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Research Article

Landscape Disturbance and Sporadic Hybridization Complicate Field Identification of Chipmunks

CHRISTINA F. FRARE,[1] *Fordham University, 441 E. Fordham Road, Bronx, NY 10458, USA*
MARJORIE D. MATOCQ, *University of Nevada, Reno, 1664 N. Virginia St., Reno, NV 89557, USA*
CHRIS R. FELDMAN, *University of Nevada, Reno, 1664 N. Virginia St., Reno, NV 89557, USA*
ANGELA M. WHITE, *Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618, USA*
PATRICIA N. MANLEY, *Pacific Southwest Research Station, 2480 Carson Road Placerville, CA 95667, USA*
KATHLEEN D. JERMSTAD, *Pacific Southwest Research Station, 2480 Carson Road Placerville, CA 95667, USA*
EVON R. HEKKALA, *Fordham University, 441 E. Fordham Road, Bronx, NY 10458, USA*

ABSTRACT Chipmunks (*Tamias* spp.) in western North America are important for their numerical abundance, their role in pathogen transmission, and the composition and structure of food webs. As such, land management agencies (e.g., U.S. Forest Service) often conduct field surveys to monitor the diversity and abundance of chipmunk species as a measure of forest health. These small mammal communities often include several morphologically similar chipmunk species, some of which occasionally hybridize, which can make field identification of species difficult. However, species-specific differences in both spatial distribution and habitat use make it imperative that biotic inventories correctly identify chipmunk species. We compared molecular-based and field-based, external phenotypic identifications of 4 chipmunk species in the Lake Tahoe Basin of the Sierra Nevada in California and Nevada, USA. Across all years and sites, we found an error rate of 14% for field-based identifications with significantly lower rates of misidentification in relatively undisturbed wildlands in comparison to recently burned wildlands or urbanized sites. We also found evidence for sporadic hybridization between focal species, including cases of mito-nuclear mismatch. Our study highlights the utility of molecular tools in corroborating field identifications of chipmunks in changing landscapes. © 2016 The Wildlife Society.

KEY WORDS DNA barcoding, hybridization, Lake Tahoe Basin, monitoring, post-fire response, species identification, *Tamias*, urbanization.

Many ecosystems are threatened by anthropogenic changes (e.g., habitat fragmentation, climate change), which may result in potentially devastating losses of biodiversity. Organismal responses to such change may include range shifts, habitat shifts, and numerical decline (Davis et al. 2005). These responses have the potential to greatly affect ecosystem function and services (Travis 2003, Davis et al. 2005, Moritz et al. 2008). Land use managers and conservation practitioners have undertaken large-scale monitoring programs to inventory and document changes in wildlife communities to assess changes in ecosystem dynamics (Hall and Langtimm 2001, Manley and Van Horne 2004). Occupancy models based on species detection are frequently used to predict habitat quality as a function of current and potential future environmental conditions, and are increasingly being used to predict and monitor trends in wildlife populations across continental scales (Royle and Dorazio 2008). These models rely primarily on traditional survey data to quantify presence-absence for individual taxa or functional guilds (Wilson et al. 1996, MacKenzie, 2005, 2006). Such methods are typically dependent upon trained practitioners able to identify targeted taxonomic groups through direct observation, trapping, acoustic detection, or other indirect observations.

Two problems frequently arise during surveys that can result in incorrect inferences, false positives, and false negatives (MacKenzie et al. 2002, 2003). Although the problem of false negatives (i.e., failing to record a species that was present but went undetected) has been recognized and addressed analytically (MacKenzie et al. 2002, 2006), the problem of false positives (i.e., recording a species incorrectly as present) is more problematic and can lead to over-estimation (Royle and Link 2006) and biased estimators (McClintock et al 2010). In addition, misidentification of a species can result in false positive and false negative errors

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[1]*E-mail: cfrare@fordham.edu*
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occurring simultaneously. These detection errors are likely to be most prolific in surveys of phenotypically similar and sympatric species, even under close physical examination (Shea et al. 2011), and are particularly detrimental when species have narrow ecological niches. Because chipmunks (*Tamias* spp.) are commonly used as indicators of forest health in the western United States, we compared molecular and field-based patterns of error in species identification for 4 broadly sympatric chipmunk species in the Lake Tahoe Basin in the Sierra Nevada Mountains of California and Nevada, USA, to improve accuracy of species monitoring programs: yellow-pine chipmunk (*Tamias amoenus*), long-eared chipmunk (*T. quadrimaculatus*), shadow chipmunk (*T. senex*), and lodgepole chipmunk (*T. speciosus*).

