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2

3 Genetics of Invasive Parrot Populations

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6

7 Introduction

8 Since publication of *The Genetics of Colonizing Species* (Baker and Stebbins 1965), genetics has

9 played a key role in the study of invasive species, both from the standpoint of using such systems

10 for investigating ecological and evolutionary principles related to colonization of novel

11 environments as well as for informing management strategies. Documenting the population

12 genetics of invasive lineages has been instrumental for testing evolutionary theory related to

13 adaptation and population bottlenecks, reconstructing the complex history of biological invasions

14 to provide insights on the invasion process, and, more recently, uncovering the genetic basis of

15 features associated with invasion success (Barrett 2015). The sheer impact of invasion genetics

16 over this period was recently highlighted by a symposium marking the 50th anniversary of the

17 seminal work that covered the current state of the field, which was subsequently communicated

18 in a special issue of *Molecular Ecology* (2015) as well as an expanded edited volume (Barrett

19 2015). Aided by our ever-improving ability to mine the genomes of living organisms, such work

20 has been carried out over a wide taxonomic breadth, from zooplankton, terrestrial plants and

21 fungi, to fish, amphibians, reptiles, birds and mammals. Despite the relative frequency with

22 which psittacines invade new habitats (Joseph, 2014), only a limited number of invasion genetics

23 studies have been conducted in parrots. These have largely focused on understanding the factors
24 contributing to invasion success, namely investigating the source(s) of introduction, identifying
25 the factors involved in the establishment of self-sustaining populations, and reconstructing
26 dispersal pathways and modes of spread (Edelaar et al. 2015; Goncalves da Silva et al. 2010;
27 Jackson et al. 2015a; Jackson et al. 2015b; Russello et al. 2008). While these studies have
28 provided new insights into these topics in a select number of species, the relative dearth of
29 studies on the genetics of invasive parrot species represents an open challenge for investigators
30 seeking to understand how and why parrots are so successful at colonizing new habitats.

31 In this chapter, we will first summarize the broader literature regarding how genetic
32 information can be used for studying the origin(s), establishment and spread of invasive species,
33 with an emphasis on avian invaders. We will then review recent studies demonstrating the utility
34 of genetics for enhancing our understanding of parrot population history, structure and behavior;
35 these provide an important baseline for understanding genetic patterns in invasive parrots. This
36 section is followed by a case study of monk parakeets (*Myiopsitta monachus*), arguably the most
37 intensively studied parrot species with regard to the genetics of invasion success. We conclude
38 with a discussion of future directions afforded by genomic technologies that could provide
39 deeper insights into genetic and epigenetic mechanisms of invasion success as well as enhance
40 our toolkit for monitoring and management of invasive species.

41

42 Genetics of Invasion History

43 Genetic information has proven instrumental in studying all phases of the invasion process,
44 including origin(s), establishment and spread of invasive species (Sakai et al. 2001). All of these
45 features are critical for improving our understanding of the ecological and evolutionary

46 mechanisms underlying invasion success. As such, molecular approaches have allowed us to
47 identify the: 1) native source population(s) and number of introductions from each source
48 (Lockwood et al. 2005); 2) number of individuals introduced from each event; and 3) dynamics
49 of expansion following establishment (Cristescu 2015; Estoup and Guillemaud 2010). Such
50 information is critical for understanding how invasions occur, which in turn can inform strategies
51 for prevention, eradication and/or containment (Mack et al. 2000).

52

53 *Origin: source and number of introductions*

54 The number and origin(s) of source populations are key considerations for reconstructing
55 invasion history. For example, multiple introductions have been frequently correlated with the
56 success of invasive species' establishment and spread (Barrett and Husband 1990; Sakai et al.
57 2001). Indeed, two of North America's most successful invasive bird species, European starlings
58 (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*), became established only after
59 repeated introductions (Ehrlich 1989). For parrots, genetic reconstructions of the number and
60 origin(s) of source populations have been conducted for monk parakeets (reviewed below) and
61 rose-ringed parakeets (*Psittacula kramera*). Native to Asia and sub-Saharan Africa, rose-ringed
62 parakeets have established self-sustaining breeding populations in over 35 countries (Lever
63 2005) and are considered one of Europe's top 100 worst alien species (DAISIE European
64 Invasive Alien Species Gateway 2008). Using mitochondrial DNA haplotypic and nuclear
65 microsatellite genotypic data from across the native and invasive ranges, Jackson et al. (2015b)
66 identified native populations in Asia, specifically from Pakistan and northern India, as the
67 predominant source for invasive populations in Europe and on islands in the Indian Ocean
68 (Mauritius and Seychelles; Figure 1A-D). Moreover, the most common haplotypes in the

69 invasive populations in Europe were those found in the more northerly native populations where
70 rose-ringed parakeets naturally tolerate colder parts of their range (Figure 1A-B), leading the
71 authors to hypothesize that cold tolerance may be a factor in their establishment success (Jackson
72 et al. 2015b). Interestingly, a number of haplotypes ($n = 30$) were identified in the invasive range
73 that were not previously detected in the native range. This disparity was most likely due to
74 unequal sampling (96 native vs. 696 invasive samples). Yet, in tandem with results based on
75 nuclear genotypic data, the authors also suggested this pattern could be attributed to admixture
76 between invasive rose-ringed parakeets from widely distributed sources in Asia and Africa
77 (Figure 1D) (Jackson et al. 2015b). Admixture between divergent genotypes originating from
78 different source populations have been found in other systems (reviewed in Dlugosch and Parker
79 2008), offering the potential for positive genetic interactions among previously isolated alleles
80 and for adaptive evolution that can increase fitness (Keller and Taylor 2010; Kolbe et al. 2004),
81 although such benefits may be constrained by negative genetic interactions (Barker et al. 2018;
82 Bertelsmeier and Keller 2018).

