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ORIGINAL PAPER

The desire for variety: Italian wall lizard (*Podarcis siculus*) populations introduced to the United States via the pet trade are derived from multiple native-range sources

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Abstract Tests of invasion success often require comparisons between introduced and native populations, but determining the native-range sources for introduced populations can be difficult. Molecular markers can help clarify the geographic extent of native-range sources, helping to identify which populations are appropriate for comparative studies. The Italian Wall Lizard (*Podarcis siculus*) was introduced multiple times to the United States with extant populations in California, Kansas, New Jersey, and New York. We used phylogeographic analysis of mtDNA sequences (*cytb* gene) for individuals sampled from these introduced populations and across the native range to identify the number of independent introductions and the location of the source populations. Haplotypes sampled from introduced populations were nested within three geographically distinct, well-supported clades that together encompassed a large portion of the native range. Combining these phylogeographic results with documentation of the introductions revealed putative sources: California individuals are derived from Sicily; Kansas and New York populations are from Tuscany near Florence; and the New Jersey population is likely from the Adriatic coastal region, but a more specific locality is not possible. The pet trade dominates the invasion pathway for *P. siculus* introductions to the US. The genetically and geographically diverse sampling of its native range may be driven by the desire for phenotypic variety in the pet trade, a hypothesis that needs future testing.

Keywords Introduced species · Invasion history · Mitochondrial DNA · Non-native range · Phylogeography · Reptile · *Podarcis siculus*

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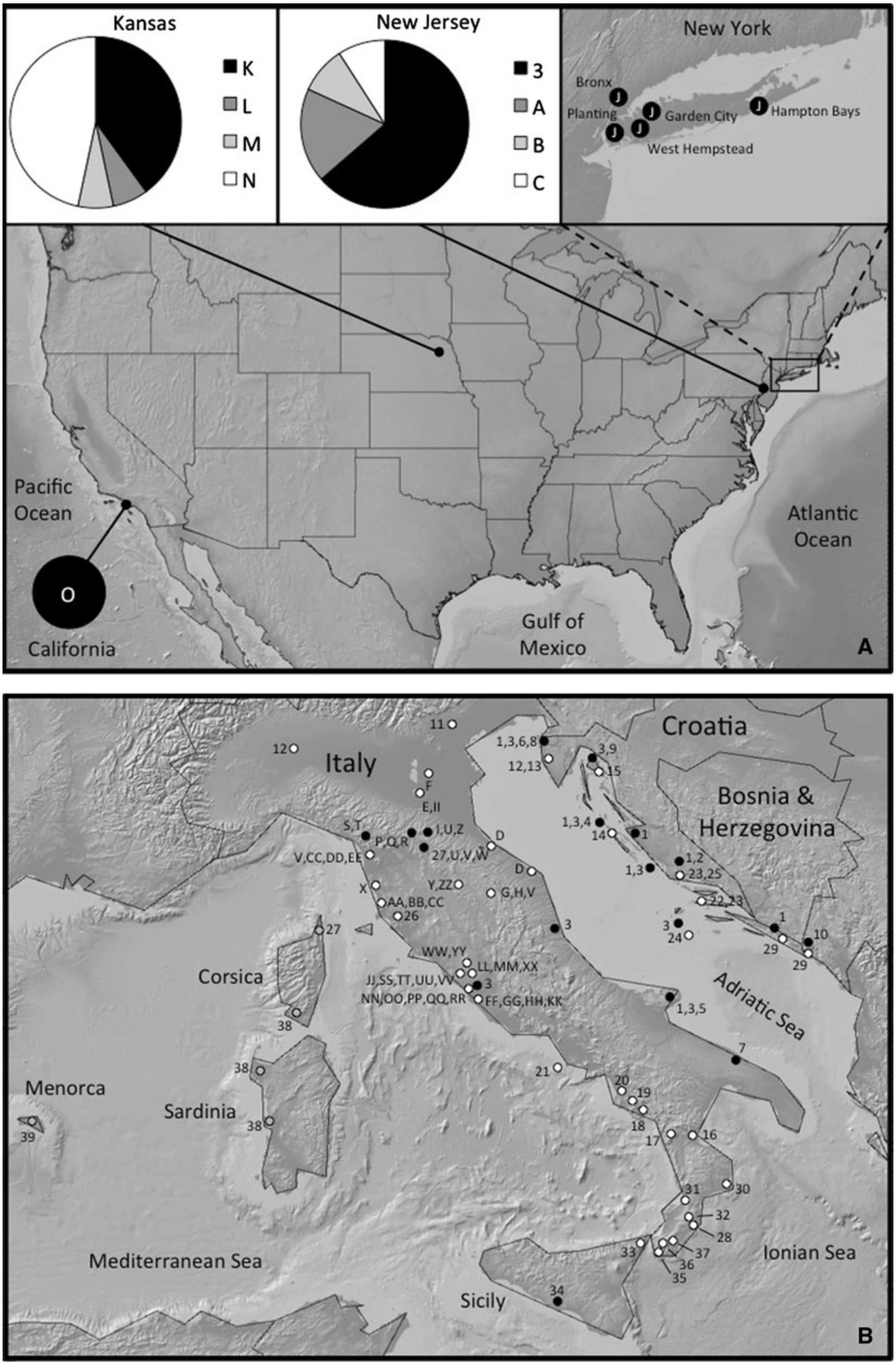
Introduction

