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Heritability of Important Phenotypic Traits in Bird Populations

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Abstract Phenotypic traits in bird populations are influenced by both genetic and environmental factors, and understanding their heritability is crucial for evolutionary studies. This study explores the heritability of important phenotypic traits in bird populations, covering morphological, behavioral, and physiological traits, discusses factors that influence heritability, such as environmental effects and gene-environment interactions, and presents a case study on the heritability of plumage coloration in zebra finches, providing insights into the genetic and environmental contributions to this trait and comparing findings with other avian species. This study emphasizes the importance of heritability in natural selection, its impact on population dynamics, and implications for conservation strategies. Future research should focus on exploring the genetic basis of a broader range of traits and the interplay between genetics and environmental influences in various bird species.

Keywords Phenotypic traits; Heritability; Bird populations; Zebra finch; Evolutionary biology

1 Introduction

Phenotypic traits in birds encompass a wide range of characteristics, including morphological, behavioral, and physiological attributes. These traits are crucial for survival and reproduction, influencing factors such as foraging efficiency, predator avoidance, and mating success. For instance, morphological traits like bill size and shape, wing length, and body mass are often subject to natural selection and can vary significantly among populations (Silva et al., 2017; Subasinghe et al., 2021). Behavioral traits, such as migratory patterns and exploratory behavior, also play a vital role in the adaptability and fitness of bird species (Winney et al., 2018; Dochtermann et al., 2019; Lin et al., 2024).

Understanding the heritability of phenotypic traits is essential for predicting how bird populations will respond to environmental changes and selection pressures. Heritability estimates indicate the proportion of phenotypic variation attributable to genetic factors, providing insights into the potential for evolutionary change (Cava et al., 2019; Walsh, 2022). For example, high heritability in traits like bill morphology suggests a strong genetic basis, which can facilitate rapid adaptation to changing environments (Lundregan et al., 2018). Conversely, traits with low heritability may be more influenced by environmental factors, highlighting the need for conservation strategies that consider habitat management (Cohen and Dor, 2018).

This study synthesizes current knowledge on the heritability of important phenotypic traits in bird populations, highlights the genetic architecture underlying these traits and discuss the implications for evolutionary dynamics and conservation, and provides a comprehensive understanding of how genetic and environmental factors interact to shape phenotypic diversity in birds, with the aim of identifying gaps in the current literature and suggest directions for future research to enhance our understanding of heritability and its role in avian evolution.

2 Fundamentals of Heritability

2.1 Definition of heritability

Heritability is a measure that quantifies the proportion of phenotypic variation in a population that can be attributed to genetic variation among individuals. It is a dimensionless measure that allows for the comparison of the importance of genetic factors in explaining individual differences within a population. Heritability does not provide information about the genetic architecture of traits but is crucial for predicting how populations will respond to selection pressures (Yadesa, 2022).

2.2 Types of heritability (narrow vs. broad)

Heritability can be categorized into narrow-sense heritability (h^2) and broad-sense heritability (H^2). Narrow-sense heritability refers to the proportion of phenotypic variance that is attributable to additive genetic variance alone. This type of heritability is particularly important in predicting the response to selection because it considers only the additive effects of genes, which are directly passed from parents to offspring (Ge et al., 2016; Yang et al., 2017). Broad-sense heritability, on the other hand, includes all genetic variance components, such as additive, dominance, and epistatic variances. It provides a more comprehensive measure of the genetic contribution to phenotypic variance but is less useful for predicting selection response because it includes non-additive genetic effects (Gamma and Liebrenz, 2019).

2.3 Methods for measuring heritability

Several methods are used to estimate heritability, each with its own advantages and limitations. Traditional methods often involve studying closely related individuals, such as twins or family members, to partition phenotypic variance into genetic and environmental components. Twin studies, for example, compare the similarity of traits between monozygotic and dizygotic twins to estimate heritability (Sanfilippo et al., 2010). More recently, advances in genomic technologies have enabled the estimation of heritability using genome-wide association studies (GWAS). These studies use single nucleotide polymorphisms (SNPs) to estimate the proportion of phenotypic variance explained by genetic variants across the genome, known as SNP heritability (Speed et al., 2016). Additionally, statistical models such as linear mixed models and structural equation modeling (SEM) are employed to derive heritability estimates from complex datasets, including high-throughput sequencing data (Rudra et al., 2017). Each method has its own set of assumptions and potential sources of bias, making it essential to carefully consider the context and population characteristics when interpreting heritability estimates (Dochtermann et al., 2019).