83

84 FIGURE 1 HERE

85

86 *Establishment: propagule pressure*

87 In addition to identifying the geographic location(s) and number of source populations, the
88 number of individuals per introduction event is a key consideration in the ultimate establishment
89 of self-sustaining breeding populations outside a species' native range. Together with the number
90 of independent introductions, the number of individuals introduced is collectively known as
91 propagule pressure (Carlton 1996). This has been a particularly important factor in the

92 establishment success of invasive birds (Blackburn and Duncan 2001). The simultaneous
93 introduction of many individuals has been shown to buffer against genetic bottlenecks
94 (Simberloff 2009), with some introduced populations having levels of genetic variation similar to
95 or higher than native populations (Kolbe et al. 2004). As a result, propagule pressure may help
96 guard against the effects of demographic stochasticity (Lockwood et al. 2005). For parrots,
97 propagule pressure exerted by the legal and illegal pet trade has been implicated in their
98 successful establishment outside of their native range (Cassey et al. 2004). For example, most
99 rose-ringed parakeet populations in Europe likely resulted from intentional or unintentional
100 release of caged birds (Strubbe and Matthysen 2009). Subsequent genetic investigation revealed
101 that the relative proportion of Asian vs. African-origin birds were consistent with European
102 importation records further implicating the pet trade as a source of propagule pressure (Jackson
103 et al. 2015b), similar to what has been found for monk parakeets (see below).

104

105 *Spread: dynamics of geographical expansion*

106 Once non-native individuals have been introduced and established, genetic studies can
107 reconstruct the dynamics of geographical expansion. Although multiple introductions of invasive
108 species has been demonstrated to be a common phenomenon, including for many of the
109 examples above, an alternative scenario for expansion has been shown by way of widespread
110 secondary invasions from a particularly successful invasive population that acts as a source for
111 establishing populations in new areas (“invasive bridgehead effect”; Estoup and Guillemaud
112 2010). A host of genetic studies have demonstrated the invasive bridgehead effect in a range of
113 species including the harlequin ladybeetle (*Harmonia axyridis*; Lombaert et al. 2010), Western
114 corn rootworm (*Diabrotica virgifera virgifera*; Miller et al. 2005), Colorado potato beetle

115 (*Leptinotarsa decemlineata*; Grapputo et al. 2005), American bullfrog (*Rana catesbeiana*;
116 Ficetola et al. 2008) and European green crab (*Carcinus maenas*; Darling et al. 2008). Although
117 to our knowledge this phenomenon has not been demonstrated genetically in invasive parrots,
118 house sparrows do appear to have expanded due to the invasive bridgehead effect. Using nuclear
119 microsatellite genotypic data across the native and invasive ranges, Schrey et al. (2011) found
120 that introduced North American populations of house sparrows likely originated from only a few
121 sources, and that on-going gene flow is occurring in the invasive range. It is important to note
122 that this house sparrow study was not explicitly designed to test the invasive bridgehead effect,
123 but future work could employ genetic data and approximate Bayesian computation methods to
124 evaluate different invasion scenarios. Given the potential for the self-accelerating process
125 whereby invasion begets invasion, some authors recommend heightened vigilance against
126 invasive bridgehead populations (Bertelsmeier and Keller 2018; Lombaert et al. 2010). We argue
127 that, at the very least, genetic studies examining this and other invasion scenarios are warranted
128 in other systems, including for volant species with high dispersal capacity, such as parrots.

129

130 Genetic Variation and Structure in Natural Parrot Populations

131 Given the dearth of studies of parrots within their naturalized ranges, understanding patterns of
132 genetic variation in the native range may represent the best alternative for inferring how invasion
133 shapes the genetics of naturalized parrots. As these native populations are typically the source of
134 individuals that eventually establish naturalized populations through the invasion process,
135 genetic patterns of native populations provide an informative baseline for the degree of genetic
136 variation and structure that might be expected in the naturalized range. For example, if source
137 populations typically have low levels of genetic variability, then low levels of variability would

138 be expected in the derived naturalized populations, which might limit their potential for
139 evolutionary responses to changing selection regimes in their new range. There might also be
140 interesting interactions between the genetic patterns in the native range population and the
141 manner in which individuals are captured for the pet trade that would impact genetic patterns in
142 naturalized populations. For example, if natural populations tend to be highly structured, with
143 most of the genetic variability occurring between isolated populations, and naturalized
144 populations are drawn from only one of these populations (i.e. if the pet trade sources from only
145 one part of the native range), then naturalized populations would tend to be genetically
146 homogeneous. On the other hand, if sourcing of individuals for the pet trade was more
147 geographically widespread, then admixture between sources might result in any given
148 naturalized population having more variability than a single native population (e.g. rose-ringed
149 parakeets; Jackson et al. 2015b).

150 In this section, we review studies of the population genetics of wild parrot populations to
151 address the following questions: 1) how structured is genetic variation in wild parrot populations;
152 2) at what scale is this structure observed; 3) what does this tell us about gene flow among parrot
153 populations; and 4) how genetically diverse are typical parrot populations? It is important to note
154 at the outset that many (but by no means all) studies of population genetics in parrots have been
155 motivated by conservation concerns for the species studied. This focus could potentially
156 introduce a bias, because species of conservation concern tend to have small and declining
157 populations, and are less genetically diverse than non-threatened populations due to genetic drift.
158 Conclusions about genetic diversity and degree of structure might also be influenced by the
159 geographic scale and intensity of sampling of a particular study. Consequently, we organize our
160 review below by geographic scale, focusing first on range-wide studies of genetic structure, then

161 on studies of variation among populations on a smaller scale, and finally with studies of genetic
162 diversity within populations.