Chipmunks are found primarily in forested regions in the western United States where they are an important guild across many ecological communities. In particular, their role caching seed and distributing ectomycorrhizal fungi (Fogel and Trappe 1978, Coppeto et al. 2006) influences plant species diversity and forest composition. Each species' habitat preference varies according to temperature, elevation, human disturbance, and forest cover. In areas of geographic overlap, species use different microhabitats, and interact with the landscape differently (Johnson 1943, Heller 1971, Heller and Gates 1971, Chappell 1978, Vander Wall 1993). In addition, individual species respond to anthropogenic and environmental changes idiosyncratically, with some species adapting to land-use and climate change, whereas others suffer population declines and concomitant genetic erosion (Manley et al. 2006, 2007; Moritz et al. 2008; Rubidge et al. 2011). Species may respond to habitat and environmental change by shifting their habitat use or distributional limits, which could augment opportunity for interspecific contact and hybridization. Further, because field personnel rely on phenotypic characteristics and habitat associations to make field identification decisions, changes in chipmunk habitat use in response to disturbance could lead to higher rates of misidentification.

Taxonomic revision for North American chipmunks has variously placed the western United States species in the genus *Eutamias*, *Neotamias*, or *Tamias* (Patterson and Norris 2016). The western clade of the group is comprised of over 20 phenotypically similar species, some of which co-occur and occasionally hybridize (Good et al. 2003, Reid et al. 2012) adding to the complexity of current taxonomy. Pending further changes, we follow Thorington and Hoffmann (2005) by using *Tamias* here.

We focused on 4 broadly sympatric species (yellow-pine chipmunk, long-eared chipmunk, shadow chipmunk, and lodgepole chipmunk) found in the Lake Tahoe Basin of the central Sierra Nevada in California and Nevada. Within this species group, there are 2 larger-bodied chipmunks (shadow chipmunk and long-eared chipmunk) and 2 smaller-bodied chipmunk species (yellow-pine chipmunk and lodgepole chipmunk). Each similarly sized pair consists of 1 generalist species (long-eared chipmunk or yellow-pine chipmunk) and 1 specialist species (shadow chipmunk and lodgepole chipmunk; Sharples 1983, Sutton 1995). Correct species identification often requires examination of size, pelage, and genital bone morphology of vouchered specimens (Sutton 1992, 1995; Sutton and Patterson 2000).

Prior surveys indicate that each species has a unique habitat preference, and that these species may be responding differentially to environmental change (Manley et al. 2006, Moritz et al. 2008, Sollmann et al. 2015). The focal species make up a large portion of the small-mammal community in this region (Manley et al. 2007); therefore, misidentification can lead to significant mischaracterization of community composition and dynamics. Genetic methods of species identification lower rates of misidentification than traditional field methods (Borisenko et al. 2008), and are sufficiently sensitive to reveal greater diversity across different categories (e.g., taxonomic, phylogenetic, functional; Jarzyna and Jetz 2016), thereby creating a more accurate and precise picture of community composition. Thus, we sought to 1) develop a simple genetic method to identify chipmunks in the Tahoe Basin and to quantify interspecific hybridization; 2) test the accuracy of field identifications of chipmunks in the Tahoe Basin; and 3) determine whether field misidentifications are more common in disturbed habitats (i.e., fire, urbanization). We predicted that landscape disturbance would increase rates of chipmunk misidentification because, especially in the case of specialist species, field personnel naturally become accustomed to the typical habitat that particular species are trapped in, and use that to inform their species determination. In situations when those typical habitat associations were altered, we suspected that rates of misidentification would increase.

STUDY AREA

The Lake Tahoe Basin is situated in the Sierra Nevada on the border of California and Nevada (Fig. 1). The lake (elevation 1,897 m) is surrounded by the Sierra Nevada Mountains, and as a result, the elevation in the basin ranges from a low of $<$1,800 m to 3,315 m at Freel Peak. At low elevations, Jeffry pine (*Pinus jeffrei*) and white fir (*Abies concolor*) dominated the forest, whereas at higher elevations, red fir (*A. magnifca*) was the dominant species. Other common species included the lodgepole pine (*P. contorta murrayana*), quaking aspen (*Populus tremuloides*), and sugar pine (*P. lambertiana*). Squirrels (Family: *Sciuridae*), deer mice (*Peromyscus maniculatus*), shrews (*Sorex* spp.), and voles (*Microtus* spp.) were some of the dominant small-mammal species.

