POPULATION GENETICS OF KANGAROO MICE, *MICRODIPODOPS* (RODENTIA: HETEROMYIDAE)

A Thesis

by

JOHN JUDE ANDERSEN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2012

Major Subject: Wildlife and Fisheries Sciences

Population Genetics of Kangaroo Mice, *Microdipodops* (Rodentia: Heteromyidae)

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Approved by:

Chair of Committee,	Jessica E. Light
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ABSTRACT

Population Genetics of Kangaroo Mice, *Microdipodops* (Rodentia: Heteromyidae).

(May 2012)

John Jude Andersen, B.S., Texas A&M University

Chair of Advisory Committee: Dr. Jessica E. Light

Dark (*Microdipodops megacephalus*) and pallid (*Microdipodops pallidus*) kangaroo mice are ecological specialists found in arid regions of the Great Basin Desert of the southwestern United States. Historical and current habitat alterations have resulted in disjunct distributions and severely diminished abundance of both species. Phylogenetic and phylogeographic research has discovered unique mitochondrial clades within *M. megacephalus* (eastern, central, western, and Idaho clades) and *M. pallidus* (eastern and western clades). Population-genetic analyses targeting the same mitochondrial markers also have found low amounts of maternal gene flow among the clades. However, little is known about population structure and genetic demography (historical and current migration rates, historical and current effective population sizes) within each mitochondrial clade.

Herein, nuclear-encoded microsatellite loci were isolated to evaluate the underlying processes that may have molded kangaroo mouse relationships and distributions. Results from population-genetic analyses support previous findings that there are at least three genetically distinct clades within *M. megacephalus* and two such

clades within *M. pallidus*. Three clades of *M. megacephalus* appear to have undergone different demographic histories, with little to no migration among clades. The two clades of *M. pallidus* also appear to have experienced varying demographic change although there has been small but recent migration between them. Additionally, the contemporary effective population sizes of all clades within *Microdipodops* appear to be low, suggesting that these populations may have difficulty coping with environmental pressures and hence are at risk of extinction. Results of this study are consistent with the recommendation that each *Microdipodops* clade should be managed as separate units and continually monitored in an effort to conserve these highly specialized taxa.

DEDICATION

This thesis is dedicated to my parents. They have always let me follow my own path, and while sometimes that has led to unfavorable surroundings, it has taken me to a pleasant avenue.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. J. E. Light, and my committee members, Dr. J. R. Gold and Dr. W. J. Murphy, for their guidance and support throughout the course of this research. I also would like to acknowledge J. C. Hafner for providing all the samples and for his invaluable input.

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TABLE OF CONTENTS

	Page
ABSTRACT	iii
DEDICATION	v
ACKNOWLEDGEMENTS	vi
TABLE OF CONTENTS	vii
LIST OF FIGURES	ix
LIST OF TABLES	x
1. INTRODUCTION	1
Microdipodops megacephalus	5
Microdipodops pallidus	9
Proposal	10
2. MATERIALS AND METHODS	11
Specimens examined	11
Laboratory methods	11
Data analysis	13
3. RESULTS	17
Summary statistics	17
Population structure	18
Average, long term migration and long-term effective population size	21
Current effective population size and migration	23
Demographic history	24
4. DISCUSSION	28
Microdipodops megacephalus	28
Microdipodops pallidus	30

Page

5. CONCLUSION 32

REFERENCES 34

APPENDIX I 42

VITA 46

LIST OF FIGURES

Page

Figure 1 Geographic distribution of the dark kangaroo mouse, the pallid kangaroo mouse, and their overlapping ranges in the Great Basin Desert of the western United States 6

Figure 2 Geographic distributions of *M. megacephalus* and *M. pallidus* with labels corresponding to mitochondrial clades. 7

LIST OF TABLES

Page

Table 1 Populations within each species defined by *a priori* mtDNA clades......... 12

Table 2 Summary statistics for *M. megacephalus*.. 19

Table 3 Summary statistics for *M. pallidus*... 20

Table 4 Results of AMOVA... 22

Table 5 Estimates of parental effective population size and estimates of historical effective population size with 95% confidence intervals........................... 25

Table 6 Estimates of current migration rate with 95% confidence intervals 26

Table 7 Results of MSVAR... 27

1. INTRODUCTION

Molecular analyses have proven to be instrumental in species discovery and have transformed biological systematics into a science that uses genetic data to help differentiate and identify taxa. Mitochondrial DNA (mtDNA) and nuclear DNA (nuDNA) are markers that are frequently used to address systematic questions through the construction of phylogenetic trees (e.g., Jezkova *et al.* 2009; Kerhoulas & Arbogast 2010; McKnight 2005; Riddle 1995; Riddle & Hafner 2006). Phylogeographic assessments of these species, including examination of geography and biogeography of a region, can help identify evolutionary unique lineages and help explain how past events (e.g., climatic cycles, geological changes, and anthropogenic effects) may have served as potential barriers to gene flow within and among populations (Avise 2000). Discovering genetic barriers for multiple co-distributed taxa also can help elucidate the complex biogeographic history of a particular region.

Although phylogenetic reconstruction is useful for determining species relationships, understanding what is occurring at the population level can shed light upon the speciation process. While there are many different reasons how and why speciation occurs, the reality is that when gene flow among populations is discontinued, those populations often will evolve into separate entities. In addition to better understanding the speciation process, genetic studies at the population level can address other topics

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This thesis follows the style of *Journal of Molecular Ecology.*

such as conservation implications and management issues (e.g., inbreeding, migration among populations, population range contractions, and population size declines) for relevant populations and species. These studies often have attempted to identify evolutionary significant units (ESUs) targeting varying molecular markers, such as: mtDNA (Georgiadis et al. 1994), allozymes (Legge et al. 1996), RLFPs (Vogler et al. 1993), and microsatellites (Small et al. 1998). Importantly, the definition of ESUs has slowly changed over the years. The first definition came from Ryder (1986), where he explained that ESUs are units that "represent significant adaptive variation based on concordance between sets of data." In 1991, Waples stated that populations must be reproductively separate from one another and have unique adaptations to be considered an ESU. Finally, Mortiz (1994) defined ESUs in light of a conservation perspective, where units are "reciprocally monophyletic for mtDNA alleles and show significant divergence of allele frequencies at nuclear loci." Although it is sometimes difficult to determine what data are necessary to define an ESU, it is important to note that the fundamental purpose of identifying ESUs is to enhance the potential for an organisms survival (Crandall et al. 2000). Thus, to provide a broader genomic coverage and alleviate any potential bias in single-locus studies, a multi-locus approach (e.g., mtDNA and nuDNA) is needed to determine if taxonomic lineages should be characterized as ESUs.

Nuclear-encoded microsatellites, tandem nucleotide repeats found distributed across higher organism genomes, are fast-evolving, generally independent nuclear data markers used to address various conservation-genetic concerns at the population level.

Discerning distinct populations within a species and observing the presence or absence of gene flow among the populations have commonly been accomplished through microsatellite analyses (Hulya *et al.* 2010; Natoli *et al.* 2004; Piggott *et al.* 2011; Vilaca & Santos 2010). By using these fast-evolving nuclear markers, researchers are better able to identify distinct populations, and provide evidence for possible ESUs. Discovery of ESUs is an increasingly important issue, especially for management practices of rare populations or species. Rather than applying the same management standards across an entire species range, managers of wildlife can apply management planning to specific populations that are on their own evolutionary trajectory and in greater need of conservation.

The genus *Microdipodops* (kangaroo mice) is an increasingly rare member of the North American rodent family Heteromyidae, which includes five other extant genera (*Chaetodipus, Perognathus, Dipodomys, Heteromys,* and *Liomys*) distributed from northwestern North America southward into northwestern South America. Heteromyidae is a relatively ancient lineage, originating between 22 and 35 million years ago (mya; Hafner et al. 2007; Meredith et al. 2011), and *Microdipodops* is believed to have diverged from its sister taxon, *Dipodomys,* roughly 15 mya (Hafner et al. 2007). Although the genus is rather old, *Microdipodops* contains the smallest number of species and the most restricted geographic range within the family. There are two species of *Microdipodops* currently recognized: the dark kangaroo mouse (*M. megacephalus*) and the pallid kangaroo mouse (*M. pallidus*). As the common names suggest, *M. megacephalus* is darker than its paler sibling, although pelage coloration is known to

vary immensely over geography for both taxa and is therefore considered an unreliable means of identification (Hafner & Upham 2011). Both of these species are sand-obligate endemics to the Great Basin Desert (Fig. 1) and, as such, are highly specialized to survive in such an extreme environment (e.g., all fluids are derived metabolically and they are able to enter torpor at very high and low temperatures; Hall 1941).