163

164 *Phylogeography and cryptic diversity*

165 Studies of phylogeography typically examine patterns of genetic variation across large parts of a
166 species range or among members of a closely-related species complex. They may have as their
167 goal a better understanding of the evolutionary history of a species, or of relationships among
168 component subspecies. Another common goal of studies at this scale is the detection of cryptic
169 species, that is, subspecies or populations within a species that are sufficiently differentiated
170 from other such populations that they warrant full species status. Such studies often have
171 conservation implications since levels of endangerment and threat are largely determined at the
172 species level; elevating a rare or declining subspecies to full species level can, in theory, quickly
173 lead to a change in its conservation status and the protections afforded to it.

174 A number of phylogeographic studies have focused on species in the Neotropics. Among
175 the first was Eberhard and Bermingham's (2004) study of the yellow-headed amazon species
176 complex, which consist of three closely related taxa variously described as subspecies of
177 *Amazona ochrocephala* or as the full species *A. ochrocephala*, *A. oratrix*, and *A. auropalliata*.
178 Using mitochondrial and nuclear DNA sequence data, the authors found distinct differences
179 between the previously identified subspecies *A. oratrix* and *A. auropalliata* that occur in
180 Mesoamerica (Mexico and Central America) and between those lineages and the South
181 American (sub)species *A. ochrocephala*. In contrast, within South America they found less
182 genetic structure in *A. ochrocephala* sampled across the Amazon basin, as well as evidence of
183 introgression between this species and a closely related congener, *A. aestiva* (Eberhard and

184 Birmingham 2004). Another study conducted at the same scale was Wenner et al.'s (2012)
185 investigation of cryptic speciation in the mealy amazon, *A. farinosa*. These authors also used
186 genetic data from both mitochondrial and nuclear DNA to identify deep divisions between
187 Central and South American subspecies and more recent divergences between pairs of
188 subspecies found within each of these regions (Wenner et al. 2012). This study led to the
189 reclassification of the two subspecies to full species status. Similarly, Masello et al.'s (2011)
190 study of the burrowing parrot, *Cyanoliseus patagonus*, used mitochondrial DNA sequences from
191 several loci to examine the degree of differentiation among four subspecies, three found east of
192 the Andes, ranging from northern to central Argentina, and one west of the Andes in central
193 Chile. They found strong differentiation across the Andes, and evidence of genetic structure
194 between two of the subspecies to the east of the Andes, while the third subspecies appeared to
195 consist of a long-standing hybrid zone between the other two (Masello et al. 2011).

196 Studies of two other parrot species examined variation across the Amazon Basin and
197 neighboring areas of central South America. In both cases, these studies found contrasting
198 patterns in maternally-inherited mitochondrial DNA sequences versus biparentally-inherited
199 nuclear microsatellite markers. In the turquoise-fronted amazon, *A. aestiva*, mitochondrial DNA
200 sequences detected distinct variation among two subspecies found in the northeastern and
201 southwestern portions of the species range, while nuclear microsatellites showed only weak
202 differentiation across the entire range (Caparroz et al. 2009b; Leite et al. 2008). Likewise, a
203 study of the blue and yellow macaw, *Ara ararauna*, in the same geographic region detected
204 structure between eastern and western populations using mitochondrial DNA sequences, while
205 the nuclear microsatellite data did not reveal any structure (Caparroz et al. 2009a).

206 Several studies have examined the degree of differentiation between disjunct populations
207 of species distributed across either true islands, or isolated islands of suitable habitat. A series of
208 studies have examined genetic structure in the highly endangered hyacinth macaw,
209 *Anodorhynchus hyacinthinus*, of Brazil. The first used nuclear and mitochondrial DNA markers
210 to test for genetic differentiation between two populations located 100 km apart in the Pantanal
211 region and a third disjunct population in the Gerais region (Faria et al. 2008). The authors found
212 no evidence of differentiation between the two populations in the Pantanal, but significant
213 differences were found between those populations and the disjunct population in Gerais using
214 nuclear microsatellites. A more recent study expanded the scale of sampling within the Pantanal
215 region and added sampling from a third disjunct region in eastern Amazonia (Presti et al. 2015).
216 This work confirmed the previous finding of significant differentiation between the Gerais and
217 Pantanal regions, but lower differentiation between the disjunct Gerais and eastern Amazonia
218 regions. The authors also detected significant differentiation between populations in the north
219 and south of the Pantanal region located about 700 km apart, a result that was unexpected given
220 the lack of an obvious barrier to dispersal between populations within the Pantanal. Overall, the
221 level of genetic diversity exhibited by hyacinth macaws was considered low (average observed
222 heterozygosity = 0.35); a related study found that levels of genetic diversity in this species were
223 lower than those found in two other macaw species (Faria and Miyaki 2006). Surprisingly, there
224 was no suggestion in these data that the three disjunct populations represented either true or
225 incipient species, perhaps either because of relatively recent isolation of the disjunct populations
226 or because of ongoing gene flow. In contrast, Russello et al.'s (2010) study of the Cuban amazon
227 (*A. leucocephala*) species complex did detect evidence for cryptic diversity among island
228 populations within the Bahamas and across the Greater Antilles. Using both mitochondrial DNA

229 and nuclear microsatellite data, the authors found evidence for the genetic distinctiveness of the
230 previously identified subspecies found on the islands of Cuba, Grand Cayman, and Cayman
231 Brac, and also showed previously unrecognized differences among populations on three different
232 islands in the Bahamas (Russello et al. 2010).

