REVIEW

Telemetry research on elusive wildlife: an synthesis of studies on giant pandas

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Abstract

Telemetry studies that track animals through space and time can lead to advances in scientific understanding that are vital in conservation efforts. For example, telemetry studies of the giant panda (*Ailuropoda melanoleuca*) have shed light on many aspects of panda biology, but small sample sizes in each separate study make it difficult to draw broad conclusions. To overcome this problem we conducted the first synthesis of all five panda telemetry studies conducted to date. Using these data we investigated patterns in 6 main topics - home range, space-use interactions, core areas, movement patterns, seasonal migration, and natal dispersal. We found that panda home range sizes do not vary between two main mountain ranges (Qionglai and Qinling), as was previously thought. Our results

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1749-4877.12197.

also suggest that females increase their movement in the mating season - a behavior typically attributed to only males. We found and summarized widespread telemetry and genetic evidence for female natal dispersal in the giant panda. Our synthesis highlights the need for additional research relating panda behavior to human disturbance factors, and can aid future studies on giant pandas as well as other species.

Key Words

Natal dispersal, home range, giant panda, synthesis, wildlife telemetry

Introduction

Wildlife telemetry is a rapidly growing field. It has resulted in a greater understanding of wildlife biology and has important applications to wildlife conservation. Telemetry data can help answer a wide range of ecological questions, including home range, habitat use, mating behavior, and natal dispersal (Miller *et al.* 2010, White & Garrot 1990). These data can also better inform management policies and protected area establishment (Hull *et al.* 2011).

Giant pandas (*Ailuropoda melanoleuca*, David, 1869) are one of the earth's most well-known and recognizable species, acting as a global conservation icon and a national treasure to China (Liu *et al.* 2001). Pandas are an endangered species, with less than 2000 individuals in the wild distributed across six mountain ranges in southwest China (Fig. 1, Vina *et al.* 2010, State Council Information Office of China 2015). Despite their popularity and threatened status, the first formal research on giant pandas was not conducted until the late 1970s and early 1980s (Hu 1986, Schaller *et al.* 1985, Pan *et al.* 2001). Due to their elusive nature and the thick bamboo understory that characterizes their habitat, pandas are difficult to observe in the wild (Hull *et al.* 2011). This challenge has made telemetry an important method in giant panda ecology and conservation.

The first study to employ telemetry on giant pandas was a joint project funded by the World Wildlife Fund (WWF), the Chinese Association for Environmental Sciences, the Chinese Ministry of Forestry, and Academia Sinica. The project took place in Wolong Nature Reserve within the Qionglai mountain range (Schaller *et al.* 1985). The capture and radio-collaring of six pandas was a central part of the study and produced results that greatly increased knowledge of panda home ranges, spatial interactions, and feeding ecology, among other topics (Schaller et al. 1985).

One of the Chinese scientists collaborating on the project, Pan Wenshi, went on to start his own research in the Qinling mountain range. During the course of this study his team gathered telemetry data from radio collars fitted to 22 pandas (Pan *et al.* 2001). These data further enhanced the scientific knowledge of the giant panda, with novel insights into reproduction, natal dispersal, migration, and other topics (Pan *et al.* 2001). One additional study in the 1990s (Yong *et al.* 2004) conducted radio telemetry on pandas in Foping Nature Reserve, situated in the Qingling Mountains. This project collared and tracked six individuals for 1 to 4 years. Mention should be made of radio telemetry research headed by George Schaller in the Min Mountains (Schaller *et al.* 1989), but the study only captured two pandas and focused almost entirely on feeding ecology.

Animal safety concerns resulted in an 11-year ban by the Chinese government on panda telemetry from 1995 to 2006 (Durnin *et al.* 2004). This resulted in a large gap in data, with only two new collaring studies conducted in the last ten years. Both of these used the more advanced GPS telemetry technologies to gather detailed data on movement and space use (Hull *et al.* 2011, Zhang *et al.* 2014, Hull *et al.* 2015). Although several authors of collaring studies have compared their results to other research (Pan *et al.* 2001, Zhang *et al.* 2014, Hull *et al.* 2015), to date there has been no examination of all five studies in tandem.

One of the biggest problems in conducting research on rare and elusive wildlife is small sample sizes. Research on giant pandas faces this issue, and many aspects of their ecology are not fully understood because of the limited number of animals any individual study could track. The aim of this paper is to synthesize and reanalyze the results of all telemetry studies on giant pandas. We targeted 6 main topics that have been investigated across multiple studies: home range size, space-use interactions, concentrated use or core areas, seasonal migration, movement patterns, and natal dispersal. For each topic, we asked a set of key questions that are important for the species and that either could not be answered adequately with single studies, or were more effectively explored with a synthesized dataset. These questions revolved around important sources of variability for each characteristic, including sex, age, season, and mountain range. We focused only on questions we could address with available data. These topics and sources of variability are common across many wildlife species, and their investigation helps shed light on diverse factors that may influence behavior of similar species worldwide.