The Great Basin Desert is a region that has had a complex biogeographic history resulting from numerous habitat alterations caused by the rise and fall of pluvial lakes (Benson 1981), shifting climatic patterns (Atvens 1952), and floristic transitions (Reveal 1979). Many of these alterations can be attributed to the glacial-interglacial cycles of the Pleistocene (Riddle 1995); recent human induced habitat destruction, however, also has plagued the area (Hafner & Upham 2011; Hafner *et al.* 2008). These threats likely have caused a significant reduction in abundance of *Microdipodops.* Several field observations have concluded that the numbers of both *M. megacephalus* and *M. pallidus* are dwindling (Hafner & Hafner 1996; Hafner 1981; Hafner & Upham 2011; Hafner *et al.* 2008; Hall 1941). Additionally, both ancestral and current habitat alterations have fragmented the distribution for both kangaroo mouse species such that current geographic ranges are disjunct (Figs. 1 and 2; Hafner et al. 2008; Hafner and Upham 2011). Both species are listed as 'Least Concern' by the International Union for Conservation of Nature (IUCN) and are not protected (Linzey & Hammerson 2008; Linzey *et al.* 2008). As a consequence, current management of kangaroo mice is virtually non-existent.

There are four geographically isolated distributions of *M. megacephalus* and three of *M. pallidus* (Figs. 1 and 2); distributions of both species are separated either by geographic barriers or unsuitable habitat (Hafner et al. 2008; Hafner and Upham 2011). Niche specializations further isolate populations of each species; *M. megacephalus* has a tolerance for sandy soils with gravel overlay and is found primarily in association with sagebrush and/or rabbit brush (Hafner & Upham 2011; and references therein); whereas *M. pallidus* prefers greasewood and fine soils with no gravel overlay (Hafner 1981; and references therein). The unique, fragmented distributions in the Great Basin Desert, specific habitat requirements, ecological specializations, and dwindling numbers have made kangaroo mice recent subjects for phylogenetic and phylogeographic studies (Hafner et al. 2006; Hafner et al. 2008; Hafner and Upham 2011).

Microdipodops megacephalus.—Extensive studies of the dark kangaroo mouse over the past several years have revealed several evolutionary unique lineages within the species (Hafner *et al.* 2006; Hafner & Upham 2011; Light *et al.* 2012). Mitochondrial markers (16S ribosomal RNA, cytochrome *b*, and transfer RNA for glutamic acid) were used in these studies primarily for phylogenetic analyses of specimens distributed throughout the range of the species. Based on the analyses, the authors concluded that there were four distinct monophyletic mtDNA clades within *M. megacephalus*: the eastern, central, western, and Idaho clades. All four clades were strongly supported and genetically divergent. Given the fragmented distribution of the species (Fig. 2), one might expect the four clades to correspond to the four isolated ranges; however, this is not necessarily the case. The eastern and central clades are essentially parapatric yet

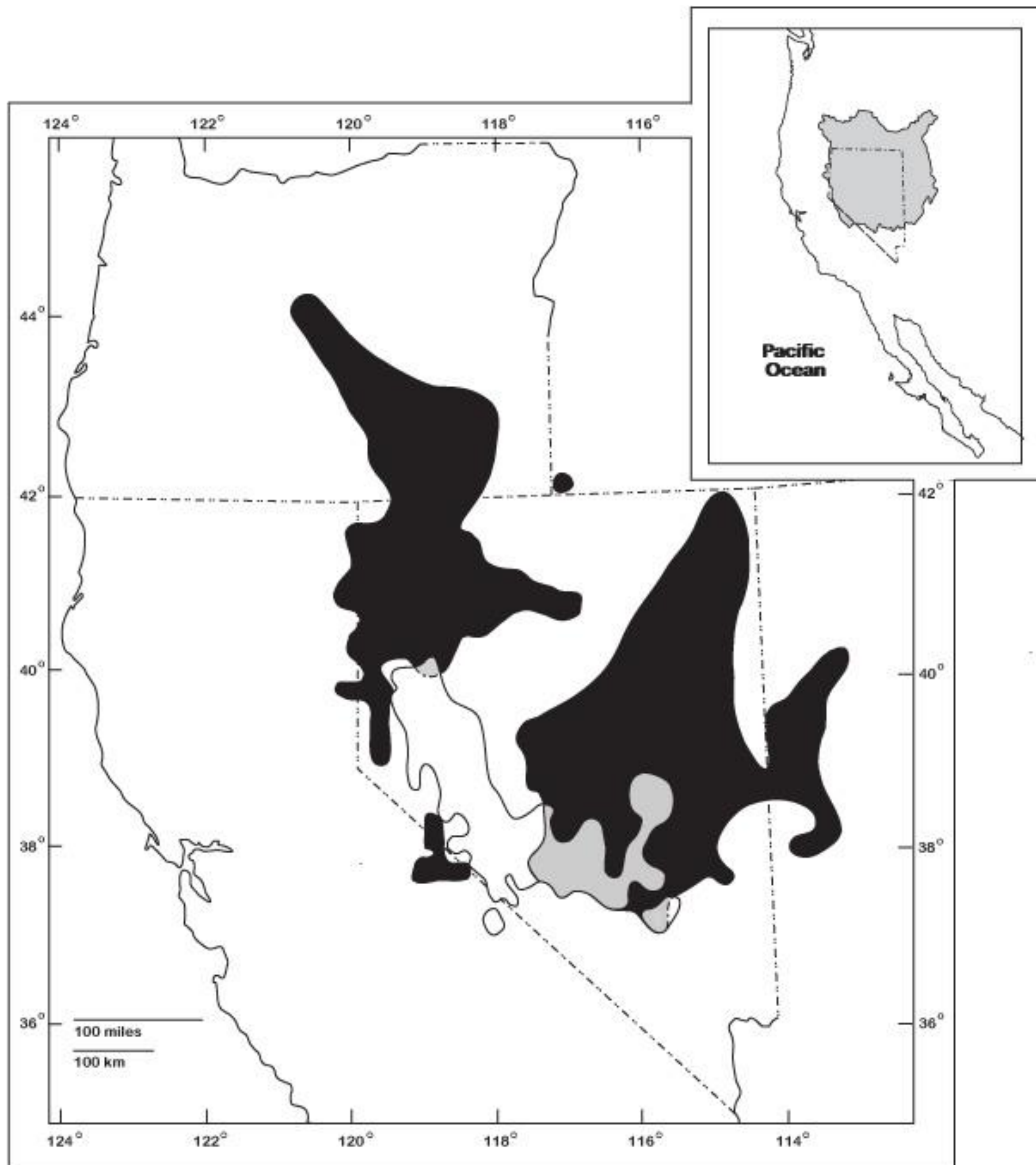
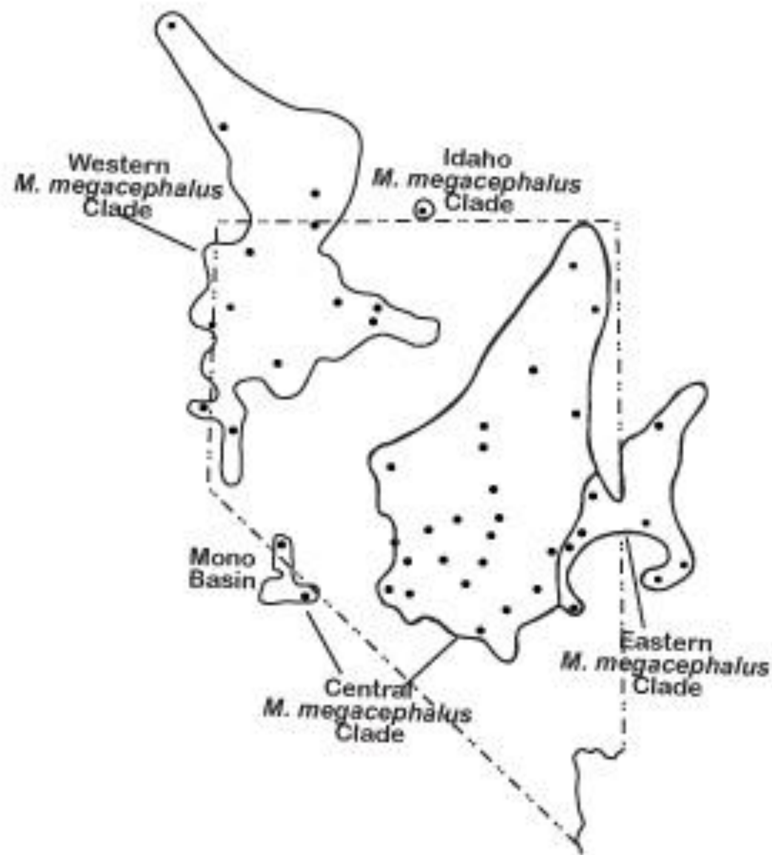


Fig. 1 Geographic distribution of the dark kangaroo mouse, *Microdipodops megacephalus* (black), the pallid kangaroo mouse, *Microdipodops pallidus* (white), and their overlapping ranges (grey) in the Great Basin Desert of the western United States.

