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Progress in the ecology and conservation of giant pandas

Fuwen Wei,[*] ‡ Ronald Swaisgood,† Yibo Hu,[*] Yonggang Nie,[*] Li Yan,[*] Zejun Zhang,[*] Dunwu Qi,[*] and Lifeng Zhu[*]

[*]Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beichenxilu 1-5, Chaoyang District, Beijing 100101, China

†Applied Animal Ecology, San Diego Zoo Institute for Conservation Research, 15600 San Pasqual Valley Road, Escondido, CA 92027, U.S.A.

Abstract: *Giant panda (*Ailuropoda melanoleuca*) conservation is a possible success story in the making. If extinction of this iconic endangered species can be avoided, the species will become a showcase program for the Chinese government and its collaborators. We reviewed the major advancements in ecological science for the giant panda, examining how these advancements have contributed to panda conservation. Pandas' morphological and behavioral adaptations to a diet of bamboo, which bear strong influence on movement ecology, have been well studied, providing knowledge to guide management actions ranging from reserve design to climate change mitigation. Foraging ecology has also provided essential information used in the creation of landscape models of panda habitat. Because habitat loss and fragmentation are major drivers of the panda population decline, efforts have been made to help identify core habitat areas, establish where habitat corridors are needed, and prioritize areas for protection and restoration. Thus, habitat models have provided guidance for the Chinese governments' creation of 67 protected areas. Behavioral research has revealed a complex and efficient communication system and documented the need for protection of habitat that serves as a communication platform for bringing the sexes together for mating. Further research shows that den sites in old-growth forests may be a limiting resource, indicating potential value in providing alternative den sites for rearing offspring. Advancements in molecular ecology have been revolutionary and have been applied to population census, determining population structure and genetic diversity, evaluating connectivity following habitat fragmentation, and understanding dispersal patterns. These advancements form a foundation for increasing the application of adaptive management approaches to move panda conservation forward more rapidly. Although the Chinese government has made great progress in setting aside protected areas, future emphasis will be improved management of pandas and their habitat.*

Keywords: adaptive management, behavioral ecology, climate change, foraging ecology, landscape ecology, molecular ecology

Avances en la Ecología y Conservación del Panda Gigante

Resumen: *La conservación del panda gigante (*Ailuropoda melanoleuca*) es una historia de éxito en potencia. Si se puede evitar la extinción de esta especie emblemática en peligro, se convertirá en un programa de escaparate para el gobierno chino y sus colaboradores. Revisamos los principales avances en la ciencia ecológica del panda gigante mediante la evaluación de cómo han contribuido a su conservación estos avances. Las adaptaciones morfológicas y conductuales del panda a una dieta de bambú, las cuales tienen una fuerte influencia sobre la ecología del movimiento, han sido bien estudiadas, lo que proporciona conocimiento para guiar las acciones de manejo desde el diseño de una reserva hasta la mitigación del cambio climático. La ecología de la búsqueda de alimento también ha proporcionado información esencial que se utiliza en la creación de modelos de paisaje del hábitat del panda. Ya que la pérdida del hábitat y la fragmentación son los principales conductores de la declinación de la población de la especie, se han realizado esfuerzos para ayudar*

‡*Address correspondence to Fuwen Wei, email weifw@ioz.ac.cn*
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a identificar áreas núcleo de hábitat, establecer en dónde se necesitan corredores de hábitat y para priorizar áreas para su protección y restauración. Por esto, los modelos de hábitat han proporcionado una guía para la creación de 67 áreas protegidas por parte del gobierno chino. Las investigaciones conductuales han revelado un sistema eficiente y complejo de comunicación y han documentado la necesidad de proteger al hábitat que sirve como una plataforma de comunicación para juntar a los sexos al momento del apareamiento. Investigaciones más detalladas muestran que los sitios de guarida en los bosques primarios pueden ser un recurso limitante, lo que indica un valor potencial en la dotación de sitios de guarida alternos para las crías. Los avances de la ecología molecular han sido revolucionarios y se han aplicado a los censos poblacionales, a la determinación de la estructura poblacional y la diversidad genética, a la evaluación de la conectividad después de una fragmentación de hábitat y al entendimiento de los patrones de dispersión. Estos avances forman una base para el incremento de la aplicación de estrategias de manejo adaptativo para avanzar la conservación del panda de manera más rápida. Mientras el gobierno chino ha hecho un gran avance en la creación de las áreas protegidas, un énfasis futuro será el manejo mejorado de los pandas y su hábitat.