Materials and Methods

A summary of telemetry methods and data collection used in the studies we reviewed is presented in Table 1. A key difference between radio and GPS telemetry is the greater spatial accuracy of GPS telemetry. None of the studies that used radio telemetry reported tests for error, which can range from 2-400m (White & Garrot 1990). Only Hull *et al.* (2015) reported average error in their test of GPS accuracy, which ranged from 16-23 m. Zhang *et al.* (2014) had GPS collar location acquisition rates ranging from 14% to 70% and Hull *et al.* (2015) had acquisition rates ranging from 24% to 54%. Using pre-deployment static testing, Hull *et al.* found no evidence for a bias in acquisition success based on habitat types. Even with missed fixes, the amount of data gathered by the GPS collars far surpassed the earlier radio telemetry methods (Table 1).

An animal's home range is most simply defined as the area it uses to forage, mate, and raise young (Burt 1943). Knowing the spatial extent of this area is important in developing an ecological understanding of a species, and conserving adequate habitat for its survival. To analyze home range size, we synthesized results obtained from Minimum Convex Polygon (MCP) calculations, the only method that all studies used (Table 1). The vast majority of published home ranges were calculated based on 1 year of telemetry data, while the ranges of a few individuals were a result of less or more than 1 year of data (Schaller *et al.* 1985, Zhang *et al.* 2014, Hull *et al.* 2015). We only included home range results based on 1 year ± 1 month in our analysis to avoid a potential bias, since multiple studies found larger home ranges when including data from periods longer than 1 year (Schaller et al. 1985, Yong et al. 2004, Hull et al. 2015). We analyzed two hypotheses tested in previous studies with our larger, synthesized dataset. These were comparisons of home range size between males and females and between two major mountain ranges (Qionglai and Qinling). We used two-tailed Mann Whitney U tests, with the significance level set at $p = 0.05$, for both analyses. For the test on sex differences, data from Zhang *et al.* (2014) had to be excluded because the MCP ranges in their published results were an average of all four pandas (2 males and 2 females).

We also compared results on home range overlap between pandas, which is a measure of space-use interaction. Spatial overlap can influence social behavior, mating patterns, competition risk, and disease transmission (Sanchez and Hudgens 2015). We were only able to consolidate and analyze home range overlap data from the two GPS studies, as the lack of published data and some discrepancies prevented the inclusion of the earlier studies. Zhang *et al.* (2014) reported separate values for winter range overlap and summer range overlap between pandas. To allow for comparison with Hull et al. (2015), we added the two values to obtain year-long overlap (an effective method because summer and winter ranges are spatially separate in this study).

In addition to home range overlap, we synthesized data on simultaneous spatial interactions among panda individuals. Schaller *et al.* (1985) and Hull *et al.* (2015) attempted to quantify this by recording all instances in which pandas were within 200 m of each other, which we summarized as a percentage of total simultaneous tracking locations a pair was within this distance (Fig. 2).

"Core areas" refer to preferred locations within an animal's home range that are used significantly more than would arise from random use, potentially resulting from differing levels of resource distribution and/or territoriality (Powell 2000). Nearly all of the telemetry studies recognized and/or performed an analysis of core areas. Methods for defining and measuring them varied between studies (Table 1), which makes quantitative comparison difficult. Additionally, only two studies reported quantitative results - Schaller *et al.* (1985)

and Hull *et al.* (2015). We compared these as well as any discussions of concentrated space use in other studies.

Movement patterns and how they change over time are increasingly recognized as important aspects of animal ecology (Fryxell *et al.* 2008). We collected data from studies that reported telemetry-derived average distances moved in one day to synthesize and compare results. Zhang *et al.* (2014) reported average movement speeds (meters/hour) between consecutive locations. We converted these average speeds to average movement distance per day by multiplying by 24 hours. Additionally, we gathered and summarized all evidence of movement behavior exhibited by pandas in the mating season across studies.

Seasonal migration is an aspect of panda ecology that has been observed in several mountain ranges within the panda's current distribution (Hu & Wei, 2004). The three studies in the Qinling Mountains defined seasonal ranges in different ways. To avoid this discrepancy, we summarized monthly elevations by study, either from direct values reported in tables (Pan *et al.* 2001) or measured from figures using ImageJ software (Zhang *et al.* 2014, Liu *et al.* 2014).

Natal dispersal is a common behavioral adaptation among species to avoid inbreeding, decrease competition, and colonize new areas (Bowler & Benton 2005). Though exploratory movements may be involved, the fact that natal dispersal typically occurs once in a subadult's life makes it difficult to gather data on the phenomenon. This is particularly the case in studies that only last 1-2 years (Zhang *et al.* 2014, Hull *et al.* 2015). Nevertheless, we summarized the available data on the topic. This analysis included data for juvenile (0-2 year old) and subadult (2.5-3.5 year old) pandas.

Results

Home Range

Home range size using MCP calculations varied between 5.14 km^2 and 13.2 km^2 between studies (Table 2). Across studies, male panda home ranges were significantly larger than that of females (Mann-Whitney U test, U=54.8, P=0.01). The mean female range was 5.63 km^2, while the mean male range was 1.52 times as large at 8.55 km^2. Home range size was not significantly different between the Qionglai (mean=7.28 km^2, n=6) and Qinling (mean=7.99 km^2, n=26) mountain ranges (Mann-Whitney U test, U=36.9, P=0.66), which differs from what was previously thought (Pan *et al.* 2001, Liu *et al.* 2014).