A



B

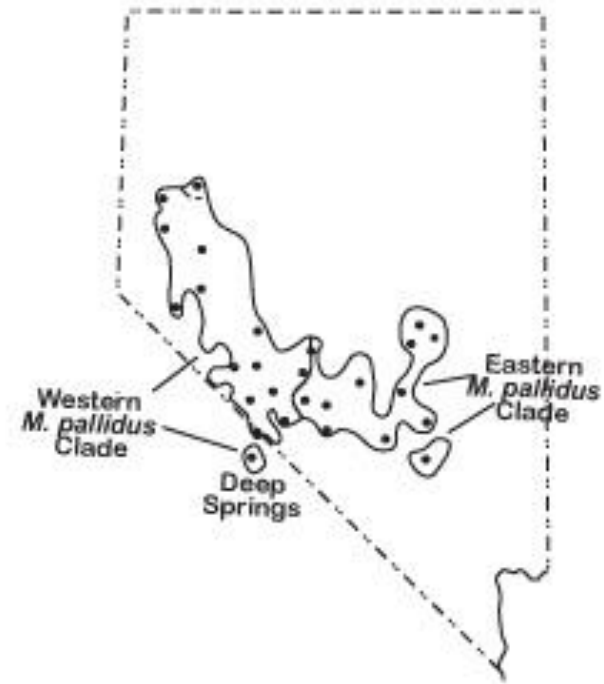


Fig. 2 A) Geographic distribution of *M. megacephalus*, with labels corresponding to mtDNA clades (eastern, central, western, and Idaho) discussed in prior studies (Hafner et al. 2006, Hafner and Upham 2011); the isolated population in the Mono Basin region (which nested within the central clade; Hafner et al. 2006) also is labeled. B) Geographic distribution of *M. pallidus,* with labels corresponding to mtDNA clades (eastern and western) from prior studies (Hafner et al. 2008); the isolated Deep Springs locality (which nested within the western clade; Hafner et al. 2008) also is labeled.

distinct genetically, with collection sites from each clade separated by as little as 25 km (Hafner and Upham 2011). Furthermore, kangaroo mice from the isolated Mono Basin (Fig. 2A) were once thought to represent a distinct lineage because they physically are separated from other mice by more than 100 km of unsuitable habitat (Hafner et al. 2006). More recent studies (Hafner & Upham 2011), however, have found that even though haplotypes from the Mono Basin are physically isolated, they are nested within the central clade. Based off the population-level analyses, using the same mitochondrial markers, the authors concluded that each clade has undergone different demographic histories (Light et al. 2012). The central clade has likely undergone historic population expansion, the western clade has undergone possible population contraction, and the eastern clade may have experienced slight population expansion (Light et al. 2012). While these findings are noteworthy, many other aspects of the evolutionary history of each clade remain unclear. For instance, it is unclear whether migration is occurring among clades. Light et al. (2012) used Wright's F_{ST} to examine mitochondrial divergence among the clades and found significant differences among the clades. However, there are two critical assumptions in Wright's F_{ST}: effective population sizes are equal and migration between populations is symmetric. If migration is asymmetric, or effective population sizes are unequal, use of the F_{ST} is possibly compromised (Beerli 1998). Thus, it is important to assess gene flow bi-directionally so that future management practices can be more effective.

All previous molecular studies on *Microdipodops* have used mitochondrial data. Support for the mtDNA clades and previous demographic findings need to be assessed

using nuclear data. Furthermore, population level analyses using fast-evolving nuclear markers, such as microsatellites, are necessary to better understand the evolutionary history within and among *M. megacephalus* mtDNA clades.

Microdipodops pallidus.—Similar to *M. megacephalus*, *M. pallidus* also has been studied using phylogenetic analyses of mitochondrial markers (Hafner et al. 2008; Light et al. 2012). Results of these studies indicated existence of two strongly supported genetically divergent clades: the eastern and western mtDNA clades (Fig. 2B). The biogeographic history of each clade is complex as the boundaries of both clades coincide with a series of mountain chains (Hafner et al. 2008). In addition, pluvial maxima in the Pleistocene likely shifted the range of *M. pallidus* to the south, and when conditions stabilized, *M. pallidus* adjusted its range back to the north (Hafner et al. 2008). The Lahontan Trough (Reveal 1979), which is the current distribution of the western clade, most likely acted as a corridor for northward range expansion from a southern refugia (Hafner et al. 2008).

Light et al. (2012) also used mitochondrial data and found that the eastern and western clades of *M. pallidus* had significantly diverged from one another and likely underwent past population expansions. While these findings are important, it is still unclear when demographic changes occurred or if migration is asymmetric based on nuclear data. A better understanding of the population demography within *M. pallidus* via analyses of nuclear data will help to address issues of management, conservation, and systematic concerns (Busch et al. 2007; Buzan et al. 2010; Vega et al. 2007).

Proposal.—*Microdipodops* has been studied extensively to provide a basis for systematic revision. While there have been a combination of phylogenetic and population-genetic analyses which have converged on some of same conclusions, all these previous studies only have utilized mtDNA. Analysis of both nuclear and mitochondrial data can facilitate a better understanding of genetic lineages within a species (Avise 1994), especially since these markers often have different evolutionary histories (e.g., Yang & Kenagy 2009).

Herein, I use microsatellite markers to genotype previously sampled specimens in order to provide an assessment of nuclear variation within *Microdipodops*. Population-level analyses, using the microsatellite data, are performed on mtDNA clades (defined as populations) and results are compared to findings based on mtDNA in previous studies. These findings will help identify ESUs in need of conservation and possibly systematic revision.

2. MATERIALS AND METHODS

Specimens examined.—A total of 184 specimens of *M. megacephalus* from 46 localities, and a total of 105 specimens of *M. pallidus* from 27 localities, were used in this study (Appendix I). The *M. megacephalus* specimens were collected between 1975 - 1976 and 1999 – 2007, and in 2011 by John C. Hafner (JCH). The *M. pallidus* specimens also were collected by JCH between 1999 and 2005, with one individual sampled in 1975. All tissues were stored in a -80°C freezer (Appendix I). For some of the analyses, test groups within each species were defined based on previously identified mtDNA clades and subclades, as shown in Table 1 (Hafner et al. 2008; Hafner and Upham 2011).

Laboratory methods.—DNA extracts and tissues were provided by JCH. When necessary, DNA was extracted from liver or kidney tissues as described by Hafner et al. (2006). Seventeen polymorphic microsatellite loci developed for *Microdipodops* by Lance et al. (2010) were genotyped as part of this study. Polymerase-chain-reactions (PCR) amplifications followed Boutin-Ganache et al. (2001) and contained a forward primer with an attached 16-bp tail sequence (5'-CAGTCGGGCGTCATCA-3'), a 6-FAM or 6-HEX (Dye Set D, Applied Biosystems) labeled tail sequence (defined above), and an unlabeled reverse primer. Amplified DNA from each PCR reaction was combined with a 400 HD Rox size-standard DNA ladder (Applied Biosystems) and electrophoresed on an ABI PRISM 377 DNA Sequencer (Applied Biosystems).

Table 1 Populations within each species defined *a priori* by mtDNA clades (Hafner et al. 2008; Hafner at Upham 2011). Sub-divisions within populations is defined by haplotype networks in Light et al. (2012).

Taxon	*N*
M. megacephalus	184
Eastern Clade	49
Eastern subclade	25
Western subclade	24
Central Clade	69
Central subclade	19
Western subunit	50
Western Clade	62
Valley Falls	9
Remainder of Western clade	53
Idaho Clade	4
M. pallidus	105
Eastern Clade	42
Eastern subunit	15
South-central subunit	23
Western Clade	63
Deep Springs isolate	10
Remainder of Western clade	53

Plates used for sequencer machines were soaked in 2 M NaOH several times prior to genotyping, and gel temperatures were consistently set to 47°C. This aided in preventing formation of acrylamide bubbles which can migrate through gels and distort gel images. Sizes of microsatellite fragments were visualized in GENESCAN v. 3.1.2 (Applied Biosystems) and assessed using GENOTYPER v. 2.5 (Applied Biosystems).

Data analysis.—Each microsatellite locus was tested for conformance to Hardy-Weinberg equilibrium, using GENEPOP v. 4.0 and default parameters with correction for multiple tests applied across all loci (Raymond & Rousset 1995; Rice 1989). Loci that differed significantly from Hardy-Weinberg equilibrium expectations were assessed either by re-scoring gels and/or re-running PCRs. GENEPOP also was used to calculate expected and observed numbers of heterozygotes, genotypic disequilibrium, and gene frequencies when null alleles were present. Number of alleles and allelic richness for each locus were calculated with FSTAT v. 2.9.3.2 (Goudet 1995).

