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Evolutionary Dynamics of Mitochondrial and Nuclear Genomes in Geese: Implications for Phylogenetic Reconstruction

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Abstract Geese, due to their complex evolutionary history and multiple hybridization and domestication processes, have become an important model for studying the phylogeny and genomic evolution of birds. This study reviewed the research achievements on the evolution of mitochondrial and nuclear genomes in geese in recent years, explored the roles of these two types of genomes in speciation, lineage differentiation and trait domestication, and emphasized some factors affecting phylogenetic analysis, such as gene infiltration, incomplete lineage separation and inconsistency between mitochondrial and nuclear genomes. This study also summarized the origin, population structure and genetic diversity of Chinese domestic geese, and combined with case analysis, revealed the geographical distribution characteristics of mitochondrial haplotypes. This study hopes to provide a theoretical basis for a further understanding of the complex evolutionary process of geese and other waterfowl.

Keywords Goose phylogeny; Mitochondrial and nuclear genomes; Genomic introgression; Lineage diversification; Domestication and genetic diversity

1 Introduction

Geese belong to the genera Anser and Branta and are very important in the study of bird evolution. They have a relatively complete fossil record and have blazed a unique evolutionary path within the Anatidae family. The evolutionary history of geese is complex, featuring both rapid speciation processes and ancient hybridization events. Therefore, it serves as an excellent model for studying the genetic diversity and speciation mechanisms of birds. Although different species of the genus Anser have obvious differences in appearance and behavior, their kinship is actually very close, which makes their evolution more difficult to explain and also indicates that we need to use systematic genomic data to further clarify their relationships (Ottenburghs et al., 2017).

Mitochondrial DNA (mtDNA) has a high mutation rate, is inherited only through the maternal line, and has a compact structure. It has always been applied in the phylogenetic research of birds and is also a commonly used molecular marker for reconstructing evolutionary relationships and species identification (Pacheco et al., 2011; Liu et al., 2013). However, the nuclear genome can also provide a lot of information that mtDNA cannot display, such as genetic recombination, incomplete separation of lineages and other evolutionary processes. These are all very crucial factors when studying the evolution of geese. The phylogenetic trees drawn from mitochondrial and nuclear genomes often show inconsistencies. Such inconsistencies are generally caused by hybridization, gene infiltration or incomplete lineage sequencing, which also indicates that it is necessary to integrate the two genomic data simultaneously (Ottenburghs et al., 2017; Princepe and De Aguiar, 2020; DeRaad et al., 2023).

This study explored how the mitochondrial and nuclear genomes of geese evolved, with a focus on their roles in phylogenetic research. It analyzed the genetic differences, hybridization, and lineage division methods of these two genomes to illustrate the evolutionary relationships among different goose species, and also evaluated the reliability of different genetic markers in addressing phylogenetic issues. This study hopes to help researchers understand the evolutionary process of birds more comprehensively and provide better phylogenetic research methods for species groups with complex evolutionary histories.

2 Taxonomy and Domestication History of Geese

2.1 Wild progenitors of domestic geese

Domestic geese mainly come from the two wild geese, Greylag goose (*Anser anser*) and Swan goose (*Anser cygnoides*). The Greylag goose was domesticated in Europe, while the Swan goose was mainly domesticated in East Asia, especially in China. They are the ancestors of most domestic goose breeds worldwide. Greylag goose mainly developed into various European domestic goose breeds. Swan goose is the ancestor of Chinese goose and African goose breeds. Both archaeological and genetic studies support that these two domestication processes occurred independently. The domestication of Greylag goose began approximately around 4 000 BC, while that of Swan goose was around 2 000 BC (Heikkinen et al., 2015; Honka et al., 2018; Kozák, 2019; Eda et al., 2022).

2.2 Domesticated goose lineages and breed diversity

More than 180 species of domestic geese have been bred from these two wild ancestors, and they vary greatly in appearance and behavior. In China, most domestic geese, except for the Yili goose, share a common ancestor. However, geese from different regions have become significantly differentiated in terms of body size and traits. The origin of European domestic geese is more complex, and some breeds have even undergone genetic hybridization with Chinese geese. During the domestication process, domestic geese have undergone significant changes in many aspects, such as weight, feather color, and egg production. Geese like Toulouse and African geese weigh much more than their wild ancestors. Some domestic geese lay about 12 times more eggs than wild geese. Wild geese are generally monogamous, while domestic geese have transformed into a breeding method where one male goose gives birth to multiple female geese (Kozák, 2019; Chen et al., 2023; Zhang et al., 2023).

