of each panda by each ecological season. In addition, we estimated the daily movement distance of pandas by calculating the straight-line distance between all points spaced 24-h apart from one to another. Then, we analyzed the relationship between movement and the sum of all panda activity counts recorded by the vertical sensor over the 24-h period. We also compared the daily movement distance among ecological seasons for each panda using nonparametric tests—the Kruskal–Wallis test and Mann–Whitney *U*-test. According to the panda's seasonal behavior established from previous field surveys, the year can be divided into 3 ecological seasons in Wolong (**Schaller et al. 1985**). Spring is from April to June when pandas mainly forage on the shoots of umbrella bamboo and stems of arrow and Yushan bamboos; summer–autumn is from July to October when pandas primarily consume leaves of arrow and Yushan bamboo, and winter is from November to March of the following year, when pandas eat old shoots, stems, and arrow and Yushan leaves.

In order to determine if the pandas' activity patterns were crepuscular, we compared the activity level among 4 periods of day: dawn, daytime, dusk, and nighttime. Periods were defined by sunlight: dawn was the period during sunrise, dusk was the period during sunset, the interval between dawn and dusk was daytime and the interval between dusk and dawn was nighttime. Sunrise and sunset shifted seasonally. During spring, dawn was 0500–0700 and dusk was 1800–2000; during summer–autumn, dawn was 0600–0800 and dusk was 1800–2000; during winter, dawn was 0700–0900 and dusk was 1700–1900. We used a 1-way ANOVA to evaluate differences in activity across these 4 periods in each season (significance level at $P < 0.05$).

Relationship between weather and activity.

We constructed generalized additive mixed models (GAMM) with a temporal autoregressive component to analyze the impact of weather factors on the activity patterns of the pandas. We chose this model because it allowed for modeling of nonlinear patterns of activity on the hourly scale. We subset the panda activity data to only include the time frame of available weather data (June 2010–September 2011). We specified individual regression equations for each panda because the tracking period was different among them.

The dependent variable in all models was the mean hourly activity level. Independent variables included binary variables (0, 1) to represent seasonal differences. Other independent variables included hour (1–24) and Julian date accurate to the hourly scale. Hour and date were included as nonlinear smoothed terms. We also included 4 weather variables: barometric pressure, temperature, solar radiation, and relative humidity. We included 3 interaction terms: air temperature and solar radiation, air temperature and barometric pressure, and solar radiation and relative humidity. These interactions were chosen according to previous studies (**Beier and McCullough 1990**). Although both temperature and barometric pressure vary with elevation, we did not include elevation as an independent variable, since during each season, the elevational range occupied by pandas varied little on the hourly scale. To reduce collinearity among independent variables, predictor variables were standardized ($[X_i - \overline{X}]/SD$) before interaction terms were generated (**Marquardt 1980**). For each model, we tested for multicollinearity using the variance inflation factor (VIF) and removed variables with values larger than 10. The models were performed using the mgcv package in R (**R Development Core Team 2005**; **Wood 2006**).

RESULTS

Activity patterns.

We acquired 469,672 activity counts at 5-min intervals on a total of 1,869 monitoring days (**Table 1**). Throughout the monitoring period, the total percent active time across the 5 pandas averaged 55% (range: 49–63%). The mean horizontal and vertical activity counts across the 5 pandas were 12±2 and 12±1 ($\overline{X} \pm SE$; range: 6–18 and 8–19, respectively). Regarding seasonal patterns in activity, pandas exhibited peaks in activity in spring, valleys in activity in summer–autumn, followed by an increase in activity again in winter. These seasonal patterns were consistent for both percentage of active time and activity level (**Fig. 2**). Activity level significantly increased from both April to May and from May to June (April versus May: $t = -8.692$, $d.f. = 117$, $P < 0.001$; May versus

