



Passer domesticus: An evolutionary genomics perspective on adaptation, Allee effects

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Passer domesticus is an avian which is believed to be under extinction. In India, many Passerines existed, but urban life paving the way for, and the rural habitation dwindling, there is a threat for these birds to go under extinction. In recent years, electromagnetic radiation (EMR) from mobile communication infrastructure and power systems has also been hypothesized as a contributing stressor, with reported associations between high EMR exposure and altered avian behaviour, reproductive success, and embryonic development in birds. This review integrates ecological, physiological, and genomic perspectives to evaluate potential mechanisms underlying *Passer domesticus* population decline. Particular emphasis is placed on urban ecological disruption, chronoecological mismatches affecting breeding cycles, and the Allee effect in small or fragmented populations. Overall, *Passer domesticus* emerges as both a sensitive bioindicator of urban environmental change and a valuable model for studying human-driven ecological and genomic impacts. The synthesis underscores the need for integrative conservation approaches combining ecological monitoring, reproductive biology, and genomic tools to better understand and mitigate ongoing population declines in urban avifauna.

Keywords: Adaptation, Avians, Electromagnetic radiations, Extinction, House sparrows, Passerines

Introduction

With more than 1300 species of avian comprising 13% of all known world's avians, India is rich with avian diversity. But regrettably, India is ranked 3rd in having rare and threatened avian species in the world¹. *Passer domesticus* (House Sparrow) was introduced in Europe from North Africa and Eurasia by the ancient Romans². Between 1970 and 1990, the *Passer domesticus* population was very large, with over 63 million breeding pairs. However, from 1990 to 2000, there was a decline of more than 10% across the continent, particularly in the Turkish population (<https://farmlandbirds.net/> last accessed on September 20, 2024). The Netherlands and UK considered *Passer* an endangered species³, as their population has dropped since the 1980s. Multiple hypotheses have

been proposed explaining the house sparrow population decline after them being added to the UK Red List of endangered species in 2002, that include; lack of food, particularly aphids, which adults feed to nestlings, pollution from automobiles running on unleaded fuel, increased predation by domestic cats or sparrow hawks (*Accipiter nisus*). Additionally other factors such as, reduced foraging opportunities due to cleaner streets, competition for food from other urban species, loss of nesting sites, particularly under the eaves and in the roofs of houses and uses of pesticides which leads to unavailability of insects of interest to feed³. The Allee effect contributes to a significant reduction in their population⁴. Allee effect is a measure in endangered birds where low population density leads to reduced individual fitness associated with demographic loss. Recent research, including full genome sequencing of species like the Indian house sparrow is being used to understand the genetic underpinnings of these declines and how birds adapt

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Graphical abstract

to or suffer from Allee effects. House sparrows can be considered a good biological indicator for detecting the effect of radiation since they live in urban environments where electromagnetic radiation (EMR) is higher. Although some reports suggest that they avoid places with high levels of EMR signals, where they co-relate their disappearance and introduction of the cell phone mast tower³. According to this calculation, no sparrows would be expected to be found in an area with field strength >4 V/m. Another study with sparrows in Flanders (Belgium) state higher levels of radiation negatively affects the abundance or behaviour⁵. A decline in several species of urban birds is seen in the U.K. than those in Spain, where radiation was 20 times higher than the allowed standard by law. In India, the sparrows are disappearing from areas around mobile towers where EMR contamination is at large⁶. Electromagnetic fields (EMFs) generated from power lines have been reported to affect the reproductive system in birds⁷, while comparative studies in mammals suggest that such effects may be mediated indirectly through the central nervous system (CNS) rather than direct gonadal action⁸. Exposure to EMR from anthropogenic sources such as mobile phone masts and power infrastructure has also been associated with altered avian behaviour, neural activity and reproductive performance³. In particular, chronic exposure to high-frequency radiofrequency fields has

been linked to reduced breeding success and increased embryonic mortality in birds³ (Table 1). The broad occurrence of avian hybridization⁹ in birds order, viz. Passeriformes, Galliformes, Anseriformes, and Charadriiformes with slow evolution of intrinsic postzygotic isolation enabling backcrossing, increase the potential for introgression¹⁰, a commonly seen phenomenon in avians documented by numerous studies¹¹. Many molecular techniques development are mirrored by the study of these model systems, e.g. mitochondrial DNA, microsatellites¹², SNPs and whole genome data¹³ all have been used in the flycatcher system, leading to molecular markers. Various studies focused on developing the reconstruction of phylogenetic networks considering both incomplete lineage sorting and hybridization¹⁴⁻¹⁵. Although this approach has not been used in avian genomics yet, it looks a promising strategy, and with this advent of genomic data phylogenetics might require a shift from tree to networks¹⁶⁻¹⁷.