Our survey took place around the entire lake, in California and Nevada. The Lake Tahoe basin spans all but 1 life zone found across the entire Sierra Nevada, and is home to $>$200 vertebrate species (Storer et al. 1963, Laws 2007). The Tahoe Basin and surrounding areas have undergone commercial and residential development, including development for recreational purposes such as hiking and skiing, creating a mosaic of forested wildlands (Lindstrom et al. 2000) and varying levels of urbanization. Another important source of disturbance in the Tahoe Basin are wildland fires, the most severe of which was the Angora fire of 2007 (Fig. 1). Localities included in our analysis reflected 3 types of sites: relatively undisturbed wildlands, recently burned wildlands, and urbanized sites. Burned sites were those in the path of the 2007 Angora fire (Fig. 1). Urbanized sites were those that

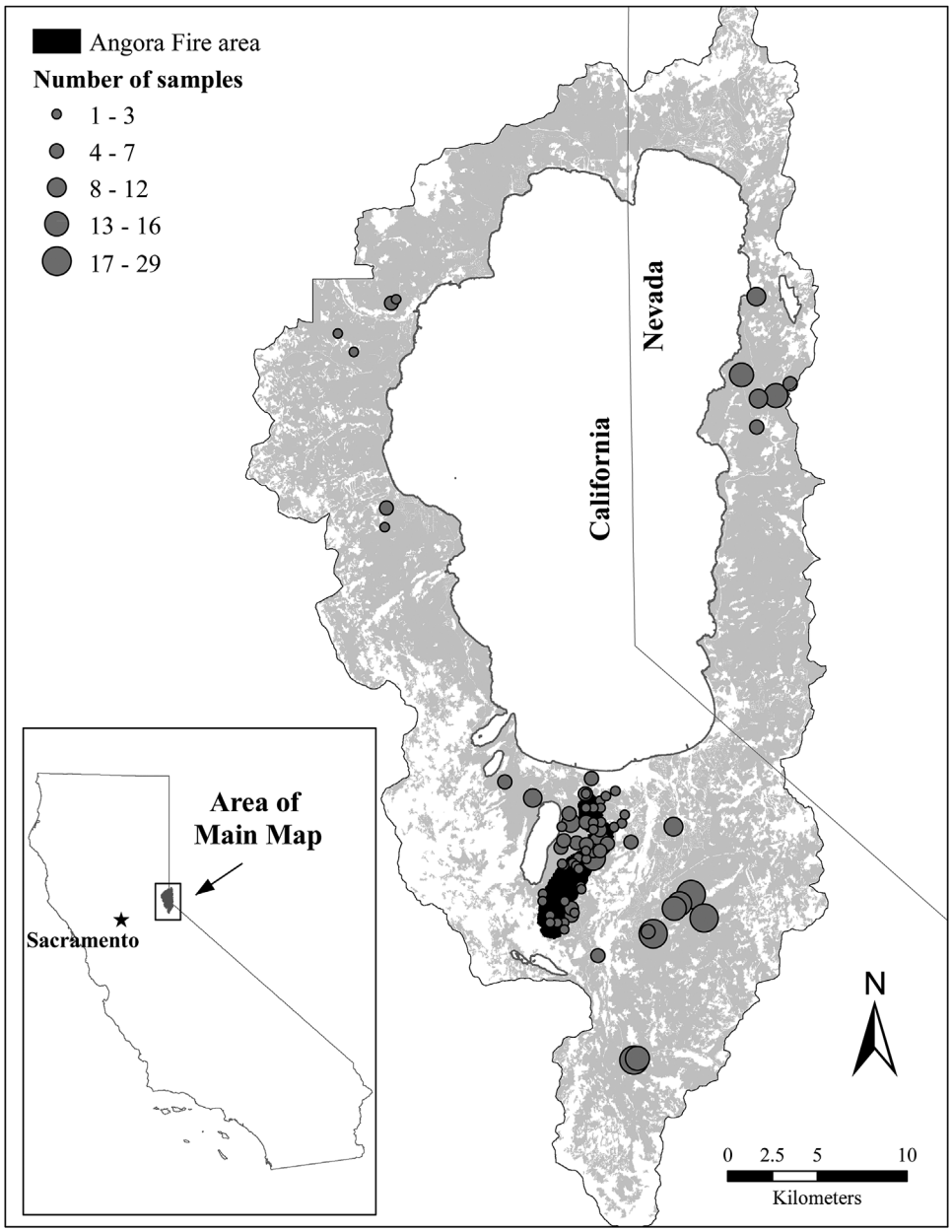

Figure 1. Distribution of chipmunk sampling localities across the Lake Tahoe Basin, USA, 2009–2010. Diameter of circles denotes sample sizes. The dark underlay in the southern part of the map shows the extent of the 2007 Angora fire.

had >10% urban development within a 150-m radius of each site calculated as the percent of land use and road density at a 30-m pixel resolution (Manley et al. 2006). Undisturbed wildlands were those located in coniferous forests outside of urbanized areas that had not burned in several decades.

