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Movement and activity of reintroduced giant pandas

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Abstract: Wild populations of giant pandas (*Ailuropoda melanoleuca*) have steadily increased in the past 2 decades, but the species' distribution remains highly fragmented. Since 2009, an introduction program has worked to rescue the giant panda population of Liziping National Nature Reserve in southwestern Sichuan Province, China. Using Global Positioning System and activity collar data collected between May 2011 and March 2016, we investigated the post-release behavior of the first 5 pandas introduced to Liziping, 4 of which were bred in captivity. Using a change-point analysis, we tested several models of post-release adjustment to the habitat. We found that it took 3–4 months for captive-bred individuals to exhibit movement patterns characteristic of their long-term behavior. Furthermore, we found that, for these individuals, post-adjustment behavior varied by season, with activity levels peaking between May and July, a period of high resource availability. This also corresponded with a decrease in large movement events, where individuals were less likely to travel long distances quickly during these months. Unlike wild giant pandas in more northerly reserves, the 5 pandas released in Liziping (both captive-bred and translocated) did not exhibit any seasonal migration between elevations. Finally, we found that our study individuals had 2 daily periods of activity, which was comparable to those reported in the literature for wild individuals. Our results suggest that captive-bred giant pandas are able to successfully adjust to the wild and, after a period of adjustment, settle into long-term behavior patterns.

Key words: acclimation, activity, *Ailuropoda melanoleuca,* altitudinal migration, change-point analysis, giant panda, habitat, movement ecology, translocation

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Introducing captive-bred individuals back into the wild is the ultimate goal of ex situ conservation (Frankham et al. 2010). Such actions are beneficial, in part, because the release of captive-bred wildlife into small, isolated populations can be an effective method for rescuing the populations from extinction due to demographic, environmental, or genetic stochasticity (Griffith et al. 1989). However, the survival and reproduction of released individuals—the key outcomes of captive-breeding and translocation programs—remain variable (Batson et al. 2015). Post-release monitoring is an important tool for evaluating release programs, and studies of the persistence and performance of released wildlife provide valuable feedback for future efforts (Sheller et al. 2006).

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Giant panda (*Ailuropoda melanoleuca*) populations and habitat have expanded over the past 20 years (Forestry Department of Sichuan Province 2015). However, the species remains vulnerable (Swaisgood et al. 2016). Threats include climate change and population fragmentation (Qing et al. 2016, Swaisgood et al. 2016), with as many as 18 of the 33 of the subpopulations containing fewer than 10 individuals (Forestry Department of Sichuan Province 2015). Of these populations, Liziping National Nature Reserve, in the Xiaoxiangling Mountain Range, contains an extremely endangered population of giant pandas (Forestry Department of Sichuan Province 2015). To reinforce this population, 9 giant pandas have been released in Liziping National Nature Reserve since 2009. This study seeks to explore the movement and activity patterns of the first 5 of these released pandas. Four of these pandas were born in captivity and the fifth was a wild-born, translocated individual.

Tracking data have been used for many years to investigate the behavior of wild individuals, and opportunities for such efforts are increasing as modern Global Positioning System (GPS) technology becomes more widely used (Hu et al. 1985; Hu 2001; Pan et al. 2001; Zhang et al. 2014, 2015). Activity and movement, including long-distance movement events, peak during the mating season (from Mar to May) for both male and female wild giant pandas (Hu et al. 1985, Hu 2001, Pan et al. 2001, Zhang et al. 2014). Generally, wild giant pandas are least active in August and September, but the reason remains unclear. Wild giant pandas exhibit seasonal altitudinal migration in both the Qinling Mountain Range (Zhang et al. 2014) and Qionglaishan Mountain Range (Hull et al. 2016). The hypothesized driver of these altitudinal migrations is a seasonal shift in the availability of bamboo (Family Poaceae, Subfamily Bambusoideae) shoots, which are the highest quality food in the giant panda diet (Pan et al. 2001, Zhang et al. 2014). Wild giant panda activity seems to peak either twice (Hu 2001, Pan et al. 2001, Zhang et al. 2014) or 3 times (Hu 2001, Zhang et al. 2015) daily, though the timing of these peaks varies substantially among individuals.

For animals released from captivity, the post-release acclimation period is characterized by an elevated level of stress hormones (Turner et al. 2002, Franceschini et al. 2008, Aguilar-Cucurachi et al. 2010), and a decrease (Zidon et al. 2009, Clapp et al. 2014) or increase (Quinn et al. 2012) in locomotion. The time for post-release acclimation varies among species, and the periods of acclimation appear to last much longer for animals released into new environments than for those released where they were captured. In previous studies, normal movement or hormone levels resumed 4–6 weeks after release for black rhinoceros (*Diceros bicornis;* Turner et al. 2002), 4 weeks for bighorn sheep (*Ovis canadensis*), and 11–18 weeks for Grevy's zebra (*Equus grevyi;* Franceschini et al. 2008).

In this study, we aimed to explore the behavior of giant pandas released into Liziping National Nature Reserve. We tested the hypothesis that giant pandas show an early 'adaptation period,' during which movement data would be demonstrably different from later movements. Using data from GPS collars, we studied the post-release performance of these introduced giant pandas both by analyzing their post-release changes in movement and activity and by comparing these measures with those from previous studies of wild giant pandas. As a result, we hoped to find useful indicators of the successful release of giant pandas into the wild and better understand the transitions they undergo after introduction.

