

Invasion genetics: Lessons from a ubiquitous bird, the house sparrow *Passer domesticus*

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Abstract Following an introduction, non-native species are exposed to environments that differ from those found in their native range; further, as these non-native species expand beyond the site of introduction, they must constantly adapt to novel environments. Although introduced species are present across most ecosystems, few species have successfully established themselves on a truly global scale. One such species, the house sparrow *Passer domesticus*, is now one of the world's most broadly distributed vertebrate species and has been introduced to a great part of its current range. To date, work on four continents suggests both genetic and phenotypic variation exists between native and introduced ranges. As such, house sparrows represent an excellent opportunity to study adaptations to novel environments and how these adaptations are derived. The global distribution of this species and the multiple independent introductions to geographically isolated sites allow researchers to ask questions regarding genetic variation and adaptation on a global scale. Here, we summarize the molecular studies of invasive house sparrows from the earliest work using allozymes through more recent work on epigenetics; using these studies, we discuss patterns of dispersal of this species. We then discuss future directions in techniques (e.g. next generation sequencing) and how they will provide new insight into questions that are fundamental to invasion biology. Finally, we discuss how continued research on the house sparrow in light of these genetic changes and adaptations will elucidate answers of adaptation, invasion biology, range expansion, and resilience in vertebrate systems generally [*Current Zoology* 61 (3): 465–476, 2015].

Keywords House sparrow, Invasive, *Passer domesticus*

1 Introduction

Introduced species are the second largest threat to global biodiversity. In the face of ecosystem impacts (Bakker and Wilson, 2004), economic costs (Mack et al., 2000), and the likelihood of growing commerce increasing the threat of new introductions (Levine and D'antonio, 2003), invasive species research has grown recently. However, in addition to invasive species management, studying invasive species in an ecological or evolutionary context will lend great insight to fundamental questions in biology such as the general spatial structure of species interactions, allopatric speciation, and response to environmental stressors and challenges (Holt, 2003).

Following an introduction, organisms cannot only endure novel environments but must also thrive in them to be successful. Additionally, as introduced species expand beyond the site of initial introduction, novel environments will likely continue to be encountered so

that individuals must continuously adjust phenotypes to cope. Most introductions involve bottlenecks and founder effects that can reduce genetic diversity initially. Unlike many threatened species facing the same challenge, introduced species are often able to overcome these reductions in genetic diversity to generate novel adaptations and adjust to novel environments; this presents a genetic paradox (Dlugosch and Parker, 2008).

In novel environments, phenotypes should match new environments, thus creating phenotypic gradients consistent with age of population (Sol et al., 2002, Rehage and Sih, 2004, Russell et al., 2010). However, the underlying mechanisms of this variation in phenotypes, particularly on such short timescales, are less clear. These phenotypic changes may be due to changes in the frequency of genes across space and time, i.e. driven by natural selection, genetic drift, founder effects (Clegg et al., 2002), or spatial sorting of genes as the population expands (Shine et al., 2011). Alternatively, phenotypic variation across ranges may be determined by other fac-

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tors such as epigenetic changes (Richards et al., 2012, Schrey et al., 2012, Liebl et al., 2013a) and phenotypic plasticity or flexibility in response to variable environments (Sol et al., 2002, Yeh and Price, 2004, Richards et al., 2006, Davidson et al., 2011). Epigenetic changes such as methylation induce changes in gene expression, which induce changes in phenotypes (Richards, 2006). Phenotypic plasticity and flexibility, which may be influenced by epigenetic and/or genetic factors, allow individuals to rapidly adjust to environmental variation (Agrawal, 2001). Factors other than genetic-based evolution are likely to contribute to phenotypic variation in introduced species given the likelihood of significant reductions in genetic diversity due to bottlenecks and founders effects at the time of initial introduction and throughout range expansion (Dlugosch and Parker, 2008).

Despite considerable challenges in successfully colonizing novel habitats following an introduction, some species have been repeatedly and successfully introduced throughout the world. In part, this success will reflect the amount of effort invested in introducing these species (Cassey et al., 2004, Blackburn et al., 2011). However, it is also recognized that some species have inherent characteristics that enable them to succeed in new environments, i.e. “weedy” species (Cassey et al., 2004). One such species, the house sparrow *Passer domesticus*, native to Europe and Asia, has been introduced and become established on four continents (Fig. 1), making it one of the most broadly distributed vertebrate species in the world (Anderson, 2006). House sparrows

have been introduced intentionally (e.g. as a familiar species or pest control) or unintentionally (Anderson, 2006), however, unlike many other species, the house sparrow has successfully expanded its range in most introduced environments (Robbins, 1973; Anderson, 2006), indicating an incredible ability to overcome genetic bottlenecks and adjust to variable climates and environments.

House sparrows were introduced to North America in the 1850s and 60s from Europe and rapidly expanded its distribution to cover all of the United States and most of Canada and Mexico by the early 1900s (Grinnell, 1919). In South America, house sparrows have been introduced multiple times including to Argentina in the late 1800s, and Chile and Brazil in the early 20th century; since, house sparrows have spread to occupy most areas of South America including Tierra del Fuego (Lever, 2005). In Australia and New Zealand, house sparrows were introduced in the early 1860s (Long, 1981), currently occupying all of New Zealand and the eastern half of Australia (Higgins and Peter, 2002). Finally, house sparrows were introduced to South Africa around 1900, from where they expanded in a northerly direction reaching southern Tanzania in the early 1980s (Anderson, 2006); additionally, a secondary introduction from South Africa into the ports of Mombasa, Kenya and Dar Salam, Tanzania occurred in the 1950s (Anderson, 2006). Another introduction (of unknown origin) brought house sparrows to Senegal and western Africa in the late 1970s (Anderson, 2006) (Fig. 1).

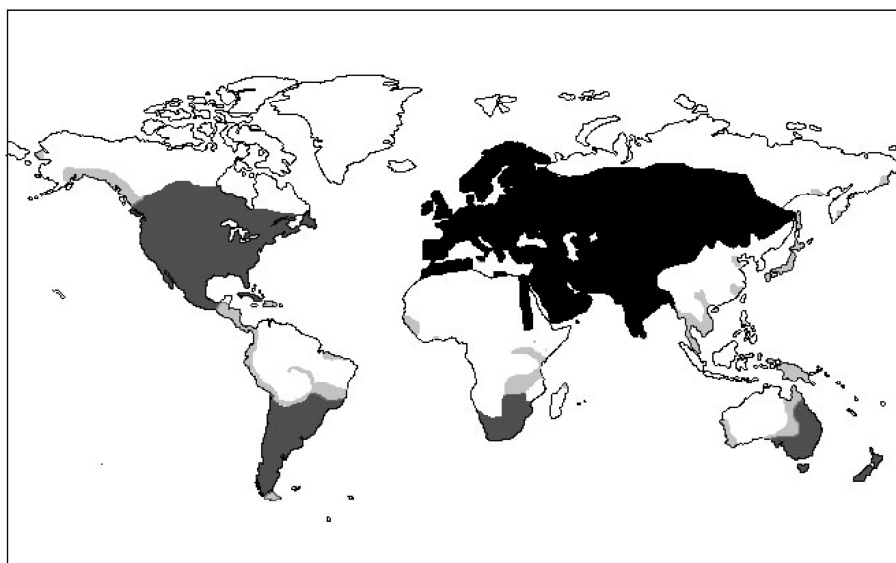


Fig. 1 Map of current distribution of house sparrows

Black area indicates native range; dark gray indicates long-established introduced (> 100 years since introduction); light gray indicates recently introduced (< 100 years).