June: $t = -4.838$, $d.f. = 120$, $P < 0.001$). Activity level reached the highest peak in June, then began to drop in July; statistically significant decreases occurred from June to July and from July to August (June versus July: $t = 15.401$, $d.f. = 120$, $P < 0.001$; July versus August: $t = 11.8$, $d.f. = 122$, $P < 0.001$). After the lowest activity in August and September, panda activity level increased significantly from month to month from October to December (October versus November: $t = -3.034$, $d.f. = 120$, $P < 0.001$; November versus December: $t = -6.271$, $d.f. = 120$, $P < 0.001$) (**Fig. 2**). Similarly, the percentage of active time for each collared panda was the highest in May and June (56–71% active), followed by the period from December to February (42–68% active), with a pronounced low in August and September (21–51% active) (**Fig. 2**). However, the variation in percentage of active time was small across seasons. For example, the adult female Mei Mei had higher activity in the spring of 2010 (a year in which she was pregnant) compared to 2011 and 2012, but her percentage of active time was similar across years (**Figs. 3** and **4**). There were some differences of panda activity by age-class, for example, the (male) older individual had a slightly lower percent active time (49%) than all other adult and subadult individuals (mean was 57%, range from 53% to 63%). The percent active time of subadult (Long Long) was similar with adults, but her activity level was lower than adults (**Figs. 3** and **4**).

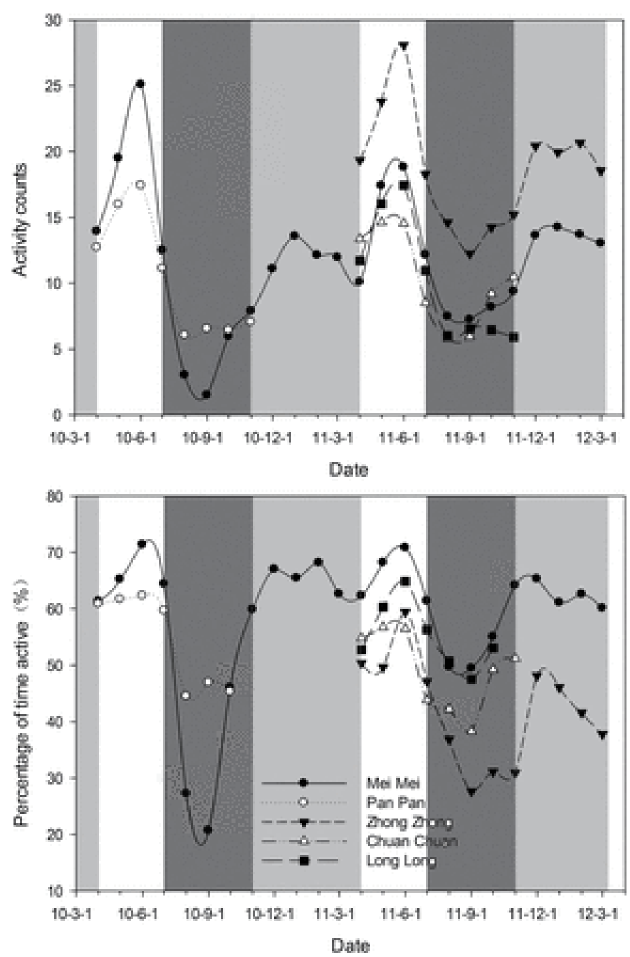

Fig. 2.

Mean monthly activity level and percentage of time active for 5 wild pandas (*Ailuropoda melanoleuca*) in Wolong Nature Reserve, China, from 2010 to 2012. The light shadow, dark shadow, and no shadow represent winter, summer–autumn, and spring, respectively.