233 There have been fewer such studies outside the Neotropics, but those that have been
234 conducted typically show similar patterns to those seen in the Americas. A study of the declining
235 eastern ground parrot (*Pezoporus wallicus*) in Australia found deep genetic divisions between
236 eastern and western populations that are found on different sides of the continent and are
237 currently separated by more than 1500 km of inhospitable habitat (Murphy et al. 2011). A recent
238 study by Jackson et al. (2015a) examined the evolutionary relationships among extant and extinct
239 species in the genus *Psittacula* from Madagascar and surrounding islands in the western Indian
240 Ocean. They found that most of the populations endemic to various islands had diverged to the
241 level of distinct species, indicating low levels of gene flow after initial colonization.
242 Interestingly, the phylogenetic diversity of this region initially decreased with European
243 colonization and subsequent extinctions, but was partially restored by another human-mediated
244 influence, namely the introduction of the invasive rose-ringed parakeet (Jackson et al. 2015a).
245 Finally, a recent study of the red-tailed black cockatoo (*Calyptorhynchus banksii*) is one of the
246 first to combine the power of genome-wide sampling of single nucleotide polymorphisms
247 (SNP's) with the expanded sampling provided by museum specimens (Ewart et al. 2019) to
248 examine phylogeographic questions. The authors examined variation in samples from across this
249 species' continent-wide range in Australia and detected robust geographic structure among
250 different regions that only partially corresponded to established subspecies boundaries (Ewart et
251 al. 2019).

252 Four general patterns have emerged from these studies of phylogeography. The first is
253 that populations are often structured over large geographic scales, such as between Central
254 American and South American populations, among islands in the Caribbean Sea or Indian
255 Ocean, or on opposite sides of the continents of South America or Australia. Such divisions often
256 correspond to contemporary barriers to dispersal like mountains, oceans, or inhospitable habitats,
257 or to past barriers created by Pleistocene climate shifts and sea level changes. The second general
258 pattern to emerge is that these divisions often correspond to subspecies boundaries previously
259 identified using plumage and morphology. Examples include studies of the mealy amazon and
260 the turquoise-fronted amazon, which identified genetic differences between some preexisting
261 subspecies (Caparroz et al. 2009b; Wenner et al. 2012). In many cases, confirmation of these
262 evolutionary differences has directly impacted the conservation status of the taxa in question. In
263 other cases, there are more complex patterns identified, such as where secondary hybridization
264 and introgression has reduced historically-present genetic differences in the burrowing parrot
265 (Masello et al. 2011) or the yellow-headed amazon *A. ochrocephala*/*A. aestiva* species complex
266 (Eberhard and Bermingham 2004; Leite et al. 2008). More rarely, such studies identify true
267 cryptic diversity among populations that have not previously been identified as genetically
268 distinct; a prime example is Russello et al.'s (2010) study that found consistent differences
269 among populations on three different islands in the Bahamas, one of which had already become
270 extinct at the time of the study. The third general pattern is that less structure is apparent between
271 populations sampled at smaller scales than species-wide, suggesting that dispersal-mediated gene
272 flow is relatively strong in parrots, a point that is reinforced by studies in the next section. The
273 fourth general pattern is that structure is more likely to be detected with some types of genetic
274 markers than others. In particular, mitochondrial DNA, with its maternal transmission, has a

275 smaller effective population size than bi-parentally inherited and recombining nuclear autosomal
276 markers such as microsatellites, which can lead to a greater degree of structuring at
277 mitochondrial DNA. This structure can be further compounded if males tend to disperse and
278 females are more philopatric, leading to less mixing of mitochondrial DNA haplotypes. Both
279 factors may have been at play in the studies of the blue and yellow macaw and turquoise-fronted
280 amazon that found more structure using mitochondrial DNA sequences than microsatellite alleles
281 (Caparroz et al. 2009a; Caparroz et al. 2009b; Leite et al. 2008). These results have interesting
282 implications for naturalized populations of parrots. In particular, the suggestion that dispersal-
283 mediated gene flow is high in many species reinforces the idea that parrots are candidates for the
284 invasive bridgehead effect described above, in which initial founding populations give rise to
285 many dispersed naturalized populations.

286

287 *Population structure*

288 While the distinction between studies of phylogeography and population structure is somewhat
289 arbitrary, there have been a number of studies in parrots that have focused on investigating the
290 degree of genetic structure among populations on a smaller scale than range-wide. Typically,
291 these studies focus on inferring gene flow between populations that are hypothesized to be
292 isolated either behaviorally or through habitat fragmentation. Among the first of such studies
293 were two by Wright and colleagues (2001, 2005) that employed both mitochondrial DNA
294 sequences and nuclear microsatellites to examine genetic structure among populations of the
295 yellow-naped amazon (*A. auropalliata*) in Costa Rica distributed over a 100 km span. The
296 primary focus of these studies was testing whether behavioral differences represented by two
297 vocal dialects in learned contact calls corresponded to differences at neutral genetic markers.

298 Both types of markers found no evidence of genetic differences across dialect boundaries, and
299 instead indicated genetic panmixia among populations at this scale (Wright et al. 2005; Wright
300 and Wilkinson 2001).