Space-use Interactions

The spatial overlap in home ranges was 2.55 times as large among pandas in the Qinling mountains compared to pandas in the Qionglai mountains, a significant difference (Mann-Whitney U test, U=45.39, P=0.0003). A statistically significant difference in spatial overlap was not found between sexes, but our results appear to agree with previous studies (Schaller *et al.* 1985, Pan *et al.* 2001) that found less overlap between females (14%) than between males and other males/females (52%/23%, Table 3). Changes in spatial overlap over time were a common finding in previous studies, with large variation between months (Schaller *et al.* 1985) or seasons. Change in spatial overlap by season was found by multiple studies in the Qinling mountains, with larger overlap in winter compared to summer (Pan *et al.* 2001, Zhang *et al.* 2014).

Schaller *et al.* (1985) and Hull *et al.* (2015) found evidence for spatial interactions in some panda pairs, with multiple pairs within 200 m of each other between 5% and 29% of the time (Fig. 2). In Hull *et al.* (2015) one subadult female was found to spend time near an adult male and an adult female. These groupings occurred at distinct times - the subadult female was found together with the male during 2 weeks in late July and throughout September, and was found close to the adult female for a 2-week period in late August. Unlike the two studies in Wolong (Schaller *et al.* 1985, Hull *et al.* 2015), Zhang *et al.* (2014) found no evidence of attraction or avoidance among their study animals.

Core Areas

Panda core areas were 0.33-1.02 km^2 in size. Schaller *et al.* (1985) and Pan *et al.* (2001) identified age, sex, and season as factors contributing to differences in space use among individuals. Concerning age, Schaller *et al.* (1985) found that subadults had a centralized pattern of space use, the 2 collared individuals in this age class in their study remaining relatively sedentary. In contrast, Pan *et al.* (2001) found that subadults had a generally dispersed pattern of space use, and that young cubs and old individuals adopted a centralized pattern of space use.

Both Schaller *et al.* (1985) and Pan *et al.* (2001) found that females exhibited centralized space use among a small number of core areas. In contrast, both studies found that males roamed widely in a dispersed pattern. In their analysis of space use Hull *et al.* (2015) found that the collared male did have core areas (16 total), albeit less than the females (mean = 30). The male also made more revisits to more core areas (10 cores revisited a total of 25 times) than the females (mean of 3 cores revisited a mean of 3.5 times).

Movement Patterns

Pandas on average moved 331-605 m a day. It should be noted that in the case of Zhang *et al.* (2014), the total distance presented may represent up to 8 relocations (from GPS fix attempts every 3 hours), resulting in more distance than the 1 relocation used in the radio telemetry studies. Even excluding these data, it would appear that pandas in the Qinling mountains move further per day (418 m) than pandas in the Qionglai mountains (369 m). Lack of reported individual data and small sample size prevented us from completing statistical tests for this relationship.

There were temporal trends in daily distances moved. Schaller *et al.* (1985) and Zhang *et al.* (2014) found that movement was greatest in the spring, decreased in the summer-autumn, and increased slightly in the winter. In the case of Zhang *et al.* (2014), daily distances moved were 2.6 times as large in March and April than the rest of the year, whereas we found that spring movement was only 1.4 times as large as the rest of the year in Wolong (Schaller *et al.* 1985). In their analysis of data from the Qinling, Liu *et al.* (2014) found daily distances moved were 1.3 times as large in March-June than the rest of the year, and 1.6 times as large in September than the rest of the year.

First passage time (FPT) analysis by Zhang *et al.* (2014) showed high tortuosity in collared pandas' movement paths until a lag distance of 700 m. The authors suggested that this is the spatial scale within which pandas focus their search efforts for bamboo resources. They also compared panda movement paths to those expected from a correlated random walk, and found little difference. They concluded that the pandas exhibited unoriented movement within seasonal ranges.

It was a common finding that males increased their movement for the spring mating season (Schaller *et al.* 1985, Pan *et al.* 2001, Hull *et al.* 2015). Schaller *et al.* (1985) and Pan *et al.* (2001) also found increased movement among females in the spring, but both studies attributed this behavior to foraging for emerging bamboo shoots. Mating is not addressed in Yong *et al.* (2004), but in another study using the same data (Liu *et al.* 2002), the authors suggest that the two adult females made mating season movements, potentially as far as their seasonal migration between habitats. Zhang *et al.* (2014) reported that a GPS-collared adult female panda made two long-distance movements during the mating season, which took her through areas outside both her seasonal ranges. These were significant undertakings, the first lasting 36 days in March/April and covering 55.4 km, and the second lasting 25 days in April/May and covering 17.8 km. The authors suggest that this finding was perhaps evidence of a temporary dispersal for breeding.

Seasonal Migration

Most pandas exhibited a distinct seasonal migration, but the nature of the migration pattern varied across studies (Fig. 3). In the Qionglai mountains, pandas stayed at high elevations above 2700 m for most of the year, and descended to lower elevations in May and June. Seasonal ranges were found to be adjacent (Hull *et al.* 2015), or very close to one another (Schaller *et al.* 1985). In contrast, the studies conducted in the Qingling mountains found that pandas spent most of the year at a low elevation, ascending in summer to higher elevations. These seasonal ranges were spatially distinct and separated by up to 6.5 km (Pan *et al.* 2001, Yong *et al.* 2004, Zhang *et al.* 2014).