Palabras Clave: cambio climático, ecología de forrajeo, ecología de comportamiento, ecología molecular, ecología de paisaje, manejo adaptativo

Introduction

The giant panda's (*Ailuropoda melanoleuca*) iconic conservation status and the global effort to rescue it from extinction make a compelling model for species conservation carried out within and led by a developing nation. Two decades ago, leading conservationists were pessimistic about the future prospects of the giant panda, motivating George Schaller, who conducted much of the foundational research on pandas, to pen *The Last Panda* (Schaller 1994). What he and others did not foresee was China's rapid economic rise and concerted effort to apply science, management, and policy to arrest the decline of a species referred to as "China's national treasure" (Swaisgood et al. 2010).

It was once believed that pandas were the perpetrators of their own demise because they were poorly adapted to their environment (Wei et al. 2015). For example, their notoriously low levels of interest in mating were the subject of ridicule; however, pandas in the wild experience no mating problems and have high reproductive rates (Pan et al. 2014). Once a better understanding of the biology and behavior of the species was incorporated into husbandry practices, captive pandas began to mate and experienced exponential population growth (Swaisgood et al. 2006). Moreover, its well-known specialization on bamboo is not an evolutionary cul-de-sac; rather, this strategy opens up a foraging niche with plentiful resources and few competitors (Wei et al. 2015). For the panda, dietary specialization may not be an extinction risk factor because bamboo is widespread and abundant bamboo. In addition to the pseudothumb and skull morphology that enable efficient processing of bamboo, the panda has specialized symbiotic gut microbes that aid in bamboo digestion (Zhu et al. 2011). Rather than arising from inherent maladaptations, the panda's conservation problems arise from anthropogenic alterations to its environment and in some cases from direct persecution.

We sought to show the great progress, over a short period, of China's giant panda conservation initiative. Much of this progress has occurred as a result of governmental policy and rapidly advancing conservation science, sometimes in a mutually supportive fashion. Given that so much ground has been gained in so short a period, it is instructive to bring together a synthesis of significant findings on the ecology of giant pandas. We researched major advancements made in several areas of conservation and ecology relative to the giant panda and considered a path for future conservation research. That such progress can be made with a difficult-to-study species suggests that similar approaches may also deliver large benefits if applied to other species in need of conservation.

Foraging Ecology

In the order Carnivora, the giant panda had evolved to specialize on a diet of bamboo. Although bamboo is a poor food source and pandas have lower digestive efficiency than herbivorous mammals (Schaller et al. 1985), they meet their nutritional needs through a number of behavioral and morphological adaptions. Research across different mountain ranges by Schaller et al. (1985), Wei et al. (1999), and Pan et al. (2014) identified panda foraging strategies—preference for new shoots, young leaves, stems in small proportions and young bamboo plants—governed by seasonal changes in availability.

Studies of nutritional ecology indicate that many aspects of the panda's life history influence and are influenced by the panda's foraging strategy. For example, pandas' foraging decisions may be governed by changing ratios of important nutrients, such as Ca, P, and N, across species and parts of bamboo plants (Nie et al. 2015). Nutrient availability appears to have large effects on the reproductive ecology of the species. Delayed implantation, a period of sustained embryonic diapause characteristic of panda reproduction, may be a strategy for delaying fetal growth until sufficient Ca is available in bamboo leaves to support bone growth and lactation.

As a bamboo specialist, the giant panda may also affect bamboo. For example, panda herbivory is associated with rapid compensatory growth, particularly in dense stands of bamboo (Hull et al. 2011), and thus may affect carrying capacity. As the panda's habitat becomes fragmented, possibly exacerbated by climate change (Songer et al. 2012; Tuanmu et al. 2013), localized impacts of foraging may become more limiting because pandas will have fewer options for dispersal to bamboo patches.

Movement Ecology

Animal movement is a fundamental aspect of a species' ecology, and understanding the factors influencing movement patterns is important to conservation and provides evidence that can be used to link individual behavior with population- and community-level effects (Nathan et al. 2008). Early coarse-scale radio tracking with VHF transmitters provided foundational data on home range size and documented the panda's solitary nature (Schaller et al. 1985; Pan et al. 2014). Although panda home ranges overlap generously, direct encounters are rare. Seasonal elevational migration was documented first in Wolong (Schaller et al. 1985), then later in the Qinling mountains (Pan et al. 2014). At both sites, the seasonal movements track changes in resources and facilitate access to bamboo species with greater nutritional value (i.e., higher concentrations or a more balanced intake of key nutrients such as N, P, and Ca) (Nie et al. 2015).