Given its broad range and the commensal nature of the species, house sparrows have been studied extensively as a model for general ecological, behavioral, and evolutionary questions (Anderson, 2006). For example, house sparrows have been used to study many phenotypic traits such as morphology (Johnston and Selander, 1964; Johnston and Selander, 1971; Johnston and Selander, 1973), personality (Martin and Fitzgerald, 2005; Lendvai et al., 2011; Bókonyi et al., 2012; Bókonyi et al., 2014), stress physiology (Lendvai and Chastel, 2010; Koren et al., 2012; Liebl et al., 2013b; Lattin and Romero, 2014), and sexual selection and reproduction (Griffith et al., 1999a; Nakagawa et al., 2007; Partecke and Schwabl, 2008; Lendvai and Chastel, 2010; Ouyang et al., 2011). The extensive research conducted in this species provides a good opportunity to draw comparisons between different populations (e.g. Griffith et al., 1999b), or different outcomes (e.g. Nakagawa et al., 2007). Such intra-specific comparisons are more powerful than inter-specific comparisons because inter-population variation is composed of ecological, rather than phylogenetic variation.

Although most of the studies conducted on house sparrows have not specifically addressed differences according to invasion status, considerable work on house sparrow biology (reviewed in Anderson, 2006), which means that we know a great deal about this species, which allows researchers concerned with invasiveness to better design and interpret research in this area. David Lack first identified house sparrows as a good model for studies of evolutionary biology recognizing that introduced house sparrows in North America provided an excellent opportunity to understand how adaptive processes could work over a relatively short timeframe (Lack, 1940). In fact, the work by Johnston and Selander (1964; 1967) on range expansion and morphological variation in American house sparrows has become one of the text book examples of selection and adaptation; these studies showed rapid morphological differentiation among house sparrow populations over a period of ~100 years, which challenged previous predictions on estimated population differentiation (Johnston and Selander, 1964; Selander and Johnston, 1967). This work has been followed by studies of other aspects of adaptiveness and invasiveness in relation to traits such as response to novelty (Martin and Fitzgerald, 2005; Liebl and Martin, 2012; Liebl and Martin, 2014), stress physiology (Liebl and Martin, 2012; Liebl and Martin, 2013), immune regulation (Martin et al., 2010; Martin et al., 2014; Martin et al., *in press*) and dispersal (Skjelseth et al.,

2007). Additionally, researchers can use the large research base which exists on house sparrows for single-species meta-analyses (e.g. Nakagawa et al., 2007), which are often stronger than those conducted on multiple species. Although phenotypic patterns have been documented, a major challenge that remains is to resolve the extent to which this variation is due to changes in gene frequencies across populations, to phenotypic plasticity, or epigenetic variation (see below); these mechanisms not only remain unresolved to the extent of invasion, but also in relation to other patterns, such as the latitudinal cline in body size first identified by Johnston and Selander (1964).

Though studies over many decades have focused on invasive populations of the house sparrow to answer evolutionary questions, only relatively recently has attention focused on characterizing the nature of invasions themselves. One of the most comprehensively understood house sparrow introductions and range expansions is that of the Kenyan house sparrow. House sparrows were introduced to Mombasa, on the coast of Kenya in the 1950s (Anderson, 2006) and subsequently expanded their range in a north-westerly direction colonizing most major cities in Kenya by 2007 (Martin et al., 2014); this introduction was most likely a secondary introduction from an introduced population from South Africa (Anderson, 2006). As expected due to the recency of the introduction, Kenyan house sparrows have reduced genetic diversity compared to other house sparrow populations around the world (both native and those introduced into North America) (Schrey et al., 2011b). Despite an overall reduction in genetic diversity, throughout Kenya, house sparrows display dramatic phenotypic patterns consistent with time since colonization: house sparrows at the range edge are more exploratory (Liebl and Martin, 2012) and more likely to approach and eat novel food (Liebl and Martin, 2014) than individuals from more established areas. Further, at the range edge in Kenya, where stressors are likely less predictable, individuals release more corticosterone in response to stressors (Liebl and Martin, 2012) and have a lower ratio of mineralocorticoid to glucocorticoid receptors (Liebl and Martin, 2013); combined, this likely allows individuals at the range edge to better cope with stressors, whereas individuals in areas of longer establishment mitigate the negative effects of elevated stress hormones. Immunologically, house sparrows at the range edge expressed more Toll-like receptors responsible for identification of parasites, potentially allowing better surveillance of novel parasites (Martin et al., 2014). Although

individual genetic differences associated with particular traits were not studied in these studies, some data indicates that epigenetic changes (Liebl et al., 2013a) and phenotypic flexibility (Liebl and Martin, 2014, Martin and Liebl, 2014) are at least partially responsible for the patterns observed throughout this range expansion.

Below, we argue that house sparrows make a particularly adept model species to study invasion and range expansion of a vertebrate species. Its broad distribution and relatively well-documented invasion history throughout the world alone make house sparrows a valuable resource for invasion biologists. However, researchers using house sparrows as a model of invasive species also benefit from the fact that so much phenotypic and molecular background and resources already exist. Here, we focus on and summarize the molecular studies conducted on house sparrows throughout the world, beginning with allozymes through to recent work on epigenetic patterns. We discuss how particular patterns of dispersal through an introduction event and/or range expansion of this species has contributed to the genetic patterns observed. Finally, we discuss the future in invasion genetics and how using house sparrows as a model for invasion genetics will be particularly enlightening for the field of invasion biology as well as adaptation generally (Fig. 2).

2 Insights from the House Sparrow

Although not always in the context of invasion or range expansion, house sparrows have been the focus of molecular research for many years (Table 1). The investigation of genetic changes across global populations has and will continue to use cutting edge molecular tools. For example, the house sparrow was the focus of the first study of extra-pair parentage using DNA fingerprinting (Burke and Bruford, 1987), some of the earliest studies using microsatellite markers in molecular ecology (Neumann and Wetton, 1996; Griffith et al., 1999b), and the more recent use of SNP chip technology (Hagen et al., 2013). Most commonly, genetics have been used to investigate population structure (Table 1) or behavioral attributes of populations (e.g. extra-pair paternity (Table 1)). Although most of this work was not conducted from a perspective of invasion biology or range expansion, it provides a foundation of knowledge with validated molecular tools for future work in these areas.