The Bayesian-inference based program STRUCTURE v. 2.3.3 (Pritchard et al. 2000) was used to detect separate clusters of genotypic variation within *M. megacephalus*, within *M. pallidus*, and within each mtDNA clade (the eastern, central, western, and Idaho clades of *M. megacephalus* and the eastern and western clades of *M. pallidus*). The population admixture model was used with 10 runs from $K = 1$ to $K = 10$ where K is a user-defined number of clusters. Each run consisted of a burn-in of 10,000 Markov chain-Monte Carlo repetitions followed by 100,000 additional repetitions. To evaluate the most likely K value, Structure Harvester (Earl & vonHoldt 2011) was used

to graph both the mean estimated ln Prob(Data) and ΔK as suggested by Evanno et al. (2005).

The computer program Arlequin v. 3.5 (Excoffier et al. 2005) was used to calculate measures of genetic divergence. F_{ST} and R_{ST} statistics were calculated with 10,000 Markov-chain steps. Population structure within each species was assessed with an analysis of molecular variance (AMOVA; Excoffier et al. 2005); populations were defined *a priori* by mtDNA clades and subclades (Table 1) and significance was assessed by 10,000 randomization replicates.

Migrate-N v. 3.0.3 (Beerli & Felsenstein 1999) was used to estimate theta (Θ; where $\Theta = 4N_e u$) and average, long-term estimates of gene flow among mtDNA clades within each species (except for the *M. megacephalus* Idaho clade; Appendix I). Preliminary short runs were performed to estimate the priors M (mutation-corrected migration) and Θ for final runs. Final runs were run twice at different starting points to verify data convergence with 3 and 1 long chain(s) used for *M. megacephalus* and *M. pallidus*, respectively. A heated-chain scheme was used for all chains to effectively search through parameter space. Burn-in for each chain was set to 100,000 and 10,000 followed by 1,000,000 and 100,000 repetitions for *M. megacephalus* and *M. pallidus*, respectively.

IMA (Hey & Nielsen 2007) also was used to determine Θ and M between mtDNA clades of *M. megacephalus* and *M. pallidus*. While both Migrate-N and IMA use the Metropolis-Hastings criterion, IMA incorporates a Metropolis-Coupled version of the algorithm which enables multiple heated chains to search the parameter space

simultaneously and can provide a more thorough mixing of chains (Hey & Rasmus 2004). IMA also differs from Migrate-N in that it assumes there is an ancestral panmictic population for each extant population. This assumption allows the estimation of the ancestral effective population size and time since divergence (*t*). Final runs consisted of a burn-in of at least 1,000,000 generations followed by at least 90,000 generations. Each run consisted of 50 chains and geometric heating, and all final runs were executed twice at different starting seeds to ensure convergence.

The program LdNe (Waples & Do 2008) was used to estimate parental effective population size via the linkage-disequilibrium approach (Waples 2006) for each mtDNA clade within *M. megacephalus* and *M. pallidus*. *Microdipodops* do not have overlapping generations (JCH pers. comm.), meaning that estimates are of N_e rather than effective number of breeders (N_b). Because allele frequencies close to 0 or 1 can skew N_e results (Waples 2006), alleles that had a frequency of less than 2% were omitted from analyses. For all analyses, a random mating model was assumed and 95% Jackknife confidence intervals, rather than parametric tests, were assessed in an attempt to correct for narrow confidence intervals (Waples 2006).

Bayesian inference of immigration rates (BIMr; Faubet & Gaggiotti 2008) was used to estimate current migration rates among populations. A burn-in period of 20,000 iterations, followed by additional 100,000 and 60,000 iterations for *M. megacephalus* and *M. pallidus*, respectively, were chosen. Additionally, preliminary pilot runs (each at a length of 2,000) were executed to provide a rough estimation of starting points for final

runs. Density graphs, which provide a visualization of data convergences, were critically analyzed and the mode, 2.5 percentile, and 97.5 percentile were noted.

Migrate-N and IMA estimates of Θ can be applied generate estimates of historic effective population size (N_{eLT}). Average mutation rate per generation (u) must be known before one can solve for Θ. Although microsatellites are known to exhibit between $5x10^{-3}$ to $5x10^{-5}$ mutations per generation (Dallas 1992; Dib *et al.* 1996; Estoup & Angers 1998; Goldstein *et al.* 1995; Weber & Wong 1993), MSVAR v. 1.3 (Beaumont 1999) was used to estimate the long-term average mutations per generations (u). MSVAR also was used to estimate other demographic variables: current effective size (N_1), ancestral effective size (N_0), effective population size change (r), and generations since population size change (t_a). Initial parameters were set to a generation time of one year (JCH, pers. comm.), with priors of effective sizes, mutation rate, and time of change set by recommended starting parameters (MSVAR manual). Runs used 20,000 data points with a burn-in of 2,000. Output was analyzed using JMP v. 5.0 (SAS Institute Inc.) and assessed for density estimated mode, 2.5 percentile, and 97.5 percentile values.

3. RESULTS

Summary statistics.—Eleven of the 17 polymorphic loci (*Mime2, Mime3, Mime11, Mime12, Mime21, Mime24, Mime29, Mime32, Mime33, Mime35,* and *Mime36*) and 10 (*Mime2, Mime4, Mime5, Mime11, Mime12, Mime24, Mime29, Mime32, Mime33,* and *Mime35*) were used in the population-genetic analysis of both species, due to amplification failure in the remaining loci. Summary data are shown in Table 2 and Table 3. One locus (*Mime33*) in *M. megacephalus* was monomorphic in the western and Idaho clades but polymorphic in the eastern and central clades. After correction for multiple tests, genotypes at two loci (*Mime11* and *Mime32*) in *M. pallidus* from the western clade deviated significantly from Hardy-Weinberg equilibrium. This was due to the isolated population from Deep Springs where homozygote excess occurred in both loci. When Deep Springs was excluded from analysis, all loci conformed to Hardy-Weinberg equilibrium. Preliminary runs of less computationally intensive analyses (AMOVA, STRUCTURE, R_{ST}), including and excluding *Mime11* and *Mime32*, showed no difference. Therefore, results reported in this study include all loci. The most polymorphic locus in *M. megacephalus* and *M. pallidus* was *Mime29* (20 and 21 alleles, respectively), while the least polymorphic loci were *Mime35* (8 alleles) and *Mime33* in *M. megacephalus* and *M. pallidus* (4 alleles), respectively (Tables 2 and 3). Allelic richness averaged across all loci was greatest in the *M. megacephalus* central clade (4.01) and the *M. pallidus* western clade (9.08). No significant differences among clades in allelic richness or gene diversity (H_E) were found.

Population structure.—STRUCTURE analyses revealed that $K = 3$ was the most likely and $K = 1$ the least likely number of clusters of nuclear variation for both *M. megacephalus* and *M. pallidus* (when plotting ln Prob (Data)). However, results from the ΔK metric suggested by Evanno et al. (2005) indicated that $K = 2$ was the most strongly supported (Δ ln Prob(Data) = 388.02 and 551.32 for *M. megacephalus* and *M. pallidus*, respectively) while $K = 3$ was the next most strongly supported (Δ ln Prob(Data) = 106.02 and 24.86 for *M. megacephalus* and *M. pallidus*, respectively). When individual mtDNA clades were analyzed separately, $K = 1$ was the most likely number of clusters of nuclear variation for all clades with the exception of the *M. pallidus* western clade, where $K = 2$ was most likely number of clusters (corresponding to Deep Springs and the rest of the western clade).

Analysis of molecular variance (AMOVA) revealed significant population structure among clades and among populations within clades in both species (Table 4). Pairwise estimates of R_{ST} among clades within *M. megacephalus* ranged from 0.159 (eastern and central clades) to 0.605 (eastern and Idaho clades) and the R_{ST} estimate between *M. pallidus* clades was 0.888. AMOVA of mtDNA subclades (see methods above; Light et al. 2012) repeatedly showed the majority of variation distributed within individuals (pairwise ϕ_{IT} ranged from 0.6517 to 0.8333), however significant variation was found among subclades in the *M. megacephalus* central clade and the *M. pallidus* western clade (pairwise ϕ_{ST} = 0.1672 and 0.1071), respectively

Table 2 Summary statistics of 11 microsatellite loci found within *M. megacephalus* from the eastern, central, western, and Idaho clades. Values of number of individuals (N), observed heterozygosity (H_O), gene diversity (expected heterozygosity; H_E), probability of conformance to Hardy-Weinberg (HW), number of alleles (A), and Allelic Richness (A_R) are reported. Locus *Mime33* was found to be monomorphic for the western and Idaho clades.