2.3 Challenges in phylogenetic resolution

Heikkinen et al. (2015) and Honka et al. (2018) found that there has always been gene exchange between wild geese and domestic geese, as well as among different domestic goose strains, which makes the genetic relationship very complex. The genomes of many European domestic geese contain a large amount of genetic components from Chinese domestic geese, indicating that they have undergone multiple hybridization. Heikkinen et al. (2020) demonstrated that the genetic diversity of domestic geese is not high, with most individuals carrying only a small amount of mitochondrial haplotypes, which affects the resolution of phylogenetic analysis. Heikkinen et al. (2020) and Chen et al. (2023) hold that wild geese and domestic geese are difficult to distinguish clearly in archaeological research because they look very similar and there are not many ancient DNA samples.

3 Evolutionary Features of Mitochondrial Genomes in Geese

3.1 Structural and evolutionary characteristics of mtDNA

The mitochondrial genome structure of geese is stable, generally consisting of 13 protein-coding genes, 2 rRNA genes, 22 tRNA genes and 1 control region. This arrangement is very similar to that of other Anseriformes. The research conducted by Liu et al. (2013), Colom and O’Brien (2024) demonstrated that most protein-coding genes use ATG as the start codon, and there are also some conserved sequences in the control region that are crucial for DNA replication and transcription. In the mitochondrial tRNA genes of geese, tRNA^Ser (AGY) and tRNA^Leu (CUN) often lack DHU arms, which is a common feature in the mitochondria of birds. The differentiation rate of mitochondrial DNA in geese is approximately 2% per million years, which is similar to that of mammals. Liu et al. (2013) also found that the genetic sequence difference between the genera Anser and Branta was approximately 9%. Although different species of the genus geese show significant differences in appearance and behavior, their genetic differences are not significant, generally ranging from 0.9% to 5.5%. This indicates that they underwent rapid differentiation and the formation of new species during the late Pliocene to Pleistocene periods.

3.2 Phylogeographic patterns and haplotype diversity

There are many different types of mitochondrial DNA in geese, and their distribution is also rather complex. Research on the lesser snow geese has found that their mitochondrial DNA can be divided into two major categories, with a difference of approximately 6.7% between them. This difference might have been caused by geographical separation during the Pleistocene. Among these two categories, some are closely related to geographical locations, while others do not have obvious geographical distribution characteristics, indicating that they might have been separated before and later had some gene exchanges. Ely et al. (2017) found that the mitochondrial differences among different populations of the white-fronted goose were quite obvious, which might be related to their loyalty to the breeding ground, population structure and the way resources were used. In China, the mitochondrial DNA of some local goose breeds is also very diverse. The diversity index (Hd) of some breeds exceeds 0.9, and gene exchange often occurs among different goose flocks. Qi et al. (2024) identified a total of 81 different haplotypes in their study, which were classified into six major groups.

3.3 Mitochondrial introgression across goose populations

The evolutionary process of geese may have been influenced by the infiltration of mitochondrial genes, hybridization between different species, and the fact that their lineages have not yet been completely separated. The different species of the genus Goose do not match the evolutionary tree of mitochondria in terms of appearance, suggesting that several situations might be at play. Ancestors originally had multiple genetic types, hybridization occurred among different species, or they evolved similar appearances. Genetic exchange among some goose breeds in China is also relatively frequent, which further indicates the existence of genetic infiltration. Qi et al. (2024) hold that this situation might make the geographical distribution among different species unclear and also make it more difficult to reconstruct their evolutionary relationships.

4 Nuclear Genome Evolution and Diversity

4.1 Advances in nuclear genomic sequencing in geese

By using advanced technologies such as PacBio, Bionano and Hi-C, researchers have completed the high-quality genome assembly of multiple goose breeds, such as the pink-footed goose and the lion-head goose. All these assemblies have reached the chromosomal level. And more than 20 000 protein-coding genes were identified (Jing et al., 2022; Zhao et al., 2022; Colom and O'Brien, 2024). These data have laid a very good foundation for subsequent genomic comparisons, adaptability studies, and the analysis of breed characteristics (Gao et al., 2016; Jing et al., 2022; Zhao et al., 2022). Jing et al. (2022) and Zhao et al. (2022) also conducted large-scale gene resequencing on nearly 1 000 geese, supporting the claim that "domestic geese have two ancestral sources", and also identified many genetic markers related to important economic traits.