An important component of invasion biology is testing hypotheses for invasion success, such as adaptation to novel environments, release from enemies, evolution of increased competitive ability, as well as other hypotheses (Sakai et al. 2001; Sax et al. 2005; Lockwood et al. 2007). Many tests for invasion success rely on identifying appropriate contrasts between introduced populations and their native-range sources (Dlugosch and Parker 2008). Such comparisons establish the ecological or evolutionary baseline necessary to detect and polarize changes occurring during an invasion. For example, Colautti et al. (2004) suggest that robust tests of the Enemy Release Hypothesis need to identify the native-range sources for introduced populations, and then sample parasites and predators in these source populations to compare with the introduced populations. In most instances, however, the specific source of an introduced population is not known, multiple undocumented introductions are always possible, and putative routes of introduction and transport vectors may not be reliable. In these cases, molecular markers can help to reconstruct the history of an invasion, identifying the number of native-range source populations, their geographic location and extent, and the distribution of variation from these sources in the non-native range (e.g., Kolbe et al. 2004; Wares et al. 2005; Fitzpatrick et al. 2012). Then comparisons can be made between these native-range sources and introduced populations to detect ecological and evolutionary changes.

The simplest scenario is that all populations in the non-native range are derived from a single source population in the native range (e.g., *Anolis chlorocyanus* in Kolbe et al. 2007a). In such a case, direct comparisons between introduced populations and their native-range source population are possible. Recent studies suggest that more often introductions occur from multiple native-range populations (Kolbe et al. 2007a; Dlugosch and Parker 2008). In these cases, multiple comparisons must be made between introduced populations and their respective native-range sources. When introductions from multiple sources occur, it is possible that individuals from different native-range sources admix within introduced populations. Direct comparisons to native-range sources may not be appropriate in these cases, so the pattern of admixture must be accounted for in other ways (Kolbe et al. 2007b; Keller and Taylor 2008). The key point is that rigorous tests of hypotheses for invasion success must account for the invasion history, whether it is an introduction from a single native-range source or a more complicated scenario with multiple sources and admixture within introduced populations.