	Mime2	*Mime3*	*Mime11*	*Mime12*	*Mime21*	*Mime24*	*Mime29*	*Mime32*	*Mime33*	*Mime35*	*Mime36*
Eastern											
N	49	49	49	49	49	49	48	48	49	49	47
H_O	0.91837	0.73469	0.67347	0.7551	0.85714	0.77551	0.72917	0.72917	0.77551	0.87755	0.76596
H_E	0.84683	0.83947	0.80391	0.8077	0.88239	0.73175	0.76425	0.77697	0.80454	0.80623	0.80599
HW	0.62137	0.01491	0.0108	0.0097	0.06952	0.0209	0.2349	0.33228	0.37365	0.10825	0.18306
A	9	8	9	12	14	6	9	8	9	7	9
A_R	4.17	4.097	3.819	3.971	4.539	3.244	3.553	3.598	3.886	3.789	0.5625
Central											
N	68	69	69	69	69	68	66	68	68	69	69
H_O	0.83824	0.71014	0.72464	0.76812	0.82609	0.86765	0.74242	0.82353	0.80882	0.75362	0.81159
H_E	0.85261	0.83233	0.79816	0.81847	0.85507	0.79869	0.79517	0.8244	0.84564	0.78536	0.88681
HW	0.45032	0.02758	0.0832	0.56024	0.56024	0.47868	0.26346	0.59097	0.25529	0.66839	0.44048
A	11	10	8	10	13	7	9	8	10	8	14
A_R	4.248	4.033	3.751	3.954	4.26	3.737	3.735	3.983	4.187	3.684	4.586
Western											
N	59	62	62	62	61	61	58	59	61	62	61
H_O	0.79661	0.79032	0.77419	0.74194	0.77049	0.85246	0.84483	0.84483	-	0.62903	0.63934
H_E	0.80878	0.80698	0.76882	0.81655	0.88227	0.87197	0.88516	0.88516	-	0.72712	0.79217
HW	0.16764	0.44102	0.04119	0.15546	0.00669	0.19183	0.06831	0.06831	-	0.1071	0.07473
A	9	9	8	8	14	9	17	7	1	6	8
A_R	3.869	3.864	3.533	3.958	4.533	4.396	4.598	3.288	1	3.261	3.718
Idaho											
N	4	4	4	4	4	4	4	4	4	3	3
H_O	1	1	0.5	0.5	0.75	0.25	1	1	-	1	0.667
H_E	0.67857	0.71429	0.67857	0.42857	0.75	0.46429	0.75	0.89286	-	0.6	0.8
HW	0.31266	0.5433	1	1	1	0.14273	1	1	-	0.39954	0.60073
A	3	3	3	2	4	3	3	5	1	2	4
A_R	2.75	2.929	2.75	1.964	3.464	2.5	2.964	4.393	1	2	4

Table 3 Summary statistics of 10 microsatellite loci found within *M. pallidus* from the eastern and western clades. Values for number of individuals (N), observed heterozygosity (H_O), gene diversity (expected heterozygosity; H_E), probability of conformance to Hardy-Weinberg (HW), number of alleles (A), and Allelic Richness (A_R) are reported. Loci with asterisk (*) represent deviation from Hardy-Weinberg after correction for multiple tests.

	Mime2	*Mime4*	*Mime5*	*Mime11*	*Mime12*	*Mime24*	*Mime29*	*Mime32*	*Mime33*	*Mime35*
Eastern										
N	42	41	42	42	42	42	41	42	42	42
H_O	0.69048	0.73171	0.7381	0.7619	0.80952	0.8333	0.85366	0.54762	0.38095	0.7381
H_E	0.82387	0.75008	0.73896	0.80034	0.79231	0.79346	0.90003	0.71572	0.31211	0.77653
HW	0.50682	0.99956	0.64144	0.17348	0.47011	0.49504	0.07527	0.12538	0.31231	0.80186
A	7	8	6	9	9	7	13	6	2	7
A_R	6.976	8	5.976	8.952	8.952	6.976	13	5.976	2	7
Western										
N	62	63	57	56	63	62	63	63	63	63
H_O	0.64516	0.77778	0.89474	0.78571	0.69841	0.838971	0.77778	0.65079	0.04762	0.77778
H_E	0.75138	0.78756	0.90545	0.88095	0.80698	0.89156	0.76825	0.77168	0.07759	0.75949
HW	0.01113	0.87267	0.03936	0.00136*	0.052	0.13845	0.2815	0*	0.03251	0.19073
A	9	7	17	12	8	15	11	7	3	7
A_R	8.496	6.302	16.522	11.194	7.946	14.485	9.809	6.301	2.839	6.945

However, two clades (the *M. megacephalus* western clade and the *M. pallidus* eastern clade) had differences between estimates of F_{ST} and R_{ST} statistics, which could indicate recent genetic drift (Hardy et al. 2003).

Average, long term migration and long term effective population size. Estimates of M from Migrate-N for *M. megacephalus* were low, with modes ranging from 0 (western -> central and central -> to western) to 0.049 (central -> to eastern). Mutation-scaled migration from eastern -> central were higher (0.18), however the 2.5% and 97.5% confidence intervals were 0.01 and 0.92, respectively. With such a large confidence interval it was therefore unclear how much (if any) historical migration was occurring between these two clades due to such a large confidence interval. Theta (ϴ) estimates for the eastern, central, and western clades of *M. megacephalus* were 12.182 (95% CI: 9.284 – 16.232), 17.078 (95% CI: 13.028 – 21.884), and 13.982 (95% CI: 9.93 – 19.364). Theta values were homogeneous among all clades.

Estimates for average, long term mutation-scaled migration within *M. pallidus* were 0.009 (western -> eastern) and 0.026 (eastern -> western). The lower bound of both estimates reached 0 and the upper bound was 0.069 and 0.045 for eastern -> western and western -> eastern, respectively. Theta (ϴ) estimates for the *M. pallidus* eastern and western clades were 11.35 (95% CI: 8.26 – 15.84) and 15.58 (95% CI: 11.52 – 20.88), respectively.

Table 4 Analysis of molecular variance (AMOVA) among for the four mtDNA clades of *M. megacephalus* (eastern, central, western, and Idaho clades) and the two clades of *M. pallidus* clades (eastern and western clades), indicating the degree and significance of population structuring based on the R_{ST} statistic. Significance of variance component (*P*) was tested by permutations according to Excoffier et al. (1992)

Source of Variation	Variance components	% of variance	Fixation indices	*P*
M. megacephalus				
Among clades	48.6338	51.87	0.5187	$P < 0.0001$
Among populations within clades	8.9543	9.55	0.1984	$P < 0.0001$
Within individuals	36.1794	38.58	0.61416	$P < 0.0001$
M. pallidus				
Among clades	263.45782	88.79	0.8879	$P < 0.001$
Among populations within clades	8.24233	2.78	0.2478	$P < 0.0001$
Within individuals	25.01905	8.43	0.9157	$P < 0.0001$

Results from IMA analysis of *M. megacephalus* are currently unavailable because the analysis is still running. IMA analysis of *M. pallidus* revealed that the lower bound of time since divergence (*t*) did not include zero, indicating that divergence did occur from one ancestral panmictic population. Estimated migration rates were slightly higher than Migrate-N results, where eastern -> western and western -> eastern were 0.085 (95% CI: 0.025 – 0.225) and 0.035 (0.005 – 0.155), respectively, indicating low levels of possible historic migration. When migration was graphed in relation to time, it was observed that only very recent migration was occurring. Theta estimates for the eastern and western *M. pallidus* clades were 8.09 (95% CI: 5.15 – 11.04) and 11.05 (95% CI: 6.63 – 15.46), respectively.

There are 16 nested models in which IMA can test against the null model, all of which vary effective population sizes among ancestral and extant populations and presence and directionality of migration. For example, a model of ABCDD tests against the null where the effective population sizes vary among the ancestral (A), eastern (B), and western lineages (C), however migration rate is equal from eastern -> western (D) and western -> eastern (D). Of these 16 models, the only significant models were AAC00, AAA00, ABA00, and ABB00. All of these models claim no migration between the eastern and western clades with varying effective population sizes. However, only one model (AAC00) makes biological sense because it would be unlikely for the ancestral population size to be similar in size to extant populations.

Current effective population size and migration.—LdNe mode, minimum, and maximum estimates (based on 95% jackknife confidence intervals) of the parental

effective population size (N_e) for *M. megacephalus* and *M. pallidus* are presented in Table 5. The eastern clade of *M. megacephalus* and the eastern clade of *M. pallidus* were the only clades with upper limits of infinity (∞). Minimum estimates of N_e (based on 95% confidence intervals) which may be indicative of bottlenecks (Waples & Do 2010) ranged from 108.8 individuals (western clade) to 179.8 (central clade) in *M. megacephalus*, and were 95.1 and 80.5 in the eastern and western clades of *M. pallidus*, respectively.

Modal estimates of current migration rate, estimated in BIMr, among clades of *M. megacephalus* ranged from 2.19×10^{-11} to 3.56×10^{-16} (Table 6), indicating effectively no migration across clades within the last generation. Modal estimates for *M. pallidus* (Table 6) indicated low but current migration between the eastern and western clades.