301 A number of studies have examined the effects of human-induced habitat fragmentation
302 on gene flow and population genetic structure. A study of the threatened red-tailed amazon, *A.*
303 *brasiliensis*, found no evidence of greater DNA fingerprint band sharing within than between two
304 populations in Brazil (Caparroz et al. 2006). This result suggests that there is no genetic
305 differentiation between these two populations separated by 100 km, despite extensive
306 fragmentation of this species' coastal Atlantic Forest habitat (Caparroz et al. 2006). A study of
307 the nomadic and critically endangered swift parrot, *Lathamus discolor*, examined the degree of
308 population structure among several populations nesting on different parts of Tasmania and
309 neighboring offshore islands (Stojanovic et al. 2018). Population genetic analyses based on
310 microsatellite genotypic data suggested panmixia of these populations despite extensive habitat
311 fragmentation; while the lack of inbreeding might be viewed as a positive for species
312 conservation, the authors point out that their results emphasize the need to treat the entire species
313 as a single conservation unit in population viability models (Stojanovic et al. 2018). Another
314 study from Australia examined genetic variation among populations of two species collectively
315 known as white-tailed black cockatoos, *Calptorhynchus baudinii* and *C. latirostris*, in the
316 southwestern portion of mainland Australia (White et al. 2014). These two species have
317 undergone dramatic declines as this region has experienced extensive habitat fragmentation due
318 to clearing for intensive agriculture. The authors used both contemporary and historical samples
319 and a large panel of microsatellites to assess whether population isolation had led to genetic
320 differentiation. They found clear genetic differences between populations to the east and the west

321 of a large wheatbelt; interestingly, this geographic differentiation was much stronger than that
322 separating samples from the two putative species. The authors suggested that this geographic
323 differentiation was driven primarily by the loss of allelic diversity in the contemporary eastern
324 population following isolation from the western population (White et al. 2014). Finally, a study
325 by Raisin and colleagues (2012) examined changes in genetic differentiation among populations
326 of the echo (or Mauritius) parakeet (*Psittacula echo*) prior to and following extensive
327 translocations undertaken to maximize population growth of this highly-endangered island
328 endemic. They found that prior to translocations, the population most geographically isolated by
329 extensive habitat fragmentation was the most genetically distinct from other populations. Perhaps
330 unsurprisingly, this difference disappeared after individuals were translocated into this
331 population. The authors suggested that loss of genetic structure was a beneficial, albeit
332 unintended, outcome of conservation efforts and that the new genetic panmixia likely mimicked
333 the uniform genetic structure of the species hypothesized to exist prior to human-mediated
334 habitat loss (Raisin et al. 2012).

335 To date, few papers have examined population structure of parrots in relatively-
336 undisturbed settings. One exception is a study by Olah and colleagues (2017) of scarlet macaw
337 (*Ara macao*) populations in the lowlands of the Peruvian Amazon. They used microsatellite
338 markers to examine variation among samples collected at clay licks and nest sites from three
339 populations along an 80 km stretch of the Tambopata river. They found weak, but statistically
340 detectable differentiation among the three sites driven primarily by the higher elevation site that
341 was separated from the others by a mountain ridge (Olah et al. 2017).

342 In summary, these studies suggest that, under undisturbed conditions, gene flow among
343 populations tends to be high in parrots with an absence of marked population structure. When

344 human actions lead to habitat fragmentation, however, gene flow can be reduced, leading to
345 genetic differentiation among isolated populations. It should be noted, however, that most of
346 these studies have focused on larger-bodied parrots with fairly general habitat preferences; it
347 would be interesting to conduct similar studies in smaller-bodied parrots or habitat specialists,
348 both of which might be expected to disperse less widely. These predictions could also be
349 examined in naturalized species, which range in size from small lovebirds to large amazon
350 parrots.

351

352 Genetic Diversity Within Populations

353 A handful of studies have examined the patterns of genetic variation within one or a few
354 populations of parrots. Without exception these have all focused on endangered species in which
355 a substantial portion of the population is maintained in captivity, with the primary questions
356 being how much genetic diversity remains in captive population(s) and how can it be maximized
357 via translocations or managed breeding. One of the earliest studies to use microsatellites to
358 characterize within-population genetic variation was conducted for the endangered St. Vincent
359 amazon (*A. guildingii*), where the authors found moderate levels of variation and detected two
360 subgroups characterized by a high and low degree of relatedness, respectively (Russello and
361 Amato 2004). This information directly led to recommendations of specific breeding pairs for
362 maximizing genetic diversity and minimizing inbreeding in this captive population of high
363 conservation value (Russello and Amato 2004). Another study, which collected microsatellite
364 and mitochondrial DNA data from two captive populations of the Cuban amazon (*Amazona*
365 *leucocephala*), found that the Zapata Swamp breeding population contained two distinct
366 lineages, one of which was also found in the other breeding population located in Managua

367 (Milian-Garcia et al. 2015). The authors hypothesized that the unique lineage in Zapata Swamp
368 might represent individuals unintentionally introduced from the Cayman Brac subspecies of *A.*
369 *leucocephala*. As the population overall had moderately high levels of heterozygosity and low
370 levels of inbreeding, the authors suggested that these two lineages should be managed separately
371 until further data could be collected to better characterize their original sources. In contrast, a
372 study of the kakapo, *Strigops habroptilus*, found high levels of inbreeding and low
373 heterozygosity as measured by microsatellites in this highly endangered island endemic species
374 (White et al. 2015). Notably, lower levels of heterozygosity in females were significantly
375 associated with lower rates of hatching and fecundity, suggesting that the genetic bottleneck
376 experienced by this species had led to inbreeding depression (White et al. 2015).