Similarities among the Qinling studies were also found in the timing and duration of ascent to summer ranges, which occurred in May or June and were completed quickly (Table 4). Discrepancies were found in the duration of the descent from summer ranges, however, which were reported to range from 1-2 days (Pan *et al.* 2001) to 3.5 months (Zhang *et al.*

2014). These differences were mainly caused by the varying definitions of seasonal ranges used by the authors, as the monthly average elevation data matched closely across the Qinling studies (Fig. 3).

Pan *et al.* (2001) noted substantial variation between individuals in seasonal migration. The dates that pandas left for summer ranges and returned to winter ranges varied greatly (Table 4), as did the total time spent in the summer range. Individuals kept to a very similar migration schedule from year to year, however. The authors did not find a significant difference between the length of time spent in summer ranges between males and females, but females were found to descend earlier and spend less time in summer ranges in years they produced cubs (average of 32.8 days) than in years they did not (average 56.5 days) (Pan *et al.* 2001). The authors also reported spoor and direct observational evidence that some pandas remained in their high elevation ranges all year, and that one radio-collared panda did not display a clear migratory pattern and also stayed at high elevation for most of the year.

Multiple studies sought to investigate the drivers of seasonal migration. In both the Qingling and Qionglai mountains, bamboo availability was found to be a main factor, with different species becoming the preferred forage in different seasons. In the Qionglai, the downward migration is driven by the emergence of *F. spacathea* shoots at lower elevations in May and June, while the stems and leaves of *B. fangiana* at higher elevations provide better forage at other times of the year (Schaller *et al.* 1985). In the Qinling, *Bashania* bamboo at lower elevations provide better forage during the long winters, while the new growth in *Fargesia* stands provide better forage in the summer.

Temperature was identified as a factor driving seasonal migration in the Qinling mountains. Pan *et al.* (2001) considered the summer temperatures of 10-12° C at the high elevation range of pandas to be optimal, while cold winter temperatures helped influence most pandas to descend to lower elevations.

Natal dispersal

In several studies, authors reported that subadult female pandas displayed evidence of natal dispersal. An instance of natal dispersal in a subadult female was documented by Johnson *et al.* (1988) as part of research derived from the Schaller *et al.* (1985) study. One month after being collared in April she traveled 15 km to the northeast, but did briefly revisit her original natal range 4 and 6 months later.

In Pan *et al.* (2001), two male offspring of the female Jiaojiao did not exhibit any long-distance movements and took up ranges in their natal areas. In contrast, her female offspring made a 17-month long ranging expedition outside of her home range before returning to an area adjacent to Jiaojiao's territory, where she gave birth. The authors reported results on two additional subadult females who made long-distance movements as they were reaching sexual maturity. One female moved 34 km over 8 months, returning to the area she was collared in an emaciated condition and with injuries. Another moved a straight-line distance of 24 km (Pan *et al.* 2001) before establishing a range approximately 4 km from the area she was collared (estimated from map figure in Pan *et al.* 2001).

Yong *et al.* (2004) noted the natal dispersal of 1 collared juvenile male, an offspring of one of the collared females in the study. Aged at 0.7 years upon capture, he was tracked for 34 months until the age of 3.53 years. The authors note that he had nearly total range overlap with his mother, but began to expand his range, perhaps to establish his own "core area" (Yong *et al.* 2004). They make no mention of the distance involved in this expansion, however, and it is likely a case of philopatry.

Zhang *et al.* (2014) observed evidence of natal dispersal in their female subadult collared panda. She made two long-distance movements, taking her up to 5 km away (estimated from figure) from her summer range before returning. The authors mention that within two weeks after their study was finished, this subadult female dispersed and established a new range. No telemetry evidence of significant male natal dispersal events have been found, but based on spoor evidence, Schaller *et al.* (1985) believed they may have just missed a natal dispersal event of a subadult male panda (Long) before they captured him.

Discussion

Home Range

We found that the average home range sizes of pandas in the Qionglai and Qinling mountains were similar. This is a different result than that found by Pan *et al.* (2001). They found significantly larger ranges than those reported by Schaller *et al.* (1985) likely because they included the migration corridor between their more spatially segregated seasonal ranges in the calculations. This results in a large increase in unused areas being included in the estimate, particularly when using the MCP method. Nonetheless, we caution that despite the lack of significant difference in home range size between the two mountain ranges, from a conservation perspective it may be that the Qinling pandas still need more protected area to maintain suitable migration routes between the more distant seasonal ranges.

We also found that male pandas had a larger home range than females, a result that previous authors noted was likely, but only Pan *et al.* (2001) concluded was significant. The fact that males have larger home ranges is probably because of the tendency for males to visit areas of several females throughout the year for securing access to mates (Schaller *et al.* 1985, Pan *et al.* 2001, Hull *et al.* 2015).

As suggested by Hull *et al.* (2015), panda home ranges may be much larger over a lifetime than any one study on a smaller timescale is able to show. Most authors separated ranges by year and/or season, but Schaller *et al.* (1985) found increases in home range size in an additional 8 months of tracking, and Yong *et al.* (2004) noted that home range sizes were larger than any one annual home range when all five years of data were considered. Hull *et al.* (2015) found a similar phenomenon, reporting that home range size continued to increase with time followed, and did not yet reach an asymptote for 2 of 3 tracked pandas by 16 months. With this in mind, conservation efforts should set aside larger areas for panda populations than short-term studies suggest, to accommodate shifts in home ranges and/or revisits to infrequently used but important areas.