3 Phenotypic Traits in Bird Populations

3.1 Morphological Traits

The size and shape of birds are critical morphological traits that can vary significantly across different species and populations. For instance, a study on ducks revealed that body size is influenced by genetic factors, with specific mutations in the *IGF2BP1* gene leading to increased body size and feed efficiency in Pekin ducks (Zhou et al., 2018). Similarly, research on helmeted Guinea fowls in Nigeria showed significant variations in biometric traits such as wing length and body length across different agro-ecological zones, indicating the influence of environmental factors on these morphological traits (Yakubu et al., 2022).

Plumage coloration is a highly variable and heritable trait in bird populations, often influenced by genetic and environmental factors. For example, the plumage color of the common barn owl varies with climatic conditions, becoming darker in regions with higher rainfall, which may aid in camouflage and water repellence (Romano et al., 2019). Additionally, the genetic basis of plumage coloration has been extensively studied, with specific genes such as *MITF* and *TYRP1* being associated with color traits in various bird species (Figure 1) (Funk et al., 2022). The interplay between genetic and environmental factors in determining plumage coloration highlights its role in adaptation and speciation.

The study of Funk et al. (2022) highlights genetic variation in rosy-finches that influences both their plumage coloration and adaptation to different elevations. The plumage coloration involves genes such as *MITF*, *EDN3*, *AP3B1*, *TYRP1*, and ASIP, resulting in differences in cheek and crown patch colors. Meanwhile, genes like *EGLN1* and *ALDH1A1* are crucial for adaptation to high elevations, supporting survival in hypoxic conditions. Unique variations in *AGGF1* and *JMY* are observed in specific high-altitude populations, indicating specialized adaptations beyond shared traits among the finches living in extreme elevations. These genetic variations are key for both aesthetic and environmental adaptations.

3.2 Behavioral Traits

Song characteristics are important behavioral traits that can influence mating success and species differentiation. In a study on the limestone wren-babbler, significant bioacoustic differences were found between populations with limited plumage differentiation, suggesting that vocalizations play a crucial role in species recognition and differentiation (Gwee et al., 2020). The genetic basis of song characteristics has also been explored, with certain genomic regions being associated with migratory orientation and song traits in Swainson's thrushes, indicating a potential link between these behavioral traits and speciation (Delmore et al., 2016).