The avian male reproductive system contains a pair of testes connected to vas deferens which in turn open to cloaca. Unlike mammals, birds do not show equivalent accessory reproductive organs such as prostate gland, seminal vesicles or bulbourethral glands in all species. However domestic poultry such as fowls, turkeys and ducks are shown to produce lymph-like fluids as accessory reproductive fluids through organs such as paracloacal vascular body,

Table 1 — Factors contributing to population decline and extinction

Category	Specific Factor	Impact on the Species
Dietary Scarcity	Lack of insects	Adults have insufficient food to feed nestlings for the first few days after hatching
Environmental Pollution	Automobile emissions and air quality	Both short-term and long-term toxicity due to the food chain
Human Infrastructure	EMR from mobile towers	Associated with loss of sparrows; affects CNS and breeding success
Human Activity	Pesticide use in parks and gardens	Cuts down food supply and inoculates the urban ecology with toxins
Habitat Loss	Loss of nesting sites	Modern construction reduces traditional urban nesting opportunities/resources
Biological Pressures	Predation and Disease	More predatory eating by domestic cats/sparrow hawks and a higher disease transmission rate
Ecological Dynamics	Allee effect	A biological phenomenon where a significant reduction in population density leads to a further decline in fitness
Chronoecology	Disrupted circadian zeitgebers	Artificial light and change of temperature leads to phenological disconnect and reproductive behavior

dorsal proctodeal glands, lymphatic folds *etc.* During breeding season, the male sparrow transfers sperm to the female through cloacal contact. While there is limited evidence regarding the impact of cell phone radiation on the male reproductive system, including factors such as overall male fertility, semen and sperm quality, sperm motility, sperm count and sexual communication, its effects on the reproductive system of the *Passer* species still need to be further investigated^{7,18,19}. In Kestrels the hatching rate has been shown to reduce with exposure to cell phone towers²⁰. Though the exact reason for this problem has not been found, the effect of pulsed magnetic field has been demonstrated to induce developmental abnormalities in the Chicken embryo²¹.

The *Passeridae* family is generally classified into eight genera, with a total of 43 currently accepted species (according to the IOC World Bird List by Gill *et al.* 2020³⁹). Among them, *Passer* is the most diverse genus with 28 recognized species³⁹, of which *Passer domesticus* is the most extensively studied species. The house sparrow (*Passer domesticus*) is a cosmopolitan human commensal distributed across all continents. It is primarily a granivorous bird commonly seen occupying cities and farmland, where it feeds on food waste and crops⁵. Passeriformes had the most explosive radiation, resulting in 6,321 currently described species. They are very abundant, making up almost 60% of all bird species. According to recent whole genome analyses and MtDNA studies, passerines originated and diversified in the Austral-Pacific at the beginning of Cenozoic period⁴⁰. Many climatic and geologic events played a role in the diversification, dispersal and speciation of passerines for example, Oligocene glaciation and inundation of