Here we reconstruct the invasion history of the Italian wall lizard (*Podarcis siculus*) into the United States. This species occurs in Italy, Sicily, Sardinia, Corsica, on the coastal regions of Slovenia and Croatia, and in some areas of Montenegro (Corti and Lo Cascio 2002). This lizard is a successful colonizer (Capula 1994), being introduced and naturalized to a number of non-native areas, including Spain (Almeria; Santander), Portugal (Lisbon), Balearic Islands (Menorca), France (Toulon; Île du Chateau d'If), Turkey (Istanbul; Sea of Marmara area), northwestern Africa (Libya; Tunisia), and the United States (Kraus 2009; Corti et al. 2011). Since the 1920s, *P. siculus* has been introduced at least five times to urban and suburban areas in the United States (Burke and Deichsel 2008, Burke 2010, Deichsel et al. 2010). The Kansas population (*P. siculus campestris*) originated in the late 1950s either as accidental escapes or deliberate releases associated with a biological supply house in Topeka (Tucker 1998; Gubanyi 1999). The New York population (*P. siculus campestris*) originated when "a number" of pet trade lizards escaped in West Hempstead in 1966 (Gossweiler 1975), and has subsequently expanded into numerous local villages, including Brooklyn, the Bronx, and other locations in Nassau County (Burke and Deichsel 2008). The New Jersey population (*P. siculus campestris*) originated in 1984 when approximately 120 individuals, purchased from a Bronx, New York commercial pet importer/dealer, were deliberately released in Mt. Laurel, New Jersey (Burke 2010) in an attempt to control pest invertebrates. The California population (*P. siculus siculus*) originated when seven adults collected in Sicily were released in an urban setting in San Pedro in 1994 (Deichsel et al. 2010). A population (*P. siculus campestris*) dating back to the late 1920s was established in Philadelphia, Pennsylvania, but is now apparently extinct (Burke and Deichsel 2008). Lizards from two of these US populations (Kansas and New York) host few helminths and no hematozoans (Burke et al. 2007), but it is unclear whether these populations are derived from the same native-range source and what parasite loads existed in the source populations.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◀ **Fig. 1** Geographic distribution of haplotypes in the non-native and native ranges of *P. siculus*. Numbers correspond to haplotypes sampled in Podnar et al. (2005) and letters to those sampled in this study. **a** Non-native range (US): pie charts indicate the frequency of haplotypes sampled from introduced populations. Inset shows the five populations sampled in New York City and Long Island. **b** Native range: *black circles* indicate sampling locations for haplotypes from the well-supported clades that also contain haplotypes sampled in introduced populations. *Gray circles* indicate similar locations except that documentation suggests these locations are recent human-mediated introductions. *White circles* indicate sampling locations for haplotypes not closely related to those haplotypes sampled in introduced populations

Three of the four extant Italian wall lizard populations in the US originated in the pet trade with two (perhaps three) of these introductions being intentional releases. The pet trade is the most common source of reptile and amphibian introductions worldwide, particularly in the past 30 years (Kraus 2009). However, the pet trade is a relatively uncommon source of introductions for lizards, making the successful establishment of these *P. siculus* populations somewhat unusual (Kraus 2009). Their connection with the pet trade led to speculation that the Kansas, New York, and New Jersey populations had come originally from the vicinity of Rome, because (1) many exporters for the international pet trade were located in Rome in the 1960s and 1970s (L. Luiselli, M. Capula, pers. comm.), (2) *P. siculus campestris* are extremely common and easily collected in and around Rome (R. Burke, pers. obs.), and (3) the particular *P. siculus campestris* color morph found in the vicinity of Rome is very similar to that of the Kansas, New York, and New Jersey populations (R. Burke, pers. obs.).

A previous study using partial *12S* mtDNA sequence data confirmed that the Kansas and New York populations belonged to the subspecies *P. siculus campestris* (Oliverio et al. 2001). Sampling of native-range populations was limited in that study, and ranges of *P. siculus* subspecies are poorly defined, so no conclusions about the origin of introduced populations could be drawn. Haplotypic variation was present in both of these introduced populations and a single common haplotype was shared between populations, suggesting a common introduction history for these introduced US populations. More recently, Podnar et al. (2005) used mtDNA sequences (including the *cytochrome b* gene, or *cytb*) in a range-wide study that identified six major *P. siculus* phylogeographic groups in the native range.

In this study, we combine these previously published *cytb* sequences from Podnar et al. (2005) with new *cytb* sequence data from the native range and the four introduced populations in the US. We use phylogenetic and population genetic analyses of mtDNA haplotypic variation to trace genetic variation sampled from introduced *P. siculus* populations in the US to its native-range sources. Our objective is to identify the native-range sources of the four extant US populations for future comparative studies. Specifically, we will determine if introduced populations are derived from a single or multiple native-range source populations, delimit the geographic extent in the native range of haplotypes sampled from introduced populations, and, if multiple sources exist, test for evidence of population-level admixture within introduced populations. Reconstructing the history of *P. siculus* populations introduced to the US will help in interpreting previous studies of behavioral, ecological and phenotypic variation (Burke and Mercurio 2002; Burke and Ner 2005; Burke et al. 2007) and identify the native-range populations to sample for future comparative studies testing invasion hypotheses.