Study area

Our data were collected between May 2011 and March 2016 from giant pandas released into Liziping National Nature Reserve, Shimian County, Sichuan Province, China (Table 1). The reserve, whose elevation ranges from 2,100 to 3,500 m, is part of the larger system of panda reserves in China that stretches along mountain ranges in Sichuan, Gansu, and Shaanxi provinces. The Liziping reserve covers an area of 47,940 ha and primarily contains suitable giant panda habitat with *Bashania spanostachya* and *Yushania lineolata* as the dominant bamboo species. This reserve contains 22 wild pandas (Forestry Department of Sichuan Province 2015) and has been the release site for 9 pandas from 2009 through 2016, the first 5 of which are the subject of this study (Table 1).

The giant pandas of Liziping National Nature Reserve constitute the largest local population in the Xiaoxiangling Mountain Range, which lies in the southwest corner of the distribution range of giant panda. The habitat in Xiaoxiangling Mountain Range is highly fragmented by roads and human settlements (Qing et al. 2016), and the Xiaoxiangling population, totaling approximately 30 giant pandas, is the smallest one of all populations. Therefore, the Xiaoxiangling population is believed to be the most endangered population of giant panda (Forestry Department of Sichuan Province 2015). Panda releases, primarily from captive breeding programs but also from translocations, have been undertaken to bolster this precariously small population.

Table 1. Individual giant pandas (*Ailuropoda melanoleuca*) released into Liziping National Nature Reserve, China, 2007–2013.

Panda name	Sex	Birth year	Release date	Data duration	Elevation range	Comments
LuXin	Female	2007	29 Apr 2009	696 days	2,619–3,537 m	Gave birth; Data missing from first 748 days
TaoTao	Male	2010	11 Oct 2012	888 days	1,935–3,880 m	2 collars
ZhangXiang	Female	2011	11 Nov 2013	825 days	1,106–3,463 m	2 collars
XueXue	Female	2012	14 Oct 2014	38 days		Died
HuaJiao	Female	2013	9 Nov 2015	135 days	1,667–3,312 m	

Methods

Study individuals

The 5 individuals examined in this study were the first 5 pandas reintroduced into the wild (Table 1). Female LuXin was a wild giant panda rescued from the Qionglaishan Mountains. She was released into Liziping National Nature Reserve 1 month after her capture and veterinary treatment; she was approximately 5 years old. The other giant pandas were all 2.5 years old and had been captive-bred in Wolong Nature Reserve, where they were cared for by their mothers in an outdoor enclosure mostly covered by forest. Females XueXue and ZhangXiang were soft-released (at 2,100 m elevation). They were kept in an outdoor enclosure in Liziping Nature Reserve for approximately 1 month, and then the fence of the enclosure was opened and they left the enclosure by themselves. Male TaoTao and female Huajiao were hard-released (at 2,050 m elevation). They were released into the wild immediately after they were transported from Wolong to Liziping.

These 5 pandas were released into Liziping National Nature Reserve, between 2009 and 2015 (Table 1). Female LuXin is the only individual in our study to give birth during the study period. Unfortunately, a collar defect meant that movement data for female LuXin were not available for the first 2 years after release. Four of the 5 released pandas are still alive in the reserve. Both male TaoTao and female ZhangXiang were briefly recaptured after their first GPS collars fell off, so that they could be fitted with a second collar.

Global Positioning System collars

Working under permission of the State Forestry Administration of China (Chuanlinfa [2018] No. 43), researchers fitted individual pandas with GPS tracking collars (GPS7000MU; Lotek Inc., Newmarket, ON, Canada), which were used to record both the location of individuals at 1- or 3-hour intervals, as well as activity counts every 5 minutes. Researchers fastened collars around the neck of the study animals, with the bulk of the device resting on the underside of the neck. Activity was measured as count data on 2 axes, vertical and horizontal, where an individual count represented the number of times that the collar's accelerometer was tripped along each axis (Naylor and Kie 2004).

The GPS collar data ranged from 135 to 888 days in duration for surviving individuals; female XueXue died 38 days into data collection (Table 1). We removed erroneous GPS data points that deviated from surrounding data points by several kilometers or more. We deemed these points erroneous through both the unlikelihood of a giant panda traveling an extreme distance in one hour only to return the next, and because they represented travel speeds far exceeding the capability of giant pandas.

We assigned each GPS location an activity value through the summation of activity counts from the midpoints between the preceding and following GPS fixes. This approach linked frequently measured activity data (every 5 min) with less frequently measured movement data (1 or 3 hr). As in many studies (Zhang et al. 2015, He et al. 2016), a high correlation existed among the horizontal, vertical, and summed vertical plus horizontal activity counts from the accelerometers. However, we used the vertical-axis activity count throughout this study, because of indications of higher accuracy on this axis.