4.2 Genetic signals of domestication and breed differentiation

Zhao et al. (2022) and Zhang et al. (2023) identified several candidate genes related to growth, reproduction, and morphological characteristics, such as TGFBR3L, CMYA5, FOXD1, ARHGEF28, SUCLG2, LDLRAD4, and GPR180. The allele frequencies of some genes increased rapidly under the influence of artificial selection. For instance, when people specifically selected geese with white feathers, some common gene types in domestic geese were formed (Figure 1) (Jing et al., 2022). Jing et al. (2022) and Zhang et al. (2023) found that compared with European geese, local goose breeds in China have higher genetic diversity. Gene exchange often occurs among different breeds, and gene infiltration makes the differences between breeds more obvious.

4.3 Gene flow and incomplete lineage sorting

Genome-wide analyses have found that in the genera Anser and Branta, there were early and modern hybridization events, which made their evolutionary relationship as complex as a web, and mixed structures also emerged in the genome (Ottenburghs et al., 2017). Wilson et al. (2022) and Zhang et al. (2023) found that there was also a considerable amount of gene infiltration among domestic geese, and some small genetic aggregations occurred within certain populations, indicating that both the natural environment and human selection have jointly influenced the current genetic structure of geese. Incomplete phylogenetic differentiation is the result of many geese rapidly forming new species, which makes their evolutionary relationships more difficult to understand. Ottenburghs et al. (2017) proposed that to solve these problems, more advanced statistical methods and network models need to be used to distinguish which are caused by hybridization and which are due to a common ancestor.

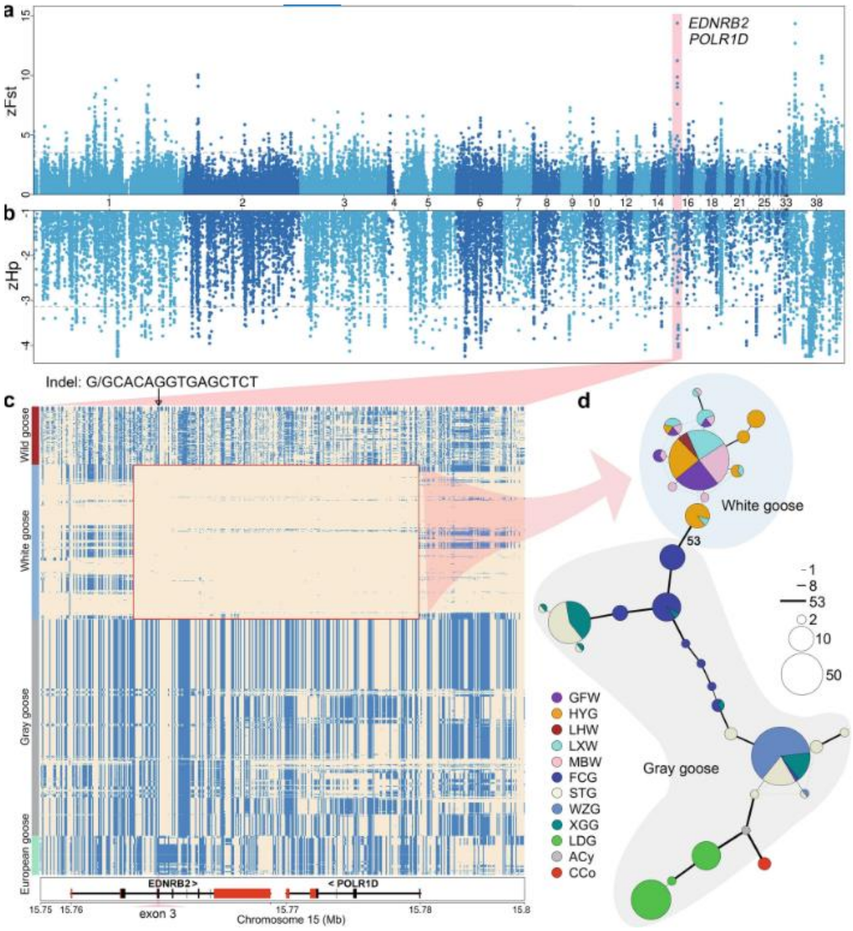

Figure 1 Selective signals for the white plumage phenotype of geese (Adopted from Jing et al., 2022)