Inevitably, VHF-based radio tracking data had large gaps when animals at more distant locations could not be detected. Thus, it is unsurprising that the advent of geographic positioning system (GPS) tracking revealed larger home range and core area sizes than radio tracking. (Zhang et al. 2014*a*; Hull et al. 2015). Fine-scale movement data show that most daily movements by pandas are characterized by short tortuous movements within a habitat patch, infrequent long-distance movements to gain access to other habitat patches, and avoidance of steep slopes. Anthropogenic disturbance may have disproportionate effects on a species that relies on conservative spatial movements. The energetic impacts of increased movement to access fragmented bamboo patches or avoid human activities could have population-level effects and have implications for habitat protection, reserve design, and wildlife corridors.

Landscape Ecology and Climate Change

Habitat loss and fragmentation are widely acknowledged as the major reasons behind the decline of giant panda populations (Schaller et al. 1985; Pan et al. 2014; Wei et al. 2015). This habitat loss and fragmentation were brought about by rapid development in China, including the expansion of agricultural and forestry activities (Liu et al. 2003; Zhao et al. 2013). Large-scale surveys indicate that the panda's range is subdivided into about 33 small populations separated by mountain ranges, rivers, roads, forest clearings, and human settlements (State Forestry Administration 2015); thus, they are demographically and genetically vulnerable and in need of knowledge-based meta-population management (Wei et al. 2012).

Because habitat loss and fragmentation are major drivers of the panda population decline, a great deal of attention has been directed to landscape ecology to determine the extent, quality, and fragmentation of the panda's remaining habitat. Habitat protection has been the vanguard of the Chinese government's response to panda endangerment and has led to the creation of 67 protected areas. However, approximately 46% of remaining habitat (33% of the panda population) remains unprotected (State Forestry Administration 2015), which presents further opportunities for protected status of additional landscapes, although in some cases protected status is not sufficient to prevent further degradation of habitat (Liu et al. 2001). The presence of pandas and existence of habitat outside reserves also presents opportunities for private sector involvement, such as payment for ecosystem services in collective forests (approximately 15% of the remaining habitat) (Yang et al. 2013). This endeavor would be particularly effective if key areas that link fragmented panda populations were targeted (Yang et al. 2015).

Efforts to map panda habitat, based on difference measures of habitat quality, have proven valuable (Qi et al. 2012). Broad-scale approaches to landscape conservation made possible by remote sensing helped move panda conservation from single reserve approaches to approaches that incorporate a matrix of reserves and unprotected habitat (Loucks et al. 2003; Shen et al. 2008; Viña et al. 2010). The resulting habitat models provide guidance for identifying core habitat areas, prioritizing areas for future protection, and recommendations on linkages between habitat areas to counter fragmentation. The Chinese government has relied on these analyses in selecting the location of some of the 67 reserves established for pandas.

However, these habitat models, and the recommendations that stem from them, are only as good as the underlying data and assumptions. Some factors used to predict giant panda presence, which are important to habitat models, lacked empirical documentation until recently. Range-wide analyses of ground-collected data yielded the discovery that giant pandas are associated with old-growth forests, a finding previously undetected in studies implemented on smaller spatial scales (Zhang et al. 2011). This finding points to the danger of a mismatch between data collected on one scale and policy decisions implemented on another. Researchers on this study included governmental decision makers, and the results influenced forest management policy, including the renewal of the logging ban. Recent advances in remote sensing techniques made possible the inclusion of understory bamboo in habitat models, which was long ignored because of limitations in remote sensing. Compared with earlier research that did not account for the presence of bamboo in the understory, new models including bamboo show much lower estimates of available habitat and higher estimates of fragmentation (Wang et al. 2009; Viña et al. 2010).

The availability of remote sensing data also makes possible the documentation of changes in habitat quality over time, as exemplified in its application to show continuing habitat degradation inside protected areas (Liu et al. 2001). Several teams of investigators made good use of this technology to rapidly document the consequences of a large earthquake centered on panda habitat in 2008, which caused the temporary loss of panda habitat and an increase in habitat fragmentation (e.g., Wang et al. 2008; Xu et al. 2009). The ability to quickly document these events allowed for actions to be devised to address earthquake impacts, the revision of conservation strategies, and, ultimately, the monitoring of natural recovery and restoration efforts (Zhang et al. 2014*b*).