Data analysis

Change-point analysis. These animals were each introduced into novel habitats; therefore, a key question was how their behavior changed as they gained experience with, and developed spatial memories of, their new homes (Fagan et al. 2013). We expected that such learning would not be instantaneous, but rather would develop over a period of adjustment following release. To detect and quantify the duration of any adjustment period for released individuals, we conducted a likelihood-based change-point analysis (Gurarie et al. 2009) on the GPS-collar movement and activity data for each of the 2 individuals for which we had substantial post-release data (male TaoTao and female ZhangXiang; Table 1). For movement data, we calculated the log of the total daily

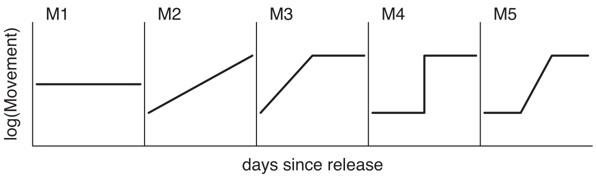


Fig. 1. Schematic representation of 5 different models fit to the total daily displacement of giant panda (*Ailuropoda melanoleuca*) movement, from data collected between May 2011 and March 2016. Numbers M1–M5 correspond to the model descriptions in text (Methods: Data analysis). Including the variance, each is specified with 2, 3, 4, 4, and 5 parameters, respectively.

displacement for each individual separately as the sum of all distances between GPS fixes during a day. To these data, we fit 5 different models, each of which pertained to a different hypothesis concerning the panda's adjustment to its habitat (Fig. 1):

1) A flat mean that represents no change over the time period (i.e., no period of adjustment).
2) A linear model with a positive slope that represents a constant increase in movement over time (i.e., behavior changes continually following the release).
3) One change point with a positive slope in the first time period and a slope of zero in the second time period (i.e., adjustment begins immediately after release, such that a model containing one change point with an initial negative slope followed by a slope of zero—indicating a high level of initial movement followed by settlement—could also be tested for in a similar fashion).
4) One change point between 2 different flat means (i.e., there is a period of adjustment followed by an immediate switch to 'normal' behavior). We include this model for completeness, but deem it unlikely for wild animals.
5) Two change points between a flat mean, a positive slope, and a second flat mean (i.e., a period of adjustment featuring constant, but reduced behavior, followed by a gradual [linear] transition to 'normal' behavior).

We fit models to the data, and calculated change points, slopes, and means using the Nelder–Mead method for optimization (Nelder and Mead 1965) implemented with the 'optim' function in Program R (R Core Team 2018). The Nelder–Mead method, also called the downhill simplex method, is a standard numerical method for finding the minimum of a multidimensional objective function. Models 1, 2, and 3 and, separately, Models 1, 4, and 5, constitute nested series; therefore, we used likelihood ratio tests to identify the best fit model after penalizing the more complicated models for their additional free parameters. We report pairwise likelihood ration test *P*-values and associated Akaike Information Criterion (AIC) values for each of the pairwise model comparisons, for each individual separately, in Table S1.

Adjustment period. To determine the length of time (if any) before individuals adjusted to their release, we considered the period of time before any potential change point to be the adjustment period. If the best model fit produced no change point, then the individual would be considered to have either not finished adjusting or not needed to adjust. In the case of 2 change points (Model 5), we did not consider the individual to be adjusted to their new environment until after the second change point. We further calculated the convex hull area for each individual over time to quantify the expansion of their range over time.

Post-adjustment. To compare the behavior of these pandas released from captivity with the published behavior of wild giant pandas, we analyzed the movement and activity patterns of each of the 3 individuals for which extensive post-adjustment data were available (male TaoTao and female ZhangXiang from the change-point analysis above, plus female LuXin, for which 2 years of data were missing after its release [Table 1], but which we assumed to have adjusted to its new habitat sometime during those missing year). Thus, all 3 of these animals had >1 year of data in their post-adjustment period.

We looked at the seasonal changes in movement, activity, elevation, and daily activity patterns by fitting generalized additive models to each individual's movement rate, activity, and elevation data. We assigned elevation to each GPS fix using the Digital Elevation Model (30 m × 30 m), provided by the International Scientific & Technical Data Mirror Site, Computer Network Information Center, Chinese Academy of Sciences (http://www.gscloud.cn). We used the generalized additive models to estimate the peak and nadir of movement, activity, elevation across the year, and also to provide a statistical test for the presence of seasonal patterns. We used the gam function in the mgvc R package (Wood 2011), log-transforming the movement rates and taking the square root of the activity means to normalize the residuals, and subsampling to 1 observation every 6 hours to eliminate autocorrelation. Similarly, we looked at the frequency of long- and very-long-distance movement events, which we defined as displacements 150–350 m/hour and >350 m/hour, respectively,

Table 2. Statistics of activity peaks and nadirs for 3 released giant pandas (*Ailuropoda melanoleuca*) from data collected between May 2011 and March 2016. Estimates and 95% confidence intervals are derived from the generalized additive model fits illustrated in Figure 3C.

	Peak		Nadir	
Panda name	Day	Activity count (95% CI)	Day	Activity count (95% CI)
LuXin	16 Jun	17.1 (15.0–19.2)	29 Aug	5.8 (4.5–7.3)
TaoTao	7 Jun	12.7 (11.3–14.1)	15 Sep	5.1 (4.3–6.0)
ZhangXiang	11 Jun	11.7 (10.6–12.9)	19 Sep	1.1 (0.8–1.5)

corresponding to approximately 4% and 2% of the longest distance displacement.