2.1 Allozymes and microsatellites

Early work using allozymes unfortunately detected very little variation among populations (Klitz, 1973; Cole and Parkin, 1981; Parkin and Cole, 1984; Väi-

sänen and Lehtväslaiho, 1984). These markers, however, did detect differences among house sparrows across vast geographic distances: England, Western Europe, Australia, and New Zealand were determined to be differentiated (Parkin and Cole, 1985). As would be expected in introduced populations, house sparrows from Australia and New Zealand had fewer rare alleles and lower levels of heterozygosity (New Zealand) or higher levels of genetic differentiation (Australia). This allozyme-based work set the table for future studies by identifying a genetic pattern consistent with introduction history and showing that genetic markers could identify important ecological characteristics of these populations. Population genetic work in house sparrows, however, expanded significantly with the development of microsatellite markers (Neumann and Wetton, 1996; Griffith et al., 1999b; Richardson et al., 2000; Dawson et al., 2006; Griffith et al., 2007; Dawson et al., 2010; Dawson

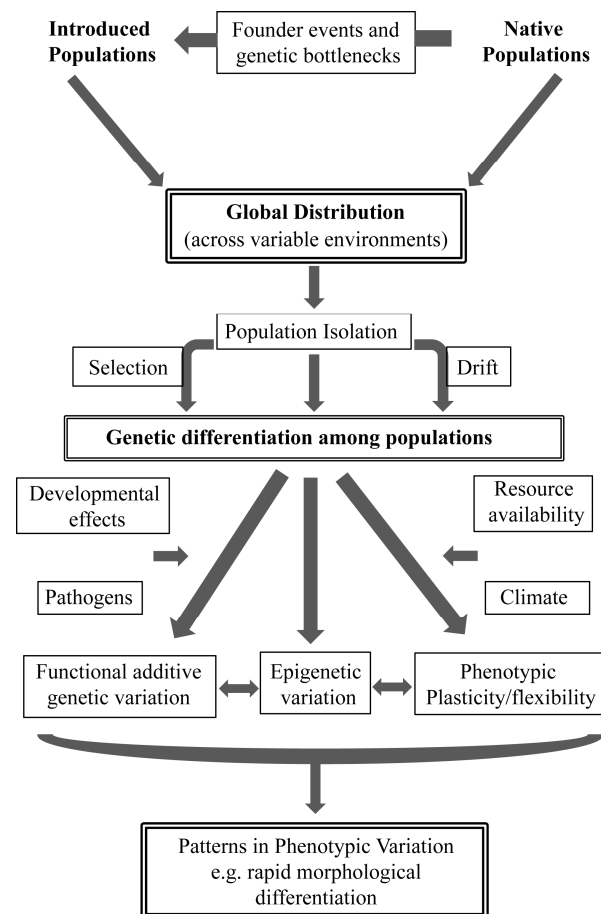


Fig. 2 House sparrows, native to Europe and Asia, have been introduced all over the world

Among populations, considerable phenotypic variation exists. This variation is a direct result of many environmental factors influencing different molecular factors, including bottlenecks, founder effects, genetic isolation, epigenetic diversity, and phenotypic plasticity and flexibility.

Table 1 Genetic studies using house sparrows as a model species. Studies are divided by type of study, genetic tool used, the location of the populations studied (I: introduced, N: native), and sample size of each study

Type of study	Type of genetic tool used	Population Location	Sample size	Citation
Effective population size	Microsatellites	Europe (N)	6 island populations	Engen et al., 2007.
Effective population size	Microsatellites	Europe (N)	15 populations	Baalsrud et al., 2014.
Genetic diversity	Microsatellites	North America (I)	42	Wetzel et al., 2012.
Genetic diversity	Allozymes	Australia (I)	174	Manwell and Baker, 1975.
Genetic diversity	Allozymes	Europe (N)	133	Cole and Parkin, 1981.
Genetic diversity	Allozymes	Europe (N)	145	Väisänen and Lehtväslaiho, 1984.
Genetic diversity	Allozymes	North America (I)	186	Bates and Zink, 1992.
Genetic diversity	Microsatellites	Europe (N)	169	Jensen et al., 2007.
Genetic diversity	Microsatellites	Europe (N)	355	Billings et al., 2012
Marker discovery	Microsatellites	Europe (N)	40	Neumann and Wetton, 1996.
Marker discovery	Microsatellites	Europe (N)	37 - 54	Griffith et al., 2007.
Marker discovery	Microsatellites	Europe (N)	64 from 2 populations	Dawson et al., 2012.
Parentage	DNA-fingerprinting	North America (I)	136	Whitekiller et al., 2000.
Parentage	Microsatellites	Europe (N)	1 population (3 years)	Ockendon et al., 2009.
Parentage	Microsatellites	Europe (N); North America (I)	133 broods from 92 pairs, from 2 populations	Griffith et al., 1999b.
Parentage	Microsatellites	North America (I)	164	Stewart et al., 2006.
Parentage	Microsatellites	Europe (N)	188 from 5 populations	Liker et al., 2009.
Parentage	Microsatellites	Europe (N)	600 from 26 populations	Vangestel et al., 2011b.
Parentage	Microsatellites	Europe (N)	61	Tóth et al., 2009.
Parentage	Allozymes	Europe (N)	420	Wetton et al., 1992.
Parentage	DNA fingerprinting	Europe (N)	183 broods	Wetton and Parkin, 1991.
Parentage	DNA fingerprinting; allozymes	Europe (N)	144 broods	Wetton et al., 1995.
Parentage	Single locus DNA profiling	Europe (N)	109	Cordero et al., 1999.
Parentage	Minisatellites; DNA fingerprinting	North America (I)	528	Edly-Wright et al., 2007.
Permanent genetic resources	Microsatellites	Europe (N)		Garnier et al., 2009.
Phenotypic association	Allozymes	North America (I)	621 from 4 populations	Fleischer and Johnston, 1982.
Phenotypic association	Microsatellites	Europe (N)	600 from 26 populations	Vangestel et al., 2011a.
Phenotypic association	Microsatellites	Europe (N)	238 from 10 populations	Kekkonen et al., 2012.
Phenotypic association	Microsatellites	South America (I)	150 from 10 populations	Lima et al., 2012.
Phenotypic association	Microsatellites	Europe (N)	705 from 12 populations	Brommer et al., 2014.
Population structure	Allozymes	Europe (N)	14 populations	Parkin and Cole, 1984.
Population structure	Allozymes	Europe (N)	11 populations	Björdal et al., 1986.
Population structure	Allozymes	Europe (N); Australia (I); New Zealand (I)	30 - 160 per population from 21 populations	Parkin and Cole, 1985.
Population structure	Allozymes	North America (I)	303 from 10 populations (serum) and 122 from 5 populations (tissue)	Klitz, 1973.
Population structure	Allozymes	North America (I)	447 from 5 populations	Fleischer et al., 1983.
Population structure	Microsatellites	Africa (I)	233 from 10 populations	Schrey et al., 2014.
Population structure	Microsatellites	Europe (N)	4 populations	Hole et al., 2002b.
Population structure	Microsatellites	Europe (N)	472 from 14 populations	Kekkonen et al., 2011b.
Population structure	Microsatellites	Europe (N)	600 from 26 populations	Vangestel et al., 2012.
Population structure	Microsatellites	Europe (N)	636 from 14 populations	Jensen et al., 2013.
Population structure	Microsatellites	North America (I); Europe (N); Africa (I)	316 from 16 populations	Schrey et al., 2011b.
Population structure	Microsatellites; MHC	Europe (N)	20 - 85 per population from 13 populations	Loiseau et al., 2009.
Population structure	Mitochondrial DNA; 3 nuclear loci	Worldwide	181	Sætre et al., 2012.
Population structure	SNP chip	Europe (N)	>160 adults	Hagen et al., 2003.
Population structure	Microsatellites	Europe (N)	986 from 2 populations	Kekkonen et al., 2011.

et al., 2012), which have been used to estimate population metrics in house sparrows throughout the world (e.g. heterozygosity, inbreeding coefficient, effective population size, relatedness, and estimates of genetic differentiation (see citations within Table 1)). These markers have proven much more powerful than allozymes at resolving the often subtle patterns of genetic differentiation found among introduced populations of house sparrow.