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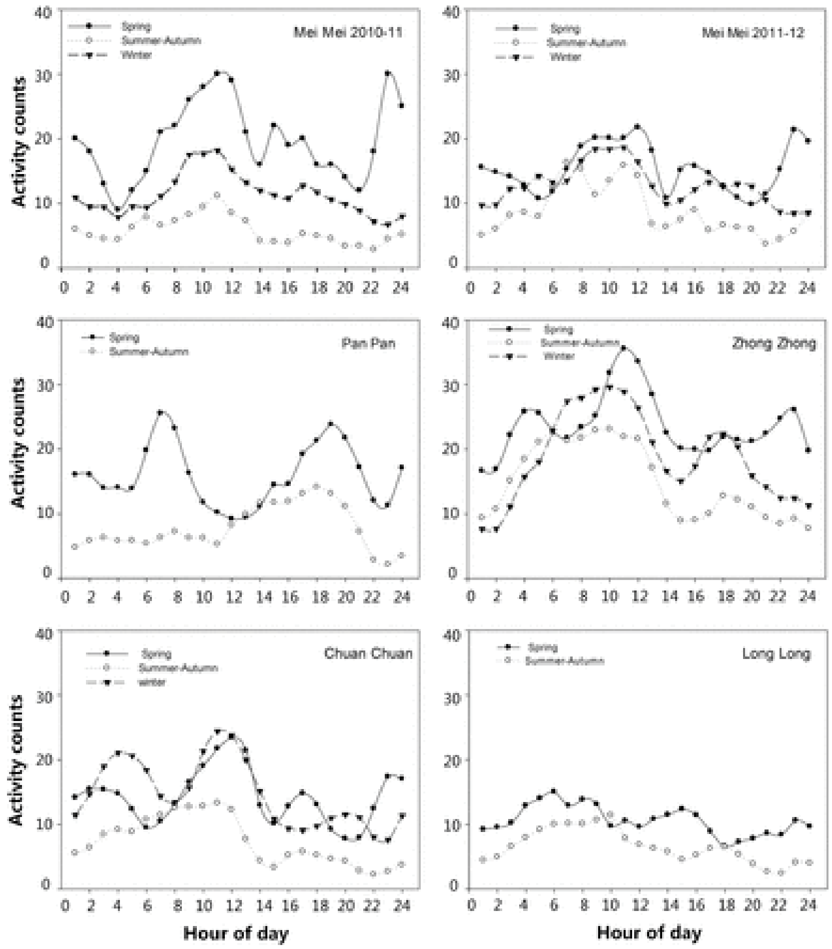

Fig. 3.

Mean hourly activity level of 5 pandas by ecological season in Wolong Nature Reserve, China, from 2010 to 2012.

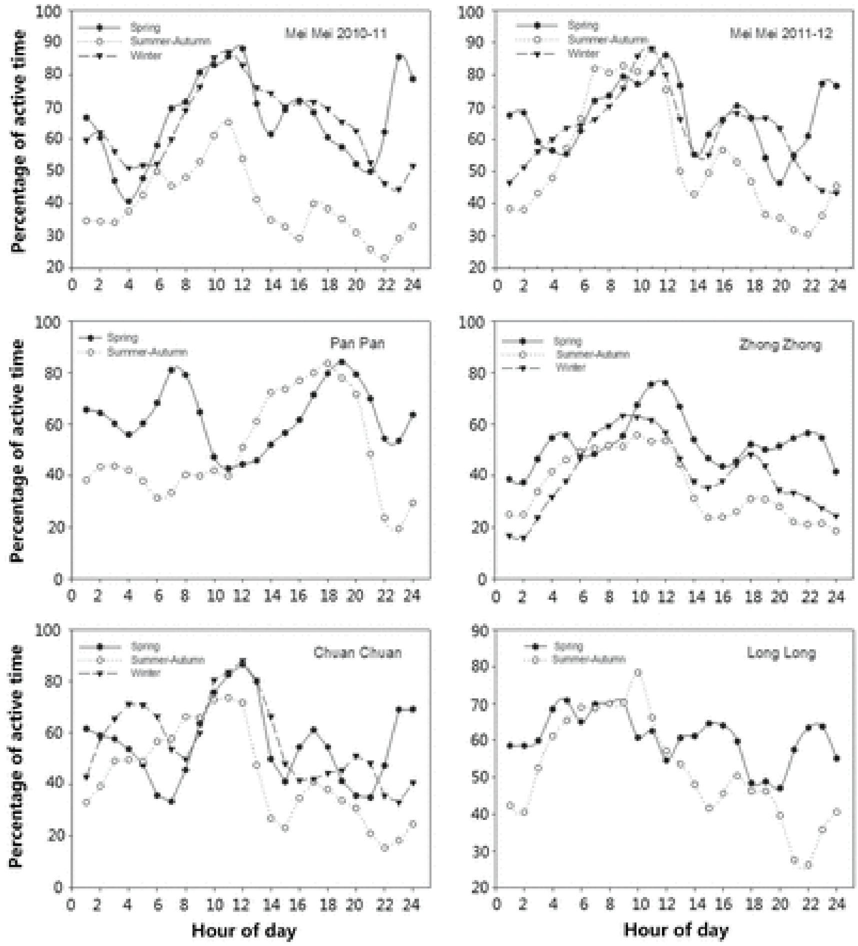

Fig. 4.

