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EDITORIAL

Fuwen Wei–Recipient of the 2021 Molecular Ecology Prize



1 | INTRODUCTION

Dr. Fuwen Wei obtained his Bachelor Degree in Biology in 1984 and his Masters Degree in Zoology in 1987 from China West Normal University. He carried out his doctoral studies from 1994 to 1997 and obtained his Ph.D. degree in 1997 from the Institute of Zoology, Chinese Academy of Sciences (CAS). Since then, he has been working as a Principal Investigator in the Institute of Zoology, CAS and served as the Deputy Director of the Institute from 2008-2017. Dr. Wei received the National Science Fund for Distinguished Young Scholars from the National Natural Science Foundation of China in 2001. He was elected as an Academician of Chinese Academy of Sciences in 2017, an Academician of The World Academy of Sciences in 2018, and an Academician of Academia Europaea in 2021. He won the CAS Outstanding Science and Technology Achievement Award in 2018 and the China Natural Science Award in 2019.

Dr. Wei's research has focused on conservation biology and molecular ecology of endangered animals, and he is a pioneer in the conservation genomics and metagenomics of endangered animals. He has applied genetic and genomic techniques to assess the evolutionary past, present and future of giant panda populations; infer the processes and causes that threaten them; reveal their adaptive mechanisms to specialized bamboo diet; and propose science-based conservation strategies for their long-term survival. His research offers a framework for endangered animal study. Below we summarize his main research advances.

2 | NONINVASIVE GENETICS AND ITS APPLICATION IN STUDIES OF GIANT PANDAS

Dr. Wei's research team established a noninvasive genetic method to eliminate sampling bottlenecks in population surveys and conservation genetics studies of giant pandas. Zhan et al. (2006) comprehensively collected fresh fecal samples of giant pandas in a key panda reserve in Minshan Mountains and obtained a molecular census of 66-72 individuals, more than doubling the previous estimate of 27 individuals, suggesting the underestimation of population size by traditional population censuses. This method has been widely applied in mammal population studies, including the giant and red panda studies from Dr. Wei's team (Hu et al., 2011; Hu, Nie, et al., 2017; Hu, Qi, et al., 2010; Hu, Zhan, et al., 2010; Zhan et al., 2007; Zhang et al., 2007, 2011; Zhu, Zhan, Wu, et al., 2010). For example, Zhan et al. (2007) used noninvasive genetics to analyze the spatial genetic structure of related giant panda individuals and found a female-biased dispersal pattern at a fine reserve scale, in contrast to the male-biased dispersal pattern of many mammals. This pattern was also confirmed by two noninvasive genetic studies of giant pandas in Liangshan and Qinling Mountains, respectively (Hu, Nie, et al., 2017; Hu, Zhan, et al., 2010). The establishment of the noninvasive genetics method greatly facilitated conservation genetic and molecular ecology studies of giant pandas (Wei et al., 2012). This method was adopted as one of critical methods for the Fourth National Survey of Giant Pandas and was also used in research programs of other endangered animals such as the red pandas (Hu et al., 2011), snub-nosed monkeys and Asian elephants.

3 | PROCESSES AND DRIVING FACTORS THREATENING GIANT PANDAS

The giant panda has existed for more than eight million years. However, its population history and the processes currently threatening it have been elusive. After sequencing the giant panda genome (Li et al., 2010), Dr. Wei's research team performed the first population genomics study of the species (Zhao et al., 2013). Their results revealed two population expansions, two bottlenecks and -WII FY-MOLECULAR ECOLOGY

two population splits during the species' evolutionary history. Their results also highlighted the existence of three genetically distinct populations of extant giant pandas: Qinling, Minshan, and Qionglai-Liangshan-Daxiangling-Xiaoxiangling. These population fluctuations and differentiations were attributed mostly to Quaternary climate changes. In particular, the last glaciation and Holocene human activities were found to have resulted in serious population declines and consequent endangerment (Zhao et al., 2013). This research truly represented pioneering and innovative work on the population genomics of endangered species. It also established a research paradigm for this field and facilitated conservation genomics studies of other endangered species, including the snub-nosed monkey, tiger, yak, and red pandas (Hu et al., 2020).