Increased scientific understanding of panda habitat and foraging requirements has provided the basic data needed to develop models to predict the impacts of climate change on pandas (e.g., Songer et al. 2012; Tuanmu et al. 2013; Fan et al. 2014; Li et al. 2015). These models all had similar forecasts: substantive habitat loss (up to 60% in some models), a shortfall of food supplies, increasing fragmentation, and northward and elevationally upward range shifts. Most of these analyses did not address the implications of the panda's history. Prior to anthropogenic disturbance pandas were distributed at much lower elevations in warmer climates and consumed different species of bamboo (i.e., those that thrive in warmer climates) (Schaller et al. 1985). In a warming climate, one might predict that more habitat will become available at elevations above the current distributional range. Areas that currently contain panda habitat may no longer be suitable for the bamboo species present but should become suitable for bamboo species that previously existed at lower elevations and in more southerly latitudes. These bamboo species once sustained panda populations before pandas were displaced by human activities. However, Li et al. (2015) suggest that the slow rate of bamboo colonization would create a lag time in recovery of habitat for pandas. This may be true, but the implication is that, for example, mitigation should be devised to buy time for habitat recovery or to expedite recovery through plantings of bamboo adapted to a warmer climate. Eventually areas may become suitable for pandas again, provided proper environmental stewardship.

Less predictable is how humans will respond to changing climate and how their response will affect pandas. The development of agriculture in China has been limited by climate, and the panda has been allowed to thrive only at elevations above which agriculture is productive. Climate change models predict that the agricultural value of land in current panda habitat will increase. For example, the increased elevational range of viticulture is predicted to affect panda habitat (Hannah et al. 2013). These observations point to an increased need for protection measures in low-elevation panda habitat in the future.

Landscape ecology has had significant impacts on giant panda conservation policy and practice and has focused attention on establishment of reserves in optimal locations, increasing connectivity between reserves through corridor establishment, and development of better management of anthropogenic threats and key ecological limiting factors within protected and unprotected areas (Loucks et al. 2003; Swaisgood et al. 2011). As China continues to reform social and economic systems, this system of reserves will continue to face challenges from modernization and development (Liu et al. 1999), and landscape ecology will continue to provide knowledge for the better management of human activities and impacts.

Behavioral Ecology

Communication plays a vital role in the regulation of reproduction and competition. It determines mating strategies, reproductive success, and how animals are distributed on the landscape (Smith & Harper 2003); thus, understanding and managing communication processes are important for conservation (Campbell-Palmer & Rosell 2011). Experimentation with captive pandas demonstrates a complex and sophisticated chemical communication system conveying information about individual identity, sex, age, reproductive condition, and competitive ability (reviewed in Swaisgood et al. [2004]). Application of this knowledge has contributed substantially to greatly improved captive mating success and helped turn around the conservation breeding program for the species (Swaisgood et al. 2004, 2006). Recent field research on chemical communication has added to understanding of habitat requirements for pandas, demonstrating that pandas use a different type of habitat for communication (open-forest ridges) than they use for foraging and other activities (Nie et al. 2012*a*). If habitat that promotes communication is not maintained, then pandas may have difficulty coming together for mating. That panda sexual motivation is strongly influenced by chemosignals (Swaisgood et al. 2004) suggests that reduced communication opportunities may impede breeding in the wild as has been shown for captive pandas.

Similar investigations have also determined the role of acoustic signals in governing panda social and reproductive behavior. Studies on captive pandas show that panda vocalizations provide information to discriminate potential mates (Charlton et al. 2009), that male vocalizations signal testosterone levels (Charlton et al. 2011), and that female vocalizations advertise fertility (Charlton et al. 2010). These acoustic signals are primarily used once pandas have come together for mating and are critically important for assessing potential mates and coordinating mating.

In small populations, whether captive or wild, understanding the mating system is of vital importance for conservation because mating patterns have profound effects on effective population size, maintenance of genetic heterozygosity, population persistence, and ability to adapt to environmental change (Anthony & Blumstein 2000). The giant panda, typically fragmented into populations of <50 individuals, is vulnerable to reproductive problems associated with small populations, including reproductive skew in mating contributions. Intervention may be necessary in some cases, but a thorough understanding of reproductive biology and ecology is a prerequisite for informed management action.

Much has been learned about giant panda mating behavior and reproduction in captive research programs, and this knowledge has been successfully applied to conservation breeding (Wildt et al. 2006). Basic reproductive endocrinology of the species is now well understood and provides a thorough picture of the temporal dynamics of and social influences on estrogen, progesterone, testosterone, glucocorticoids, and other hormones associated with estrus, conception, and pregnancy (Kersey et al. 2010; Willis et al. 2011). The behavioral dynamics involved in mating, especially the role of communication, have been well documented (Swaisgood et al. 2004, 2006). Data derived from technologies such as GPS satellite tracking and fecal hormone analysis have supplemented early observations and provided new insights into reproductive behavior in wild pandas (Nie et al. 2012*b*, 2012*c*). Male pandas are able to locate females across large areas and demonstrate fierce and injurious aggression in competition for access to females. Wild male pandas may be energy limited and unable to sustain elevated levels of energetically expensive testosterone when not needed for mating and intra-sexual competition Nie et al. (2012*c*). The picture that emerges from this research is that panda reproduction may be limited by the ability to access, process, and conserve energy and that, as a species, pandas may be especially vulnerable to anthropogenic threats that have energetic costs.