METHODS

Sample Collection

We collected samples for genetic analyses from chipmunks during 3 small mammal surveys conducted in the Lake Tahoe Basin Management Unit in 2009 and 2010 by the United States Forest Service (Fig. 1). We conducted 2 of the surveys at multiple sites in unburned forest to quantify how habitat features (e.g., forest structure, elevation, urbanization) influenced the density of small mammals and used the third survey to examine the influence of habitat features on the density of small mammals in recently burned forest. Ten (2009) and 13 (2010) field technicians were involved with data collection, 4 of whom collected data in both years. Field technicians collected data across surveys. To ensure consistency in capture and identification of small mammals, we trained all field technicians together at the start of each field season. We conducted 2 weeks of training prior to data collection. Training consisted of trap setting, animal handling, species identification, and an examination of study skins housed in the University of Nevada, Reno and University of California, Davis collections to learn the range of phenotypic variability observed in each chipmunk species.

The trapping design varied by project, but in all cases. we used a rectangular trapping grid with a 30-m spacing between trap stations (48–72 stations). Each station consisted of either an extra-large Sherman (10 × 11.5 × 38 cm, H.B. Sherman Traps, Tallahasse, FL) or a Tomahawk live trap (12.5 × 12.5 × 40 cm, H.B. Sherman Traps). We placed Sherman traps at the base of trees, along larger logs or under shrubs, and covered them with natural materials for insulation. We attached Tomahawk traps to trees >50 cm diameter at breast height, 1.5–2 m above the ground with the back third of the trap wrapped in polytarp to provide cover for trapped animals. We pre-baited traps for 3–4 days with a mixture of oats, peanut butter, raisins, and molasses with subsequent trapping occurring over the next 3–4.5 days. We conducted live-trapping of chipmunks under a California Scientific Collection Permit (no. 8732).

We marked each chipmunk captured with a uniquely numbered ear tag (model 1005-1, National Band and Tag Co., Newport, KY) and identified it to species (at each capture event) based on phenotypic characteristics (e.g., size, coloration) and known habitat associations (Jameson and Peeters 1988; Table 1). At the end of the field season we assigned each individual to species based on the majority of field identifications across all captures, or when a majority did not exist, we based species assignment on the field identification of the more experienced technician.

For molecular genetic confirmation of each individual, we collected a 2-mm tissue sample from the ear of each captured chipmunk. We stored the tissue sample in a small wax paper envelope to dry. The samples we obtained coarsely reflect relative abundance of these species in the Lake Tahoe Basin (Appleby 2015). For example, long-eared chipmunk is the most abundant taxon; nonetheless, because long-eared chipmunk and shadow chipmunk are the most difficult species to tell apart in this region, we maximized our inclusion of these samples in our dataset. For each species, we selected samples to represent full coverage across all sampling sites around the lake, while maximizing number of samples selected from areas that had documented recent disturbances due to development and wildfires.

DNA Sequencing

We extracted genomic DNA for all tissue samples (ear clips) using the Qiagen DNeasy tissue kit (Qiagen, Valencia, CA) according to manufacturer's instructions. We amplified and sequenced cyt *b* from 170 individuals, including a larger fragment of cyt *b* (784 bp) from half the sample (80 individuals) to robustly place individuals in the western *Tamias* complex, and then a smaller fragment (243 bp) from the remaining samples to assign individuals to these mtDNA lineages. We amplified the larger cyt *b* fragment using primers MVZ 05 and MVZ 16 (Smith and Patton 1993), and the smaller fragment with primers TAMH4F and TAMH3R (Rubidge et al. 2014).

To obtain a nuclear perspective and assess the potential of hybridization in misidentifications, we sequenced most of intron 9 (588 bp) of zona pellucida glycoprotein 2 (*Zp2*) from 70 individuals. We targeted these 70 individuals for sequencing because their other genetic markers indicated they may have been either misidentified in the field or were hybrids. We amplified *Zp2* using primers ZP23F and ZP24R (Reid et al. 2012).