4 | EVOLUTIONARY POTENTIAL OF GIANT PANDAS

Previously, lack of genetic diversity was thought to be one of intrinsic factors resulting in the endangerment of giant pandas. Dr. Wei's research team performed genetic diversity assessment using a large sample size, mtDNA and microsatellite markers, and found that giant pandas possess higher genetic diversity than previously estimated, also suggesting a higher evolutionary potential and genetic resilience than previously thought (Zhang et al., 2007). This research was listed as one of the 2007 Top-10 News Stories for Chinese Basic Research by the Ministry of Science and Technology of China. Later, more studies also detected relatively high levels of microsatellite and mtDNA diversity (Hu, Qi, et al., 2010; Zhu, Zhan, Meng, et al., 2010), a finding which was also supported by genome-wide genetic variation assessment (Zhao et al., 2013). The rapid population decline of giant pandas caused by periodic massive bamboo flowering, poaching and zoo capture, did not lead to significant decreases of either genetic diversity or effective population size (Zhu et al., 2013). In addition, Dr. Wei's research team found that the captive giant panda populations also maintain high genetic diversity (Shan et al., 2014).

5 | GENETIC CONSEQUENCES OF SMALL POPULATIONS

For the smallest and most isolated Xiaoxiangling giant panda population, Dr. Wei's team detected the signal of a strong and recent 60fold population reduction, starting about 250 years ago (Zhu, Zhan, Wu, et al., 2010). This event was postulated to have been a consequence of a known dramatic increase in the local human population facilitated by the use of non-native crops at the peak of the Qing Empire. Hu, Qi, et al. (2010) reconstructed the demographic history of the southernmost Liangshan population and found evidence for a population decline on the order of 95–96% during the last millennium, most likely due to anthropogenic habitat loss.

6 | LANDSCAPE GENETICS OF GIANT PANDAS

Landscape features may play important roles in genetic structure of wildlife. Dr. Wei's research team found that the Dadu River resulted in the divergence of Xiaoxiangling and Daxiangling giant panda populations, and the National Road No.108 further hindered gene flow within the two populations (Zhu, Zhang, et al., 2011). Zhu, Zhan, Meng, et al. (2010) and Hu, Zhan, et al. (2010) found that habitat heterogeneity affected the dispersal paths and gene flow of giant pandas, and least-cost path distance explained more variation in genetic distance than Euclidean distance in the Xiaoxiangling and Liangshan Mountains, respectively. In the Qinling giant panda population, the fragmented landscape did not lead to genetic structuring, but the gene flow was found to be significantly affected by two topographic factors, slope aspect and topographic complexity (Ma et al., 2018).

7 | MECHANISMS OF ADAPTATION TO SPECIALIZED BAMBOO DIET

Being a carnivorous mammal, giant pandas live almost entirely on bamboo which is a low nutrient and low energy food. Using a stable isotope technique, Dr. Wei's research team found that the isotopic trophic and ecological niche widths of ancient pandas were approximately three times larger than those of modern pandas. Thus, ancient pandas had more complicated food structure and habitat type than their modern counterparts. During diet specialization, they propose that this genus underwent two major dietary shifts, the first was completed before the Pleistocene from carnivory or omnivory to herbivory, and the second from herbivory to an obligate bamboo diet, which possibly was not finished until the mid-Holocene (Han et al., 2019). In other words, these studies suggested that giant panda evolved from a relatively generalist toward a very specialized species in terms of its diet. For a long time, how the giant pandas evolved to adapt to this specialized bamboo diet has remained a mystery. Dr. Wei's research team performed a series of studies involving morphology, genetics, behavior, and physiology, and identified adaptive evolutionary mechanisms for dealing with the specialized bamboo diet in giant pandas.