New Zealand²³. Within the *Passer* genus, the house sparrow is part of the "Palearctic black-bibbed sparrows" group and a close relative of the Mediterranean "willow sparrows". Among the members of genus *Passer* (Old World sparrows) House sparrow (*Passer domesticus*), Spanish sparrow (*P. hispaniolensis*), and tree sparrow (*P. montanus*), are human commensals; as most *Passer* species nest readily in man-made constructions. The relationships between the species within genus *Passer* and to other finches (*Passeridae* and New World sparrows) have not been fully understood. To address this, multi-locus phylogenetic analysis and computational tools are being increasingly used. Päckert *et al.*, 2021⁴² amplified and sequenced four molecular markers using 65 samples from 22 species of the *Passeridae* genera *Passer*, *Petronia*, *Gymnoris*, *Montifringilla*, *Pyrgilauda* and *Onychostruthus* performing a multi-locus analysis with a broader taxon sampling across different genera of *Passeridae* to generate a comprehensive phylogenetic hypothesis⁴². Their analysis confirmed that Old World sparrows exist as a monophyletic group and were sister to another well-supported clade including weavers (*Ploceidae*), Przewalski's finch (*Urocynchramus pylzowi*), estrildid finches and wydahs (*Estrildidae* and *Viduidae*). Around 17.5 million years ago (mya) the basal split in old world sparrows occurred separating the cinnamon ibon (*Hypocryptadius cinnamomeus*) from all other *Passeridae*. Approximately 10 mya, the old world sparrow further divided into two major groups as rock sparrows (genus *Petronia*) and the snowfinches (*Montifringilla*, *Pyrgilauda*, *Onychostruthus*). Around 6.9 mya these three snow finches genera went through the diversification process.

According to the multi-locus phylogeny by Päckert *et al.*, 2021⁴², during the late Miocene, around 6 mya, two major radiations of Old World sparrows emerged in different geographic regions i.e. the Palearctic and the afrotronic⁸⁸. The Afrotronic radiation includes seven species from Sub-Saharan Africa. Three species of grey-headed sparrows were included in one Sub-Saharan region namely *P. griseus*, *P. diffusus* and *P. gongoensis* while the two species from South Africa viz., *P. melanurus*, *P. motitensis* and the east african chestnut sparrow (*P. eminibey*). The second major radiation, focused in the Palearctic and Oriental regions include 12 species, this radiation started diversifying approximately 5.5 Mya, with an initial separation of the Asian russet sparrow (*P. cinnamomeus*) from other *Passer* species. Further diversification produced the tree sparrow (*P. montanus*) and the Central Asian Saxaul sparrow (*P. ammodendri*). In the early Pleistocene, a final diversification phase created a cluster of closely related species: the house sparrow (*P. domesticus*), the Spanish sparrow (*P. hispaniolensis*), the Italian sparrow (*P. italiae*), and the Socotra sparrow (*P. insularis*), highlighting the complex evolutionary history within the *Passeridae* family as confirmed by Päckert *et al.* (2021)⁴².

Avian sequencing projects and the role of regulatory elements

Over the years, mtDNA nucleotide substitution patterns with DNA restriction enzymes were attempted in birds which later restriction fragment length polymorphism (RFLP) analysis was used for broader application in the field of ornithology²². Due to the limited power of resolution and with PCR and DNA sequencing developed, RFLP was later abandoned paving way for sequencing-based approaches. As on today, 80% of species are nearly complete with genome sequencing efforts, for example Furnariidae, Emberizidae, etc are available. Given the lack of fossil evidence regarding their point of divergence, and considering that this group—which comprises approximately 60% of extant bird species evolved relatively late in Australia around 47 million years ago, it appears that the molecular clock operates at a different speed for this specific order²³.

Regulatory elements, loss of function, and gain of function constructs can be identified, designed, and quickly introduced respectively, by comparing noncoding regions of chicken and mammalian genomes, thus making Chicken Genome particularly