Denning ecology is an important field of study among ursids, and other species giving birth in dens, because access to adequate dens can be important for offspring survival. As one of the most altricial of all eutherian mammals, the giant panda may be more reliant on the quality of denning habitat for successfully rearing vulnerable offspring. Giant pandas give birth every 2–3 years and rear offspring in a cave or tree den for the first few months of life (Schaller et al. 1985; Zhu et al. 2001; Pan et al. 2014). Research detailing the characteristics of preferred dens provides a management blueprint for suitable den sites to support panda reproduction (Zhang et al. 2007). Den quantity and quality may be important factors limiting giant panda population size.

Data on habitat factors that predict giant panda presence provide support for the hypothesis that panda populations may be limited by suitable den sites available in old-growth forests (Zhang et al. 2011). Tree dens, which can only be found in old-growth trees large enough to contain a cavity of sufficient size, may afford better protection and a more suitable microclimate for rearing cubs. Unfortunately, many panda reserves are dominated by second-growth forest, the old-growth having been logged long ago. Artificial dens may be the only practical way to address this potentially limiting resource in the short term. At the Foping Nature Reserve managers have used this information to begin testing the use of artificial dens.

Molecular Ecology

It can be stated without hyperbole that advances in the molecular ecology of giant pandas have been nothing short of revolutionary, mirroring the revolution in the application of non-invasive genetic techniques in many aspects of ecology and conservation relative to other species. Major advancements for the giant panda in this field have been reviewed recently (Wei et al. 2012, 2015) and are summarized briefly here. These advancements center around genetic diversity; population genetic structure; population size; and sex-biased dispersal.

Maintenance of genetic diversity is a cornerstone of conservation because this diversity reflects the ability of populations to adapt to environmental change and, therefore, persist (Frankham et al. 2002). Early studies found low levels of genetic diversity in giant pandas, a finding consistent with the panda's endangered status and beliefs regarding its long, slow decline due to maladaptation. However, this belief was supplanted when moderate levels of genetic diversity were revealed through the application of microsatellite markers and whole-genome sequencing. Results of these procedures suggest pandas have not yet lost the ability to adapt to environmental change. New genetic tools also revealed population structure and subdivision, providing knowledge vital for identifying management units, determining vulnerable subpopulations, and implementing meta-population management. Population divergence is the product of several operating factors, including fluctuations in climate, natural barriers, and anthropogenic habitat loss and fragmentation. Some genetic clusters, however, are the product of natural processes, not recent human-caused fragmentation, and therefore should be managed as conservation units to retain genetic structure and any localized adaptation (Zhu et al. 2011; Zhao et al. 2013).

Conservation strategies are also reliant on information about population size so that trends through time and space can be documented and addressed and appropriate conservation status can be assigned. The large and approximately once-a-decade national survey attempts to document panda population size based on its idiosyncratic feeding styles that yield individual differences in the size of bamboo stem fragments left in feces (State Forestry Administration 2015). The advent of genetic sampling from feces can provide a more accurate way to identify and count pandas. In one reserve, molecular methods led to a population estimate that more than doubled the previous estimate based on bite size (Zhan et al. 2006). Accurate estimation of population size will provide the foundation for more effective protection and management of pandas. Quantifying successful dispersal patterns is yet another important application of molecular ecology because dispersal influences population-genetic structure, such as degree of inbreeding. Unlike their ursid and most other mammalian kin, pandas show a surprising female-biased dispersal pattern, providing good reason to select females as candidates for reintroduction (Zhan et al. 2007).

Past, Present, and Future of Giant Panda Conservation

That the giant panda still exists in the wild is due to the Chinese government's commitment and visionary policies and management actions to arrest the panda's decline (Table 1). Initially the primary limiting factors facing pandas included poaching and habitat destruction. Since enactment of the 1988 Wildlife Protection Law, which banned poaching, this once-important threat has become almost nonexistent (Zhu et al. 2013; Wei et al. 2015). As part of China's National Conservation Plan, the number of protected areas for pandas has increased from 4 to 67, protecting approximately 58% (1.4 million ha) of occupied panda habitat (State Forestry Administration 2015). Strict forest protection measures and an active reforestation program have established China as one of the few countries with increasing forest cover (Li et al. 2013).