2.2 Patterns of genetic differentiation

Many ecological factors, some related to invasion and range expansion, affect the genetic differentiation of house sparrows. Native populations show genetic differentiation, even at rather short geographic distances, whereas introduced populations often have less differentiation. In house sparrows, several factors may contribute to the observed genetic differentiation; these include a sedentary lifestyle with low dispersal (Hole et al., 2002), isolation by distance (Loiseau et al., 2009), barriers to migration (Hagen et al., 2013; Jensen et al., 2013), habitat fragmentation (Bjordal et al., 1986; Hole et al., 2002), human commensalism (Bjordal et al., 1986), population declines (Hole et al., 2002; Kekkonen 2011), bottleneck/founder effect and genetic drift associated with island colonization (Hagen et al., 2013; Jensen et al., 2013), and biased dispersal over developed habitats (Vangestel et al., 2011a; Vangestel et al., 2012a). In fact, a decline in population size, along with habitat fragmentation and the sedentary nature of house sparrows likely played an important role in generating genetic differentiation among populations within 24 km on farmland in England (Hole et al., 2002) and a striking increase in genetic differentiation was detected after 40 years of population decline among Finnish house sparrow populations (Kekkonen et al., 2011a; Kekkonen et al., 2011b). In addition, introduced populations face several other unique circumstances leading to genetic differentiation including multiple sources of introduced individuals, human-mediated long-distance dispersal, dispersal contingent on introduction history, and multiple patterns of dispersal during range-expansion following the initial introduction (Parkin and Cole, 1985; Schrey et al., 2011a; Lima et al., 2012; Schrey et al., 2014).

Often, there is less genetic differentiation among introduced populations following a range expansion than among native populations over a similar geographic scale. Introduced house sparrows in North America have low genetic variation at allozyme loci (Klitz, 1973) with no genetic structure within a 12 km² area in Kansas (Fleischer, 1983). Further, introduced North American

(Schrey et al., 2011) and Brazilian populations (Lima et al., 2011) had lower levels of genetic differentiation compared to native European populations. It is important to note, however, that the introduction of house sparrows into novel areas can generate genetic differentiation via founder effects and genetic drift; house sparrows in Australia and New Zealand (Parkin and Cole, 1985) and Kenya (Schrey et al., 2011), for example, showed genetic differentiation from native populations following introduction.

The studies of recent introductions into Brazil (Lima et al., 2011) and Kenya (Schrey et al., 2011, 2014) suggest genetic characteristics of house sparrow populations change immediately following an introduction event (Schrey et al., 2011; Lima et al., 2012). A global comparison including house sparrow populations from North America, Europe, and Kenya showed that the most recently introduced population (Kenya), had the lowest genetic diversity, whereas the North American populations had seemingly recovered genetically in the 150 years since introduction. In a second, similar study, Brazilian house sparrows (long-established introduced population) had slightly reduced levels of genetic diversity compared to European house sparrows (Lima et al., 2012).

2.3 Patterns of range expansion following an introduction

Interestingly, the genetic characteristics of house sparrow populations also change as the population undergoes range expansion (Lima et al., 2012; Schrey et al., 2014). Depending on the mechanism of range expansion, from serial stepwise expansion with multiple bottlenecks to multiple introduction events with long distance dispersal, genetic diversity and differentiation can either increase or decrease throughout an expansion (Kolbe et al., 2004; Schrey et al., 2014). Lima et al. (2012) showed little genetic differentiation among Brazilian house sparrows, suggesting expansion occurred from a single, large source population (Lima et al., 2012); at the time of the study, however, house sparrows had been established in Brazil for over 100 years. A second study, addressing population-level genetic changes in Kenyan house sparrows, was conducted less than 60 years from the initial introduction in a population still expanding its range (Schrey et al., 2014). The study found evidence of genetic admixture (local populations including individuals with diverse genetic backgrounds) increasing with range expansion along routes commonly traveled by humans, yet evidence of contemporaneous stepwise expansion in less traveled areas. The pattern of

genetic differentiation observed was consistent with two types of range expansion. One occurred with multiple (likely human-based) movements of birds between an introduction source and cities along more traveled routes. The other occurred via step-wise expansion with little to no genetic admixture along less well-traveled human routes.

2.4 Patterns of dispersal

Dispersal is a critical process that influences genetic structure and likely has a tremendous impact on invasiveness. Generally, individual house sparrows do not disperse far (Fleischer et al., 1984; Altwegg et al., 2000; Hole et al., 2002b; Skjelseth et al., 2007). Dispersal is most common among juveniles (Fleischer et al., 1984; Altwegg et al., 2000), although it is not related to body mass, condition, clutch size, or hatch date (Altwegg et al., 2000) suggesting local dispersal may be affected more by breeding productivity and population size than nest or genetic effects. Globally, the distribution of house sparrows tends to be highly fragmented in a manner consistent with human habitation (Anderson, 2006), and human activity has been implicated in its current distribution (Anderson, 2006; Schrey et al., 2014). In particular, the range expansion of introduced house sparrows in North America and Kenya was highly influenced by human-based long distance dispersal (Robbins, 1973; Schrey et al., 2011a; Schrey et al., 2014), which has likely had a profound effect on the genetic patterns observed in these areas.

Studies have detected barriers to dispersal as having profound consequences on genetic structure. Within Finland, for instance, dispersal has maintained connectivity between mainland populations but the sea between Finland and Sweden, which acts as a dispersal barrier has led to population differentiation (Kekkonen et al., 2011). This result is analogous to allozyme results in Norway, where strong differentiation occurred between Norway and mainland Europe (Bjorndal et al., 1986). Additionally, island and mainland house sparrow populations show different patterns of genetic differentiation: island populations tend to have greater differentiation due to bottlenecks, founder effects, and genetic drift (Hagen et al., 2013; Jensen et al., 2013), but mainland populations show stronger isolation by distance (Jensen et al., 2013). Finally, how landscapes are developed (i.e. degree of urbanization) contributes to dispersal patterns, even at small scales (Vangestel et al., 2012). Urban populations tend to have more fine-scale structure than rural ones, possibly due to reduced dispersal or by attracting greater numbers of migrants from

surrounding suburban and rural (Vangestel et al., 2012). The evolutionary ecology of the urban environment is an area of growing importance, and not surprisingly, being a highly urbanized species, the house sparrow has been the focus of a number of important studies in this area. The gradient between the urban and rural landscape represents a number of ecological challenges for a species, and the study of behavioral (Bókony et al., 2009; 2012), physiological (Gavett and Wakeley, 1986), and morphological variation (Liker et al., 2008) across this gradient is highly informative about adaptiveness, resilience, and invasiveness broadly.