efficient for the purpose²⁴. A study by Peona and colleagues in 2021 used *Paradisaea raggiana* (bird-of-paradise) as the model animal to identify the cause consequences of assembly gaps using a multiplatform genome assembly²⁵. Since, avian genomes have very less repeat content of 10% and with a genome size small among all amniotes, thus, regions such as repeat-rich W sex chromosomes, GC-rich microchromosomes, or eukaryotic genomes of any size and complexity that possess a challenge to assemble can be focused. Birds-of-Paradise provides a good system in the study of speciation, hybridization, and sexual selection due to their rich radiation²⁶. Peona *et al.* suggested W chromosomes and previously inaccessible microchromosomes can be assembled via a multiplatform approach. Also, repeat categories like satellites and LTR retrotransposons can be reported substantially, which is missing from most types of de novo assemblies²⁵. This approach identified the major cause of assembly fragmentation as repeats and LTR retrotransposons. While chromosome 16 is the most complex avian chromosome comprising MHC²⁷, the birds have a ZW sex chromosome system, the female being heterogametic, comparable to Mammalian Y chromosome the W chromosome is difficult to assemble and highly repetitive²⁸ like human Y chromosome. Previous studies on avian sex chromosomal evolution are biased toward Z²⁹, W chromosome evolves rapidly by the accumulation of transposable elements, with a few regions syntenic and collinear between paradise crow and chicken.²⁵ The efficiency of available sequencing technologies in assembly and completeness through summary statistics of scaffold N50 and BUSCO values were assessed³⁰, giving minimum scaffold size among the largest scaffold and genome completeness. Various degrees of fragmentation, suggest that avian genome can generate short-read assemblies with score more than 95% on BUSCO gene completeness³¹, although during the identification of gene models in PacBio data, and the sequencing errors in it, limits the BUSCO. BUSCO fails, at least partially, in recognizing genes in the assembly even after multiple rounds of corrections³². Similar BUSCO tendency was observed in multiple studies working with long reads^{25,31}, so a sequence polishing step is necessary to get good gene annotation and BUSCO score. Due to GC content in avian genomes, hundreds of core genes are missing from short-read assemblies, hence from BUSCO gene set³³. Theoretically implying that with assembly polishing,

both short and long-read assemblies can have a high BUSCO score, but will inevitably ignore the presence and quality of core genes that are difficult to assemble. Additional gene-based approaches for quantification of presence and completeness are needed in avian genomes where the BUSCO scores are high³¹. When gene models of Z and W chromosomes, which indicate genes from challenging regions of genomes, are aligned to all assembly versions complete/partial/absent genes also referred to as differences in gene content in the short-read and linked-read-based assemblies are identified²⁵.

Repetitive regions and elusive chromosomes can potentially be assembled by long reads, therefore, genome completeness and quality by characterising and quantifying these regions and not that were already obtained by previous technologies²⁵. Repeat modeller predicted 71 new consensus sequences using PacBio assembly, because the respective repeats were too fragmented /assembled in few copies in Illumina assemblies from three birds -of paradise species, this helped base pair masking by Repeatmasker by up to 38% within the same assembly²⁵. Repetitive elements also consist of multicopy genes, such as MHC which is involved in adaptive immune response, and are located on chromosome 16 in birds²⁷. Several scaffolds of this chromosome were recovered of which only a fragmented assembly exists from chicken²⁷. Using exon 2 and 3 as a proxy in blast hits the maximum number of MHCII B copies in lucPyrPB and lycPyr6 were found, suggesting MHC genes are affected by the CHiCAGO map misassembly correction²⁵. For complex regions such as MHC, the use of ultralong reads of bacterial artificial chromosomes (BAC) sequencing looks necessary to resolve the number of gene copies and structures. LAI³⁴ for assessment of the quality of an assembly in terms of completeness of the LTR retrotransposons present, was tested which resulted in LAI scores that represent a high-quality reference genome as indicated in Ou *et al.*, 2018, higher than Chicken genomes. Indicating gap filling and polishing curation process of multiplatform assemblies quality improvement in case of large LTR retrotransposons representations²⁵. The authors manually curated multiplatform assembly and three de novo draft assemblies of the same sample, characterizing and measuring genome completeness, which resulted in long-read assemblies much better than short-read assemblies. Statistics, Scaffold N50 and BUSCO

values, which are optimised for short reads do not reflect the full potential and strengths of new sequencing technologies. While there are challenges to make (a) chromosome-level assembly are a primary assembly based on long reads, (b) data for correcting mis assemblies that should be independent like CHiCAGO map or linked reads, and (c) polishing sequencing errors for both short and long reads and Hi-C map for chromosomes-level scaffolding. Correction of nucleotide and assembly errors can be done using Illumina libraries, but polishing should be done with great care, short-reads might over-homogenize repetitive sequences for base calling errors and short indels, thus advisable to correct only outside repeats. In addition, 10x Genomics linked reads can also be used to correct both sequencing errors and misassemblies (*e.g.*³⁵) and to scaffold the genome (arcs³⁶, arks³⁷, fragscaff³⁸). In case of budgets and sample material constraints, linked reads may be more suitable than short reads alone in obtaining a genomic overview.