Space-use Interactions

We found nearly double the home range overlap in the Qinling mountains compared to the Qionglai mountains, which makes sense, as the former population is believed to have the highest density of pandas per unit area (Hu & Wei, 2004). Nonetheless, the potential biasing factor of sex differences, as well as the limited sample size, should be pointed out in this comparison (Qionglai: 1 male, 4 females; Qinling: 2 males, 2 females).

Multiple studies found evidence of non-mating spatial interactions among pandas. The closeness of panda pairs, particularly proximity outside the breeding season found by Hull *et al.* (2015), suggests that there is the potential for social interaction throughout the year. Behavioral observations by Schaller *et al.* (1985) and Pan *et al.* (2001) corroborate this, which ranged from possibly territorial behavior to amicable co-foraging of family members.

This latter behavior was found through behavioral observation of the relatively habituated female Jiaojiao and her progeny by Pan *et al.* (2001). It is unclear, however, if familial relatedness can fully explain the attraction between some individuals and absence of it in others. According to Schaller *et al.* (1985), the subadults exhibiting social attraction in their study were likely not siblings due to their closeness in age, and the rarity of surviving multiple-cup litters in pandas. More research, and the additional protocol of taking a genetic sample from captured individuals, is needed to further explore the phenomenon of familial and non-familial social interactions.

Both Schaller *et al.* (1985) and Pan *et al.* (2001) made observations of aggression between pandas outside the mating season. These included adults acting aggressively towards subadults (Schaller *et al.* 1985), mothers with cubs fighting or chasing nearby adults, and fights between adult males (Pan *et al.* 2001). The first and last observations could indicate some degree of territoriality, but the evidence is too sparse to draw conclusions at the species level.

Core Areas

Females had a more centralized pattern of space use than males, a result Pan *et al.* (2001) attributed to the raising of cubs in dens and the need for stable, plentiful resources. The more dispersed pattern of space use in males was explained by the tendency for males to patrol their range to monitor females throughout the year (Schaller *et al.* 1985, Pan *et al.* 2001, Hull *et al.* 2015).

The discrepancy in the space-use patterns of subadults found by Schaller *et al.* (1985) and Pan *et al.* (2001) is perhaps explained by the lack of natal dispersal events observed by the former study. Pan *et al.* (2001) reported several instances of this behavior which led them to describe subadults as maintaining a “dispersed” pattern of space use.

In a discussion of core areas, it is interesting to consider Zhang *et al.*’s (2014) analysis of movement patterns, which led them to conclude that pandas maintained unoriented movements within their seasonal ranges. In contrast, Hull et al. (2015) detected up to 39 separate core areas in panda home ranges which they returned to after several month-long periods. Captive studies have found that pandas have excellent spatial memory (Perdue *et al.* 2011, Tarou *et al.* 2004). The authors of both studies stated that their findings did not necessarily indicate the tendency to remember certain forage, though. Pandas’ ability to return to seasonal home ranges (which was quantified through movement path analysis by Zhang *et al.* 2014) suggests spatial memory at a broad scale, and the numerous small core areas found by Hull *et al.* (2015) suggests spatial memory at finer scales as well.

Perdue *et al.* (2011) found that males had greater spatial memory than females, particularly a greater “working memory” indicative of the need to remember varying information, such as the location of females and scent marking locations. This finding supports the idea that males “check-up” on females (Schaller *et al.* 1985, Pan *et al.* 2001), and would explain Hull *et al.*’s (2015) results that the male returned to many more core areas than any female.

Movement Patterns

Multiple studies found that males travel extensively in the spring mating season (Schaller *et al.* 1985, Pan *et al.* 2001), and attribute this increased movement to the search for mates. We believe that our study has highlighted enough evidence to suggest that females make similar increases in movement during the mating season. With this in mind, we think it possible that some of the increased spring movement in females that Schaller *et al.* (1985) and Pan *et al.* (2001) attribute to bamboo shoot forage may be attributable to movement behavior for mating.

Female pandas can mate with multiple individuals during a single estrus (Schaller *et al.* 1985, Pan *et al.* 2001). This promiscuous mating system could partially explain an increased movement during the mating season in both sexes. Whether this behavior in females is widespread or unique to certain populations is uncertain. In Wolong, long-distance adult female movements during estrus were not reported in Schaller *et al.* (1985) or by Hull *et al.* (2015, pers. observations). The two studies that found explicit evidence of this behavior were both conducted within Foping Nature Reserve in the Qinling mountains (Liu *et al.* 2002, Zhang *et al.* 2014). A final point on movement is that variation in distances moved by individual pandas within a population can be large, as evidenced by the large variance in mean daily distances moved reported by Pan et al. (2001).

Seasonal Migration

It has been well documented that seasonal migrations up and down in elevation occur in panda populations, and that migration patterns differ in direction and intensity between the Qionglai and Qinling mountains. Our synthesis confirmed these differences between the mountain ranges. We also addressed the discrepancies in migration timing and duration among Qinling pandas by plotting average monthly elevation across studies (Fig. 3). The monthly elevations of pandas from all three Qinling studies match closely, indicating the discrepancies were a function of range definitions rather than results.