2.5 Beyond microsatellites

One key factor that many of the above described studies do not address is that microsatellite diversity usually measures changes in neutral markers rather than diversity of functional genes. To truly understand how invasions are genetically influenced, we will need to transition from the use of neutral markers to determining how variation of particular genes influence introduction and range expansion success. In fact, one study comparing neutral marker diversity using microsatellites with major histocompatibility complex (MHC) divergence showed that MHC differentiation was stronger than that of the neutral markers (Loiseau et al., 2009); MHC are some of the most polymorphic loci in vertebrates and code for a major part of the immune system. Using variation in the functional gene (i.e. MHC), the authors also reported a stronger association of genetic diversity with geographic distance than with microsatellites (Loiseau et al., 2009).

Recent advances in molecular tools (e.g. next generation sequencing) undoubtedly will provide major contributions to genetic studies of house sparrows. A recent study (Hagen et al., 2013), which took advantage of the house finch genome to support SNP-based technology, demonstrates the promise of this technique, which is even more powerful than microsatellites. Future studies will likely take advantage of transcriptomics techniques (i.e. RNAseq) to assay global pattern of gene expression. The increased statistical power, the potential to screen expression data, and the availability of large scale DNA sequence variation data will allow a deeper investigation of the genetic factors underling the well-documented ability of the house sparrow to invade new environments. Additionally, these techniques will likely uncover fundamentally important factors for evolutionary change, which may be applied to other species.

2.6 A role for epigenetic mechanisms

Populations can undergo phenotypic adjustment by

other means than genetic-based to best match variable environments (Pigliucci and Muller, 2010). Phenotypic changes that occur within a population as it transitions from new to colonized have been observed in just a few generations (Duckworth and Badyaev, 2007). This rate of change is unlikely to be explained by genetic evolution alone, especially in introduced populations with reduced genetic diversity. Thus, epigenetic mechanisms or phenotypic plasticity may contribute to changes observed during an introduction or range expansion. Invaders at the vanguard of an expanding wave are exposed to rapidly fluctuating and novel environments; within-individual mechanisms of rapidly adjusting phenotypes to the ensuing environments would be particularly useful in these areas. It is even possible that once phenotypes are determined epigenetically or through plasticity, that canalization of those phenotypes would occur through traditional genetic evolution (Waddington, 1942).

Epigenetic control of phenotypes is one mechanism by which phenotypes are able to adapt rapidly to novel environments. Epigenetic effects induce a change in gene expression without an underlying change in the genomic sequence (Richards, 2006). The most commonly studied epigenetic effect is DNA methylation, which has been shown to generate ecologically important phenotypes (Bossdorf et al., 2010). Epigenetic changes typically increase or decrease expression of particular genes, thus influencing phenotypes. Epigenetically mediated phenotypes are both heritable (Slatkin, 2009) and influenced *de novo* by environments. Thus, epigenetic variation may be particularly impactful during an introduction event, particularly given the timescale over which introductions and range expansions occur. In other words, as epigenetic marks are influenced by novel environments, they provide a mechanism for modifying, and increasing the expression of particular phenotypes, over and above the underlying genes responsible for the inheritance of that phenotype. Additionally, as the epigenetics marks responsible for expressing (or not) a particular gene can also be heritable, they can themselves be quickly fixed (Waddington, 1942). Indeed, epigenetic variation has been shown to be important in multiple invasions (Richards et al., 2012) including that of house sparrows (Schrey et al., 2012, Liebl et al., 2013a). Compared to a long-established population of introduced house sparrows (Florida, North America), a recently introduced population (Kenya) had more frequent methylation throughout the genome (Schrey et al., 2012). Further, within Kenya, groups with the lowest

genetic diversity had the highest epigenetic diversity (Liebl et al., 2013a). This suggests that epigenetic diversity may compensate for the reduced levels of genetic diversity that are often experienced following bottlenecks and founder effects from introduction events.

Although not greatly pursued in the ecology literature, we recommend that future work focus on the importance of epigenetic change for individual fitness and adaptive change during invasions and range expansions. Again, given the distribution of house sparrows and their genetic similarity to passerine species with known genomes, they make ideal candidates to study epigenetic differentiation as it relates to a vertebrate invasion. Additional studies addressing broad methylation patterns should be conducted to confirm the patterns in Kenya (that groups with the lowest genetic diversity were those with highest epigenetic diversity; Liebl et al., 2013) are wide-spread among introduced house sparrow populations. In addition, we suggest researchers address methylation and other epigenetic regulatory mechanisms of specific genes. This can be conducted via several techniques including sequencing of genomic material under epigenetic control. This effort would provide crucial information as to how epigenetic mechanisms regulate invasion in house sparrows (and other species). Potential target genes which have been identified as under epigenetic control in other species include those influencing stress regulation, (Weaver et al., 2004), beak shape (Skinner et al., 2014), and immune regulation (Skinner, et al., 2014).

3 Future Directions

To best understand invasion genetics, we believe a global collaboration by a consortium of researchers should join forces to ask questions in a coherent manner at an international level; further, we believe the house sparrow is one of the better models for such work. The house sparrow provides excellent opportunities for the field of invasive species genetics because of its distribution, abundance, and considerable background of knowledge. These characteristics prevent problems caused by low replication or sample size, at both the individual and population level. Borer et al. (2014) present the success that is achievable by an international consortium studying a single research question. Studies of globally distributed house sparrows would provide insight not only into the genetics of the invasion, but also to other major questions of global significance such as those related to biodiversity, conservation, and organismal adaptability to changing environments.

Conservation biology has focused on the study of rare species, but relatively few on abundant species expanding their range. However, focusing on these common species and what traits confer resilience will lend an important perspective to our effort of preserving biodiversity (Gaston, 2010). Unarguably, house sparrows are common throughout its range, although, ironically, may be at a lower density in parts of its native range (e.g. UK) than introduced range (Hole et al., 2002). There are a host of questions regarding the characteristics that have conferred such success on the house sparrow as an invasive species. To what extent can this success be attributed to plasticity in reproduction, diet, sociality, cognitive skills, immunity, or is there something about the genetic architecture of the species that has enabled it to respond so rapidly to such a wide range of environments?

It may be argued that house sparrow invasion success is largely dependent on the fact they are predominantly found in human modified areas, which is becoming increasingly distributed across the globe. However, it is also clear that the species is able to survive (and thrive) in variable climates, including those very different from its native range. This provides an ideal opportunity to use house sparrows across the world to understand adaptation to different and changing climates. For example, house sparrows introduced from England have become established along a clinal gradient in Australia from temperate Tasmania to monsoonal tropics of Queensland through the arid interior. Addressing variation in behavioral, physiological, morphological, and molecular traits across such clines would deliver significant insight into how climatic variation drives selection on avian biodiversity, as well as providing a detailed understanding about the mechanisms through which birds can adapt to climatic variation at an almost global level. Whereas these ideas are not specifically genetic, the addition of modern molecular techniques in conjunction with such studies would provide great additional insight such as to what extent genetic or epigenetic variation determine the responses of individuals and/or populations to different environments.