However, since the inception of the intrepid efforts to prevent the giant panda's extinction, many of the threats and limiting factors have changed, creating a need for a shift in conservation priorities. Preliminary results from an ongoing evaluation of the giant panda's International Union for Conservation of Nature Red List status show that habitat loss is not as big a threat to panda populations as it was previously (R.S., personal observation). Instead, anthropogenic habitat degradation, climate change, road and other construction projects in proximity to panda habitat, increasing ecotourism, pathogens, and environmental pollutants are considered the paramount threats pandas face. An optimistic view of the panda's conservation status suggests the panda population is larger than once believed (Zhan et al. 2006), that the amount of habitat is expanding, and that the population is increasing (up 17% in the past decade) (State Forestry Administration 2015). A more pessimistic view of the panda's future emphasizes the severe population fragmentation (33 isolated subpopulations, only 6 of which have more than 100 pandas), continuing threats that degrade and fragment panda habitat (e.g., roads, hydroelectric dams, mining, tourism [State Forestry Administration 2015]), and climate change (Li et al. 2015). Much of the knowledge gained from the national surveys is the direct result of the government's incorporation of ecological knowledge generated by scientists. Examples include use of home range size and bite-size analysis in the methods of population estimation, use of remote sensing and habitat models to estimate range, and, more recently, incorporation of molecular censusing to estimate population size and genetic diversity and isolation.

Against the backdrop of shifting threats and conservation opportunities, more of the same is not likely to carry panda conservation much further forward. The remaining opportunities to establish more protected areas for giant pandas will be limited, making better management of pandas and panda habitat within protected areas an increasing priority. Protected status does not necessarily confer full protection (Liu et al. 2001), and threats will need to be curtailed. Protection measures will need to extend into unprotected privately held or communal property through incentives, regulation, and local community stakeholder engagement (Yang et al. 2013, 2015).

The past two decades have witnessed a remarkable increase in the biological and ecological knowledge of giant pandas, making the panda an excellent candidate for testing the much-touted but little-used adaptive management approach (Nichols & Williams 2006) for endangered species conservation (Swaisgood et al. 2011). Management requirements should guide scientific research and scientific research should inform management actions, specifically through the development and testing of a priori hypotheses. For several examples of potential application of adaptive management to pandas, see Table 2. This general approach has already served the panda well, with science helping to move the captive population from vulnerability to sustainability (Swaisgood et al. 2006, 2011). In 2013, there were 375 individuals in the conservation breeding program and captive breeding is changing its focus from quantity to quality.

Whereas creation of protected areas and anti-poaching efforts were the primary conservation tools of the past, strategies to offset habitat fragmentation will dominate

Table 1. The Chinese government's giant panda conservation efforts and main achievements.

Threat	*Action*
Poaching	enactment in 1988 of Wildlife Protection Law banning poaching establishment of 67 nature reserves and nature reserve management facilities
Habitat loss and degradation	Grain to Green Project (conversion of agricultural land with a slope >25° to forest or grassland)
Loss of forest cover	natural forest protection program (prohibition of large-scale deforestation since 1998); Grain to Green Project
Habitat fragmentation	established, constructing, or planning corridors in Qinling, Minshan, and Daxiangling Mountains
Population subdivision	genetic rescue: translocation and reintroduction plan (pilot releases of 2 wild and 3 captive-born pandas, includes pre-release training for captive pandas and post-release monitoring for all pandas)
Lack of information on population and habitat trends	regular monitoring in most nature reserves (important for developing adaptive management)

the future. Habitat corridors to increase connectivity are currently under development (Wei et al. 2015). The government's corridor strategy has benefited immensely from ecological knowledge. They used information about what constitutes habitat and landscape mapping that expose habitat gaps. Although this does not quite constitute adaptive management, it does point to the fact that policy makers have had some dialogue with ecologists. Good science will be required to document whether pandas—and other wildlife—use these corridors and whether they achieve the genetic and demographic goals they are designed to address (Table 2). Routine monitoring conducted in many reserves provides some of the needed information on the effects of management, and plans for expansion of monitoring effort will position the program well for capturing lessons learned. Short-term tests of this strategy will involve the use of camera traps or fecal surveys to determine corridor use, and long-term tests will involve genetic tools to evaluate genetic exchange between subpopulations. If newly established corridors are determined insufficient to meet meta-population management goals, then the design of those corridors will need to be modified (Table 2) or other measures taken to encourage pandas to use them. For example, it has been proposed that conspecific cues (such as scent signals) could be planted in corridors to encourage pandas to use them; this strategy may require experimentation to determine the optimal set of cues (Swaisgood et al. 1999).