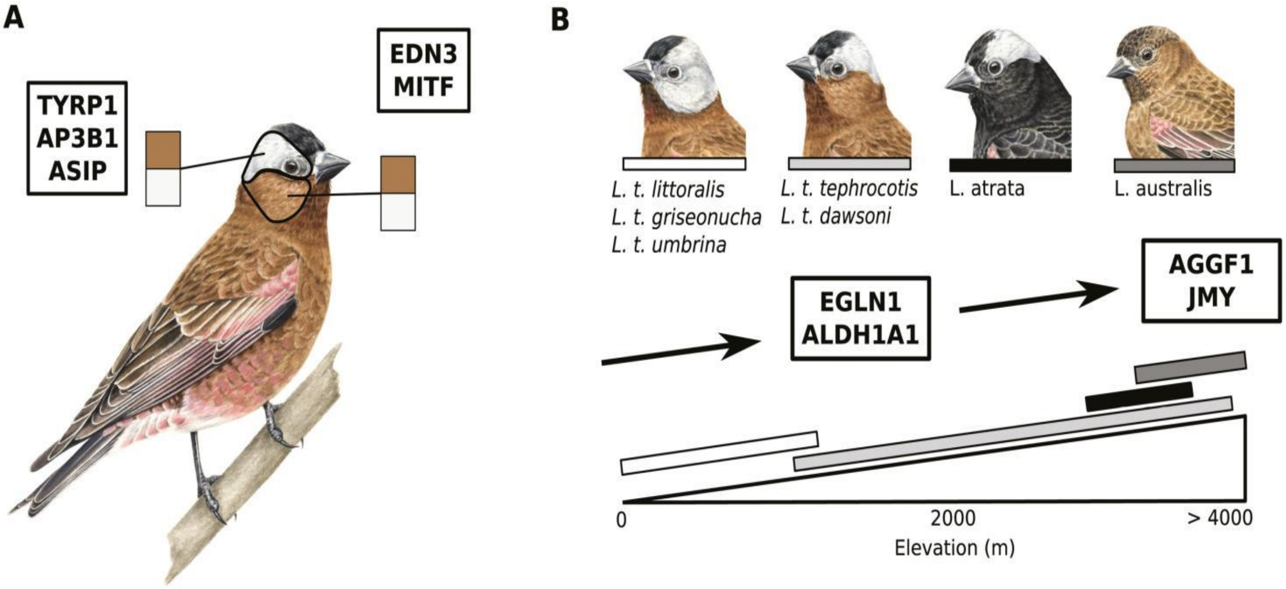

Figure 1 Genes underlying plumage coloration and elevational adaptation. (A) Five primary candidate plumage genes and their function in rosy-finch phenotype. Variation in *Mitf* and *Edn3* result in cheek patch differences, while variation in *Ap3b1*, *Tyrp1*, and *Asip* result in crown patch differences. (B) Four candidate elevation genes showing shared variation at *Egln1* and *Aldh1a1* among high-elevation birds, and unique variation in *Aggf1* and *Jmy* in brown-capped rosy-finches (Adopted from Funk et al., 2022)

Nesting behavior is another critical behavioral trait that can impact reproductive success and survival. Although specific studies on the heritability of nesting behavior in birds were not provided in the data, it is well-known that nesting site selection, nest construction, and parental care behaviors are influenced by both genetic and environmental factors. These behaviors can vary widely among species and populations, contributing to their ecological adaptation and evolutionary success.

3.3 Physiological Traits

Metabolic rate is a key physiological trait that affects energy expenditure and overall fitness in birds. While the provided data did not include specific studies on the heritability of metabolic rate, it is understood that metabolic rate can be influenced by genetic factors, environmental conditions, and individual health. For example, the adaptation to high elevations in North American rosy-finches involves genetic regions associated with hypoxia-related genes, which likely impact their metabolic rate and ability to thrive in low-oxygen environments.

The stress response is a physiological trait that can influence an individual's ability to cope with environmental challenges. Although the data did not provide specific studies on the heritability of stress response in birds, it is known that stress response can be affected by genetic predisposition, early-life experiences, and current environmental conditions. Understanding the genetic and environmental factors that influence stress response can provide insights into how bird populations adapt to changing environments and cope with stressors.

4 Factors Influencing Heritability

4.1 Environmental influences

Environmental factors play a significant role in shaping the heritability of phenotypic traits in bird populations. For instance, in a study on Great Lakes piping plovers, it was found that environmental factors such as breeding site had a major influence on traits like natal dispersal distance and female breeding time, which were not significantly heritable (Saunders and Cuthbert, 2014). Similarly, in house sparrows, early-life telomere length was primarily driven by environmental variance, including annual and brood effects, rather than genetic factors (Pepke et al., 2021). These findings underscore the importance of environmental conditions in determining phenotypic variation and heritability in wild bird populations.

4.2 Genetic architecture

The genetic architecture of traits, including the number and effect size of contributing loci, significantly impacts heritability. For example, a study on the genomic architecture of clutch size and egg mass in great tits revealed that these traits are influenced by many loci of small effect distributed across the genome, with no single locus having a large impact (Santure et al., 2013). This polygenic nature of traits suggests that heritability is spread across numerous genetic factors, making it complex to predict evolutionary responses. Additionally, the heritability of early-life telomere length in house sparrows was found to be low, indicating a polygenic trait strongly affected by environmental conditions.