Methods

We sampled the four extant populations of introduced *P. siculus* in the US, including Topeka, Kansas; Mt. Laurel, New Jersey; San Pedro, California; and New York (which included five sites: the Bronx, Garden City, Hampton Bays, Planting Fields Arboretum, and West Hempstead (Fig. 1a; Table 1). Podnar et al. (2005) sampled widely throughout the native range of *P. siculus* in Bosnia & Herzegovina, Croatia, France (Corsica), Italy (including Sardinia and Sicily), Montenegro, and Spain (Menorca) (Fig. 1b). Preliminary analyses of these mtDNA (*cytb* gene) sequences identified localities in Tuscany with individuals closely related to those sampled from Kansas and New York in the US. We therefore focused additional sampling in Tuscany and other parts of central and northern Italy, and due to its purposed connection with the pet trade, we also sampled intensively in the vicinity of Rome.

Lizards were captured in the field by hand or by noosing. A distal tail segment was removed from each

Table 1 Sampling of individuals (N), haplotypes, and mtDNA (*cytb* gene) sequence divergences within introduced populations and between introduced and native populations of *P. siculus*

Introduced Population	N	Number of haplotypes	Mean pairwise within-population sequence divergence (%)	Sequence divergence to the most closely related native-range haplotype (%)
Kansas (Topeka)	15	4	0.08	0.34
New York City area	29	1	0	0.34
New Jersey (Mt. Laurel)	11	4	0.16	0
California (San Pedro)	5	1	0	0.90

lizard by gently pulling on the end of the tail until a small segment broke off along a fracture plane. These lizards have autonomous tails, so the wound quickly sealed and rarely bled. Lizards were released at the point of capture. Total genomic DNA was extracted using a standard salt extraction method (Sambrook and Russell 2001). We amplified and sequenced an ~900 bp fragment of mtDNA including the *cytb* gene. Due to the presence of a nuclear pseudogene of the mitochondrial *cytb* gene in *P. siculus* (Podnar et al. 2007), we used highly selective PCR primers designed by to amplify exclusively mtDNA following the protocol of Podnar et al. (2005). PCR products were purified using ExoSAP-IT (USB Corp.). These purified PCR products were used as template for standard Big Dye Terminator v.3.1 sequencing reactions, which were cleaned with Sephadex and visualized on an ABI 3730 in the Museum of Vertebrate Zoology at the University of California, Berkeley.

We inferred the relationships among all *cytb* haplotypes using both Bayesian inference and maximum likelihood (ML). In addition to *P. siculus* ingroup samples, outgroup taxa for each analysis taken from Genbank included *Podarcis muralis muralis* (AY185096), *Podarcis melisellensis melisellensis* (AY185057), and *Podarcis melisellensis fuimana* (AY185029). We used MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001) to infer the relationship among haplotypes under Bayesian inference and RAxML (Stamatakis et al. 2008) to generate ML trees. We used a three-partition strategy that estimated separate models of sequence evolution for each codon position (Brandley et al., 2005). We chose models for each partition by comparing the AIC scores generated by MrModeltest 1.1b (http://www.abc.se/~nylander/; Posada and Crandall 1998). We conducted four independent Bayesian phylogenetic analyses of 20 million generations each, sampling trees every 1000 generations. We generated a consensus topology and calculated posterior probabilities from post burn-in trees sampled from all analyses (a burn-in time of 5 million generations was used for each run) in MrBayes. The ML analysis used the GTR model for each partition due to less flexibility in choosing models in RAxML and generated 1000 bootstrap replicates. We used PAUP v.4b10 (Swofford 2002) to calculate uncorrected sequence divergences.

We delimited native-range source populations by identifying the least inclusive, well-supported native-range clades that also contained haplotypes sampled in introduced populations. Then we examined the geographic distribution of haplotypes from these well-supported, genetically distinct clades. Non-overlapping haplotype distributions suggest a phylogeographic structure in the native range necessary to identify the geographic extent of putative sources. Finally, we interpreted the phylogeographic reconstruction of the introduction history in conjunction with the documented history of introduction. This allowed us to identify haplotypes previously linked to human-mediated transport within the native range and to exclude these locations as likely sources of introduced populations (Podnar et al. 2005).