In conclusion, due to its widespread distribution and up-and-coming molecular tools, house sparrows make an ideal model in which researchers can study invasion and range expansion. The factors deemed important in the successful invasion potential of house sparrows should prove to be important for management decisions concerning invasive species as well as for conservation of threatened species undergoing range expansions and

shifts due to environmental changes. Because house sparrows have been independently introduced all over the world, researchers can identify the molecular correlates of invasion and range expansion without the problems experienced in singly introduced species. Given the global distribution pattern of house sparrows, they also present the opportunity for researchers around the world to collaborate on a similarly focused goal, of identifying the genetic mechanisms of range expansion. Finally, those characters identified as major contributors to invasion and range expansion success in the house sparrow likely are not unique to the house sparrow. However, the identification of such characters in such a well-developed invasion trajectory allows research to identify key traits important to invasions that can be pursued in other, invasive species.

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References

- Agrawal AA, 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* 294: 321–326.
- Altwegg R, Ringsby TH, Sæther BE, 2000. Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus*. *Journal of Animal Ecology* 69: 762–770.
- Anderson TR, 2006. *Biology of the ubiquitous house sparrow: From genes to populations*. New York: Oxford University Press.
- Baalsrud HT, Sæther BE, Hagen IJ, Myhre AM, Ringsby TH et al., 2014. Effects of population characteristics and structure on estimates of effective population size in a house sparrow metapopulation. *Molecular Ecology* 23: 2653–2668.
- Bakker JD, Wilson SD, 2004. Using ecological restoration to constrain biological invasion. *Journal of Applied Ecology* 41: 1058–1064.
- Bates JM, Zink RM, 1992. Seasonal variation in gene frequencies in the house sparrow *Passer domesticus*. *The Auk* 109: 658–662.
- Björda H, Cole S, Parkin D, 1986. Genetic differentiation among some populations of the house sparrow *Passer domesticus* from southwestern Norway. *Hereditas* 105: 107–114.
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP et al., 2011. A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333–339.
- Bókony V, Kulcsár A, Liker A, 2009. Does urbanization select for weak competitors in house sparrows. *Oikos* 119: 437–444.
- Bókony V, Kulcsár A, Tóth Z, Liker A, 2012. Personality Traits

- and behavioral syndromes in differently urbanized populations of house sparrows *Passer domesticus*. PLoS ONE 7: e36639.
- Bókonyi V, Lendvai ÁZ, Vágási CI, Pátraş L, Pap PL et al., 2014. Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. Behavioral Ecology 25: 124–135.
- Borer ET, Harpole WS, Adler PB, Lind EM, Orrock JL et al., 2014. Finding generality in ecology: A model for globally distributed experiments. Methods in Ecology and Evolution 5: 65–73.
- Bossdorf O, Arcuri D, Richards CL, Pigliucci M, 2010. Experimental alteration of DNA methylation affects the phenotypic plasticity of ecologically relevant traits in *Arabidopsis thaliana*. Evolutionary Ecology 24: 541–553.
- Brommer JE, Hanski IK, Kekkonen J, Väisänen RA, 2014. Size differentiation in Finnish house sparrows follows Bergmann's rule with evidence of local adaptation. Journal of Evolutionary Biology 27: 737–747.
- Burke T, Bruford M, 1987. DNA fingerprinting in birds. Nature 327: 149–152.
- Cassey P, Blackburn TM, Russell GJ, Jones KE, Lockwood JL, 2004. Influences on the transport and establishment of exotic bird species: An analysis of the parrots (Psittaciformes) of the world. Global Change Biology 10: 417–426.
- Clegg SM, Degnan SM, Kikkawa J, 2002. Genetic consequences of sequential founder events by an island-colonizing bird. Proceedings of the National Academy of Sciences 99: 8127–8132.
- Cole SR, Parkin DT, 1981. Enzyme polymorphisms in the house sparrow *Passer domesticus*. Biological Journal of the Linnean Society 15: 13–22.
- Cordero PJ, Wetton JH, Parkin DT, 1999. Extra-pair paternity and male badge size in the house sparrow. Journal of Avian Biology 30: 97–102.
- Davidson AM, Jennions M, Nicotra AB, 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14: 419–431.
- Dawson DA, Burke T, Hansson B, Pandhal J, Hale MC et al., 2006. A predicted microsatellite map of the passerine genome based on chicken-passerine sequence similarity. Molecular Ecology 15: 1299–1320.
- Dawson DA, Horsburgh GJ, Küpper C, Stewart IRK, Ball AD et al., 2010. New methods to identify conserved microsatellite loci and develop primer sets of high cross-species utility: As demonstrated for birds. Molecular ecology resources 10: 475–494.
- Dawson DA, Horsburgh GJ, Krupa AP, Stewart IRK, Skjelseth S et al., 2012. Microsatellite resources for Passeridae species: A predicted microsatellite map of the house sparrow *Passer domesticus*. Molecular ecology resources 12: 501–523.
- Dlugosch KM, Parker IM, 2008. Founding events in species invasions: Genetic variation, adaptive evolution, and the role of multiple introductions. Molecular Ecology 17: 431–449.
- Duckworth RA, Badyaev AV, 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proceedings of the National Academy of Science 104: 15017–15022.
- Edly-Wright C, Schwagmeyer P, Parker PG, Mock DW, 2007. Genetic similarity of mates, offspring health and extrapair fertilization in house sparrows. Animal behaviour 73: 367–378.
- Engen S, Ringsby TH, Saether BE, Lande R, Jensen H et al., 2007. Effective size of fluctuating populations with two sexes and overlapping generations. Evolution 61: 1873–1885.
- Fleischer RC, Johnston RF, 1982. Natural selection on body size and proportions in house sparrows. Nature 298: 747–749.
- Fleischer RC, 1983. A comparison of theoretical and electrophoretic assessments of genetic structure in populations of the house sparrow *Passer domesticus*. Evolution 37: 1001–1009.
- Fleischer RC, Johnston RF, Klitz WJ, 1983. Allozymic heterozygosity and morphological variation in house sparrows. Nature 304: 628–630.
- Fleischer RC, Lowther PE, Johnston RF, 1984. Natal dispersal in house sparrows: Possible causes and consequences. Journal of Field Ornithology 55: 444–456.
- Garnier S, Durand P, Arnathau C, Risterucci AM, Esparza-Salas R et al., 2009. New polymorphic microsatellite loci in the house sparrow *Passer domesticus*. Molecular Ecology Resources 9: 1063–1065.
- Gaston KJ, 2010. Valuing common species. Science 327: 154–155.
- Gavett AP, Wakeley JS, 1986a. Blood constituents and their relation to diet in urban and rural house sparrows. Condor 88: 279–284.
- Griffith SC, Owens IPF, Burke T, 1999a. Female choice and annual reproductive success favour less-ornamented male house sparrows. Proceedings of the Royal Society, B. 266.
- Griffith SC, Stewart IRK, Dawson DA, Owens IPF, Burke T, 1999b. Contrasting levels of extra pair paternity in mainland and island populations of the house sparrow *Passer domesticus*: Is there an 'island effect'? Biological Journal of the Linnean Society 68: 303–316.
- Griffith SC, Dawson DA, Jensen H, Ockendon N, Greig C et al., 2007. Fourteen polymorphic microsatellite loci characterized in the house sparrow *Passer domesticus* (Passeridae, Aves). Molecular Ecology Notes 7: 333–336.
- Grinnell J, 1919. The English sparrow has arrived in death valley: An experiment in nature. American naturalist 53: 468–472.
- Hagen IJ, Billing AM, Rønning B, Pedersen SA, Pärn H et al., 2013. The easy road to genome-wide medium density SNP screening in a non-model species: Development and application of a 10 K SNP-chip for the house sparrow *Passer domesticus*. Molecular Ecology Resources 13: 429–439.
- Higgins P, Peter J, 2002. Handbook of Australian, New Zealand and Antarctic Birds. Vol. 6: Pardalotes to Shrike-thrushes. Victoria: Oxford University Press.
- Hole DG, Whittingham MJ, Bradbury RB, Anderson GQA, Lee PLM et al., 2002a. Widespread local house-sparrow extinctions. Nature 418: 931–932.
- Holt RD, 2003. On the evolutionary ecology of species' ranges. Evolutionary Ecology Research 5: 159–178.
- Jensen H, Bremset EM, Ringsby TH, Saether BE, 2007. Multilocus heterozygosity and inbreeding depression in an insular house sparrow metapopulation. Molecular Ecology 16: 4066–4078.
- Jensen H, Moe R, Hagen IJ, Holand AM, Kekkonen J et al., 2013. Genetic variation and structure of house sparrow populations: Is there an island effect? Molecular Ecology 22: 1792–1805.
- Johnston RF, Selander RK, 1964. House sparrows: Rapid evolution of races in North America. Science 144: 548–550.