Results

Change after release

We found that for female ZhangXiang and male TaoTao, movement behavior changed after an initial period of 3–5 months, best fitting Model 5 (Figs. 1 and 2). For TaoTao, our model indicated an initial breakpoint at 83 days, and the second change point (corresponding to the end of the estimated adjustment period), at 130 days. For ZhangXiang, the breakpoints were 157 and 177 days, respectively. These changes in movement behavior are visualized in Figure 2 by the movement tracks and increasing convex hull area, where the area covered is much greater post-adjustment than during the initial period. For TaoTao, the daily mean displacements from the 3 time periods were 388, 588, and 955 m, respectively. For ZhangXiang, these same displacements were 294, 445, and 630 m, respectively (Fig. 2). At the conclusion of the adjustment period, male TaoTao was 2.3 km from the release site and female ZhangXiang was 2.1 km away from the release site.

In contrast, activity did not exhibit statistically distinguishable change points (Fig. 2). Activity for both female ZhangXiang and male TaoTao increased quasi-linearly in approximately the first 100 days, but never reached the stable long-term patterns that we saw for movement. Hence, the change-point analysis did not identify separate periods of activity (Fig. 2). For male TaoTao, Model 1 provided the best fit to activity data, indicating that all 3 years of data shared very similar activity readings. Females ZhangXiang (Fig. 2) and HuaJiao (not shown) exhibited greater variability in activity, and did not exhibit consistent patterns that conformed to any of our models.

Seasonal changes

Post-adjustment movement patterns were relatively stable through the calendar year for the 3 pandas with data sets longer than 1 year (Fig. 3A). Female Luxin displayed the lowest movement rates (median = 10.2 m/hr, inter-quartile range [IQR] = 4.9–22.9), with the P-value on the day-of-year effect >0.05, suggesting no seasonal structure. Female Zhangxiang and male Taotao displayed similar movement-rate statistics: median = 15.4 and 17.3 m/hour (IQR: 8.1–29.7 and 8.4–42.7, respectively). Peak movement occurred in early summer (May–Jun), but the differences across seasons were small, ranging from a maximum of 24 m/hour to a minimum of 16 m/hour. In contrast, a clear pattern emerged when we look at long-distance dispersal events (Fig. 3B). These events peaked during February and March and were at a minimum during the summer months (May–Aug). Activity counts showed a slightly shifted seasonal trend, with peaks in mid-June and distinct minima at late August and September (Fig. 3C). Activity peaked in mid-June, but then declined rapidly by estimated mean factors of ≥ 3 to the lowest levels during late August to mid-September, and stayed fairly low through the winter (Table 2). Unlike wild pandas in other reserves, we found no elevational seasonal migration for females LuXin and Zhangxiang, or male Taotao, in Liziping National Nature Reserve (Fig. 3D). Except for sporadic forays to lower and higher elevation, these 3 individuals tended to stay at a similar elevation year-round (approx. 3,000 m), and none of the years for which we have data showed any sign of vertical seasonal migration.

Taken together, these results indicate that, during the summer months (a period of abundant food resources in the form of bamboo shoots), the movement speed of giant pandas was generally similar throughout their day but they had higher activity levels and were much less likely to cover long distances in rapid movement bouts (Fig. 3A–3C).

Using data following the end of the calculated adjustment periods of male TaoTao and female ZhangXiang, and the end of the assumed adjustment period for female LuXin (early data were missing due to collar malfunction [Table 1]), we found positive, statistically