Mean hourly percentage of time active of 5 pandas (*Ailuropoda melanoleuca*) by ecological season in Wolong Nature Reserve, China, from 2010 to 2012.

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With respect to daily activity patterns, 3 of the adult pandas (Mei Mei, Zhong Zhong, and Chuan Chuan) exhibited similar patterns. There were 3 activity peaks and 3 rest periods (occurring between 2 of the activity peaks) throughout the day in every season (**Figs. 3** and **4**). The timing of activity peaks and rest periods was nearly synchronous across the 3 adult pandas, the first activity peak occurring in the morning (1000–1200), the second peak in the afternoon around dusk (1600–1900), and the third peak at midnight (2300–0300; **Figs. 3** and **4**). The subadult, Long Long, displayed 3 activity peaks and 3 rest periods as well, but her activity peaks and valleys were not as apparent as the adult individuals. Activity peaks for the three adults shifted around 1–2h later from the spring season to the summer–autumn season (spring activity peaks—0600–0800, 1500–1600, 2200–2400; summer activity peaks—0800–1000, 1600–1800, 0000–0100; **Figs. 3** and **4**). An exception to the aforementioned patterns was Pan Pan, an adult female who exhibited a crepuscular activity pattern in spring with activity peaks at dawn (600–800) and dusk (1700–1900) and a unimodal activity pattern in summer–autumn with a single activity peak from afternoon to dusk (1400–2000, **Figs. 3** and **4**).

There were significant differences in activity level of the 5 study pandas based on time of day (dawn, daytime, dusk, and nighttime) in all studied seasons (ANOVA, all $P < 0.05$). Activity level was significantly lower at dusk than daytime in every season for most pandas ($P < 0.05$). The only exception was the adult Pan Pan, for whom the mean activity level at dusk was significantly higher than daytime and nighttime in spring and summer–autumn ($P < 0.05$). Significance of differences for the rest of the time of day comparisons varied considerably across individuals and did not support previous results from earlier studies showing crepuscular activity in pandas (**Table 4**; **Fig. 5**).

Table 4.
Activity level ($\bar{X} \pm SE$) of GPS-collared pandas (*Ailuropoda melanoleuca*) by season, comparing activity at nighttime, dawn, daytime, and dusk.

	Mei Mei	Pan Pan	Zhong Zhong	Chuan Chuan	Long Long
Spring					
Night	9.2 ± 0.2^{a}	12.2 ± 0.9^{a}	23.7 ± 0.7^{a}	14.1 ± 0.5^{a}	10.3 ± 0.4^{a}
Dawn	13.1 ± 0.4^{b}	25.1 ± 2.5^{b}	22.3 ± 1.5^{b}	9.9 ± 1.1^{b}	13.9 ± 1.3^{b}
Day	12.4 ± 0.2^{b}	16.9 ± 1^{c}	25.7 ± 0.6^{c}	16.2 ± 0.4^{c}	10.7 ± 0.4^{a}
Dusk	8.4 ± 0.3^{c}	26.1 ± 2.6^{d}	21.4 ± 1.4^{d}	8.5 ± 0.8^{d}	7.5 ± 0.7^{c}
Summer–Autumn					
Night	6.1 ± 0.2^{a}	5 ± 0.2^{a}	14.1 ± 0.5^{a}	5.3 ± 0.3^{a}	5.6 ± 0.3^{a}
Dawn	10.3 ± 0.5^{b}	6.8 ± 0.7^{b}	21 ± 1.1^{b}	10.7 ± 1^{b}	10.1 ± 0.7^{b}
Day	7.9 ± 0.2^{c}	9.8 ± 0.3^{c}	15.6 ± 0.5^{c}	7.9 ± 0.3^{c}	7.1 ± 0.3^{c}
Dusk	4.8 ± 0.3^{d}	12.1 ± 0.2^{d}	11.7 ± 0.9^{d}	3.9 ± 0.4^{d}	4.6 ± 0.5^{a}
Winter					
Night	9 ± 0.2^{a}		16.2 ± 2.2^{a}		
Dawn	15.5 ± 0.7^{b}		17.7 ± 4.4^{b}		
Day	13.9 ± 0.3^{b}		22.4 ± 2^{c}		
Dusk	11.2 ± 0.6^{c}		11.2 ± 3.5^{d}		

Different superscript letters (a–d) indicate significant differences across the 4 times of day for each panda season according to analysis of variance.