Pan *et al*. (2001) found exceptions to the normal migration pattern in the Qinling. The authors recorded direct and indirect evidence (tracks, spoor, and sightings) that some un-collared pandas did not descend during the winter months. A single collared female also lacked the normal migration pattern. They also reported two instances of individuals fighting or contesting for mating privileges at high elevation (2500 m and 2800 m) in April, 6 and 12-15 days later than the latest date the authors reported seeing all other courtship events at lower elevations. More research is needed to determine how widespread this phenomenon is and if it has led to genetic differences in populations in the Qinling population based on elevation.

In addition to the importance of bamboo distribution in driving seasonal migrations among panda populations, temperature appears to influence this behavior in the Qinling. This effect that was not found in the Qionglai, where pandas experience lower mean temperatures and spend early summer at lower elevations (Liu *et al*. 2014). Pandas in the Qinling migrated upwards in elevation when maximum temperatures rose (Pan *et al.* 2001, Zhang *et al.* 2014, Liu *et al.* 2014). This is an important consideration given the potential temperature increases in the coming century from anthropogenic global climate change. Coupled with the recent predictions that the preferred bamboo species in the Qinling will face significant reductions to their range under a warming climate (Tuanmu *et al.* 2012), the need to avoid high temperatures means this subpopulation of pandas could be facing the most severe threats to survival in the coming century.

Natal dispersal

Natal dispersal among pandas is a difficult behavior to capture in telemetry studies, and the data are limited. One issue is that the number of juveniles and subadults followed in any one study has been small. Another is that the study duration has in many cases been too short to have much chance of detecting a natal dispersal event. Nonetheless, the findings made thus far are revealing. It would seem that there is a risk involved in natal dispersal, as one female returned to her original capture site after traveling outside the study area in an emaciated and badly wounded condition, dying shortly after (Pan *et al.* 2001). This suggests she faced conflict in new areas and could not integrate into the local population. Long-range movements by female subadults to new areas before returning to near their original home range (Xiwang in Pan *et al.* 2001), or their original capture area (females in Johnson *et al.* 1988, Pan *et al.* 2001, and Zhang *et al.* 2014), is a recurring phenomenon. This suggests female subadults may make exploratory movements before permanently establishing a new range elsewhere, as suggested by Zhang *et al.* (2014).

Fecal genetics studies have found that in the Liangshan and Minshan mountains female natal dispersal coupled with male philopatry is indeed the behavioral norm (Hu *et al.* 2010, Zhan *et al.* 2007). Hu *et al.*'s (2010) results indicated some short-range natal dispersal in males, and another fecal genetics study (Zhu *et al.* 2011) found evidence of an even larger male natal dispersal event of potentially 20 km. This suggests that like many aspects of panda ecology, there is some variation in this behavior between and within mountain ranges.

Human disturbance and habitat fragmentation have been identified as genetic barriers on large and small scales (Zhu *et al.* 2011, Hu *et al.* 2010), but there is also evidence that disturbance features such as roads are not absolute barriers (Zhu *et al.* 2011). Additionally, habitat restoration (Liu *et al.* 2008) and corridor construction efforts are underway (Zhu *et al.* 2011), which will help increase habitat connectivity. More study will help to further explain the natal dispersal patterns of the giant panda amid varying degrees of habitat fragmentation, knowledge that is important in conserving the remaining wild populations.

Conclusions

Our study was the first effort to review and synthesize findings of telemetry studies on giant pandas, an important undertaking due to the low sample sizes involved in the individual studies reviewed. Through this process we corroborated previous findings that males have larger home ranges than females. We also obtained results that differed from previous studies, including the lack of a difference in home range size between the Qinling and Qionglai mountain ranges. The results of our synthesis support the conclusion that both females and males alter their movement patterns in the mating season, and highlight the behavioral differences in seasonal elevation migrations between populations. We also point out the possibility of a behavioral split and divergence among pandas in the Qinling mountains, based on seasonal elevation migration.

There is much yet to be learned about wild panda biology and ecology, and perhaps the most apparent theme in our paper is that of variation and exceptions across study individuals and panda populations. Although our synthesis has shed new light on several aspects of panda ecology, more research is needed to further explore many of the topics we covered in different populations and reach broader conclusions. While telemetry studies are the most effective technique in gathering data on panda movement, fecal genetics sampling has advanced enough to make important contributions to the knowledge of panda population structures and dispersal tendencies (Hu *et al.* 2010, Zhu *et al.* 2011). The possibilities of this technique on large, population-level scales are intriguing.

The effects of human disturbance on giant panda movements remains understudied. Though some mention was made of this potential interaction, no telemetry studies explicitly attempted to measure this factor. Research into the effects of human disturbance on giant pandas has been more common in presence/absence studies (Pan *et al.* 2001) and fecal genetics sampling (Qi *et al.* 2011), but there is more to learn regarding the response of pandas to disturbance and their ability to utilize recovering habitats (Hull *et al.* 2014). There has been much progress in panda research and conservation (Swaisgood *et al.* 2009), but there is also increased anthropogenic presence and development across the panda distribution range (Liu 2015a). A coupled human and natural systems approach (Alberti *et al.* 2011, Liu *et al.* 2013, Liu *et al.* 2015b) is needed to integrate panda movement information with other types of information to better understand and mitigate negative human impacts.