- Johnston RF, Selander RK, 1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25: 1–28.
- Johnston RF, Selander RK, 1973. Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. *American Naturalist* 107: 373–390.
- Kekkonen J, Hanski IK, Jensen H, Väisänen RA, Brommer JE, 2011a. Increased genetic differentiation in house sparrows after a strong population decline: From panmixia towards structure in a common bird. *Biological Conservation* 144: 2931–2940.
- Kekkonen J, Seppä P, Hanski IK, Jensen H, Väisänen RA et al., 2011b. Low genetic differentiation in a sedentary bird: House sparrow population genetics in a contiguous landscape. *Heredity* 106: 183–190.
- Kekkonen J, Jensen H, Brommer JE, 2012. Morphometric differentiation across house sparrow *Passer domesticus* populations in Finland in comparison with the neutral expectation for divergence. *Ibis* 154: 846–857.
- Klitz W, 1973. Empirical population genetics of the North American house sparrow. *Ornithological Monographs* 14: 34–38.
- Kolbe JJ, Glor RE, Rodriguez Schettino L, Lara AC, Larson A et al., 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature* 431: 177–181.
- Koren L, Nakagawa S, Burke T, Soma KK, Wynne-Edwards KE et al., 2012. Non-breeding feather concentrations of testosterone, corticosterone and cortisol are associated with subsequent survival in wild house sparrows. *Proceedings of the Royal Society B: Biological Sciences* 279: 1560–1566.
- Lack D, 1940. Variation in the introduced English sparrow. *Condor* 42: 239–241.
- Lattin CR, Romero LM, 2014. Chronic stress alters concentrations of corticosterone receptors in a tissue-specific manner in wild house sparrows *Passer domesticus*. *The Journal of Experimental Biology* 217: 2601–2608.
- Lendvai ÁZ, Chastel O, 2010. Natural variation in stress response is related to post-stress parental effort in male house sparrows. *Hormones and Behavior* 58: 936–942.
- Lendvai ÁZ, Bókony V, Chastel O, 2011. Coping with novelty and stress in free-living house sparrows. *Journal of Experimental Biology* 214: 821–828.
- Lever C, 2005. *Naturalised Birds of the World*. London: T & A D Poyser.
- Levine JM, D'Antonio CM, 2003. Forecasting biological invasions with increasing international trade. *Conservation Biology* 17: 322–326.
- Liebl AL, Martin LB, 2012. Exploratory behaviour and stressor hyper-responsiveness facilitate range expansion of an introduced songbird. *Proceedings of the Royal Society B: Biological Sciences* 279: 4375–4381.
- Liebl AL, Martin LB, 2013. Stress hormone receptors change as range expansion progresses in house sparrows. *Biology Letters* 9: 20130181.
- Liebl AL, Schrey AW, Richards CL, Martin LB, 2013a. Patterns of DNA methylation throughout a range expansion of an introduced songbird. *Integrative and Comparative Biology* 53: 351–358.
- Liebl AL, Shimizu T, Martin LB, 2013b. Covariation among glucocorticoid regulatory elements varies seasonally in house sparrows. *General and Comparative Endocrinology* 183: 32–37.
- Liebl AL, Martin LB, 2014. Living on the edge: Range edge birds consume novel foods sooner than established ones. *Behavioral Ecology* 25: 1089–1096.
- Liker A, Papp Z, Bokony V, Lendvai AZ, 2008. Lean birds in the city: Body size and condition of house sparrows along the urbanization gradient. *Journal of Animal Ecology* 77: 789–795.
- Liker a, Bókony V, Kulcsár A, Tóth Z, Szabó K et al., 2009. Genetic relatedness in wintering groups of house sparrows *Passer domesticus*. *Molecular Ecology* 18: 4696–4706.
- Lima MR, Macedo RHF, Martins TLF, Schrey AW, Martin LB et al., 2012. Genetic and morphometric divergence of an invasive bird: The introduced house sparrow *Passer domesticus* in Brazil. *PLoS ONE* 7: e53332.
- Loiseau C, Richard M, Garnier S, Chastel O, Julliard R et al., 2009. Diversifying selection on MHC class I in the house sparrow *Passer domesticus*. *Molecular Ecology* 18: 1331–1340.
- Long JL, 1981. *Introduced Birds of the World*. New York: Universe Books.
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M et al., 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710.
- Manwell C, Baker CMA, 1975. Molecular genetics of avian proteins XIII. Protein polymorphism in three species of Australian passerines. *Australian Journal of biological Sciences* 28: 545–557.
- Martin LB, Fitzgerald L, 2005. A taste for novelty in invading house sparrows *Passer domesticus*. *Behavioral Ecology* 16: 702–707.
- Martin LB, Alam JL, Imboma T, Liebl AL, 2010. Variation in inflammation as a correlate of range expansion in Kenyan house sparrows. *Oecologia* 164: 339–347.
- Martin LB, Coon CAC, Liebl AL, Schrey AW, 2014. Surveillance for microbes and range expansion in house sparrows. *Proceedings of the Royal Society B: Biological Sciences*. 281: 20132690.
- Martin LB, Liebl AL, 2014. Physiological flexibility in an avian range expansion. *General and Comparative Endocrinology* 206: 227–234.
- Martin LB, Liebl AL, Kilvitis H, *in press*. Stress-immune interactions in a range expanding bird. *General and Comparative Endocrinology*.
- Nakagawa S, Ockendon N, Gillespie DOS, Hatchwell BJ, Burke T, 2007. Assessing the function of house sparrows' bib size using a flexible meta-analysis method. *Behavioral Ecology* 18: 831–840.
- Neumann K, Wetton JH, 1996. Highly polymorphic microsatellites in the house sparrow *Passer domesticus*. *Molecular Ecology* 5: 307–309.
- Ockendon N, Griffith SC, Burke T, 2009. Extrapair paternity in an insular population of house sparrows after the experimental introduction of individuals from the mainland. *Behavioral Ecology* 20: 305–312.
- Ouyang JQ, Sharp PJ, Dawson A, Quetting M, Hau M, 2011. Hormone levels predict individual differences in reproductive success in a passerine bird. *Proceedings of the Royal Society B: Biological Sciences* 278: 2537–2545.
- Parkin DT, Cole SR, 1984. Genetic variation in the house sparrow *Passer domesticus* in the East Midlands of England. *Biological*