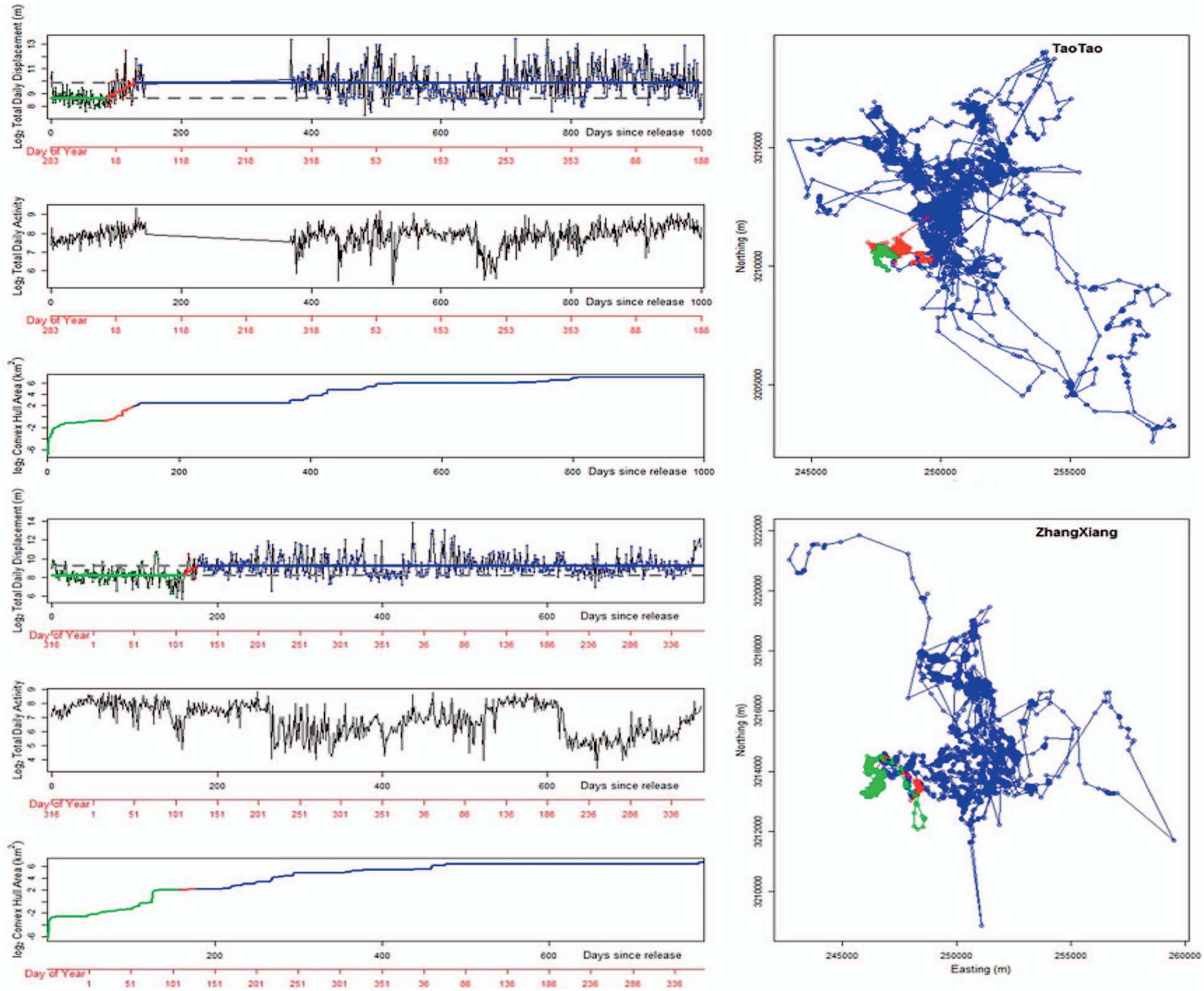


Fig. 2. Movement, activity, and Global Positioning System (GPS) tracks for the giant pandas (*Ailuropoda melanoleuca*)—male TaoTao (top) and female ZhangXiang (bottom)—that were released into Liziping National Nature Reserve, China, over the lifespan of their GPS collars. Data were collected between May 2011 and March 2016. The log (base 2) total daily displacement for each individual is shown with the best model fit from the change-point analysis. Green points represent the period before the first change point, red points represent the period between change points, and blue points represent the period after the second change point. These same colors are used to show the trajectories of each individual after release. Activity is shown as the log (base 2) of the summed activity readings for each day. The bottom panel indicates how the convex hull area (log base 2) of the total movement tracks increased over time after release.

indistinguishable relationships among individuals between total activity and daily displacement in all 4 seasons (Fig. 4). Activity levels were highest in April to June, but all 4 seasons exhibited comparable ranges of daily displacement. The relatively loose coupling between activity and displacement helps explain why breakpoints exist so clearly in the movement data, but not in the activity data (Fig. 2).

Diel activity

Daily activity for each of the 3 pandas in our study with >1 year of data tended to follow a pattern of 2 active periods daily, separated by low-activity resting periods (Fig. 5). For the 2 captive-bred individuals (male TaoTao and female ZhangXiang), daily activity was separated into one long active period during the day and a shorter period of activity during the middle of the night.