Demographic history.—Estimates of mutation rate (u), population contraction/expansion (r), and time since demographic change (t_a) are reported in Table 7. Average mutation rates ranged from 1.48×10^{-4} to 2.2×10^{-4}. Estimates of population contraction/expansion were shown to vary across populations. While the *M. pallidus* western clade ($r = 0.997$; $P > 0.05$) and the *M. megacephalus* eastern clade ($r = 0.76$; $P > 0.05$) showed population contraction within the last 68,121 and 12,935 years, respectively, the *M. pallidus* eastern clade ($r = 2.0$; $P < 0.05$) and *M. megacephalus* central ($r = 1.51$; $P > 0.05$) and western ($r = 1.434$; $P > 0.05$) clades showed population expansion within the last 25,000 years (Table 7).

Table 5 Mode and putative 95% jackknife confidence intervals of parental effective population size. Alleles with a frequency less than 2% were excluded from analysis (see text).

Sample	Parental N_e
M. megacephalus	
Eastern Clade	378.1 (166.3 – ∞)
Central Clade	341.0 (179.8 – 1,914.5)
Western Clade	213.2 (108.8 – 1,385.9)
M. pallidus	
Eastern Clade	287.9 (95.1 – ∞)
Western Clade	128.3 (80.5 – 270.3)

Table 6 Estimates of current migration rates, calculated with BIMr. Modal values and their 95% quartiles are given for migration rate from the previous generation.

Sample	2.5%	Mode	97.5%
M. megacephalus			
Eastern -> Central	1.59×10^{-5}	2.86×10^{-16}	7.8×10^{-3}
Eastern -> Western	2.74×10^{-16}	1.82×10^{-15}	4.8×10^{-4}
Central -> Eastern	4.71×10^{-9}	3.56×10^{-16}	1.15×10^{-6}
Central -> Western	5.63×10^{-9}	1.82×10^{-15}	9.18×10^{-7}
Western -> Eastern	2.43×10^{-9}	2.19×10^{-11}	5.93×10^{-10}
Western -> Central	1.26×10^{-12}	2.19×10^{-11}	5.9×10^{-10}
M. pallidus			
Eastern -> Western	0.00034	0.00223	0.04538
Western -> Eastern	0.00023	0.0017	0.03241

Table 7 Mode estimates and 95% quartiles for mutation rate (*u*), population contraction/expansion (*r*), and time since population change in years (t_a) as calculated in MSVAR. Generation time was set to 1 year to solve for t_a.

Sample	2.5%	Mode	97.5%
M. megacephalus			
Eastern Clade			
u	2.2×10^{-4}	2.0×10^{-4}	1.7×10^{-4}
r	0.3957	0.7645	1.1344
t_a	4,673	12,935	40,058
Central Clade			
u	2.0×10^{-4}	1.78×10^{-4}	1.5×10^{-4}
r	0.533	1.51	8.062
t_a	17,570	25,579	40,140
Western Clade			
u	2.02×10^{-4}	1.78×10^{-4}	1.5×10^{-4}
r	0.529	1.434	7.099
t_a	11,465	25,387	47,136
M. pallidus			
Eastern Clade			
u	2.2×10^{-4}	1.9×10^{-4}	1.7×10^{-4}
r	1.0	2.0	5.0
t_a	12,777	20,921	40,171
Western Clade			
u	1.97×10^{-4}	1.72×10^{-4}	1.48×10^{-4}
r	0.619	0.997	1.845
t_a	7,447	68,191	83,115

4. DISCUSSION

This study demonstrates that nuclear microsatellite markers support previous mitochondrial studies in that *M. megacephalus* and *M. pallidus* are comprised of at least three (eastern, central, and western clades) and two (eastern and western clades) genetically distinct clades, respectively. The clade of *M. megacephalus* in Idaho could not be analyzed rigorously due to our small sample size. This study differs from past phylogenetic and phylogeographic studies by using nuclear data to assess patterns of migration among mitochondrial lineages, effective population sizes, current population structure, current migration, and demographic history. Results of the study should improve understanding of how current populations in both species have diverged, how recently populations have exchanged genes (if at all), and if different management strategies might be useful for different evolutionary significant units (ESUs).

Microdipodops megacephalus.—There is significant population structure within *M. megacephalus* supporting the eastern, central, and western clades as distinct lineages. In agreement with previous phylogenetic analyses, population genetic analyses of microsatellite data reveal a close affinity between the eastern and central clades, but a clearly diverged western clade (Hafner and Upham 2011). The closer affinity between the eastern and central clades is consistent with their geographic proximity as these two clades are parapatric, whereas the western and Idaho clades are completely isolated (Fig. 2A). Historically, little to no gene flow appears to have occurred between the eastern/central and western clades. However, it is unclear how much migration, if any,

has occurred between the eastern and central clades. Molecular evidence suggests lineage divergence within *M. megacephalus* occurred much earlier in the Pliocene (Hafner and Upham 2011; Hafner et al. 2008). Fossil evidence outside of the Great Basin Desert from the late Blancan (1.9 – 2.9 mya) further supports that kangaroo mice diversified prior to the Pleistocene and not within the Great Basin Desert (Mehringer 1986; Smith 1982). Therefore, a plausible hypothesis is that there were multiple lineages of *M. megacephalus* at one time, and some or all of those lineages invaded the Great Basin Desert in the early Pleistocene (Hafner and Upham 2011). This early Pleistocene migration has been observed in other taxa, such as brown creepers and mountain chickadees (Manthey et al. 2011; Spellman et al. 2007). It appears that unsuitable habitat (i.e., habitats lacking sandy soils with gravel overlay, sagebrush, and rabbitbrush) is all that is separating the eastern and central clades, sometimes by as little as 25 km (Hafner and Upham 2011). Thus, it is possible that both clades represented one lineage that invaded the Great Basin Desert, and then diverged from one another after an uprising of unsuitable habitat during the Pleistocene.

No current migration is occurring among clades. This finding, along with evidence of reciprocal monophyly of mtDNA clades and significant differences in microsatellite allele and genotype distributions, supports the notion that each clade should be managed as a separate unit. In fact, the need for conservation practices for each of the *M. megacephalus* clades has never been greater. According to the 50/500 rule (Franklin 1980), at least 50 adults are needed to avoid inbreeding and 500 to avoid extinction due to an inability to cope with environmental change. However, this rule has

recently been disputed and it may be that a minimum viable population size should be much higher (Traill et al. 2010) or will vary among populations (Flather et al. 2011). Regardless, our results report low numbers which imply the possibility of inbreeding, the inability to adapt to environmental change, and therefore, possible extinction. It is unknown if the Pleistocene glacial-interglacial periods solely affected the abundance of *M. megacephalus*, however, a combination of historic (Pleistocene and pre-Pleistocene) and recent habitat changes have likely played a role in depressing current sizes (Hafner and Upham 2011). Appropriate measures must be taken to conserve each genetically distinct lineage with appropriate management techniques for each population.

Microdipodops pallidus.—The eastern and western *M. pallidus* clades are genetically distinct units. Hafner et al. (2008) hypothesized that clade divergence within *M. pallidus* was mainly attributed to range adjustments caused by the Pleistocene's climatic oscillations. While the Great Basin Desert was never directly affected with glaciations, it did have extended pluvial periods (Lomolino et al. 2006). For instance, the last glacial maximum (Wisconsin age) gave rise to many bodies of water, such as Lahontan lake (Lomolino et al. 2006). It is plausible that during pluvial periods, the geographic range of *M. pallidus* shifted out of the Great Basin Desert, and during interglacial periods ranges adjusted back (Hafner et al. 2008). The series of mountain chains that currently serves as a boundary between the two clades (e.g., the southern end of Toquima Range, San Antonio Mountain, Lone Mountain, Weepah Hills, Split Mountain, Clayton Ridge, and Montezuma Range; Hafner et al. 2008) may have split range extensions in an eastern and western direction and subsequently blocked gene flow

between the two clades. Molecular dating, however, indicates that the divergence between the two lineages occurred earlier than the climatic oscillations of the Pleistocene (Hafner et al. 2008). Therefore, similar to *M. megacephalus*, it is possible that the ancestral population diverged outside of the Great Basin Desert, two independent lineages invaded the region at the beginning of the Pleistocene, and the series of mountain chains continued to prevent historic gene flow between these two lineages.

Contrary to our average, long term analyses, a low level of recent migration appears to be occurring between the eastern and western lineages. The mountain chain that divides the eastern and western clades appears to have been a barrier isolating the two clades, but there is one known sympatric locality (San Antonio, Nevada). This small area, which is suitable to accommodate members of these two clades, may represent a possible hybridization zone; however, further sampling is necessary to facilitate this hypothesis. Migration between the eastern and western clades, although, is extremely low. Similar to its sister taxon *M. megacephalus*, the lower bound of the parental effective population size of both the eastern and western clades is well below the 500 individual guideline. Importantly, the western clade even has an upper bound below 500. Thus, both the eastern and western clades may be in danger of extinction by not having a minimum viable population sizes; separate management practices for each clade must be enforced within the near future (Triall et al. 2010). The western clade is further at risk because previous findings indicate that it may have undergone a recent population contraction (Light et al. 2012).