We used 1× AmpliTaq Gold 360 Master Mix (Applied Biosystems, Foster City, CA) to amplify products, using standard thermal cycle parameters and the following annealing temperatures: cyt *b* long 48°C, cyt *b* short 50°C, and *Zp2* 53.5°C. We cleaned amplified products using ExoSAP-IT (Affymetrix, Santa Clara, CA) and used purified template in Sanger-sequencing reactions with the amplification primers and ABI Big Dye chemistry (Applied Biosystems). We ran cycle-sequenced products on an ABI 3730 DNA Analyzer (Applied Biosystems) in the Nevada Genomics Center (Reno, NV) or at Macrogen (Rockville, MD) sequencing all samples in both directions.

We edited and aligned sequences in Sequencher 5.4 (Gene Codes, Ann Arbor, MI) and translated coding regions into amino acid sequences using MacClade 4.08 (Maddison and Maddison 2005). For the nuclear locus, *Zp2*, we called heterozygous sites as those with double peaks, where the secondary peak was at >60% of the primary peak, and scored sites using International Union of Biochemistry ambiguity codes. We deposited all DNA sequences in GenBank (numbers pending).

Genetic Analyses

To attribute individuals to particular species, we used the 784 bp fragment of cyt *b* mtDNA sequence data and compared these field-collected samples to those of vouchered specimens held in GenBank (Good et al. 2008; Reid et al. 2010, 2012). The 48 *Tamias* samples from GenBank represented chipmunk species that included representatives of all focal species from the Tahoe Basin. We assigned field-collected individuals to a species or mtDNA lineage based on phylogenetic affinity.

Table 1. Phenotypic characteristics and habitat associations used in field identification of chipmunk species in the Lake Tahoe Basin, 2009–2010.

Species	Mass (g)	Distinguishing characteristics	Habitat associations
Shadow chipmunk	70–98	Lateral light stripes grayish to brown. Patch behind ear less conspicuous and smaller than that of long-eared chipmunk. Less overall color contrast. Tail hairs white tipped.	Dense forest with substantial shrub understories.
Long-eared chipmunk	52–100	Ears long, slender, and pointed. Large conspicuous white patch behind ear, longer than depressed ear. Lateral light strips nearly white or white. Tail hairs tipped white.	Open, brushy, and rocky areas in mixed-conifer forests.
Yellow-pine chipmunk	36–50	Inner light striped often broader and more conspicuous than outer light stripes. Outer dark stripes black.	Open brushy forests.
Lodgepole chipmunk	30–64	Outer light stripes pure white and broader than inner light stripes. Outer dark stripes nearly or quite obsolete. Dark tail tip.	Subalpine, red fir and lodgepole pine forest.

We established phylogenetic affinity of field-collected and Genbank-vouchered specimens by conducting simple distance-based phylogenetic analyses with clustering algorithms (i.e., neighbor joining and unweighted pair group method with arithmetic mean) in PAUP* 4.0a147 (Swofford 2002) under the best fitting model (general time reversible + proportion of invariable sites + gamma distribution) as determined by corrected Akaike's Information Criterion in jModelTest v2.1.7 (Darriba et al. 2012). We rooted the character matrix with the eastern chipmunk (*T. striatus*).

We used the nuclear locus *Zp2* to corroborate cyt *b*-based species identifications. Further, because this locus contains species-specific alleles (Reid et al. 2012), it can be used to identify hybrids. For the sequence analysis of *Zp2*, we used a smaller sample of individuals ($n = 70$), which included specimens that were reassigned based on genetic clustering methods.

We genotyped 416 individuals at 11 microsatellite loci using primers designed for yellow-pine chipmunk (Schulte-Hostedde et al. 2000) to quantify nuclear genetic variation with each species, to identify field misidentifications, and to identify any interspecific hybridization. We initially genotyped 280 of these individuals (70 from each target species), and then upon discovery of the high rate of misidentification between 2 species in particular (long-eared chipmunk and shadow chipmunk), we added another 136 individuals from these particularly problematic species for 416. We used 1× AmpliTaq Gold 360 Master Mix with fluorescently labeled forward primers in standard polymerase chain reactions with a 50°C annealing temperature. We resolved fragments using an ABI 3100 genetic analyzer with GeneScan™ 500 LIZ® size standard (Applied Biosystems), called alleles using GeneMarker (SoftGenetics, State College, PA) and confirmed allele sizes by eye.