Results

We obtained an aligned data set of 880 bp of the *cytb* gene for *P. siculus*. The final data set contained 89 unique haplotypes, 37 of which are previously published sequences from Podnar et al. (2005) including one shared between the ranges, and the others are newly reported in this study including 43 from the native range in Italy and nine from introduced populations in the US.

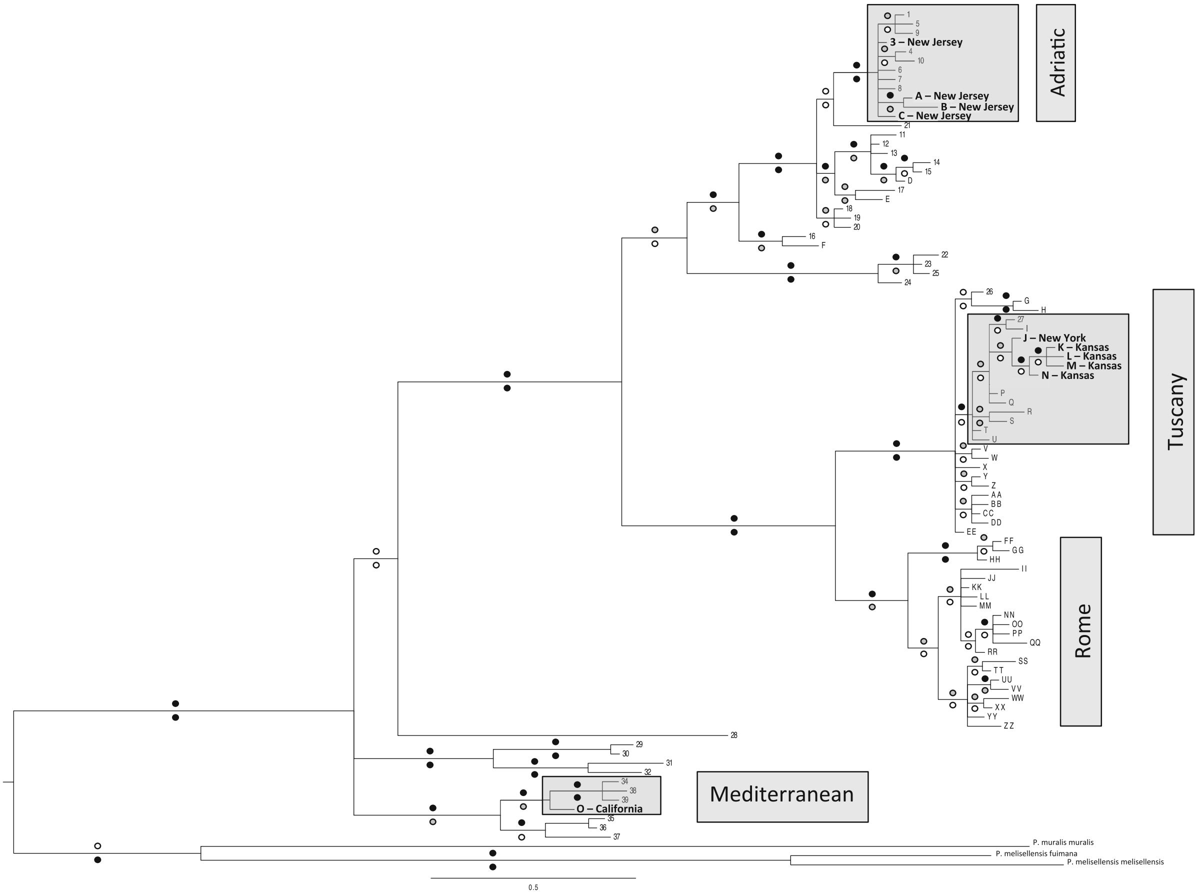

Fig. 2 Consensus phylogram obtained from the posterior distribution of trees in MrBayes. Tip labels are numbers for haplotypes sampled in Podnar et al. (2005), which correspond to their scheme (1–39), and letters for those sampled in this study (A-ZZ). For haplotypes sampled from introduced populations, we indicate the population next to the letter in *bold*. *Shaded boxes* indicate the three well-supported clades with haplotypes sampled from introduced populations, which are labeled along with the newly identified Rome clade. *Circles* above nodes indicate posterior probability (PP) values and *circles* below nodes are ML bootstrap (BS) values; *black circles* (PP or BS ≥ 0.95), *gray circles* ($0.70 \leq$ PP or BS < 0.95), and *white circles* (PP or BS < 0.70)