7.1 | Morphological and genetic adaptations

The giant panda and red panda have evolved pseudo-thumbs to facilitate grasping bamboo, representing a classical example of adaptive and convergent evolution. By *de novo* sequencing the red panda genome and using comparative genomics method, Dr. Wei's research team identified the genomic signatures of convergent evolution. Two limb development genes *DYNC2H1* and *PCNT* have been identified to be key candidate genes for pseudo-thumb development. As evolutionary responses to a specialized bamboo diet, adaptive

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convergence has also been observed in genes involved in the digestion and utilization of bamboo nutrients such as essential amino acids, fatty acids, and vitamins (Hu, Wu, et al., 2017). This research offers a novel example for understanding molecular mechanisms of diet-related convergent evolution and is one of the earliest genomelevel convergent evolution studies. A review in *Nature Reviews Genetics* commented that "this is an elegant paper that describes convergent evolution in two distantly related pandas" (Meadows & Lindblad-Toh, 2017).

7.2 | Physiological adaptation

A long-standing question pertaining to its physiology is how the giant panda lives on the low-energy bamboo to maintain its energy demand. Dr. Wei's research team found that the giant panda has an exceptionally low daily energy expenditure similar to that of the three-toe sloth. This is closely related with its morphological, physiological and behavioral characteristics, such as reduced energy-consuming organs (liver and kidney), low activity, and low levels of the thyroid hormones. Moreover, the low thyroid hormone levels may be attributed to a premature stop codon of DUOX2 gene, which is unique to the giant panda. This gene is a critical gene for thyroid hormone biosynthesis (Nie, Speakman, et al., 2015). This research is a paradigm of integrative biology research, systematically illustrating the adaptive mechanism of giant panda maintaining low energy expenditure. Furthermore, a collaborative study between his team and John Speakman's team confirmed the functional effects of DUOX2 pseudogenization by the creation and analysis of geneedited mice with the same mutation as that found in giant panda (Rudolf et al., 2021).

7.3 | Behavioral adaptation

Dr. Wei's research team has also studied the foraging strategy, activity rhythm and habitat utilization of giant pandas, and found evidence for behavioral adaptation of giant pandas to balance the bamboo nutrients and energy consumption (Nie et al., 2019; Nie, Zhang, et al., 2015). They showed that natal dispersal patterns are female-biased, which might drive inbreeding avoidance in giant pandas (Hu, Nie, et al., 2017). Recently, Dr. Wei's team described an interesting behavior of wild giant pandas, horse manure rolling, and found that horse manure containing BCP/BCPO likely bestowed the wild giant pandas with cold tolerance at low ambient temperatures (Zhou et al., 2020).

8 | CONSERVATION METAGENOMICS OF GIANT PANDAS

How giant pandas digest cellulose in bamboo has long been an unsolved question. Dr. Wei's research team used 16S rRNA gene

sequencing and metagenomic approach to identify the structure and function of gut microbiota of giant pandas (Zhu, Wu, et al., 2011). They discovered several kinds of Clostridum with the ability to degrade cellulose and identified several genes coding for cellulosedigesting enzymes. These results suggested that the gut microbiota plays a critical role in degrading bamboo cellulose. This work represented a pioneering metagenomics study of gut microbiomes of wild animals. In addition, further study found significant differences in gut microbiome abundance between shoot-feeding and leaffeeding periods. The gut microbiomes of pandas helped to enhance the crude fiber utilization efficiency during the nutrient-deficient leaf period, whereas they expanded their functional capacity to reinforce the utilization of crude protein in the protein-rich shoot period (Wu et al., 2017). A more recent study detected gut microbiome convergence in structure and function between giant and red pandas, suggesting that the specialized herbivorous diet rather than host phylogeny is the dominant driver of gut microbiome convergence within Arctoidea (Huang et al., 2021). In addition, by integrating multi-omics analysis and in vitro culture experiments, his team provided an overview of the bamboo flavonoid metabolic profiles and their roles in host health maintenance via shaping the microbiota configuration, providing novel insights into host-microbiota coevolution (Wang et al., 2021).