Human Commensalism and Adaptation

Human-commensalism house sparrow is said to have begun during the Neolithic revolution in the Middle and Near East⁴³. Ravinet *et al.*, 2018 conducted an examination of the population genomic variation in three Eurasian *Passer* sparrow species, the Spanish (*Passer hispaniolensis*), Italian (*Passer italiae*) and house sparrow (*Passer domesticus*), to understand evolutionary relationships among the species and identify candidate genes in house sparrow involved in adaptation to urban environments compared to the other wild species⁴³. They also analysed the Bactrianus sparrow, which is a subspecies that may have diverged from the main house lineage. The subspecies migrates, does not associate with human settlements, is less bold and has different skull and beak morphology owing to its divergent foraging and diet⁴⁴ and other traits associated with non-human commensal sparrow species. Hence, Bactrianus sparrows are considered proxies for the ancestral, pre-commensal house sparrow. Comparative genomics of the 2 subspecies revealed multiple regions in the sparrow genome showing signatures of house-specific positive selective sweeps. Some of the genes identified associated to divergent phenotypic traits between the 2 subspecies include xpEHH and wnt7a involved in feather development and melanogenesis in birds⁴⁵,

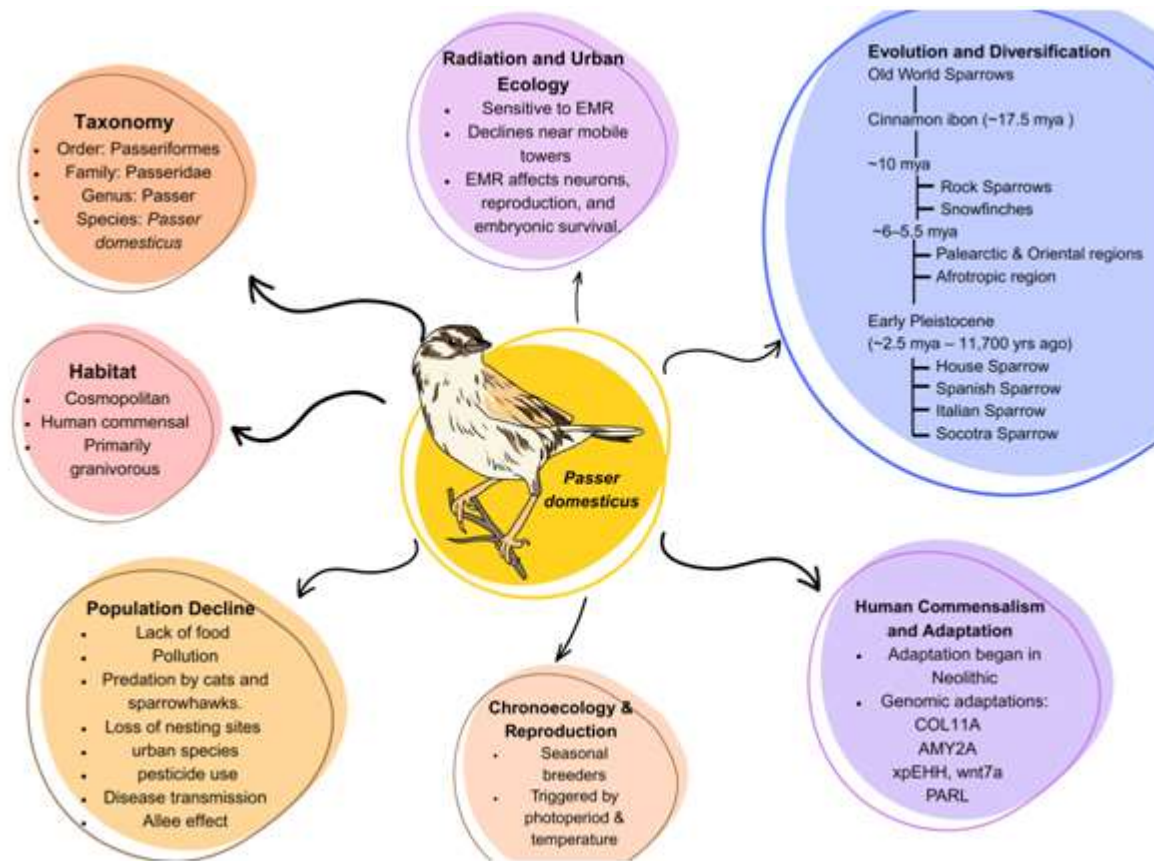


Fig. 1 — A Pictorial central figure of *Passer domesticus* and its habitation

Table 2 — Candidate Genes and Their Phenotypic Effects

Gene	Primary Biological Process	Phenotypic Effect / Significance
COL11A	Skull morphology and craniofacial structure	Associated with a heavier skull and bigger beak in house sparrows, developed to eat harder seeds of domesticated crops
AMY2A	Starch-based diet (amylase gene)	It is seen as an adaptation to human agriculture in which the house sparrows underwent a copy number gain in the Neolithic revolution
PARL	Circadian rhythm	Upregulated in the migratory Bactrianus subspecies; house sparrows (non-migratory) show divergent selection here
xpEHH & wnt7a	Feather development and melanogenesis	Linked to physical morphology and coloration differences between two subspecies

PARL gene associated with circadian rhythm during migration was upregulated in Bactrianus sparrows. This is of interest as Bactrianus sparrows migrate while house sparrows do not⁵. Two important genes associated with this divergent selection are the *COL11A* and *AMY2A* genes on chromosome 8. *COL11A* is closely associated with skull morphology and craniofacial structure, which differ between Bactrianus and house sparrows, with the latter exhibiting a more robust skull morphology and larger beak due to its adaptation to feeding on tougher seeds from domesticated crops⁴⁴. *AMY2A*, an amylase gene linked to the transition to starch-based diets in both