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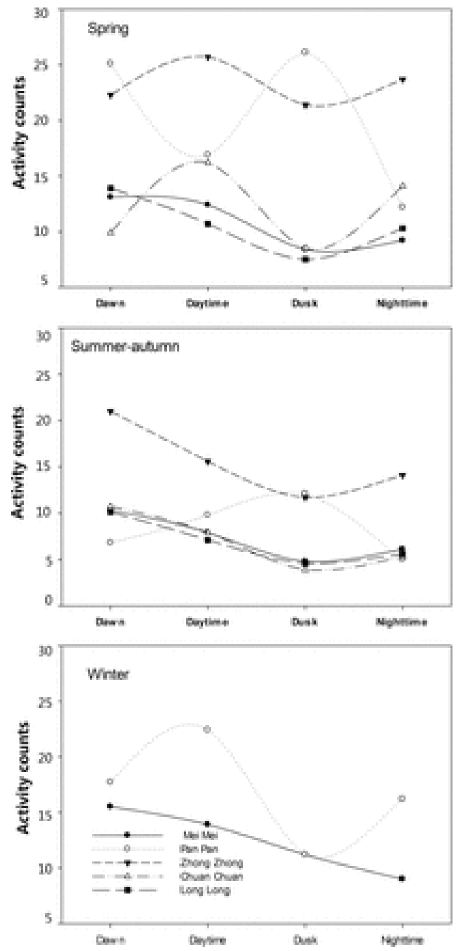

Fig. 5.
Activity level of each collared panda (*Ailuropoda melanoleuca*) by ecological season, comparing activity at dawn, daytime, dusk, and nighttime.

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Captive pilot study.

We found significant relationships between activity counts measured by the GPS collar and behaviors performed by the animal. The activity counts of inactive behavior were 0 for both axes, which were significantly lower than any active behavior (**Table 3**). Activity counts for moving were significantly higher than feeding and “other” behaviors (**Table 3**).

Movement across seasons.

The mean daily movement distance was 241±341 m (mean ± *SD*) and ranged from 0 to 4,605 m across pandas. The distribution was left-skewed, such that the median distance was 114 m (25 and 75% quartiles were 60 and 284 m, respectively). Panda activity was significantly higher when mean daily movement distance was over 500 m than within 500 m (Mann–Whitney *U*-test: $Z = 18.028$, $P < 0.001$), while activity level changed little with increasing movement when mean daily movement was closer than 500 m (**Fig. 6**). Daily movement distance was significantly shorter in summer–autumn than spring and winter across pandas (Mann–Whitney *U*-test: all $P < 0.05$), with the exception of the pregnant female Mei Mei (Kruskal–Wallis Test: $\chi^2 = 0.92$, $d.f. = 2$, $P = 0.631$). The male panda's daily movement distance was greater than others across all seasons (Mann–Whitney *U*-test: $Z = 13.041$, $P < 0.001$).

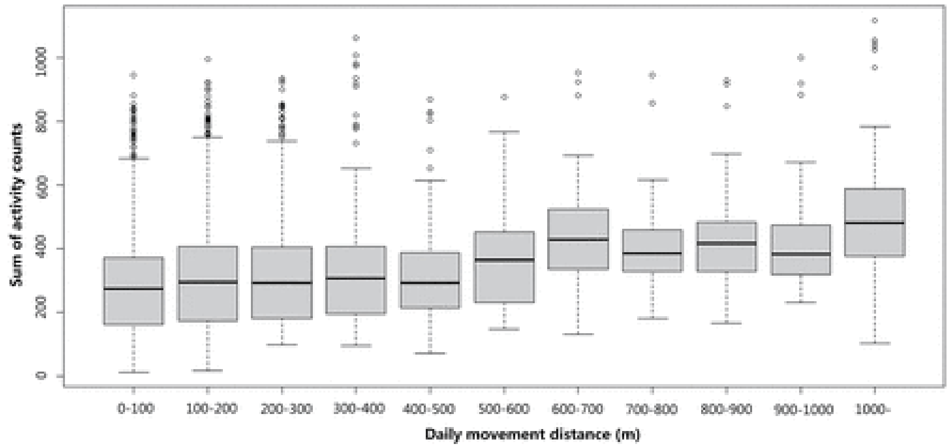

Fig. 6.