MrModeltest 1.1b identified different models of evolution for each codon position (1st position: SYM + I; 2nd position: HKY + G; 3rd position: GTR + G). Topological conflict between the Bayesian and ML trees was minimal, and limited only to tip relationships among closely related haplotypes. We report the consensus Bayesian topology with posterior probabilities and ML bootstrap values (Fig. 2).

The phylogeographic pattern in the native-range was broadly similar to findings in Podnar et al. (2005) identifying the same six well-supported phylogeographic clades. Our sampling in the vicinity of Rome yielded a new, well-supported clade sister to the Tuscany clade (Fig. 2). Two haplotypes from this clade were not sampled near Rome; haplotype II was sampled in Bologna and haplotype ZZ was from Chiusi (Fig. 1b). Haplotypes sampled from introduced populations in the US were detected in three well-supported clades: Adriatic, Tuscany, and Mediterranean (Fig. 2). Uncorrected sequence divergence among these clades ranged from 5.7 to 8.6 %, suggesting multiple genetically divergent sources.

We found 10 haplotypes in the four introduced populations in the US derived from three genetically (and in most cases geographically) distinct native-range sources. The introduced population in Topeka, Kansas had four closely related haplotypes, two at low frequency and two at moderate frequency

(Fig. 1a; Table 1). A single haplotype was detected in the five localities sampled in the New York area. This haplotype from New York was closely related to haplotypes sampled in Kansas, but no shared haplotypes were detected. However, a previous study found a shared *12S* mtDNA haplotype between these two introduced populations (Oliverio et al. 2001), suggesting a common origin. These haplotypes from Kansas and New York are closely related to those sampled in the localities of Borgo San Lorenzo, East Florence, Florence (including haplotype 27 from Podnar et al. 2005), and Pistoia (Fig. 2; Supplementary Table S1), suggesting a northern Tuscany origin for these introduced populations.

In contrast to the close association between haplotypes from Kansas and New York, samples from New Jersey and California are neither closely related to these nor to each other. Of the four haplotypes detected in New Jersey, the most common one was identical to haplotype 3 from Podnar et al. (2005) and a new sample from Rome (Nuovo Salario), Italy with the others at lower frequency (Fig. 1a). This haplotype is widespread along the coast of the Adriatic Sea in east-central Italy, Croatia, and Bosnia & Herzegovina (Fig. 1b). Furthermore, the clade containing all the haplotypes from New Jersey (i.e., the Adriatic clade in Fig. 2) has closely related haplotypes distributed along the coast of the Adriatic Sea in the native range. Therefore, it is impossible to determine the geographic location of the source population from these data. A single haplotype was detected in California (Fig. 1a), which is sister to a clade containing haplotypes 34, 38, and 39 sampled from Corsica, Menorca, Sardinia, and Sicily (Figs. 1b, 2). Despite introductions from multiple native-range sources, we did not detect population-level admixture of haplotypes from distinct mtDNA lineages within introduced populations.

Discussion

Mitochondrial DNA haplotypes sampled from introduced populations in the US are derived from three genetically distinct and well-supported native-range clades that are largely geographically distinct from each other. This provides strong support for at least three independent introductions in the US. This pattern of introductions from multiple native-range sources is common (Dlugosch and Parker 2008), particularly in lizards (Kolbe et al. 2004, 2007a; Chapple et al. 2012; Schulte et al. 2012). Haplotypes from the Adriatic clade are widely distributed within the native range, making it difficult to narrow the geographic extent of the source population for the New Jersey introduction. Future studies comparing introduced and native populations of *P. siculus* must account for these independent introduction histories, although where exactly to sample in the native range is not always clear.