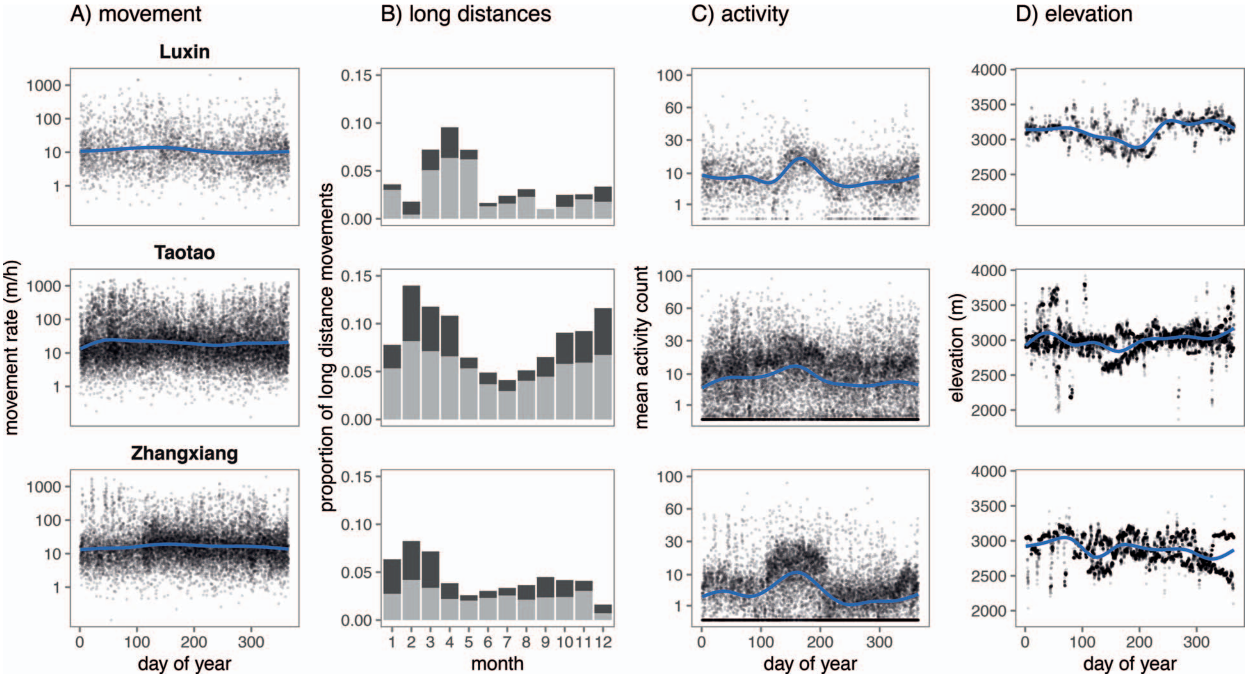


Fig. 3. Movement, activity, and elevations across the year for 3 giant pandas (*Ailuropoda melanoleuca*)—LuXin (female, top row), TaoTao (male, middle row), and ZhangXiang (female, bottom row)—that were released into Liziping National Nature Reserve, China. Data were collected between May 2011 and March 2016. All measurements are presented for the post-adjustment period. The panels represent, left to right: (A) movement rates, computed as displacement per hour; (B) proportion of long-distance movements (light grey: 150–350 m/hr; dark grey: >350 m/hr); (C) activity rate computed as the mean number of times the accelerometer sensor was triggered per day (averaged across the x and y dimensions and theoretically ranging from 0 to 255); and (D) elevation in meters. The blue curves in (A), (C), and (D) represent the fitted GAM (generalized additive model) smoothing.

However, in female LuXin, which had been born in the wild, these active periods were shifted toward a long active period during the night, with a shorter, second active period in the morning. Preliminary data for female Huajiao and data collected for female XueXue before her death (not shown) both followed similar activity timing to male TaoTao and female ZhangXiang. Note that the high activity values for female ZhangXiang during the adjustment period appear to be due to the sensitivity of her first GPS collar. No similar periods of activity at this level were found in any other individuals, whereas the high activity readings extended throughout the entirety of this first collar and ended immediately at the start of the second collar. We still present these data here because we presume the timing of activity levels to still be reliable.

Discussion

Although our inferences are necessarily limited by our small sample size, our study gives the first insight into the behavior pattern of captive-bred giant pandas after being released into the wild. Through our analysis of movement and activity for these individuals, we observed how long it took individual pandas to adjust to their new environment. Such metrics are important tools in endangered species management because movement behaviors can be strong indicators of the success of translocation and reintroduction efforts (Berger-Tal and Saltz 2014).

Armstrong and Seddon (2008) suggested that reintroduced animals go through 2 kinds of acclimation to their new environments. In that conceptualization, the first acclimation phase involves recovery from translocation stress, and the second, longer phase involves acclimation to the release site. In a comparison of so-called 'soft' or 'hard' releases of pandas into the wild using accelerometer-based activity data, L. He et al. (members of our research group, unpublished data) found that the recovery from translocation stress can happen quickly, sometimes in as little as 30 days, but typically occurs