In some cases, corridors will not be possible or sufficient. Although often hotly debated, translocation of pandas from other reserves or the release of captive-born pandas may be required for genetic rescue of many small, isolated populations. Genetic analyses and habitat mapping was used by the government to determine populations in need of genetic rescue, such as those in the Xiaoxiangling Mountains (Zhu et al. 2010). Augmentation of this population with both captive-bred and wild pandas has already commenced. Further development of reintroduction techniques, using a hypothesis-testing approach, will refine this conservation tool and ensure its successful application where necessary (Seddon et al. 2007). Although an important tool for conservation, translocations are also often misapplied or poorly executed, requiring careful planning to ensure goals are met (Germano et al. 2015). In an adaptive management context, panda reintroductions and translocations must be conducted experimentally. Various factors should be manipulated experimentally to determine what works and what does not. For example, the release habitat should be closely evaluated. It is possible that the ecological requirements of pandas released into a novel area will be somewhat different from resident pandas. The introduced pandas may require easier access to important resources initially; thus, existing ideas of what constitutes habitat may not fully apply. The composition of the release group or the social environment at the release site may also predict differences in success. For example, in another solitary mammal, releases with familiar conspecific neighbors led to a more than 20-fold increase in production of offspring and better population establishment (Shier & Swaisgood 2012). An adaptive management approach to panda reintroduction should begin with identification of the variables with the most effect on post-release survival and establishment, to guide experimentation, and should be followed by detailed post-release monitoring to capture lessons learned.

A better understanding of the ecological factors that set carrying capacity in protected areas is required so that those resources can be better managed to increase panda populations within reserves. Population viability analysis suggests that environmental carrying capacity may be one of the most important factors limiting panda

Table 2. Scenarios suitable for an adaptive management approach to giant panda conservation.

Management question	*Scientific observations supporting adaptive management initiative (reference number*)*	*Proposed management action*	*Response variables to measure management action efficacy*
Is a lack of suitable den sites limiting population size and can artificial dens increase carrying capacity?	Old-growth forest predicts panda presence, indicating that panda populations may be limited by maternal dens provided by large trees (1). Studies of characteristics of den sites provide guidance on how to design artificial dens (2).	Install artificial dens in panda habitat with little old-growth forest; variables to manipulate to influence suitability include placement, size and shape, and addition of biologically relevant cues that may promote use.	den use, (comparative) offspring survival, cause of mortality, population increase, den area avoidance, and other signs that den placement is a form of disturbance
Does the age structure of bamboo influence resource availability and carrying capacity for and can management of bamboo increase carrying capacity?	Pandas prefer to forage on younger bamboo and younger bamboo is more nutritious (3,4). Further correlative studies are desirable to establish whether panda populations are larger where bamboo is younger.	bamboo management experiment in which bamboo is cut and allowed to regenerate implemented on a large scale in multiple experimental and control plots	regrowth of harvested bamboo, change in bamboo age structure, change in use by pandas of areas with experimental regrowth, change in panda body condition, reproduction, survival, and population size
Are corridors effective tools for increasing population connectivity and what corridor design will optimize connectivity?	Populations are severely fragmented with little gene flow between subpopulations (5,6). Detailed habitat mapping identifies areas where corridors can best be established (7,8).	work with Chinese government officials to designate corridor areas and potential restoration efforts to make them more suitable for pandas; test different corridor designs based on shape and habitat characteristics and compare efficacy	frequency of use of corridors by pandas as determined by camera trapping, fecal DNA, and other measures; long-term increase in gene flow between subpopulations
Can reintroduction be a tool for increasing population viability of meta-populations and what is the most effective method for reintroducing pandas to meet this objective?	Captive populations are reaching sustainability targets (9). Preliminary efforts to translocate or release captive-bred pandas have met with some success and have provided lessons learned (10). Habitat has been defined and mapped (1,7,8) and locations in need of augmentation for population viability have been identified (8,11).	compare success of animal relocations as a function of variables such as origin (captive, wild), pre-release training methods, release group composition (age, sex, numbers), and habitat and pre-existing population characteristics at release site	post-release monitoring to determine behavioral accommodation to new environment, survival, and reproduction, long-term genetic and population monitoring to determine whether genetic and demographic goals are met
What proactive mitigation measures can be taken to combat the predicted effects of climate change?	Based on an understanding of panda and bamboo ecology, climate change models predict changes in habitat distribution and loss of habitat within the protected areas network (12).	experimental planting and assisted migration of bamboo species adapted to lower elevations or lower latitudes in northern areas or at higher elevation than their historical range; translocation or captive release to northern areas or at higher elevation than their historical range (assisted migration)	monitoring of bamboo growth and long-term establishment as a function of distance moved from historical range; post-release monitoring of pandas as above; simultaneous monitoring of bamboo and pandas in current range to assess the degree to which current models accurately predict effects of climate change on bamboo and pandas