377 While the number of genetic studies within populations is small, they do suggest that
378 populations that undergo severe bottlenecks have the potential to experience deleterious effects
379 from inbreeding. This result is quite relevant to invasive or naturalized populations, as many
380 would be expected to undergo genetic bottlenecks due to founding events involving just a few
381 breeding individuals.

382

383 Genetics of Invasion Success: The Case of the Monk Parakeet

384 Monk parakeets (*Myiopsitta monachus*) have emerged as a model species in avian invasion
385 genetics. Genetic studies have led to insights about where invasive monk parakeets originated,
386 how populations were established in climatically distinct parts of the world, and how such
387 populations may spread within the invasive range. Pinpointing source populations, a crucial step
388 when asking questions about the ecology and evolution of invasive species, has been a primary
389 focus of this research. Identifying invasive monk parakeets' original sources of genetic and

390 phenotypic variation is an undertaking that has employed broad-scale sampling across the native
391 and invasive ranges, and tracked recent innovations in genetic tools.

392 Source populations for invasive monk parakeets were first assessed with mitochondrial
393 DNA by Russello et al. (2008), who characterized patterns of genetic similarity and structure
394 among invasive populations in the United States and native populations in South America.
395 Parakeets in the United States were most genetically similar to those in northern Argentina and
396 Uruguay, a narrow region of this species' native range that has been tapped heavily for the global
397 pet trade (Russello et al. 2008). This study highlighted one of the first stages of the monk
398 parakeet invasion pathway, demonstrating that dispersal out of the native range was indeed
399 human-mediated and associated with the pet trade (Russello et al. 2008). A subsequent study,
400 relying on both mitochondrial DNA and nuclear microsatellites, and additional sampling in the
401 native and invasive ranges, provided more evidence for northern Argentina and Uruguay as a
402 source region (Figure 1 A-E; Edelaar et al. 2015). Parakeets sampled from pet shops in Spain,
403 representing an intermediate step in the invasion process between initial dispersal out of the
404 native range and population establishment in the invasive range, were genetically similar to this
405 source region (Edelaar et al. 2015), further supporting the role of the global pet trade in monk
406 parakeet invasions (Figure 2D-E).

407

408 FIGURE 2 HERE

409

410 These studies have led to important insights about potential source populations and monk
411 parakeets' invasion pathways. Some limitations remain, however, that are being addressed in
412 ongoing research to more closely evaluate origins of invasive populations. First, while both

413 studies identified northern Argentina and Uruguay as a likely source region for invasive monk
414 parakeets, sampling has been so far insufficient to identify South American source populations at
415 a finer geographic scale. The Convention on International Trade in Endangered Species of Wild
416 Fauna and Flora (CITES) documents Uruguay as the primary legal exporter of monk parakeets
417 from their native range (Convention on the International Trade in Endangered Species of Wild
418 Fauna and Flora 1973). Indeed, from 1975–2015, 97% of monk parakeets that were legally
419 imported to Mexico originated in Uruguay (Hobson et al. 2017). However, previous genetic
420 sampling of monk parakeets in Uruguay has been sparse (Edelaar et al. 2015; Russello et al.
421 2008). Second, recent innovations in sequencing technology provide the means to sample
422 genomes to a much greater degree than ever before, returning thousands of SNPs across many
423 individuals. Ongoing research is focused on extending geographic sampling to Uruguay and
424 broadening the sampling of individual genomes with restriction site-associated DNA sequencing
425 (RADseq) to shed additional light on source populations for invasive monk parakeets (Smith-
426 Vidaurre et al. unpublished data).

427 Genetic studies with monk parakeets have also identified patterns of population genetic
428 structure that provide clues about population establishment. Evolutionary theory predicts that
429 species arriving in new habitats are vulnerable to genetic bottlenecks, or decreased genetic
430 diversity (Dlugosch and Parker 2008). The impact of such bottlenecks depends on the size and
431 genetic variation of the founding population, and the length of time that the population remains
432 small (Nei et al. 1975). Stronger bottlenecks can increase inbreeding, potentially inhibiting
433 population resilience to novel selection pressures, such as disease or changing climates, and are
434 generally thought to impede establishment after introduction (Bock et al. 2015; Dlugosch and
435 Parker 2008). All genetic studies comparing invasive and native populations of monk parakeets

436 to date have found evidence of genetic bottlenecks associated with invasion (Edelaar et al. 2015;
437 Russello et al. 2008). Edelaar et al. (2015) identified decreasing genetic variation in concert with
438 increasing latitude, a pattern repeated across invasive populations in both the U.S. and Spain.
439 This pattern suggests either increasingly strong genetic bottlenecks with increasing latitude, or
440 alternatively, parallel adaptation to shared urban and climatic selection pressures (Edelaar et al.
441 2015). Some invasive populations show evidence of weaker genetic bottlenecks, such as the
442 Canary Islands, which could be due to many founders originating from a single genetically
443 diverse source population, admixture among multiple source populations after dispersal from the
444 native range, and/or weaker selection pressures in that part of the invasive range (e.g. less harsh
445 winters; Edelaar et al. 2015). Research is ongoing to better characterize genetic bottlenecks and
446 the possibility of adaptation to parallel selection pressures. Despite exhibiting genetic
447 bottlenecks, invasive monk parakeet populations in the U.S. and Spain show no signs of a
448 decline that might be attributable to inbreeding, with the possible exception of the Hyde Park
449 population in Chicago (Pruett-Jones et al. 2012). Taken together, these findings suggest that
450 founder effects and/or genetic bottlenecks do not prohibit monk parakeet population
451 establishment, as has been observed in other invasive species (Dlugosch and Parker 2008).
452 Future work should extend the assessment of genetic bottlenecks and multiple source populations
453 to other regions of the invasive range to better understand population establishment in this
454 invasive parrot.