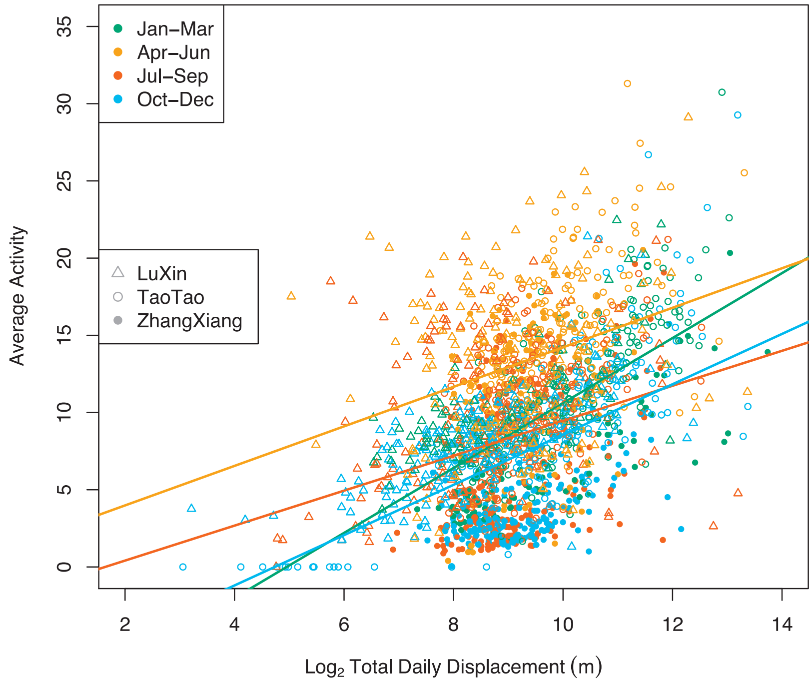
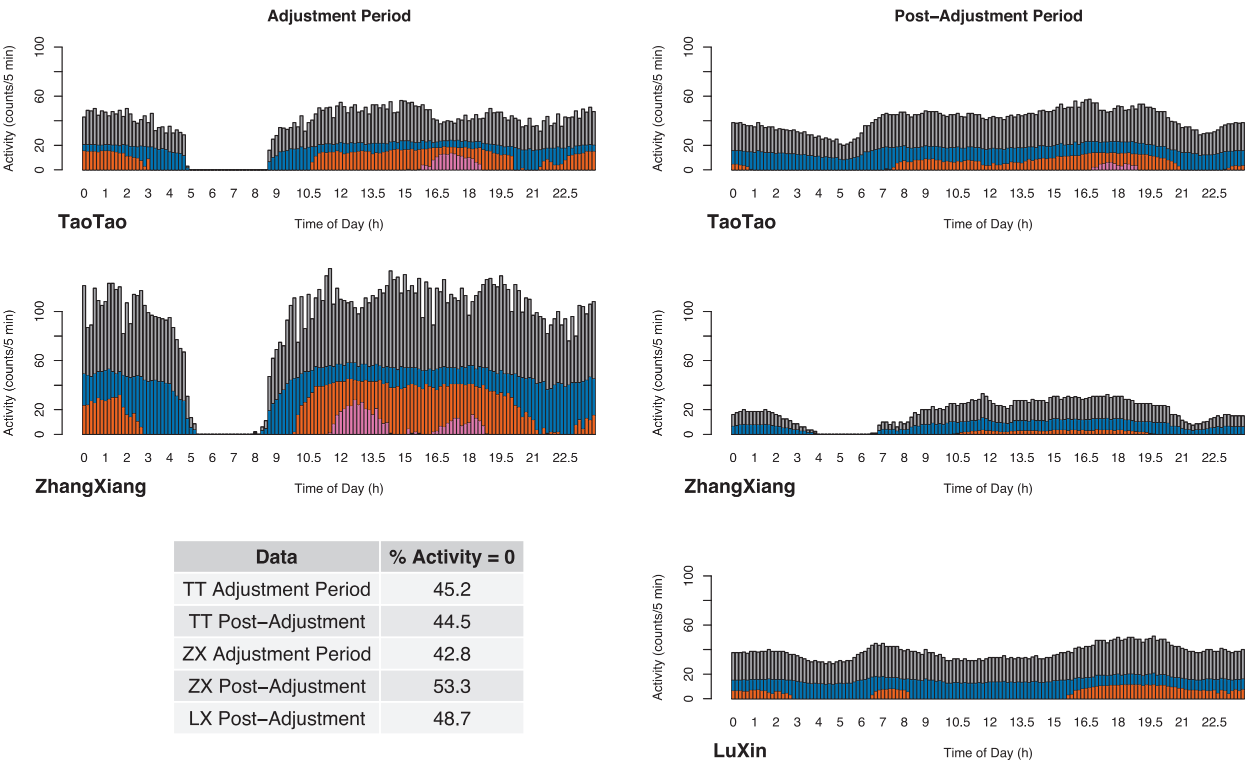


Fig. 4. Daily average activity counts (from data collected between May 2011 and Mar 2016) plotted against total daily displacement, for 3 giant pandas (*Ailuropoda melanoleuca*)—female LuXin, male TaoTao, and female ZhangXiang—that were released into Liziping National Nature Reserve, China, post-adjustment period. Colors represent binning by 3-month groups; open triangles represent female LuXin, open circles represent male TaoTao, and closed circles represent female ZhangXiang.

within 30–90 days. Our results from movement data suggest a longer acclimation period of 3–4 months for captive-bred giant pandas introduced into the wild. This is indicated by the amount of time before male TaoTao and female ZhangXiang reached their stable daily movement levels. The movement tracks of each individual reveal limited movement away from the release site during the adjustment period. For comparison, Hu (2001) reported that wild giant pandas will move and/or forage over 1–4 km within several hours. In other cases, pandas will spend up to a day feeding in one location. Encouragingly, the released individuals in this study exhibited similar behavior after their adjustment period, despite never having this opportunity in captive life. We plan to more extensively analyze these behaviors in future studies as larger sample sizes become available.

The seasonal changes in movement and activity for the released pandas highlight the importance of their foraging on bamboo shoots during summer months. During early summer, bamboo shoots, which are high in nutrients, emerge and become a key staple in the diet of giant pandas (Hu 2001, Pan et al. 2001). These months showed the highest activity levels for the year, yet long-distance movement was extremely limited when resources were abundant. Alternatively, as resources became scarce during the autumn and winter, long-distance movement increased and activity decreased. This suggests that when bamboo shoots are present, individual pandas will increase their activity to take advantage of abundant resources, but do not have to travel as far to find suitable patches.

Our study, carried out in the southernmost extent of the giant panda's range, found no consistent elevational migration during different times of the year; individuals stayed at elevations close to 3,000 m throughout the year with somewhat greater variation in elevation during the summer months. This contrasts with studies of wild pandas in other nature reserves. In Foping Reserve, located approximately 500 km north of Liziping in the northern extent of the species' range, giant pandas migrate from low-elevation habitats (<2,000 m) to high-elevation habitats (>2,000 m) for summer months, making distinct movements with a mean elevation change of 700–800 m (Yong et al. 1994, Pan et al. 2001, Liu et al.