[*]Reference key: 1, Zhang et al. 2011; 2, Zhang et al. 2007; 3, Schaller et al. 1985; 4, Nie et al. 2015; 5, SFA 2006; 6, Wei et al. 2012; 7, Shen et al. 2008; 8, Viña et al. 2010; 9, Wildt et al. 2006; 10, Wei et al. 2015; 11, Zhu et al. 2010; 12, Tuanmu et al. 2013.

population size (Zhou & Pan 1997) and that habitat may be managed to increase carrying capacity. However, a more fine-scale understanding of habitat requirements is needed (Swaisgood et al. 2010), as are bold experiments (i.e., adaptive management) to evaluate population responses to manipulation of putative limiting resources (Swaisgood et al. 2011).

An important first step in moving the panda conservation agenda forward, therefore, is to understand better what constitutes high-quality habitat that will increase carrying capacity pandas (e.g., Zhang et al. 2011). However, panda habitat is often defined on a landscape scale (Liu et al. 2001; Shen et al. 2008), and its definition neglects the understory bamboo on which pandas rely (Linderman et al. 2005). To advance giant panda conservation, experimental manipulations of bamboo forage, potential dens, and other limiting factors will need to be carefully designed and implemented (Table 2). Although the population response to such management actions is what needs to be quantified, other measures can provide informative feedback before a population response is detectable.

What would a large-scale experiment to test manipulation of putative limiting factors look like? Take the case of bamboo forage outlined in Table 2. Ecological research shows pandas prefer to consume young bamboo (Schaller et al. 1985; Nie et al. 2015). A question that stands out is whether management actions to shift the bamboo age structure would be beneficial. In many grazing species, the act of grazing increases the subsequent nutritional value of the habitat because it causes compensatory growth (McNaughton 1984), an effect pandas may have on bamboo (Hull et al. 2011). Panda populations have been low for many generations and are only now beginning to increase (State Forestry Administration 2015), raising the possibility that any beneficial effects of panda foraging behavior on bamboo habitat have been compromised. Perhaps the bamboo age structure is much older than in historical times and therefore supports a lower panda population than previously. To test this hypothesis, management intervention on a limited experimental scale may be warranted. Some plots could be cut, whereas others are left as controls. Preferential use by pandas of newly created young bamboo stands would provide a rapid indicator of the success of the management strategy, but long-term population responses to this bamboo manipulation, relative to sites with no manipulation, would be required to determine whether bamboo age structure influences carrying capacity. If policy makers and researchers joined together in such a large-scale experiment, it might be possible to develop a management tool that would help restore panda populations and habitat to historical levels within protected areas.

A second example of a large-scale manipulation of putative ecological limiting factors is the test of old-growth forest as an important denning resource influencing cub survival and population recruitment. Ecological research demonstrating that pandas are associated with old-growth forests pointed to this hypothesis and influenced forest protection policy (Zhang et al. 2011). The next step will be to undertake a large-scale test of this hypothesis. Old-growth tree dens cannot be generated over short periods, so artificial dens may be the best alternative. Research indicating the preferred characteristics of suitable dens and surrounding microhabitat (Zhang et al. 2007) will guide the design and placement of artificial dens. Measures of use by pandas and survival of cubs will be available long before a change in population size. If pandas are not using these dens, then it is not possible for the dens to affect population size.

Adaptive management will also have a large role to play in addressing predictions from climate change models and, if necessary, mitigating future effects of climate change (Table 2). The design of some research questions may have to await on-the-ground changes that need to be addressed, but proactive mitigation may be warranted in some cases. For example, assisted migration (Mawdsley et al. 2009) experiments for bamboo (and pandas in the future) may be conducted as probes to detect shifts in habitat (Table 2). The most important question to address will be determining how bamboo species that occupy lower elevational ranges and more southerly latitudes (and that pandas once foraged upon) will respond to climate change. Will these species recolonize areas now currently occupied by pandas, replacing one habitat type with another? Studies showing the rate of natural colonization and assisted colonization through plantings will be informative.

The future of giant panda conservation should be bright, and there is good reason for hope. As a global conservation icon and ample resources and political will behind its conservation, the giant panda makes an excellent test case for endangered species recovery.

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