Image caption: a: Manhattan plot of zFst between white and gray geese; b: Manhattan plot of zHp in white geese, with the positions matching zFst; the gray dashed line represents the top 1% cutoff; c: the plot of the haplotype structure of variants around the *EDNRB2* and *POLR1D* genes in all domestic geese and wild populations (the genera *Anser* and *Cygnus* in the *Anatidae* family); major and minor alleles in GFW are indicated by beige and light blue, respectively; the red box represents the unique haplotypes of white geese; the black arrow indicates the position (15 764 637 bp) of the candidate causal 14-bp insertion for the white geese; the red and black rectangles in the bottom box represent the UTRs and CDSs, respectively. d Haplotype network based on 285 SNPs and Indels from the *EDNRB2* gene (15 763 328 bp) to *POLR1D* gene (15 779 122 bp) on chromosome 15; each circle represents a haplotype, and the size of the circle is proportional to the haplotype frequency. The line width and length represent the difference between haplotypes; GFW: Guangfeng white goose, HYG: Huoyan goose, LHW: Lianhua white goose, LXW: Lingxian white goose, MBW: Mingbei white goose, FCG: Fengcheng gray goose, STG: Shitou goose, WZG: Wuzong goose, XGG: Xingguo gray goose, LDG: Landaise goose, ACy: *Anser cygnoides*, CCo: *Cygnus columbianus* (Adopted from Jing et al., 2022)

5 Mitonuclear Discordance in Phylogenetic Reconstruction

5.1 Mechanisms of phylogenetic incongruence

The research conducted by Li and Lu (2024) demonstrated that when using mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) to draw evolutionary trees, the two results sometimes differ. This situation is known as “mitonuclear discordance”. There are several reasons for this inconsistency. One is “Genealogical Inconsistencies” (ILS). Some gene types left by ancestors are still retained in different populations, which makes the drawn gene trees look inconsistent. Firneno et al. (2020) and DeRaad et al. (2023) hold that this situation is more common in groups where species evolve rapidly, as the time when mitochondria and nuclear DNA return to a common ancestor may be different. Another situation is “gene infiltration”, that is, when different species hybridization occurs and gene fragments are transferred there, “mitochondrial capture” - it is possible when the mitochondrial DNA of one species is completely replaced by another, but their nuclear DNA is still different (Layton et al., 2020; Mao and Rossiter, 2020; Berbel-Filho et al., 2022). Quattrini et al. (2023) and Zhang et al. (2024) demonstrated that different selection pressures can also affect the evolutionary speed of mitochondria. Sometimes, due to relatively low evolutionary pressure or the need to adapt to the environment, mitochondria may become much faster than nuclear DNA, thus embarking on a different “evolutionary path”.

5.2 Case examples in Chinese goose populations

Although there is still a lack of direct research on the inconsistency between the mitochondrial and nuclear genomes of Chinese goose species at present, studies on other animals can provide us with some references. Berbel-Filho et al. (2022) discovered a large number of gene infiltration events in Kryptolebias of the genus killifish, causing the types of mitochondria and the lineage of nuclear genes to not match, revealing the hidden genetic diversity and complex evolutionary process behind them. It has also been found in the studies of rotifers and toads that situations such as hybridization and lineage inconsistencies (ILS) can all lead to this genetic inconsistency. In these cases, the study found that the markers of nuclear DNA could reflect the appearance and ecological differences of animals more accurately than those of mitochondria (Papakostas et al., 2016; Firneno et al., 2020). From this, it can be inferred that in China's goose breeds, similar situations may have occurred in the past, such as historical hybridization, rapid formation of goose breeds, or incomplete lineage differentiation, etc. These processes may lead to conflicts in the evolutionary tree, making the true genealogical relationships and the origin of species less clear.