Data	% Activity = 0
TT Adjustment Period	45.2
TT Post–Adjustment	44.5
ZX Adjustment Period	42.8
ZX Post–Adjustment	53.3
LX Post–Adjustment	48.7

Fig. 5. Daily activity patterns for each of the 3 giant pandas (*Ailuropoda melanoleuca*)—female LuXin, male TaoTao, and female ZhangXiang—that were released into Liziping National Nature Reserve, China, with >1 year of data collected between May 2011 and March 2016. Different color bars represent quartiles of the data, with light grey at the upper quartile, blue and orange as the middle quartiles, and pink as the lower quartile. Missing colors for any 10-minute time window indicate values of no activity. Percentages in the table indicate the percentage of activity values that were equal to zero in the 5 given time periods.

2002, Zhang et al. 2014). This pattern has also been observed in the Qinling Mountains, but reverses seasonal movements observed in Qionglai Mountain pandas (Connor et al. 2016). Individuals in the Wolong Reserve, located approximately 200 km north from Liziping in the middle of the giant panda's range, have a much smaller elevational migration (approx. 200 m); they stay at higher elevation during the autumn and winter, and descend for late spring and summer (Liu et al. 2015).

Our study did not directly test whether the lack of migration between elevations was caused by differences in the environment of the Liziping Reserve or was due to the inexperience of individuals. Of course, it also remains possible that seasonal migration between elevations exists among the reserve's wild panda population, for which we do not have collar data. However, in our study, the 4 captive-bred individuals and the 1 wild-born individual all remained at similar elevations year-round. This suggests that seasonal migration between elevations in panda populations is not an innate behavior. Rather, altitudinal migration, when it exists, may instead reflect a combination of learned experience and a response to resource availability and other environmental conditions, which may vary among habitats and climates.

Our released individuals followed similar daily patterns of activity, with 2 active periods during the afternoon–evening hours and late at night, separated by a period of low activity during the morning. This appeared to become less defined after adjustment, but the pattern remained fairly consistent. The wild-born female, LuXin, also had 2 active spells, but shifted toward later hours of the day. Other studies have found either 2 (Hu 2001, Pan et al. 2001, Zhang et al. 2014) or 3 (Hu 2001, Zhang et al. 2015) active periods for wild giant pandas, but the reason for the difference remains unknown. Timing of activity varied in these studies, so the daily activity patterns of our released individuals seem to fit the pattern expected of a wild individual.

It is also notable that most of the seasonal variability in daily behavior occurred in activity readings, and not daily movement. Indeed, activity peaked during the summer months (May–Jul), but then declined to the lowest levels during the autumn. This trend was consistent among individuals, and is similar to that seen in wild giant pandas in Wolong National Reserve (Zhang et al. 2015). These results suggest the importance of activity readings, and not simply GPS readings, for discerning changes in seasonal behavior of individuals. This contrasts to the substantial change in movement behavior after the introduction of individuals into the wild.

Analyses of movement behavior are becoming increasingly useful as a component of reintroduction programs (Berger-Tal and Saltz 2014), and some comparisons are possible to other bear reintroductions. For example, European brown bears (*Ursus arctos*) released in Austria and the Pyrenees moved larger distances than did wild bears in southern and northern European populations (Ordiz et al. 2007). Brown bears released in the Italian Alps revealed strong sex-based differences in post-release movement (Preatoni et al. 2005). In that study males showed restricted movements in the months after release, whereas females were more variable, in some cases moving dozens of kilometers away. For endangered Louisiana black bears (*Ursus americanus luteolus*), individual female bears occupied substantially larger territories post-release than those same individuals did in their source populations (1.3–32-fold larger; Benson and Chamberlain 2007). In that study, landscape fragmentation in the area surrounding the release site may have prevented translocated bears from making even longer distance movements.

Given the very small sample size of the results presented here, it is impossible to draw any firm conclusions about the movement of reintroduced pandas, and any observed results must be interpreted cautiously. However, we can make the tentative suggestion that captive-bred giant pandas, when released into the wild, take a period of 3–4 months to adjust to their new habitat. Future work will be necessary to characterize this transition period more fully and compare the behavior of reintroduced pandas with wild individuals. It is interesting that these few reintroduced individuals did not exhibit elevational migration, but it is uncertain whether this is caused by environmental factors or as a result of the introduction. Overall movement data appear to provide a good indicator of adjustment to the wild for introduced individuals, and we suggest that both movement (in terms of large movement events) and activity levels provide important information as to how giant panda behavior changes throughout the year.

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ZY, HK, QD, XG, and XY organized the panda releases and collected the data; WFF, AF-G, EG, and MAL identified directions to take the analyses; AF-G and EG analyzed the data and created the graphics; AF-G, EG, and WFF developed the first draft; and all authors edited and extended the manuscript.

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Supplemental material

Table S1. Comparisons of results for the 5 change-point models (Fig. 1) of the movement data collected between May 2011 and March 2016 for 2 giant pandas (*Ailuropoda melanoleuca*)—male TaoTao and female ZhangXiang—that were released into Liziping National Nature Reserve, China. The matrices present results for likelihood ratio tests giving the probability of rejecting less complex models in favor of alternative more complex models of adjustment. The Akaike Information Criterion (AIC) values indicate that, for both pandas, the all-around best fit model is #5. Model fits for Model 5 are shown in Figure 2.