We analyzed the microsatellite dataset using the Bayesian clustering program STRUCTURE v.2.3.4 (Pritchard et al. 2000, Falush et al. 2007). We used the admixture and correlated alleles models and ran 10 iterations for each number of clusters (K). We allowed the number of clusters to vary from 1 to 8; 2 times the number of species expected in the dataset. We ran 1×10^6 repetitions for the burn-in period, followed by 1×10^6 searches and recorded 90% credibility intervals during all searches. We determined the number of unique genetic clusters by examining ΔK (Evanno et al. 2005) as estimated using STRUCTURE HARVESTER v 0.6.94 (Earl 2012).

To further visualize genetic diversity within each genetic cluster and degree of differentiation between groups, we conducted a principal coordinates analyses (PCoA) based on the standardized allele frequencies in the microsatellite dataset. We conducted PCoAs in GenAlEx 6.501 (Peakall and Smouse 2006, 2012). We estimated standard diversity statistics and quantified overall nuclear divergence between the species by estimating population differentiation (F_{ST}) using the analysis of molecular variance (AMOVA) subroutine in GenAlEx. For these analyses, we limited our sample to putatively genetically pure and correctly identified individuals, as indicated by our admixture analyses from STRUCTURE.

RESULTS

Field-Based Species Identification

We included in this study 1,377 chipmunk captures. During surveys, we captured individual chipmunks on multiple occasions ($\bar{x} = 3.4 \pm 3.0$ [SE], range = 1–24) and often identified the same individual as >1 species (95 of the 242 individuals caught multiple times). Based on genetic identification, field technicians varied in their ability to correctly identify chipmunks to species based on phenotypic cues. Correct species identification by field technicians was highest for yellow-pine chipmunk (average correct identification $90 \pm 11\%$) and long-eared chipmunk ($89 \pm 14\%$), followed by lodgepole chipmunk ($73 \pm 29\%$). Correct field identification of shadow chipmunk was lowest and most variable ($66 \pm 35\%$). Despite the larger field crew, correct identification of *Tamias* species was higher in 2010 (88%) than 2009 (73%). Although results varied by species (Table 2), end-of-season field assignments provided higher accuracy in species identification than identification based on capture events (86.3% for overall species assignments compared to 82.4% for overall species identifications); therefore, the following genetic results are compared to species assignments.

Genetic Species Identification

Our phylogenetic analysis revealed the same major clades as prior work on the group (Fig. 2); yellow-pine chipmunk and shadow chipmunk were close relatives in a northwestern clade, and lodgepole chipmunk and long-eared chipmunk shared affinities in a larger southwestern lineage (Piaggio and Spicer 2001, Reid et al. 2012, Sullivan et al. 2014). Mismatch between field assignments and phylogenetic affinity was seen

Table 2. Field-assigned and genetic identification (ID) of individual chipmunks in the Lake Tahoe Basin, 2009–2010. Genetic identification was based on nuclear microsatellite genotypes at 8 loci. Numbers show sample size and percentage consistent between field and genetic identification. Genetic ID columns show only those individuals that had STRUCTURE *q* values >90%; individuals with admixed genomes are shown in the rightmost column. Additional parentheses in the shadow chipmunk genetic ID column denote that 2 individuals were identified as shadow chipmunk in the field and by nuclear microsatellite genotype but had long-eared chipmunk mtDNA and, thus, had hybrid ancestry.

	Genetic ID				
Field-assigned ID	**Long-eared chipmunk (%)**	**Shadow chipmunk (%)**	**Yellow-pine chipmunk (%)**	**Lodgepole chipmunk (%)**	**Potential hybrids (%)**
Long-eared chipmunk (185)	165 (89)	12 (6)	2 (1)	1 (0.5)	5 (3)
Shadow chipmunk (93)	28 (30)	56 (60) (−2)	3 (3)	1 (1)	3 (3) (+2)
Yellow-pine chipmunk (70)	0	1 (1.5)	66 (94)	1 (1.5)	2 (3)
Lodgepole chipmunk (68)	0	0	8 (12)	59 (87)	1 (1.5)