humans and dogs during the Neolithic revolution is observed to undergo copy number gain in house sparrows⁴³ (Fig. 1 and Table 2).

Chronoecological factors shaping *Passer's* distribution

The population and distribution of any species in any given area needs the selection of a suitable habitat, for example, foraging, nesting and reproduction *Passer domesticus* like the other birds are seasonal breeders, which decide their breeding period based on seasonal photoperiod and temperature variation. In birds, β -TSH secretion is under regulation of photic signals received by SCN⁴⁶.

Longer photoperiods during early summer and spring season upregulate β -TSH synthesis which combine with alpha subunit to form active TSH which acts on tanycytes in hypothalamus. Tanycytes then release type II iodothyronine deiodinase (DIO2) which converts T4 into T3. T3 then stimulates release of GnRH (Gonadotrophin Releasing Hormone) which induces gametogenesis, steroidogenesis and reproductive behaviour⁴⁷. These biochemical pathways are aligned with the foraging behaviours like, ensuring the availability of insects during the time of giving birth which makes the breeding time more calculated and exclusive. Disrupted circadian zeitgebers, unexpected climate variations, temperature and weather fluctuations in urban environments may result in altered reproductive behaviour and phenological mismatch⁴⁸. Therefore, these chronoecological disruptions can affect chick survival and influence local population decline. The fact gets more evident in the data showing severe declination in the hyper urbanised parts of Europe and India.

Conclusion

The house sparrow, a small bird belonging to the Passeridae family, plays relatively underexplored roles in the ecosystem, highlighting the need for deeper investigation to inform effective conservation strategies. Beyond its ecological functions, the house sparrow holds significant value in tracing human history and migration, as its evolutionary path is closely linked with that of humans. Historically, this species has been associated with the spread of agriculture and the expansion of agrarian communities across Eurasia⁴⁵. Despite this, limited research has delved into these relationships in depth, particularly within the South Asian context. Recently, we developed a genomic resource for the house sparrow⁴⁹, which offers valuable potential for exploring a wide range of ecological and phenotypic questions through integrative genomic analyses. The house sparrow is a well studied ubiquitous, anthro dependent human commensal. With rapid growth of urbanisation, there is an indefatigable need to check and protect these avians. In this review, we outlined the role of urbanisation, commensal relationships, adaptation and genes associated with the environment besides allee effects exploiting the Passerines.

Conflict of interest

All authors declare no conflict of interest.

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