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Tables

Table 1. Telemetry and data collection methods for all published telemetry studies on giant pandas

Study	Schaller *et al.* (1985)	Pan *et al.* (2001)	Yong *et al.* (2004)	Zhang *et al.* (2014)	Hull *et al.* (2015)
Mountain range	Qionglai	Qinling	Qinling	Qinling	Qionglai
Collar type (brand)	VHF (Telonics)	VHF (Telonics)	VHF (Telonics)	GPS (Lotek)	GPS (Lotek)
Locating method	Triangulation	Triangulation	Cross-point of two bearings	-	-
Receiving towers	68	Not reported	59	-	-
Mapping method	1:10,000 scale map	1:50,000 scale map, later GIS	GIS software	GIS software	GIS software
Number of records	1561	5973	1639 ‡	5976	4537 §
Average # of records/panda	312.2	271.5	273.2	1494.0	907.4
Average # of records/panda/month followed	25.2	7.2 †	12.1	119.5	66.6
Home range calculation	Minimum convex polygon (MCP)	Ellipse, MCP	MCP	Brownian bridge movement model, MCP	Biased random bridge movement model, MCP
Core area calculation	Frequency of relocations in grid cells	Frequency of relocations in grid cells, surrounding cells with lesser weight	-	-	Home range area vs probability of use threshold (Van Walder and Rodgers 2012)
Social interaction	Proximity between individuals, direct observation	Direct observation	-	Jacobs D test	Proximity between individuals, Minta's test
Movement patterns	Distance between daily relocations	Distance between daily relocations	Distance between daily relocations	Speed (meters moved per hours	-

				between relocations), First passage time (FPT) analysis	
Seasonal migration	No specific methods stated	Spatial-temporal analysis of relocations	Spatial-temporal analysis of relocations	FPT analysis	-

- Not investigated or not applicable

† Relocation sampling effort reduced approximately 5 years (half way) through the study to focus on gathering behavioral data.

‡ Originally 1756 radiolocations, 117 taken out for inaccuracy.

§ For home range and core area analyses, records limited to those collected from April 2011-April 2012

Note: No specified methods were used for identifying natal dispersal behavior, except for anomalous movements outside of home range.

Table 2. Summary of key behavioral characteristics across five published studies on giant panda telemetry

Variable	Schaller *et al.* (1985)	Pan *et al.* (2001)	Yong *et al.* (2004), Liu *et al.* (2014)	Zhang *et al.* (2014)	Hull *et al.* (2015)
Home range (MCP method)†	5.14 km^2 ±1.04	7.42 km^2 ± 3.71	6.01 km^2 ± 1.41	13.2 km^2	7.08 km^2 ± 4.36
Spatial overlap	Discrepancies in results	No quantified results	No quantified results	34.4%	13.5%
Core areas	0.33 km^2	No quantified results	No quantified results	No quantified results	1.02 km^2
Average distance between daily relocations	369 m ± 145 (pandas = 4)	411 m ± 484 (pandas = 6)	425 m ± 147 (pandas = 6)	605.46 m‡ (pandas = 4)	No quantified results
Seasonal migration§	Significance test on data by Liu *et al.* (2014) found elevation difference between seasons	Elevation difference between seasons	Elevation difference between seasons	Elevation difference between seasons; evidence of linear, directed movement between seasonal ranges	No quantified results
Natal dispersal	1 case of subadult female natal dispersal reported later in project (Johnson *et al.* 1988)	3 cases of subadult female natal dispersal	No natal dispersal events	1 case of subadult female natal dispersal	No natal dispersal events

† All available records used to calculate averages

‡ Speeds in m/hour measured from figure using ImageJ and later converted to average daily distance

§ See Fig. 3, Table 4 for more detailed data.

Table 3. Spatial overlap of giant pandas within and between sexes as measured using telemetry methods. Only GPS studies (Zhang et al. 2014, Hull et al. 2015) used.

Relationship	Males overlap other males by:	Males overlap females by:	Females overlap other females by:	Females overlap males by:
Mean overlap	51.92% (Sample size = 2)	23.42% (Sample size = 6)	14.77% (Sample size = 4)	26.50% (Sample size = 6)

Table 4. Definitions of seasonal elevation ranges by the three studies in the Qinling mountains, as well as the reported timing and speed of ascents and descents from summer ranges.

Study	Winter elevation	Summer elevation	Timing of ascent	Speed of ascent	Timing of descent	Speed of descent
Pan *et al.* (2001)	1350-2000 m	Above 2000 m	May 21 – July 1	1-2 days	July 8 – October 1	1-2 days
Yong *et al.* (2004)	1400-1950 m	2150-2800 m	June 7 – 15	2-3 days	September 1 – October 6	36 days
Zhang *et al.* (2014)	988-2000 m	Above 2000 m	May	Less than one month	July – November	3.5 months

Figure Legends

Figure 1. Map of the current distribution of the giant panda in China. Suitable panda habitat across 6 mountain ranges was estimated by Viña et al. (2010). Study areas of studies reviewed in this paper are also shown, including Wolong Nature Reserve (Schaller et a. 1985, Hull et al. 2015), the Changqing Forestry District (Pan et al. 2001), and Foping Nature Reserve (Yong et al. 2004, Zhang et al. 2014).