Our phylogeographic analysis rejects Rome as the primary source for *P. siculus campestris* individuals founding the Kansas, New York, and New Jersey populations. The most common haplotype sampled in New Jersey was also the most widespread haplotype in the native range (haplotype 3), being found primarily along the southwest and northeast coasts of the Adriatic Sea (Fig. 1b). This distribution led Podnar et al. (2005) to conclude a recent and rapid colonization of the Adriatic region, perhaps human-mediated. The proximity of several distantly related haplotypes in this region also supports a history of human-mediated transport. This lack of fine geographic structure in the mtDNA haplotypic variation limits our ability to identify the location of the native-range source population. Previous studies have sometimes shown fine geographic structure in mtDNA haplotypic variation in the native range (e.g., *Anolis sagrei* in Kolbe et al. 2004), facilitating detection of both multiple sources and their geographic extent in the native range. Analyses for other taxa have found less geographic structure in the mtDNA haplotypic variation, in which case adding data from more variable markers, such as microsatellites, can narrow the geographic extent of the source (e.g., Argentine ants in Tsutsui et al. 2001). For the source of the introduced New Jersey population of *P. siculus*, more variable markers and more native-range sampling in terms of both populations and individuals per population are needed. However, if extensive human-mediated transport exists within the native range, then even more variable markers may not prove useful.

The native-range source for the introduced Kansas and New York populations is clearer. Haplotypes closely related to those sampled in Kansas and New York are restricted to northern Tuscany in the vicinity of Florence. The sole exception is haplotype 27, which was sampled in both Florence and Corsica, but the latter is likely a recent human-mediated introduction (see Podnar et al. 2005 and citations therein).

Similarly, the haplotype shared by populations in New Jersey and along the Adriatic (haplotype 3) was also detected in one individual from Rome (Nuovo Salario), Italy. In this case, the 10 other individuals sampled from Nuovo Salario had closely related haplotypes within the Rome clade (Fig. 2), which is consistent with the overall phylogeography of *P. siculus*. These two examples of haplotypes that are both associated with introduced populations and sampled in localities that contradict otherwise strong phylogeographic patterns, suggest occasional human-mediated transport within the native range. Thus, a scenario in which lizards in the pet trade are transported through Rome (with some escapees), but not collected there, is plausible.

The haplotype from California is closely related to native-range haplotypes found on several large Mediterranean Islands, which themselves may be historical introductions aided by humans (Lever 2003). For example, haplotype 38 is shared between Corsica and Sardinia (Fig. 1b). Our genetic data for the California introduction are consistent with the documentation of Sicily as the source (Deichsel et al. 2010). Human-mediated movement of lizards within the native range appears frequent as evidenced by the distributions of haplotypes 1, 3, 27, 38, and is associated with each of the three independent introductions to the US. The extent to which this phenomenon of movement of individuals within their native ranges occurs in other species is unknown.

The pet trade pathway for *P. siculus* introductions to the US has resulted in established populations that span the phylogenetic diversity and geographic extent of this species in its native range. The desire for variety in the pet trade—new species, uncommon varieties, and in this case subspecific color morphs of *campestris* and *siculus*—may have led to sampling of genetically diverse source populations with subsequent release and establishment in non-native areas. Whether the pet trade leads to the establishment of non-native populations with greater diversity compared to other pathways (e.g., biocontrol, cargo, nursery trade) remains to be tested. The numerous other introductions of *P. siculus* (Kraus 2009; Corti et al. 2011), as well as reptiles in general (Lever 2003), may serve as good subjects for tests of this hypothesis given their popularity in the pet trade.

In conclusion, phylogeographic analysis of mtDNA sequences confirms at least three independent introductions of *P. siculus* from its native range to the US. The combination of mtDNA haplotype data and historical documentation clarifies the geographic extent of the sources in the native range. The Kansas and New York populations are derived from Tuscany in the vicinity of Florence, the California population is from Sicily, and the New Jersey population is likely from the Adriatic region, but a more specific locality is not currently possible. Tests of hypotheses for invasion success therefore must account for this introduction history when selecting native-range populations for comparison. For example, a test of whether the depauperate parasite fauna found in some introduced US populations (Burke et al. 2007) is the result of escape from native-range enemies or being derived from native-range sources with low parasite loads depends critically on accurate sampling of these native-range source populations.

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