4.3 Interaction between genes and environment

The interaction between genetic and environmental factors, known as genotype-environment interactions (GxE), can significantly influence heritability. In tree swallows, the relationship between candidate genes and phenological traits such as laying date and incubation duration was found to be affected by environmental variables like breeding density and temperature (Bourret and Garant, 2015). This highlights the complexity of predicting trait evolution, as GxE interactions can modulate the expression of genetic potential under varying environmental conditions. Furthermore, a study on roe deer demonstrated that accounting for environmental similarity among relatives could reduce heritability estimates for certain traits, indicating that genetic variation for habitat selection plays a role in environmental similarity (Gervais et al., 2022).

4.4 Population-specific factors

Heritability estimates can vary significantly across different populations due to population-specific factors. For instance, a study on Savannah sparrows breeding in agricultural grasslands found varying heritability estimates for morphological traits, influenced by the specific environmental and genetic context of the population (Cava et al., 2019). Additionally, a meta-analysis of heritability in behavior across different taxa revealed considerable variation among behaviors, with migratory behaviors being the most heritable (Dochtermann et al., 2019). These findings suggest that heritability is not a fixed parameter but can vary depending on the population's genetic makeup and environmental context.

5 Case Study: Heritability of Plumage Coloration in the Zebra Finch

5.1 Background on zebra finches

The zebra finch (*Taeniopygia guttata*) is a small, socially monogamous bird native to Australia. It is widely used as a model organism in various fields of biological research due to its pronounced sexual dimorphism in plumage coloration and vocal behavior (Figure 2). Zebra finches are opportunistic breeders, and their adaptability to different environmental conditions makes them an excellent subject for studying genetic and environmental influences on phenotypic traits (Hauber et al., 2021).

The study of Hauber et al. (2021) show a clear similarity between the tutor and tutee zebra finch songs, suggesting effective vocal learning, which is a crucial element of zebra finch social behavior. Additionally, there is a marked difference between the male and female call spectrograms, highlighting sexual dimorphism in vocalization patterns. This supports the idea that vocal learning and sexual differences in calls are both key features of zebra finches, making them valuable model organisms for studying vocal communication and social learning.

5.2 Research approach

To investigate the heritability of plumage coloration in zebra finches, researchers have employed various experimental designs. One common approach involves controlled breeding experiments to isolate genetic factors from environmental influences. For instance, a study used a three-generation breeding design to homogenize the genetic background while comparing wild-type and white plumage morphs, which differ significantly in melanization (Krause et al., 2017). Another study sequenced the melanocortin-1 receptor (MC1R) gene in different plumage morphs and controlled for population structure to avoid artefactual associations.