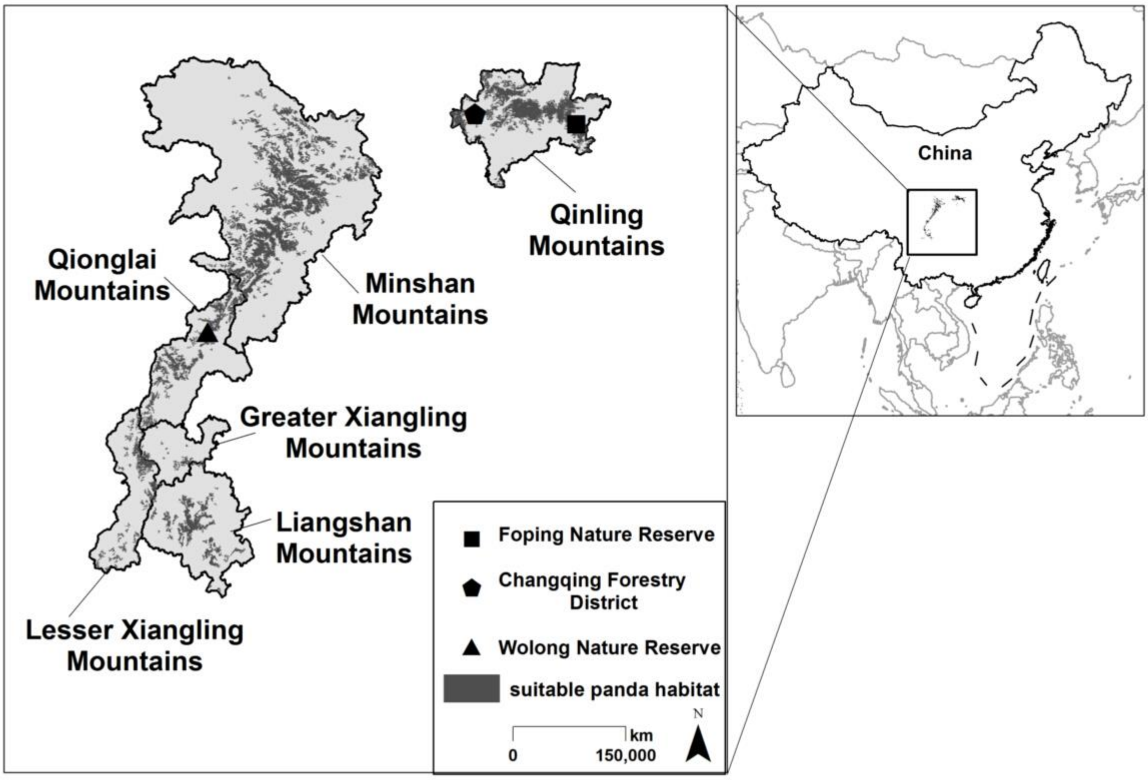

Figure 2. Percent of all simultaneous observations in which pairs of pandas were located within 200 m. Only Schaller *et al.* (1985) and Hull *et al.* (2015) performed this analysis.

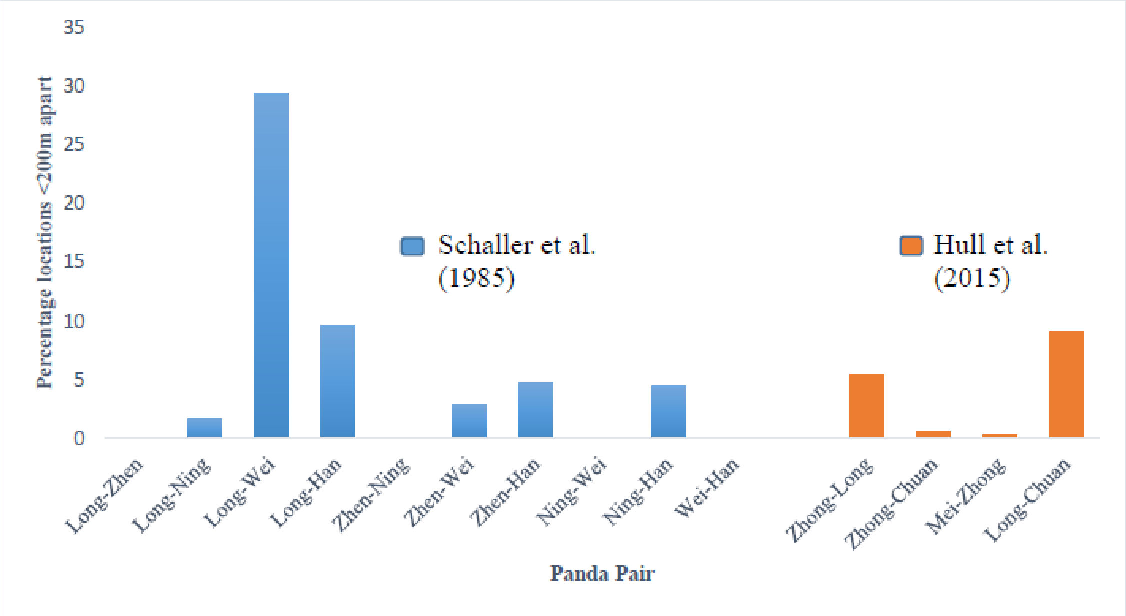

Figure 3. Mean monthly elevation of tracked pandas, separated by study.