455 Additional processes that could influence invasive population establishment and spread
456 remain understudied in monk parakeets. For instance, we know little about gene flow among
457 invasive populations over local or broader geographic scales, which could ameliorate the
458 negative effects of genetic bottlenecks by increasing genetic diversity (Dlugosch and Parker

459 2008). Most studies to date have conducted sampling at a broad geographic scale, limiting our
460 ability to ask whether monk parakeet establishment has been influenced by gene flow among
461 neighboring invasive populations, or whether populations in parts of the invasive range (e.g.
462 Florida, U.S.) have spread by splitting off from a single successful population (i.e. invasive
463 bridgehead effect). In that regard, Goncalves da Silva et al. (2010) used species-specific
464 microsatellites (Russello et al. 2007) to reconstruct a dispersal distance estimate of nearly 100km
465 for invasive monk parakeets in Florida. While this estimate is high, it suggests that invasive
466 monk parakeets could establish new populations within 100km of an existing population.
467 Second, we do not know whether introduction through the global pet trade has led to sex-ratio
468 biases in invasive populations, which could impact establishment by altering population growth
469 and/or patterns of genetic diversity. Finally, we know little about reproductive strategies in the
470 invasive range that could influence population establishment. For instance, extra-pair copulation
471 can alter the genetic diversity of a female's brood, and is known to be common across birds
472 (Jennions and Petrie 2000). Extra-pair copulation could work in tandem with standing genetic
473 variation of an invasive population and sex-ratio biases to impact establishment. Monk parakeets
474 nest colonially and communally, a strategy that provides many opportunities for extra-pair
475 copulation. A study of native monk parakeets in Córdoba, Argentina reported significant levels
476 of extra-pair paternity within broods, suggesting that monk parakeet nesting strategies are
477 associated with copulation outside the social pair bond (Martínez et al. 2013). However, whether
478 this reproductive strategy impacts invasive monk parakeet establishment success remains an
479 open question.

480 A promising approach to assess the establishment and spread of invasive monk parakeet
481 populations is the reconstruction of invasion pathways. Such reconstructed pathways, based on

482 genetic data, are hypotheses about the invasion process that complement previous studies of
483 population genetic patterns. Invasion pathways encompass estimates of historic and recent
484 population sizes, bottleneck duration, and historic or recent admixture. Multiple hypotheses can
485 be tested per invasive population, allowing for the simultaneous evaluation of hypotheses with
486 different source populations and demographic processes. Recently developed analytical tools
487 facilitate hypothesis-testing using mitochondrial DNA or microsatellite markers (Estoup and
488 Guillemaud 2010), as well as highly dimensional SNP markers that provide finer resolution of
489 individual genomes (Raynal et al. 2016; Smith et al. 2017). This research is currently ongoing
490 with monk parakeets, employing SNPs to identify source populations and potential demographic
491 and selection processes underlying invasive population establishment (Smith-Vidaurre et al.
492 unpublished data). Accounting for demographic processes that impact population establishment
493 is an important baseline to ask whether establishment has also been influenced by adaptation to
494 new selection pressures. Future research should extend these methods to more populations across
495 the invasive range, and evaluate patterns of spread by employing finer-scale geographic
496 sampling and methods such as the genetic directionality index (Peter and Slatkin 2013) to
497 identify whether new invasive populations are founded by long- or short-range dispersal from
498 existing populations (e.g. invasive bridgehead effect), versus independent colonization by
499 escaped or released birds from the pet trade.

500 Exciting and challenging directions for future research with monk parakeets include
501 assessing gene flow and genetic similarity among invasive populations at local and broader
502 geographic scales, extending such genetic studies to more areas across the invasive range, and
503 testing hypotheses about adaptation to new selection pressures, which will shed light on
504 candidate molecular markers and networks under selection following invasion. A recent study

505 with native monk parakeets identified high heritability of morphological traits, suggesting that
506 some traits, such as tarsus length and bill width, could be sensitive to new selection pressures in
507 the invasive range (Martínez et al. 2018). Cold tolerance may serve as an important selection
508 pressure underlying invasive population establishment and spread (Edelaar et al. 2015), as
509 suggested for rose-ringed parakeets (Jackson et al. 2015b). Gene networks or other molecular
510 markers associated with thermal tolerance are promising candidates for future research. As monk
511 parakeets are recent invaders that have experienced relatively few generations of natural
512 selection, endeavors to study evolutionary responses in invasive populations should consider not
513 only changes in SNP allele frequencies as signatures of selection, but also changes in molecular
514 markers sensitive to environmental change over short timescales, such as transposable elements
515 and DNA methylation (Rey et al. 2016; Stapley et al. 2015).

516

517 Future Directions

518 Advances in genomic technologies now allow us to mine the genome at an unprecedented level
519 to enhance our understanding of fundamental questions in ecology and evolutionary biology,
520 including those related to invasion success. Although parrots in general have low environmental
521 and economic impacts relative to the most invasive species on the planet (e.g. kudzu, *Pueraria*
522 *montana*; Asian long-horned beetles, *Anoplophora glabripennis*; Asian carp, *Cyprinus carpio*;
523 zebra mussels, *Dreissena polymorpha*), systems such as the monk parakeet and rose-ringed
524 parakeet may still provide opportunities for testing hypotheses related to invasion success, as
525 well as opportunities to evaluate genomics, epigenomics and genome editing as tools for more
526 effective management.