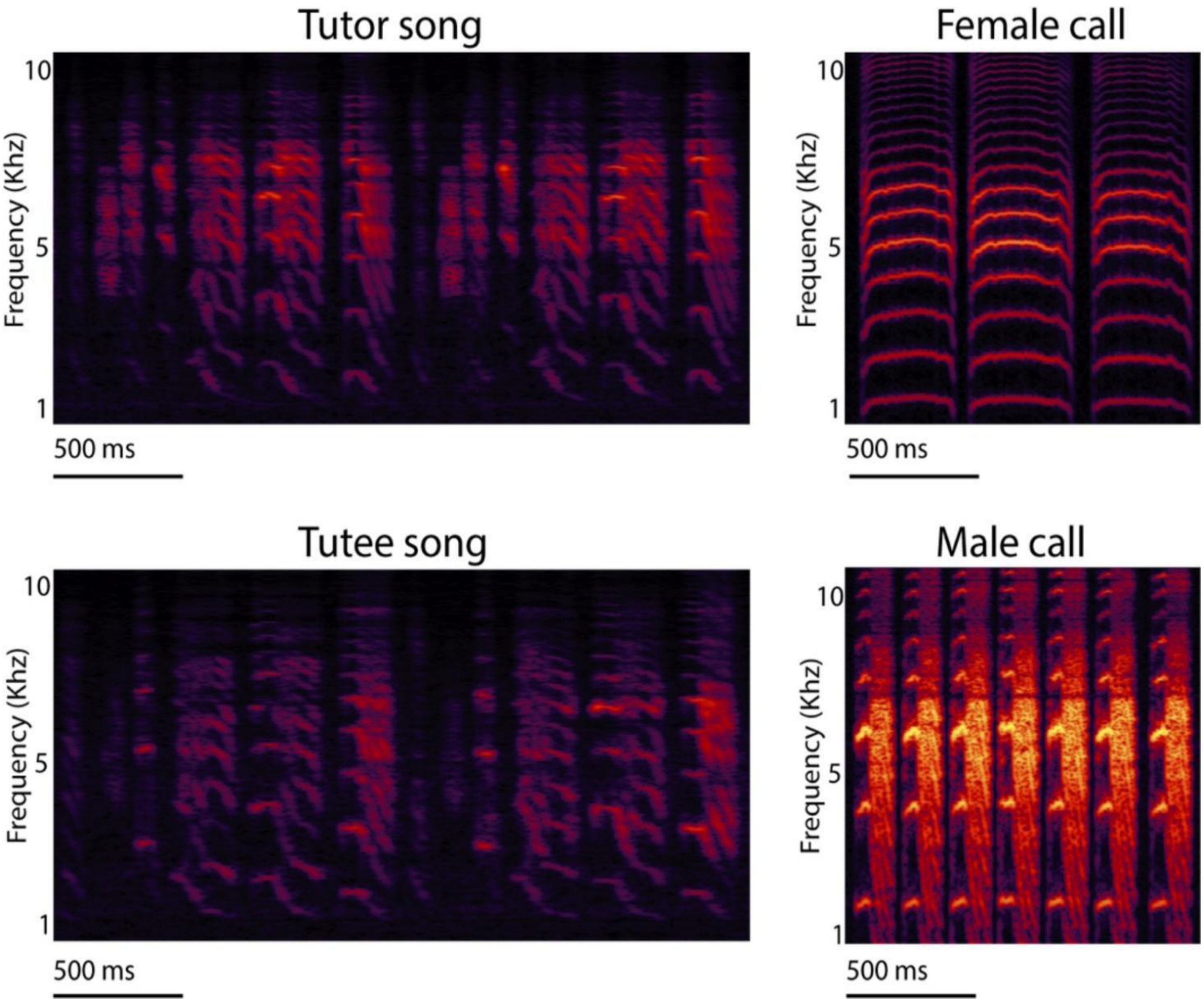

Figure 2 Spectrograms of zebra finch songs and calls (Adopted from Hauber et al., 2021)

Image caption: Spectrogram of tutor and tutee adult male zebra finch songs, and undirected contact calls of adult females and males. Spectrograms represent time (x-axes) and pitch (y-axes) with greater amplitude as increasing brightness. Note the similarity of the tutor (typically social father) and tutee (son) song pair of male zebra finches and the distinct sexual differences of the calls (Adopted from Hauber et al., 2021)

5.3 Findings and implications

Research has shown that plumage coloration in zebra finches is influenced by both genetic and environmental factors. The study using a controlled breeding design found that white plumage morphs had poorer body condition but compensated by reproducing earlier and producing heavier eggs relative to their body mass. This suggests that plumage coloration can be linked to fitness-related traits, although further studies are needed to evaluate these effects under natural conditions.

Another study on the MC1R gene found no significant association between MC1R polymorphism and plumage coloration after controlling for population structure, indicating that genome-wide divergence might explain the initial findings (Hoffman et al., 2014). This highlights the importance of considering population structure in genetic association studies.

5.4 Comparison with other species

Comparative studies in other bird species have also explored the genetic basis of plumage coloration. For example, similar to zebra finches, leaf warblers showed no association between MC1R polymorphism and plumage coloration, suggesting that other genetic factors or environmental influences might play a more significant role.

Additionally, studies on inbreeding depression in zebra finches revealed that sexually selected traits like beak color and song rate are more affected by inbreeding than morphological traits, indicating a complex interplay between genetic quality and phenotypic expression (Bolund et al., 2010).