Relationship between daily movement distance (m) and sum of activity counts for pandas (*Ailuropoda melanoleuca*) in Wolong Nature Reserve, Sichuan, China.

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Relationships between weather and activity.

In correspondence with earlier results, the effects of hour and season were significant predictors of panda activity in the GAMM, as was Julian date (**Table 5**). After controlling for these factors, the impact of most weather factors on the pandas' activity was relatively weak. An exception was solar radiation, which was significant in predicting higher activity levels for most pandas. There was also a significant negative interaction between temperature and solar radiation, such that solar radiation had a stronger positive effect on activity level when the temperature was low.

Table 5.

Generalized additive mixed models (GAMM) depicting factors influencing mean hourly activity level of pandas (*Ailuropoda melanoleuca*) in Wolong Nature Reserve, China, 2010–2011.

Variables	**Coefficients**				
	Mei Mei	**Pan Pan**	**Zhong Zhong**	**Chuan Chuan**	**Long Long**
Pressure	–0.028	0.289	–0.404	–0.505	–1.181
Air temperature	1.518	–0.111	–0.655	–1.516	–1.48
Relative humidity	0.725	–3.059**	0.992	–0.222	0.753
Solar radiation	3.654***	–0.724	2.139*	5.232*	2.043*
Season	–0.979	–2.024*	–2.234*	–2.072*	–0.883
Solar radiation × air temperature	–0.307	–0.658	–1.614*	–2.002*	–2.181*

Relative humidity × solar radiation	2.365*	1.766	−1.751	−0.454	−0.342
Pressure × air temperature	2.115*	2.804**	0.224	−0.047	−0.121
S (hour)[a]	18.03***	8.176***	14.72***	10.559***	10.799***
S (Julian date)[a]	23.24***	−0.751	7.769***	3.321*	5.358***
R^2/sample size	0.063/11,328	0.059/2,928	0.127/4,512	0.037/4,176	0.021/4,200

[a] Smoothed terms were fitted for hour and Julian date.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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Discussion

This is the first quantitative analysis of the seasonal and diel patterns of activity of the endangered giant panda using accelerometers embedded in GPS collars, an approach that helped corroborate earlier research and also yielded new information. Although our sample size is relatively small and some results should be interpreted with caution, the results are novel because they have never before been acquired for this rare, elusive, endangered, and protected species.

The seasonal pattern in giant panda activity that we found showing an activity peak in spring compared to summer–autumn and winter is in keeping with previous findings from radiotelemetry studies on the species, but our study helps add temporal precision and robustness to this finding. Based on findings from the movement analysis and the captive panda study, this activity peak likely corresponds to greater movement by the pandas. During spring, pandas migrate from high to low elevation for foraging on umbrella bamboo shoots, which contain higher nutritional concentration (e.g., calcium, nitrogen, and phosphorus) and comprise a high energy diet relative to foods consumed at other times of year (**Nie et al. 2014**). Pandas move longer distances in search of umbrella bamboo shoots, since this is a scattered resource that covers only roughly 40% of a given area (compared to over 90% for arrow bamboo—**Schaller et al. 1985**). According to optimal foraging theory (**Charnov 1976**), pandas would be expected to maximize their energy intake by spending more time and effort on foraging during this season.

Pandas may also be more active during spring because it is the mating season, a time period when male pandas allocate more energy on traveling and fighting for mating rights (**Hu and Wei 1990**; **Pan et al. 2014**). Pregnant female pandas might be more active when foraging on umbrella bamboo shoots, since the shoots have high nutritional content which is advantageous for embryonic development and improving the birthrate of offspring (**Nelson 1991**; **Shelby et al. 2006**). In our study, Mei Mei was more active (which was reflected by activity count and percentage of time active) during the spring of the year in which she was pregnant, providing support for this hypothesis (**Fig. 2**). Captive pandas also show higher activity and foraging in spring even though they do not need to search for food, suggesting that this pattern may be associated with reproduction (**Huang et al. 1999**).