5.3 Implications for species and breed classification

The research conducted by Papakostas et al. (2016) and by Campbell et al. (2020) found that mtDNA sometimes fails to accurately reflect the true boundaries between species, which may lead to classification errors or overlook some hidden genetic diversity. It is unlikely to solve these problems solely by mitochondrial data. Data on nuclear genomic information, morphological characteristics, and ecological environment, among others, need to be used together. Only by adopting a more comprehensive phylogenetic approach can genealogical conflicts be better handled and which species are independent be clearly determined (Papakostas et al., 2016; Campbell et al., 2020; Layton et al., 2020). This comprehensive approach is particularly important for geese. It is helpful for clarifying how each variety came about, gaining a deeper understanding of their evolutionary mechanisms, and formulating reasonable conservation and breeding plans.

6 Phylogenetic Methods and Multi-Locus Integration

6.1 Species tree estimation tools

Models like MP-EST and ASTRAL, which are based on the “common ancestor theory”, can specifically handle the differences between different gene trees. In the same year, Meiklejohn et al. (2016), Mirarab et al. (2016), and Ottenburghs et al. (2016) found that if a sufficiently accurate gene tree could be obtained, these methods were usually more reliable than the traditional “concatenation” method. Mirarab et al. (2016) and Kimball et al. (2019) demonstrated that there are some other methods, such as Supertree and summary methods (like MRP and MRL), which can combine many small gene trees together, improving efficiency and being suitable for analyzing large-scale genomic data. Phylogenetic analysis strategies based on super-conserved elements (UCEs) and exons have also been successfully applied to complex groups like geese, solving the problem that their evolutionary relationships are difficult to clarify (Meiklejohn et al., 2016; Ottenburghs et al., 2016).

6.2 Comparative evaluation of mitochondrial and nuclear trees

The effective population size of mitochondrial DNA is relatively small and often shows relatively obvious signals in the differentiation between species. When it is analyzed together with nuclear DNA, it can enhance the resolution ability of the evolutionary tree (Corl and Ellegren, 2013). However, if only mitochondrial DNA is relied on, the complex evolutionary history may not be clear, especially when the lineages are not completely separated (ILS) or there are hybridization cases, its information may not be sufficient (Corl and Ellegren, 2013; Ottenburghs et al., 2016). In contrast, nuclear DNA, especially genes on sex chromosomes and autosomes, can provide stronger resolution and greater stability when the sample size is sufficient (Corl and Ellegren, 2013). Although the method of combining multiple genes together can receive a high approval rate, it may also mask the inconsistencies among different genes and even increase systematic errors. Adopting the common ancestor model or consensus method can better handle the differences among these gene trees and provide more reliable results in the case of complex evolutionary processes (Mirarab et al., 2016; Farah et al., 2021).

6.3 Toward a consensus phylogeny for domestic geese

Ottenburghs et al. 's research on True Geese (Anserini) in 2016 found that combining whole-genome data and using the "connection method" and the "common ancestor model" to build a consensus tree can well solve some controversial evolutionary relationships and also more clearly determine the time point of species differentiation. The evolutionary trees drawn by these two methods are very consistent, both supporting the division of True Geese into two main lineages, Anser and Branta, and each genus has more detailed branch structures. The consensus tree also indicates that there are many rapid new species formation processes and hybridization events within the genus Anser, all of which have a significant impact on their evolutionary relationships. The research of Ottenburghs et al. (2016) further indicates that it is very important to integrate multiple gene loci when constructing a phylogenetic tree. Corl and Ellegren (2013), as well as Ottenburghs et al. (2016), discovered that if data from mitochondria and nuclear DNA could be combined and advanced establishment methods were adopted, the complex evolutionary history between domestic geese and their close relatives could be understood more effectively.

7 Functional Evolution in Mitochondrial Genes

7.1 Selection in oxidative phosphorylation genes

In mitochondria, the genes responsible for the oxidative phosphorylation (OXPHOS) process are important for cellular energy production and are usually highly functionally limited. However, these genes also show signs of adaptive evolution, especially to meet the metabolic needs of different species. Some amino acid changes in cytochrome b and other Oxphos-related genes may be related to specific metabolic or environmental stresses, such as low-energy diets, large-sized animals, or situations that require special oxygen regulation, such as diving, flying, and high altitudes. These changes are often concentrated in some regions that are particularly important for function, such as the cyclic structural region of NADH dehydrogenase, or the locations where mitochondria and nuclear coding subunits interact in cytochrome c oxidase, indicating that these genes may not only undergo structural changes but also functionally adapt to different selection pressures. The two subunits ATP8 and ATP6 show high adaptive changes, indicating that they play an important role in the assembly and function of the OXPHOS complex (Da Fonseca et al., 2008).