527 Since the seminal volume edited by Baker and Stebbins (1965), there has been much
528 debate over the primary sources of genetic variation important for invasion success: pre-existing
529 standing variation, new beneficial mutations, and/or introgression by way of hybridization of
530 naturally distinct lineages (reviewed in Bock et al. 2015). Invasive species, with their contrast
531 between ‘baseline’ source populations, and ‘experimental’ invasive populations, offer exciting
532 opportunities to employ genomic approaches like population-wide reduced representation (e.g.
533 RADseq; Baird et al. 2008) or whole genome sequencing (e.g. Therkildsen and Palumbi 2017) to
534 determine the different sources of genetic variation at work. A host of studies have already begun
535 to harness genomic scans for detecting signatures of selection, differentiation, and hybridization
536 for identifying genes and linked regions associated with invasiveness (e.g. Prentis et al. 2008;
537 Willoughby et al. 2018). These same genome-wide approaches also hold promise for improving
538 our understanding of genetic patterns in native range populations and how these change with
539 increasing rarity, population fragmentation, or environmental changes. As these processes are
540 also faced by invasive populations, genomic studies in the native range can provide a baseline for
541 understanding population history and informing invasive species management (Sjodin et al.
542 2020a; Sjodin et al. 2020b).

543 In addition to heritable genetic variation, there is increasing recognition that epigenetics
544 can affect ecologically important traits, which may also play a role in invasion success (Hawes et
545 al. 2018). Epigenetics is generally defined as the study of changes in organisms caused by
546 modification of gene expression rather than alteration of the genetic code itself. In the context of
547 invasive species, organisms that can successfully colonize and establish areas outside of their
548 native range have been generally considered to have a high stress tolerance (Al Hassan et al.
549 2016; Serafini et al. 2011; Zerebecki and Sorte 2011), which may be associated with underlying

550 epigenetic processes. For example, a recent study in corals found an association between levels
551 of DNA methylation, the most commonly studied epigenetic change, and a measure of ocean
552 acidification that is predicted to increase under various climate change scenarios (Putnam et al.
553 2016). Understanding the relative roles of genetic and epigenetic variation in invasion success
554 will continue to be a fundamental question moving forward (Hawes et al. 2018).

555 Lastly, there has been much discussion in the literature and the popular press on the
556 promise and pitfalls of emerging genome editing technologies; in terms of immediate
557 deployment outside of the laboratory, invasive species (and disease vectors) have featured
558 prominently (Burt 2003; Dearden et al. 2018). One such genome editing technique known as
559 Clustering Regularly Interspaced Short Palindromic Repeat (CRISPR) combined with CRISPR-
560 associated Protein 9 (Cas9) has been developed as a driving mechanism that increases the
561 chances that the targeted genetic change will be inherited by offspring (“gene drive”; Esvelt et al.
562 2014; Gantz et al. 2015). In the context of invasive species, application of this technology has
563 been actively considered for disrupting the sex determination process to bias offspring towards a
564 single sex as a means for heavily skewing sex ratios in order to promote negative population
565 growth and, ultimately, extirpation (Alphey 2014; Deredec et al. 2008; Esvelt et al. 2014; Gantz
566 et al. 2015). While there is considerable scope for debate on the ethical implications and risks
567 involved in deploying such technologies, the strong impact some invasive species have on their
568 surrounding environments suggest it would be wise to at least investigate their potential as
569 management tools.

570

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573

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812 Figure Legends

813 Figure 1. Distribution of mitochondrial DNA variation across the native and invasive ranges of
814 rose-ringed parakeets (*Psittacula kramera*). A. Pie charts represent the approximate locations
815 sampled in the Asia and African native ranges. Different colors relate to different haplotypes. B.
816 Pie charts represent the frequency of native mitochondrial DNA haplotypes detected within each
817 invasive population across Europe. C. Pie charts represent the frequency of native mitochondrial
818 DNA haplotypes detected within each invasive population in Mauritius and Seychelles. Black
819 proportions indicate mitochondrial DNA haplotypes detected in invasive populations that were
820 not detected in the native range. D. Bayesian clustering plot based on microsatellite genotypic
821 data collected in the native range in Africa and Asia, and the invasive range in Europe. Modified
822 from Figures 4 and 5 of Jackson et al. (2015b). Rose-ringed Parakeet image used under CC BY-
823 SA 2.0 (Imran Shah /Flickr).

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825 Figure 2. Distribution of mitochondrial DNA variation across the native and invasive ranges of
826 monk parakeets (*Myiopsitta monachus*). A. Distribution of sampled populations across the entire
827 native range (indicated by the blue dotted line). B. Location of sampled populations in the USA.
828 C. Location of sampled populations in Spain. Wild-caught birds sampled in pet shops (a stage
829 between uptake and potential introduction) do not have a location. D. Haplotype frequencies in
830 each population, with the size of each bubble being proportional to the number of individuals a
831 population with that particular haplotype. E. Bayesian clustering plot based on microsatellite
832 genotypic data collected in the northern and southern native range in South America and the
833 invasive range in Spain and the USA. Modified from Figures 2 and 4 of (Edelaar et al. 2015).
834 monk parakeet image used under CC BY 2.0 (TANAKA Juuyoh /Flickr).