Young arrow bamboo leaves with high nutrient content are the main food of during summer–autumn, a resource that has a high and even distribution across the landscape, causing movement and activity levels to be relatively low (**Schaller et al. 1985**; **Nie et al. 2014**; **Pan et al. 2014**). The relatively high activity levels and movement in winter may relate to increased travel to less available water sources or to the lower nutritional content of food compared to other times of year (**Schaller et al. 1985**). The overall variation across the year may be attributed to variation in consumption of bamboo species and components and their associated variation in nutrient composition throughout the year (**Schaller et al. 1985**; **Nie et al. 2014**; **Pan et al. 2014**). Similar studies on other species have shown that seasonal activity patterns reflect responses to seasonal changes in forage type, quantity, and quality (**Garshelis and Michael 1980**; **Beier and McCullough 1990**; **Massé and Côté 2013**; **Podolski et al. 2013**).

The daily activity patterns of pandas in this study showing 3 activity peaks differed from previous findings of crepuscular activity patterns (exhibiting 2 daily peaks at around 0500 and 1700) for pandas in this reserve (**Schaller et al. 1985**). The timing of the peaks was also different—dawn and dusk for **Schaller et al. (1985)** and late morning, afternoon, and midnight for our study. **Schaller et al. (1985)** did note that their crepuscular patterns were found after combining raw data across 5 individuals, but there was considerable variation across pandas (and seasons), although the raw data was not fully shown. Our study suggests that the activity patterns of pandas may be more variable than previously appreciated.

The variability is further apparent when comparing to pandas monitored using radiotelemetry in the Qinling mountains, which demonstrated a diurnal activity pattern with an activity peak in the afternoon from 1300 to 1700 (**Pan et al. 2014**). Researchers have suggested that this may be due to differences in diet, with pandas in the Qinling mountains commonly foraging leaves from 2 different bamboo species that are higher in nutrients but slower to digest than the stems more often consumed in Wolong, a diet which does not require as intensive and frequent foraging (**Schaller et al. 1985**; **Pan et al. 2014**). Our results showing 3 activity peaks provide further support for this hypothesis in demonstrating the potentially high metabolic demands of pandas in Wolong.

Previous studies have shown that the daily activity pattern of some bear species such as sun bears and black bears is unimodal with most activity concentrated in the daytime (**Te Wong et al. 2004**; **Yamazaki et al. 2008**; **Schwartz et al. 2009**). Other bears such as brown bears and grizzlies have been characterized as crepuscular, which is related to avoiding human activity or mimicking activity patterns of prey (**Warner 1987**; **Olson et al. 1998**; **Munro et al. 2006**). This pattern is similar to many herbivorous ungulate species (**Gogan 1973**; **Schmitz 1991**; **Ager et al. 2003**; **Kie et al. 2005**; **Forester et al. 2007**). There are also some studies on black bears and grizzly bears that have found that activity patterns alternate between unimodal and crepuscular based on food abundance and availability across seasons (**Garshelis and Michael 1980**; **Munro et al. 2006**). Pandas are a unique species with which to examine activity patterns because they share a similar diet with other large herbivores but differ in that they do not have large predators in their environment (**Schaller et al. 1985**). Their adaptation of 3 activity peaks sheds light on their unique ecology compared to other animals.

Our study provides new information about panda activity patterns through the analysis of activity level data—data that are available for the first time using GPS collars in our study. Activity level analysis helped to more comprehensively elucidate the patterns and distinguish differences in activity at a monthly and yearly scale compared to the variable of percent active time (**Figs. 3** and **4**). While percent active time was relatively stable across seasons, activity level varied and revealed a high period of activity in spring. In addition, the pregnant female Mei Mei's patterns could be more fully understood via the activity level, as although she did not show differences in percentage active time by season across years, she exhibited a higher activity levels in the spring prior to her offspring's birth and lower activity levels in the period after the young's arrival. Another instance was that the percent active time for the subadult was similar with adult individuals, but it exhibited a relative lower activity level (**Figs. 3** and **4**). These observations suggest that pandas may meet their energetic demands by increasing their activity level without compromising their total amount of rest when the seasonal or physiological demands require it. This phenomenon has not been fully explored in other species before since this technology is relatively new, thus we suggest it should be investigated in the future to determine whether it is a widespread phenomenon.