9 | CONSERVATION PRACTICES OF GIANT PANDAS

Based on his findings that small populations face higher extinction risk, Dr. Wei proposed giant panda reintroduction and habitat corridor construction projects to save these most isolated populations, which are currently being implemented by the Chinese government. Over ten giant pandas have been successfully reintroduced into the Xiaoxiangling population, and the Nibashan Corridor has been under construction in the Daxiangling population. *Science* commented on these projects as "Hope for wild pandas" (Schenkman, 2010). Dr. Wei's team conducted the field monitoring after reintroduction and confirmed that these reintroduced pandas survived in the wild and have established their own home ranges. One of which, "Luxin", even successfully reproduced and produced offspring (Yang et al., 2018).

To understand whether the investment in pandas translates into substantial returns for humanity, a research team led by Dr. Wei valued the ecosystem services that panda and its habitat provided. To conserve pandas, the Chinese government has established 67 nature reserves. The estimated ecosystem service value from pandas and their reserves falls between \$US 2.6–6.9 billion/year in 2010, including provisioning, regulating and cultural service values. Protecting the panda as an umbrella species and the habitat that supports it yields significant societal benefits, roughly 10–27 times the cost of maintaining the current reserves, motivating expansion of the reserves and other investments in natural capital in China (Wei et al., 2018).

10 | CONCLUSION

Dr. Wei's findings revealed that the endangerment of giant pandas can be attributed mostly to ancient climate change combined with more recent human activity. Giant panda has evolved a series of adaptations to bamboo diet, its reproductive viability has not declined, its population size is under gradual increase, and its genetic diversity is still relatively high. These findings suggest that the giant panda retains substantial evolutionary potential, refuting the pessimistic view that pandas have gone down an "evolutionary dead-end" (Wei, Hu, et al., 2015). Based on these research and conservation advances, in 2016 the IUCN downlisted the giant panda from Endangered to Vulnerable (Swaisgood et al., 2018).

In the light of these significant research achievements, Dr. Wei has been invited to write many reviews and perspective articles about the molecular ecology, conservation ecology, evolutionary biology, and gut metagenomics of the giant panda by the journals Molecular Ecology (Wei et al., 2012), Conservation Biology (Wei, Swaisgood, et al., 2015), Molecular Biology and Evolution (Wei, Hu, et al., 2015), Trends in Microbiology (Wei, Wang, & Wu, 2015), and Trends in Genetics (Wei, Fan, & Hu, 2020); and about the advances and trends of population genomics and evolutionary developmental biology by the journals Protein Cell (Wu et al., 2014) and Science China - Life Sciences (Wei, 2020). Based on the latest research advances and disciplinary developments, Dr. Wei proposed two subdisciplines of conservation biology: conservation evolutionary biology (Wei et al., 2019) and conservation metagenomics (Wei, Wu, et al., 2019). These two subdisciplines highlight the cross-disciplinary nature of conservation biology, as well as future research trends, which will facilitate the better development of conservation biology.

Building on his conservation biology achievements, Dr. Wei has extended his perspective to the relationship between nature and humans. After his nomination as senior consultant on biodiversity issues for the Chinese government from 2019-, Dr. Wei has been deeply involved in the preparation and negotiation for the 15th Conference of Parties to the Convention on Biological Conservation (CBD COP15) and the drafting of the Post-2020 Global Biodiversity Framework (GBF). In his recent publication, Dr. Wei proposed a novel 2050 vision of the "Unity of Nature and Man" drawn from Chinese traditional Taoist philosophy for the Post-2020 GBF, which emphasized the balance of three main goals of CBD to meet the needs of both man and nature (Ma et al., 2021). In addition, Dr. Wei promotes marine biodiversity research and conservation, calling on China to strengthen the construction of marine national parks and countries around the world to strengthen international cooperation to protect marine biodiversity (Zhou et al., 2021). He further suggested that marine endosymbiosis systems should be explored with omics techniques, which would offer insights into endosymbiosis mechanisms and conservation of marine systems (Hu et al., 2021).

In summary, Dr. Wei's phenomenal academic achievements have greatly contributed to the development of the field of molecular

ecology, especially for endangered animals, and represent stellar contributions to the field of conservation genomics and metagenomics.

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