5. CONCLUSION

This study demonstrates long-term averages and contemporary differences among previously identified mtDNA clades of *Microdipodops* using nuclear data. Analyses reveal that there are at least three genetically distinct groups within *M. megacephalus* that are not currently exchanging genes. Similarly, *M. pallidus* can be characterized by two distinct lineages corresponding to the eastern and western mtDNA clades. *Microdipodops pallidus* likely did not have any historic migration between populations, but low rates of migration appear to be occurring at present. It is clear, based upon both mitochondrial and nuclear genetic markers, that *M. megacephalus* and *M. pallidus* are made up of different evolutionary significant units (ESUs). These ESUs often have specific habitat requirements and should probably be recognized as distinct species. For example, members of the *M. megacephalus* western and eastern clades seem to occupy finer sands in lower elevation habitats, whereas representatives of the central and Idaho clades are found in sandier soils with gravel overlay (Hafner and Upham 2011)

Given impeding habitat threats in the Great Basin Desert, it is important that each ESU be managed as separate species. Indeed, Chaplin et al. (2000) ranked the Great Basin as second in imperiled species numbers among ecoregions of the United States. Habitat loss through agricultural practices, wildfires, and invasive plants has devastated the low elevation areas where kangaroo mice from the eastern and western clades of *M.*

megacephalus are distributed. Although *M. pallidus* inhabits higher elevation areas, and are not believed to be directly affected by wildfires, it is clear that both dark and pallid kangaroo mice are experiencing population declines (Linzey & Hammerson 2008; Linzey *et al.* 2008). Recent attempts to trap dark kangaroo mice from northern localities where mice were once abundant have been unsuccessful (e.g., Powell Butte, Narrows, Riddle, Quinn River Crossing, Sulphur, Winemucca, Golconda, Izenhood, Halleck, and Callao; Hafner 1981; Hall 1941). Furthermore, repeated efforts to collect *M. pallidus* in once fruitful areas (e.g, Fallon, Alamo, and Deep Springs) have either proven to be increasingly difficult or completely unsuccessful (Hafner et al. 2008).

Kangaroo mice are endemic to the Great Basin Desert and likely have persisted there through the millennia. However, abundance of these mice is diminishing and each ESU may be in critical risk of extinction. Furthermore, kangaroo mice may be integral in seed dispersal and thus necessary for the sustainability of the flora within the Great Basin Desert. Given this potential key role in seed dispersal, *Microdipodops* may serve as indicator species to healthy desert ecosystems (Light et al. 2012), and a reduction in their abundance may prove detrimental to the surrounding environmental. Species of *Microdipodops* clearly are a necessary entity in the Great Basin Desert, and this study provides further support that management efforts should be applied to each ESU in an effort to conserve these valuable taxa and the imperiled habitats of the Great Basin Desert.

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APPENDIX I

Appendix I. Localities (listed by mtDNA clade then alphabetically by general locality), number of samples (*n*) and museum vouchers of *Microdipodops megacephalus* and *M. pallidus* specimens examined in this study. Museum abbreviations are as follows: Moore Laboratory of Zoology (MLZ, Occidental College), Museum of Southwestern Biology (MSB, University of New Mexico), Monte L. Bean Life Science Museum (BYU, Brigham Young University), San Diego Natural History Museum (SDNHM), Idaho Museum of Natural History (IMNH, Idaho State University), and the Museum of Vertebrate Zoology (MVZ, University of California, Berkeley).

Locality, *n*, Museum Vouchers

Microdipodops megacephalus

<u>Eastern Clade:</u>
Beryl: 0.7 mi N, 6.3 mi E Beryl, 5125 ft, Iron Co., Utah, 8, MLZ 2145-2152
Callao: 7.7 mi S, 2.7 mi E Callao, 4500 ft, Juab Co., Utah, 1, MSB 35599
Callao: 5.5 mi S, 7.8 mi E Callao, 4400 ft, Juab Co., Utah, 1, MSB 35602
Geyser: 5.3 mi S, 1.6 mi E Geyser, 5900 ft, Lincoln Co., Nevada, 2, MLZ 1974, 1975
Geyser: 5.2 mi S, 1.9 mi E Geyser, 5900 ft, Lincoln Co., Nevada, 4, MLZ 1976-1979
Geyser: 5.1 mi S, 2.3 mi E Geyser, 5900 ft, Lincoln Co., Nevada, 4, MLZ 1980-1983
Milford: 16.1 mi S, 19.6 mi E Garrison, 5400 ft, Millard Co., Utah, 3, MLZ 2079-2081
Milford: 19.3 mi S, 18.4 mi E Garrison, 5100 ft, Millard Co., Utah, 6, MLZ 2082-2087
Milford: 11.2 mi N, 39.6 mi W Milford, 5200 ft, Beaver Co., Utah, 1, MLZ 2088
Minersville: 4.2 mi S, 15.8 mi W Minersville, 5050 ft, Beaver Co., Utah, 8, MLZ 2071-2078
Minersville: Escalante Desert, 380 09.118’ N, 1130 12.94’ W, 1540 m, Beaver Co., UT, 2, BYU 30100, 30101
Osceola: 6.0 mi S, 4.2 mi W Osceola, 5800 ft, White Pine Co., Nevada, 3, MLZ 1942-1944
Panaca: 24 mi W Panaca, 4600 ft, Lincoln Co., Nevada, 4, MLZ 1752-1755
Pony Springs: 9.0 mi N, 10.8 mi W Pony Springs, 6020 ft, Lincoln Co., Nevada, 2, MLZ 2059, 2060

<u>Central Clade:</u>
Austin: 6.2 mi S, 19.6 mi W Austin, 6150 ft, Lander Co., Nevada, 4, MLZ 1748-1751
Belmont: 3.2 mi N, 4.2 mi E Belmont, 7000 ft, Nye Co., Nevada, 4, MLZ 2027-2030
Benton: 5 mi N Benton, 5600 ft, Mono Co., California, 6, MLZ 1740-1742, MLZ 1915-1917
Cherry Creek: 7.2 mi N, 8.8 mi E Cherry Creek, 5850 ft, White Pine Co., Nevada, 1, MLZ 1965
Cobre: 0.9 mi S, 0.4 mi W Cobre, 5900 ft, Elko Co., Nevada, 2, MLZ 2067, 2068
Contact: 10.9 mi S, 2.5 mi W Contact, 5700 ft, Elko Co., Nevada, 2, MLZ 2069, 2070
Currant: 4.9 mi S, 28.2 mi W Currant, 6000 ft, Nye Co., Nevada, 2, MLZ 2005, 2006
Danville: 6.1 mi S, 2.4 mi E Danville, 6800 ft, Nye Co., Nevada, 3, MLZ 2021-2023
Duckwater: 8.4 mi N, 17.5 mi W Duckwater, 6350 ft, Nye Co., Nevada, 3, MLZ 1997-1999
N Eureka: 22.8 mi N, 3.6 mi W Eureka, 5850 ft, Eureka Co., Nevada, 4, MLZ 1956, 1957, MSB 35526, 35527

Locality, n, Museum Vouchers

W Eureka: 6.2 mi N, 9.5 mi W Eureka, 6000 ft, Eureka Co., Nevada, 2, MLZ 2031, 2032
Fletcher: 1/4 mile N Fletcher, 6100 ft, Mineral Co., Nevada, 2, MLZ 1744, 1745
Goldfield: 12.0 mi N, 2.5 mi W Goldfield, 4860 ft, Esmeralda Co., Nevada, 1, MLZ 1747
Gold Reed: 2.9 mi S, 3.1 mi E Gold Reed, 5350 ft, Nye Co., Nevada, 1, MLZ 2053
Gold Reed: 2.9 mi S, 4.0 mi E Gold Reed, 5330 ft, Nye Co., Nevada, 5, MLZ 2054-2058
N Hiko: 31 mi N, 1 mile W Hiko, 5100 ft, Lincoln Co., Nevada, 1, MLZ 1960
W Hiko: 6 mi N, 31 mi W Hiko, 4800 ft, Lincoln Co., Nevada, 2, MLZ 1815, 1816
Ruby Valley: 13.2 mi S, 0.6 mi E Ruby Valley, 6000 ft, Elko Co., Nevada, 1, MLZ 2033
San Antonio: 3.7 mi N, 3.2 mi E San Antonio, 5600 ft, Nye Co., Nevada, 2, MLZ 1761, 1762
Sunnyside: 1.3 mi S, 4.9 mi W Sunnyside, 5200 ft, Nye Co., Nevada, 1, MLZ 1966
NE Tonopah: 13.8 mi N, 7.9 mi E Tonopah, 5800 ft, Nye Co., Nevada, 4, MLZ 1961-1964
SE Tonopah: 9.8 mi S, 9.9 mi E Tonopah, 5200 ft, Nye Co., Nevada, 1, MLZ 1831
Tybo: 1.0 mi N, 8.5 mi W Tybo, 6200 ft, Nye Co., Nevada, 2, MLZ 1799, 1800
Warm Springs: 5.9 mi N, 10.2 mi E Warm Springs, 5200 ft, Nye Co., Nevada, 1, MLZ 2024
Warm Springs: 6.4 mi N, 10.1 mi E Warm Springs, 5200 ft, Nye Co., Nevada, 1, MLZ 2025
Warm Springs: 7.7 mi N, 9.5 mi E Warm Springs, 5200 ft, Nye Co., Nevada, 1, MLZ 2026
NE Warm Springs: 19.2 mi N, 13.4 mi E Warm Springs, 6000 ft, Nye Co., Nevada, 5, MLZ 1905, MLZ 1948-1951
SE Warm Springs: 12.7 mi S, 0.4 mi E Warm Springs, 6000 ft, Nye Co., Nevada, 5, MLZ 1968-1972