- Journal of the Linnean Society 23: 287–301.
- Parkin DT, Cole SR, 1985. Genetic differentiation and rates of evolution in some introduced populations of the house sparrow *Passer domesticus* in Australia and New Zealand. *Heredity* 54: 15–23.
- Pardecke J, Schwabl H, 2008. Organizational effects of maternal testosterone on reproductive behavior of adult house sparrows. *Developmental Neurobiology* 68: 1538–1548.
- Pigliucci M, Muller GB, 2010. *Evolution, the Extended Synthesis*. Cambridge, MA: MIT Press.
- Rehage JS, Sih A, 2004. Dispersal behavior, boldness, and the link to invasiveness: A comparison of four *Gambusia* species. *Biological Invasions* 6: 379–391.
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M, 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981–993.
- Richards CL, Schrey AW, Pigliucci M, 2012. Invasion of diverse habitats by few Japanese knotweed genotypes is correlated with epigenetic differentiation. *Ecology Letters* 15: 1016–1025.
- Richards EJ, 2006. Inherited epigenetic variation: Revisiting soft inheritance. *Nature Reviews Genetics* 7: 395–401.
- Richardson DS, Dawson DA, Salgueiro P, Komdeur J, Burke T, 2000. Fifty Seychelles warbler *Acrocephalus sechellensis* microsatellite loci polymorphic in Sylviidae species and their cross-species amplification in other passerine birds. *Molecular Ecology* 9: 2226–2231.
- Robbins CS, 1973. Introduction, spread, and present abundance of the house sparrow in North America. *Ornithological Monographs* 14: 3–9.
- Russell JC, McMorland AJC, MacKay JWB, 2010. Exploratory behaviour of colonizing rats in novel environments. *Animal Behaviour* 79: 159–164.
- SÆTRE GP, Riyahi S, Aliabadian M, Hermansen J, Hogner S et al., 2012. Single origin of human commensalism in the house sparrow. *Journal of Evolutionary Biology* 25: 788–796.
- Schrey A, Grispo M, Awad M, Cook M, McCoy E et al., 2011a. Broad-scale latitudinal patterns of genetic diversity among native European and introduced house sparrow *Passer domesticus* populations. *Molecular Ecology* 20: 1133–1143.
- Schrey A, Coon CAC, Grispo M, Awad M, Imboma T et al., 2012. Epigenetic variation may compensate for decreased genetic variation with introductions: A case study using house sparrows *Passer domesticus* on two continents. *Genetics Research International* doi:10.1155/2012/979751.
- Schrey AW, Grispo M, Awad M, Cook MB, McCoy ED et al., 2011b. Broad-scale latitudinal patterns of genetic diversity among native European and introduced house sparrow *Passer domesticus* populations. *Molecular Ecology* 20: 1133–1143.
- Schrey AW, Liebl AL, Richards CL, Martin LB, 2014. Range expansion of house sparrows *Passer domesticus* in Kenya: Evidence of genetic admixture and human-mediated dispersal. *Journal of Heredity* 105: 60–69.
- Shine R, Brown GP, Phillips BL, 2011. An evolutionary process that assembles phenotypes through space rather than through time. *Proceedings of the National Academy of Sciences* 108: 5708–5711.
- Skinner MK, Gurerrero-Bosagna C, Haque MM, Nilsson EE, Koop JAH et al., 2014. Epigenetics and the evolution of Darwin's finches. *Genome Biology and Evolution* 6: 1972–1989.
- Skjelseth S, Ringsby TH, Tufto J, Jensen H, Sæther BE, 2007. Dispersal of introduced house sparrows *Passer domesticus*: An experiment. *Proceedings of the Royal Society B: Biological Sciences* 274: 1763–1771.
- Slatkin M, 2009. Investigations - genetics of complex traits: Epigenetic inheritance and the missing heritability problem. *Genetics* 182: 845–850.
- Sol D, Timmermans S, Lefebvre L, 2002. Behavioural flexibility and invasion success in birds. *Animal Behavior* 63: 495–502.
- Stewart IR, Hanschu RD, Burke T, Westneat DF, 2006. Tests of ecological, phenotypic, and genetic correlates of extra-pair paternity in the house sparrow. *The Condor* 108: 399–413.
- Tóth Z, Bókonyi V, Lendvai ÁZ, Szabó K, Péntes Z et al., 2009. Kinship and aggression: Do house sparrows spare their relatives? *Behavioral Ecology and Sociobiology* 63: 1189–1196.
- Väisänen RA, Lehtälä H, 1984. Absence of genic polymorphism in a northern population of the house sparrow *Passer domesticus*. *Hereditas* 100: 161–162.
- Vangestel C, Mergeay J, Dawson DA, Vandomme V, Lens L, 2011a. Spatial heterogeneity in genetic relatedness among house sparrows along an urban-rural gradient as revealed by individual-based analysis. *Molecular Ecology* 20: 4643–4653.
- Vangestel C, Mergeay J, Dawson DA, Vandomme V, Lens L, 2011b. Developmental stability covaries with genome-wide and single-locus heterozygosity in house sparrows. *PLoS ONE* 6: e21569–e21569.
- Vangestel C, Mergeay J, Dawson DA, Callens T, Vandomme V et al., 2012. Genetic diversity and population structure in contemporary house sparrow populations along an urbanization gradient. *Heredity* 109: 163–172.
- Waddington CH, 1942. Canalization of development and the inheritance of acquired characters. *Nature* 150: 563–565.
- Weaver ICG, Cervoni N, Champagne FA, D'Alessio AC, Sharma S et al., 2004. Epigenetic programming by maternal behavior. *Nature Neuroscience* 7: 847–854.
- Wetton JH, Parkin DT, 1991. An association between fertility and cuckoldry in the house sparrow *Passer domesticus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 245: 227–233.
- Wetton JH, Parkin DT, Carter RE, 1992. The use of genetic markers for parentage analysis in *Passer domesticus* (house sparrows). *Hereditas* 69: 243–254.
- Wetton JH, Burke T, Parkin DT, Cairns E, 1995. Single-locus DNA fingerprinting reveals that male reproductive success increases with age through extra-pair paternity in the house sparrow *Passer domesticus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 260: 91–98.
- Wetzel DP, Stewart IRK, Westneat DF, 2012. Heterozygosity predicts clutch and egg size but not plasticity in a house sparrow population with no evidence of inbreeding. *Molecular Ecology* 21: 406–420.
- Whitekiller R, Westneat DF, Schwagmeyer P, Mock DW, 2000. Badge size and extra-pair fertilizations in the house sparrow. *The Condor* 102: 342–348.
- Yeh PJ, Price TD, 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. *The American Naturalist* 164: 531–542.