7.2 Mitonuclear co-evolution and compensation hypotheses

Mitochondrial genes and nuclear genes need to cooperate together in the OXPHOS complex of mitochondria to ensure the efficient progress of cellular respiration, so they must "co-evolve". The OXPHOS proteins encoded by mitochondria and the nucleus are highly correlated in the rate of evolution, which supports the claim of "mitochondrial-nuclear gene co-evolution". Changes in one genome are usually adjusted accordingly by the other genome to maintain normal functions (Sunnucks et al., 2017; Piccinini et al., 2021; Weaver et al., 2022). Regarding the hypothesis of "nuclear compensation" - that is, nuclear genes can remedy harmful mutations in mitochondria - there is currently not much direct evidence. Piccinini et al. (2021) and Weaver et al. (2022) demonstrated that some studies did indeed find an increase in the dN/dS ratio of the nuclear OXPHOS gene, but no obvious signals of compensatory positive selection were generally observed at specific locations, and the time distribution of amino acid substitution did not consistently indicate that nuclear compensation played a key role. Researchers believe that "reciprocal coevolution" or "division of labor and variation after gene replication" may better explain these evolutionary patterns (Havird and McConie, 2019; Piccinini et al., 2021). Sunnucks et al. (2017) and Morales et al. (2018) argued that some structural characteristics of the genome, such as the tight aggregation of mitochondrial functional-related genes in certain regions, might also promote this mutually adaptive evolution.

7.3 Adaptive signatures in wild vs. domesticated populations

Sunnucks et al. (2017) found in the process of studying the adaptation of bar-headed geese to the high-altitude environment that both mitochondrial genes and nuclear OXPHOS genes showed obvious selection signals when facing environmental stress. Population differentiation and local adaptation in birds change along with the mitochondrial genome and the nuclear gene clusters that control mitochondrial function. Morales et al. (2018) found that in populations living under different climatic conditions, the phenomenon of "selective sweeping" often occurs, and there are also cases where mitochondria and nuclear genes are introduced together, indicating that they work in concert during the evolutionary process. The co-evolution between mitochondrial and nuclear genes is a key mechanism that drives wild animals and domestic species to adapt to the environment and differentiate into different lineages, which is of great significance for the evolutionary study of geese and other species.

8 Case Study: Phylogenetic Analysis of Swan Goose-Derived Chinese Breeds

8.1 Background and sampling design

Most of the native rare species of Chinese geese originated from Swan goose (*Anser cygnoides*). Because they have a unique genetic background and their numbers are decreasing, they have high conservation value. To study their evolution, blood samples were collected from six representative goose breeds, namely Lingxiang White (LX), Yan (YE), Yangjiang (YJ), Wuzong (WZ), Xupu (XP), and Baizi (BZ), in this case study. Gender balance was also maintained during sampling (♂:♀ = 1:1). This case study analyzed the mitochondrial cytochrome b (CYTB) gene sequences of these geese and evaluated their genetic diversity, population structure, and historical population changes (Figure 2) (Qi et al., 2024).

Figure 2 The six geographic collection points for the endemic endangered geese (Adopted from Qi et al., 2024)

Image caption: Images of different goose breeds were captured using a digital camera (Osaka, Japan); LX, Lingxiang White; YE, Yan; YJ, Yangjiang; WZ, Wuzong; XP, Xupu; BZ, Baizi; the irregular black shapes (rectangle, triangle, etc.) in the figure represent the collection locations of the experimental animals, the rectangle in the bottom right corner is a part of Chinese territory (Adopted from Qi et al., 2024)

8.2 Results from mitochondrial and nuclear data comparison

Through the analysis of the mitochondrial *CYTB* gene, researchers discovered a total of 117 loci with variations in these six goose breeds and identified 81 different haplotypes, indicating that they have a high degree of genetic diversity. The haplotype diversity of YJ, YE and WZ is particularly prominent (Hd > 0.9), and there is frequent gene exchange among LX, YJ, YE and WZ (Nm > 15.00), indicating that the genetic relationship among these varieties is relatively close. These six varieties can be divided into six major mitochondrial lineages based on mitochondrial data, reflecting that they have diverse genetic sources. The results of the neutral test (Tajima's D and Fu's Fs) and the mismatch distribution showed that the populations of WZ and YJ were relatively stable, and no signs of recent rapid expansion or bottleneck events were found (Qi et al., 2024). The research conducted by Ely et al. (2017) demonstrated that mitochondria are maternally inherited with less gene flow, and usually can more clearly display the population structure. Nuclear DNA markers, due to a greater number of gene flows, exhibit lower genetic differentiation.