6 Implications for Evolutionary Biology

6.1 Role of heritability in natural selection

Heritability plays a crucial role in natural selection by determining the extent to which phenotypic traits can respond to selective pressures. The quantification of heritable genetic variance in fitness underscores the potential for adaptation within populations (Walsh, 2022). This heritable variation is the "fuel" for evolution, enabling populations to adapt to changing environments (Mai et al., 2024). For instance, the study on Savannah sparrows revealed varying heritabilities for morphological traits, indicating that some traits are more likely to respond to selection pressures than others. Similarly, the heritability of behavioral traits, as shown in a meta-analysis, suggests that genetic variation significantly influences phenotypic variation, which is essential for evolutionary responses to selection (Dochtermann et al., 2019).

6.2 Impact on population dynamics

Heritability also impacts population dynamics by influencing the evolutionary potential of populations. For example, the study on storm petrels demonstrated that heritability in life-history traits like laying date can vary significantly even within small spatial scales, affecting local adaptation and population dynamics (Kim et al., 2012). Additionally, genomic selection studies in wild bird populations, such as the one on great tits, highlight the potential for heritable traits to influence population dynamics through improved breeding strategies (Gienapp et al., 2019). The ability of populations to adapt to environmental changes, as seen in the study on phenotypic plasticity in blue tits, further illustrates how heritable traits can drive population-level responses to climate change (Biquet et al., 2021).

6.3 Conservation considerations

Understanding the heritability of phenotypic traits is vital for conservation efforts, as it informs strategies to maintain or enhance the adaptive potential of populations. The concept of evolutionary rescue, where partly heritable phenotypic variability can help populations avoid extinction, is particularly relevant in conservation biology (Carja and Plotkin, 2016). This approach suggests that maintaining genetic diversity and heritable variation within populations can increase their resilience to environmental changes. Moreover, the study on the heritability and evolvability of morphological traits in Savannah sparrows highlights the importance of considering heritable traits in managed habitats, such as agricultural landscapes, to mitigate human impacts on wildlife (Cava et al., 2019). Conservation strategies should, therefore, focus on preserving genetic diversity and heritable traits to ensure the long-term survival and adaptability of bird populations.

7 Concluding Remarks

The heritability of phenotypic traits in bird populations has been extensively studied across various species and traits. Research indicates that many life history and morphological traits are influenced by numerous loci of small effect rather than a few loci of large effect. For instance, studies on the great tit (*Parus major*) and house sparrows (*Passerculus sandwichensis*) have shown that the genetic architecture of traits like clutch size, egg mass, and morphological features is highly polygenic, with no single SNP explaining a large proportion of phenotypic variation. Additionally, the heritability of these traits can vary significantly between populations, as seen in zebra finches (*Taeniopygia guttata*) where genotype-phenotype associations were more consistent in captive populations compared to wild ones due to differences in linkage disequilibrium.

Moreover, environmental factors play a crucial role in shaping phenotypic traits. For example, in the endangered Great Lakes piping plovers (*Charadrius melodus*), environmental influences were found to be the main source of variation for traits like natal dispersal distance and breeding time, which were not significantly heritable. Similarly, phenotypic plasticity has been identified as a key driver of phenological changes in response to climate change, as observed in the Mediterranean blue tit population.

Future research should focus on further elucidating the genetic basis of phenotypic traits in bird populations by employing advanced genomic techniques and larger sample sizes. Studies should aim to identify specific causal variants and their interactions with environmental factors. Additionally, there is a need to explore the role of structural variants (SVs) in phenotypic variation, as they have been shown to significantly influence traits like migratory behavior in the Eurasian blackcap. Investigating the potential for local adaptation and the impact of assortative mating on genetic divergence, as seen in the white wagtail (*Motacilla alba*), could provide deeper insights into the mechanisms of reproductive isolation and speciation.

Furthermore, research should consider the implications of heritability and evolvability in the context of rapidly changing environments. For instance, understanding how agricultural practices influence the selection pressures on bird populations, as studied in Savannah sparrows, can inform conservation strategies. Finally, the application of genomic selection in wild populations, despite its challenges, holds promise for enhancing our understanding of evolutionary dynamics and could be a valuable tool for conservation genetics.

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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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