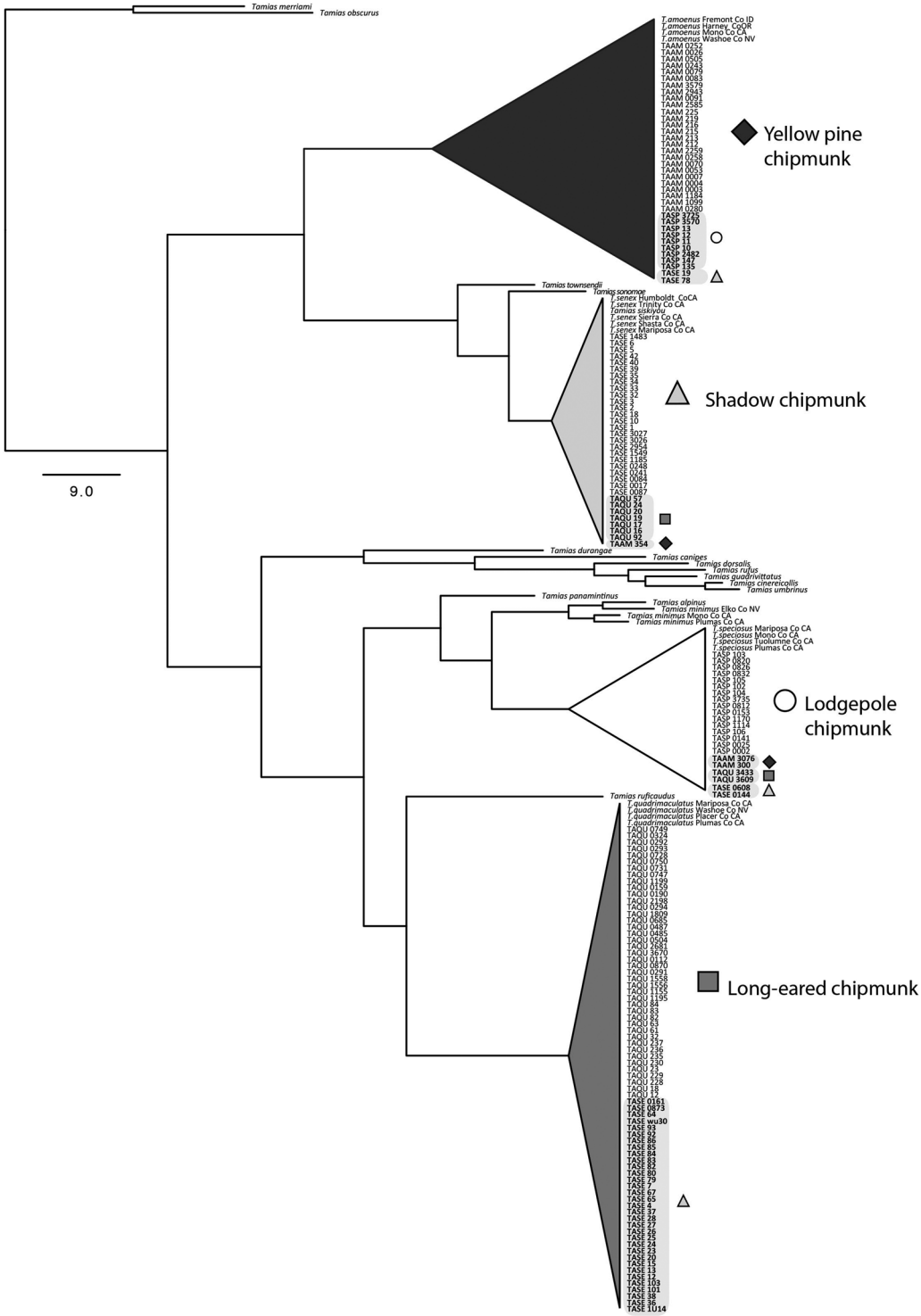

Figure 2. Phylogenetic placement of chipmunk samples in the Lake Tahoe Basin (abbreviated names; TAAM: yellow-pine chipmunk, TASE: shadow chipmunk, TASP: lodgepole chipmunk, and TAQU: long-eared chipmunk) obtained in 2009–2010 among known western chipmunk species (full scientific names, location). Dark gray diamond: yellow-pine chipmunk, light gray triangle: shadow chipmunk, white circle: lodgepole chipmunk, gray square: long-eared chipmunk. Mismatch between field identification and phylogenetic affinity was observed in all 4 sampled taxa, but was particularly striking in long-eared chipmunks (medium gray square), where >40% of individuals with these haplotypes were considered shadow chipmunks (light triangle) in the field.

in all taxa, but was particularly striking in the long-eared chipmunk clade where more than 40% of individuals with these haplotypes were considered shadow chipmunk in the field (Fig. 2). These results prompted our further analyses with a larger set of individuals and a multi-locus dataset to understand the nature and extent of misidentifications of chipmunks in the Tahoe Basin.