8.3 Implications for breeding and conservation

Some goose breeds exhibit high mitochondrial diversity and frequent gene exchange, indicating that maintaining genetic ties among breeds is very important for enhancing their adaptability. Qi et al. (2024) found that compared with European goose breeds, the Wright Fixed Index (Fst) of native Chinese geese is relatively lower, which may indicate that their adaptability is weaker and they are more vulnerable to environmental changes or reduced genetic diversity. It is extremely urgent to protect the genetic diversity of goose breeds. Scientific conservation strategies need to be formulated, not only to preserve their genetic resources but also to design targeted breeding plans to enhance their survival ability and adaptability to the environment. Conservation efforts should also make full use of genetic differences within and between populations to better support the long-term development and sustainable utilization of precious goose breeds (Qi et al., 2024).

9 Challenges and Future Directions

9.1 Sampling gaps and geographic biases

The true relationships among some species have not been fully clarified due to insufficient and broad sampling. To determine the important time points in the evolutionary process, more types of data are needed, especially the mitochondrial whole-genome data of birds (including geese). The geographical distribution of sampling is not balanced enough. The goose populations in some areas are insufficiently representative. This geographical deviation may mask their true genetic diversity and even miss the signals of gene infiltration (Jing et al., 2022).

9.2 Misleading signals from single-locus studies

If the research relies only on one genetic locus, especially only on mitochondrial DNA, it is very likely to be disturbed by factors such as incomplete lineage differentiation, hybridization between species, or gene infiltration. The research conducted by Ottenburghs et al. (2017), DeRaad et al. (2023) and Quattrini et al. (2023) indicates that these circumstances may lead to misleading results for phylogenetic analysis. The kinship among different species of the genus Anser inferred solely from mitochondrial DNA may not reflect their true evolutionary history. This is because during the rapid differentiation of species, coupled with the fact that ancestors already had multiple genetic types, the results can easily become difficult to explain. The situation of "inconsistency between mitochondrial DNA and nuclear DNA evolutionary trees" is very common. This “line-nuclear divergence” is usually caused by the simultaneous occurrence of incomplete lineage separation and gene exchange (DeRaad et al., 2023; Quattrini et al., 2023).

9.3 Data integration and computational demands

In order to reconstruct the evolutionary relationships of species more accurately, it is necessary to use the nuclear DNA and mitochondrial data of the entire genome simultaneously, but this approach also brings many computational and analytical difficulties. Compared with mitochondrial genes, nuclear DNA has a lower substitution saturation rate and stronger phylogenetic signals, and usually performs better when studying the deep-level differentiation among species. But the problem is that analyzing such large datasets containing a large number of gene loci requires more complex statistical methods and a lot of computing resources. These challenges are more obvious when hybridization, gene infiltration, and differences between different gene trees need to be considered (Ottenburghs et al., 2017; DeRaad et al., 2023; Quattrini et al., 2023).

9.4 Future directions in goose phylogenetics

Ottenburghs et al. (2017) and Jing et al. (2022) hold that future research should focus on conducting more comprehensive sampling throughout the entire distribution range of geese, combining data from both nuclear and mitochondrial genomes, in order to better understand their evolutionary history. Nowadays, there are some new statistical tools, such as hybrid network analysis and D-statistic, which are helpful for distinguishing the effects of hybridization and incomplete lineage separation (Ottenburghs et al., 2017; DeRaad et al., 2023), this is very useful for interpreting the complex signals in genetic data. Jing et al. (2022) indicated that with the development of chromosome-level genome assembly technology and the advancement of population genomics research, it will help to gain a deeper understanding of the genetic diversity, adaptive evolution, and the influence mechanism of artificial selection of domestic geese and wild geese.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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