Our study is also the first to demonstrate statistically significant relationships between weather and panda activity, a phenomenon that has been demonstrated in other species such as white-tailed deer, moose, and lynx (**Beier and McCullough 1990**; **Gillingham and Klein 1992**; **Beltrán and Delibes 1994**), but not pandas. Our data revealed there was a significant positive correlation between solar radiation and panda activity throughout all seasons, and especially in colder conditions. This relates and contributes to research demonstrating giant panda habitat selection for areas with higher solar radiation (**Liu et al. 2011**) and speaks to a broadly understood phenomenon of mammalogy in which furbearing animals absorb heat from sunshine, adding to their thermal energy (**Hamilton and Heppner 1967**; **Loveless 1967**; **Moen 1973**; **Quan et al. 2011**). Similar results have been found in other wildlife, such as the black-and-white snub-nosed monkey (*Rhinopithecus bieti*) and mule deer (*Odocoileus hemionus*) during winter (**Loveless 1967**; **Moen 1973**; **Quan et al. 2011**). Compared to the effect of weather, hour of day and season had a stronger effect on panda activity. This suggests that endogenous rhythms, occurring on daily and seasonal scales, and diet variation across seasons likely play a more important role in panda activity patterns than weather alone, a finding also seen in other species (**Aschoff 1966**).

We found differences in relationships between weather variables and panda activity across individuals in the study, suggesting that individual life history or physiological traits could affect the environment–activity relationship, although a larger sample size may be needed for more robust conclusions. In addition, our study does not capture small-scale variation in microclimate across different slopes, aspects, and elevations in the study area, a topic that is in need of further research in the future. The captive pilot study was useful in demonstrating relationships between GPS collar-recorded activity levels and behavior. However, the utility was limited by the fact that the behavior of the captive panda differed from the wild pandas. For instance the mean activity level on horizontal and vertical direction were 9±0.04 and 9±0.04 (n = 6,411), respectively (compared to

12±2 and 12±1 across the wild pandas). Captive pandas were likely more stationary while feeding due to the fact that they were handed clumps of already broken-off bamboo and they did not need to search for them and were likely less active when moving due to less space available for movement. Nonetheless, the captive study gave some perspective for interpreting the activity level data.

In this first quantitative analysis of activity patterns of the elusive giant panda, several new findings were revealed. We revised and contextualized previous knowledge on the pandas' activity pattern, and also elucidated an important behavioral strategy—the pandas' ability to adjust activity level to adapt to physiological requirements, weather, temporal variation, and forage variability. This study also informs giant panda conservation efforts, particularly with respect to the implications of our result of higher activity levels in higher solar radiation for potential future climate change scenarios, as such changes may alter behavioral states of pandas in ways not previously explored. The study also provides a baseline for giant panda reintroduction programs currently being conducted, as it may help to interpret changes in activity levels as pandas transition from captive to wild settings. This study also provides guidance for quantitative studies on the dynamics of activity patterns of many other wildlife species worldwide.

ACKNOWLEDGMENTS

We thank the Wolong Nature Reserve Administration and the staff at the China Conservation and Research Center for the Giant Panda (CCRCGP) for their support. We thank S. Fan, W. Yang, and H. Yang for carrying out field work. We acknowledge the following sources of funding: National Science Foundation (NSF), the National Aeronautics and Space Administration (NASA), Michigan AgBioResearch, the Michigan State University Distinguished Fellowship Program, the William W. and Evelyn M. Taylor International Engagement Program, the International Association for Bear Research and Management, the National Natural Science Foundation of China (40901289), the open fund of the State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences (SKLURE2008-1), the Giant Panda International Collaboration Fund (SD0631; SD1113), Sichuan Provincial Department of Science and Technology (2008SZ0115), the special fund of China West Normal University (14B001), and the Ocean Park Conservation Foundation of Hong Kong (HK09).

Footnotes

Associate Editor was I. Suzanne Prange.

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