Western Clade:
Chilcoot: 1.7 mi N Chilcoot, 5100 ft, Plumas Co., California, 1, MLZ 1756
Chilcoot: 1.5 mi N Chilcoot, 5100 ft, Plumas Co., California, 1, MVZ 158930
Denio: 0.6 mi S Denio, 4200 ft, Humboldt Co., Nevada, 2, MSB 35530, 35531
Fields: 2.4 mi N, 3.4 mi E Fields, 4050 ft, Harney Co., Oregon, 9, MLZ 2007-2015
Gerlach: 28.5 mi N, 27.8 mi W Gerlach, 4700 ft, Washoe Co., Nevada, 5, MLZ 2089-2093
Gerlach: 28.2 mi N, 27.6 mi W Gerlach, 4700 ft, Washoe Co., Nevada, 5, MLZ 2094-2098
Gerlach: 24.5 mi N, 25.0 mi W Gerlach, 4800 ft, Washoe Co., Nevada, 1, MLZ 2099
Gerlach: 24.0 mi N, 24.8 mi W Gerlach, 4800 ft, Washoe Co., Nevada, 5, MLZ 2100-2104
Gerlach: 22.4 mi N, 23.6 mi W Gerlach, 4800 ft, Washoe Co., Nevada, 5, MLZ 2105-2109
Jungo: 13.8 mi N, 11.2 mi E Jungo, 4200 ft, Humboldt Co., Nevada, 5, MLZ 2124-2128
Ravendale: 4.4 mi N, 13.6 mi E Ravendale, 5650 ft, Lassen Co., California, 2, MLZ 2110,2112
Ravendale: 4.7 mi N, 10.8 mi E Ravendale, 5350 ft, Lassen Co., California, 2, MLZ 2113-2114
Sparks: 6 mi N, 4 mi E Sparks, 4600 ft, Washoe Co., Nevada, 3, MLZ 1757-1759
Valley Falls: 36 mi N, 14 mi E Valley Falls, 4300 ft, Lake Co., Oregon, 10, MLZ 1987-1996
Vernon: 0.5 mi S, 11.5 mi W Vernon, 4450 ft, Pershing Co., Nevada, 1, MLZ 1760
Vya: 3.2 mi N, 11.5 mi E Vya, 5600 ft, Washoe Co., Nevada, 3, MLZ 1984-1986
N Winnemucca: 7 mi N Winnemucca, 4600 ft, Humboldt Co., Nevada, 1, MSB 35533
SW Winnemucca: 5.5 mi S, 9.2 mi W Winnemucca, 4300 ft, Humboldt Co., Nevada, 1, MSB 35535

Locality, *n*, Museum Vouchers

Idaho Clade:
Riddle: Starr Valley, NW ¼ Section 19, T16S, R5W, B.M., Owyhee Co., Idaho, 1, IMNH 259
Riddle: 1/2 mi N Nevada, 2 1/2 mi E Oregon, Owyhee Co., Idaho, 1, IMNH 693
Riddle: 11 mi S, 44.2 mi W Riddle, 5000 ft., Owyee Co., Idaho, 2, MLZ 2163-2164

Microdipodops pallidus

Eastern Clade:
Alamo: 4.5 mi S, 32.5 mi W Alamo, 4600 ft, Lincoln Co., Nevada, 1, MSB 35536
Currant: 4.9 mi S, 28.2 mi W Currant, 6000 ft, Nye Co., Nevada, 5, MLZ 2000-2004
Goldfield: 12.0 mi N, 2.5 mi W Goldfield, 4860 ft, Esmeralda Co., Nevada, 2, MLZ 1743, 1746
SE Goldfield: 4.6 mi S, 19.8 mi E Goldfield, 4950 ft, Nye Co., Nevada, 2, MLZ 2051, 2052
Gold Reed: 3.0 mi S, 4.3 mi E Gold Reed, 5330 ft, Nye, Co., Nevada, 2, MLZ 1958, 1959
W Hiko: 6 mi N, 31 mi W Hiko, 4800 ft, Lincoln Co., Nevada, 4, MLZ 1811-1814
Lockes: 9.6 mi S, 3.8 mi W Lockes, 4800 ft, Nye Co., Nevada, 4, MLZ 2017-2020
New Reveille: 0.9 mi N, 10.3 mi E New Reveille, 4900 ft, Nye Co., Nevada, 2, MLZ 1940-1941
San Antonio: 0.5 mi S San Antonio, 5400 ft, Nye Co., Nevada, 1, MLZ 1798
Tonopah: 0.5 mi N, 32.0 mi E Tonopah, 5600 ft, Nye Co., Nevada, 4, MLZ 1801-1804
SE Tonopah: 11.0 mi S, 10.0 mi E Tonopah, 5200 ft, Nye Co., Nevada, 5, MLZ 1821-1825
SE Tonopah: 10.6 mi S, 10.0 mi E Tonopah, 5200 ft, Nye, Co., Nevada, 5, MLZ 1826-1830
NE Warm Springs: 19.2 mi N, 13.4 mi E Warm Springs, 6000 ft, Nye Co., Nevada, 5, MLZ 1906, 1952-1955

Western Clade:
Coaldale: 1.8 mi S, 5.3 mi E Coaldale, 4797 ft, Esmeralda Co., Nevada, 1, MLZ 1817
Deep Springs: 7.2 mi S, 4.0 mi W Deep Springs, 4920 ft, Inyo Co., California, 2, MLZ 1767, 1768
Deep Springs: 4.6 mi S, 3.9 mi W Deep Springs, 5000 ft, Inyo Co., California, 2, MLZ 1769, 1770
Deep Springs: 2.4 mi S, 2.3 mi W Deep Springs, 5050 ft, Inyo Co., California, 6, MLZ 1771-1776
Dyer: 7.0 mi N, 0.5 mi W Dyer, 4900 ft, Esmeralda Co., Nevada, 5, MLZ 1785-1789
Fallon: 4.3 mi N Fallon, 3900 ft, Churchill Co., Nevada, 3, MLZ 1947, 2115-2116
Lovelock: 2.5 mi N, 22.5 mi W Lovelock, 3950 ft, Pershing Co., Nevada, 3, MLZ 1967, 2117-2118
Luning: 9.8 mi N, 10.8 mi E Luning, 5350 ft, Mineral Co., Nevada, 5, MLZ 1805-1809
Luning: 12.7 mi N, 9.2 mi E Luning, 5050 ft, Mineral Co., Nevada, 1, MLZ 1810
Marietta: 0.4 mi S, 0.5 mi E Marietta, 4950 ft, Mineral Co., Nevada, 3, MLZ 1777-1779
Mina: 8.9 mi S, 1.2 mi E Mina, 4400 ft, Mineral Co., Nevada, 10, MLZ 1780-1784, 2119-2123
Nixon: 6.4 mi N, 1.0 mi W Nixon, 4200 ft, Washoe Co., Nevada, 1, MLZ 1794
Oasis: 0.2 mi S, 1.5 mi E Oasis, 5050 ft, Mono Co., California, 2, MLZ 1790, 1791
Oasis: 1.0 mi S, 4.0 mi E Oasis, 5100 ft, Mono Co., California, 2, MLZ 1792, 1793

Locality, n, Museum Vouchers

San Antonio: 0.5 mi S San Antonio, 5400 ft, Nye Co., Nevada, 2, MLZ 1796-1797
Schurz: 7.3 mi N, 2.6 mi W Schurz, 4287 ft, Mineral Co., Nevada, 3, MLZ 1818-1820
Silver Peak: 5.1 S, 1.1 mi E Silver Peak, 4300 ft, Esmeralda Co., Nevada, 2, MLZ 1945, 1946
NW Tonopah: 9.2 mi N, 8.1 mi W Tonopah, 4850 ft, Nye Co., Nevada, 1, MLZ 1973
Wadsworth: 1.0 mi N, 1.0 mi W Wadsworth, 4200 ft, Washoe Co., Nevada, 1, MLZ 1795
Yerington: 11.7 mi S, 3.5 mi E Yerington, 4690 ft, Lyon Co., Nevada, 3, MLZ 1832-1834
Yerington: 11.1 mi S, 2.8 mi E Yerington, 4640 ft, Lyon Co., Nevada, 5, MLZ 1835 – 1839

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