Of 11 nuclear microsatellites tested, 3 failed to amplify in all species (loci 114, 138, 166) and were omitted. Bayesian clustering analysis and assessment of ΔK showed greatest

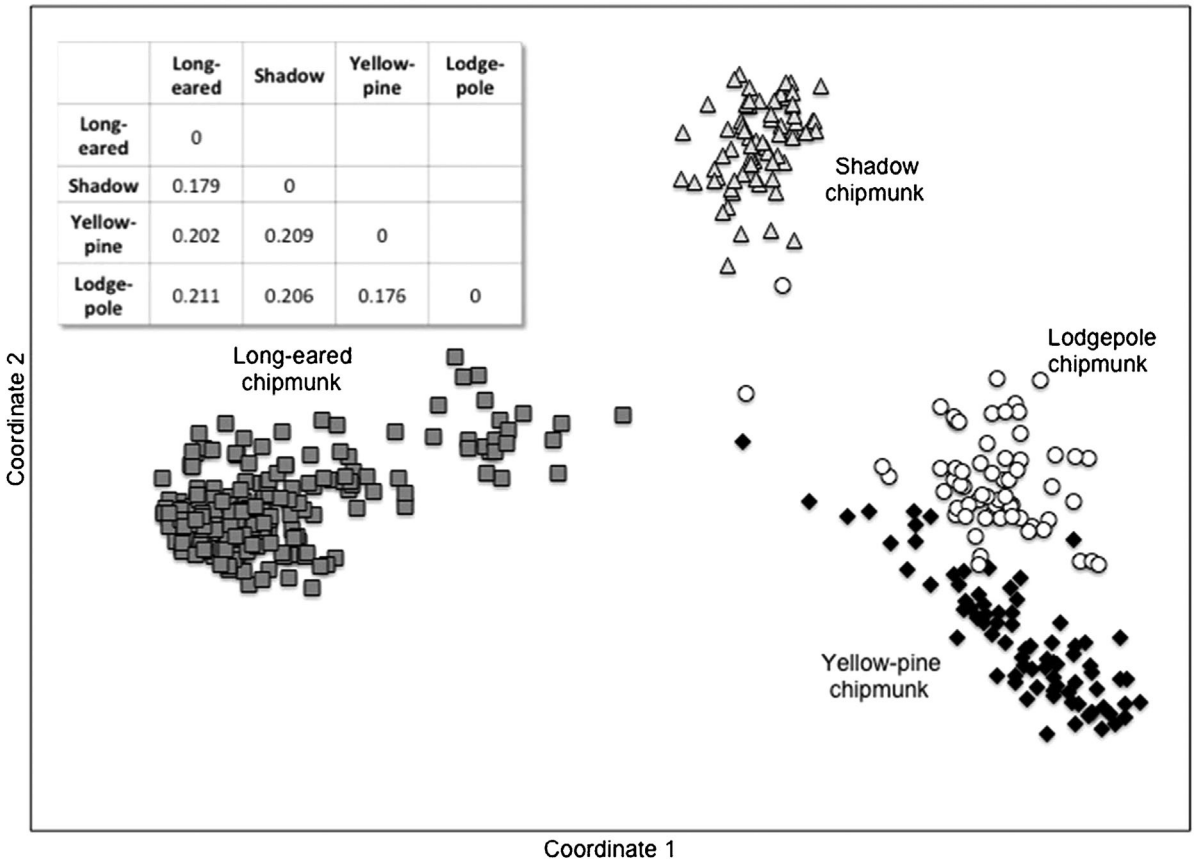

Figure 3. Coordinate 1 versus 2 of a principal coordinates analysis of 8 nuclear microsatellite loci for chipmunk species (long-eared chipmunk [gray square], shadow chipmunk [light gray triangle], yellow-pine chipmunk [dark gray diamond], and lodgepole chipmunk [white circle]) in the Lake Tahoe Basin, USA, 2009–2010 Inset shows pairwise F_{ST} between the species.

support for 5 genetic clusters. Each cluster was largely consistent with our expectations based on mtDNA and field assignments, although 2 of the 5 clusters were from within the long-eared chipmunk genetic cluster. Because the focus of this study was limited to species-level identification rather than more subtle subdivisions within taxa, we combined the 2 long-eared chipmunk clusters for further inference of individual genetic assignment and assessment of potential hybridization among species. The majority of individuals assigned to 1 genetic cluster with high q values (population membership coefficient, >0.95). We considered any assignment >0.90 as inclusion in a particular genetic cluster or taxonomic group. Despite overall concordance between field assignments and nuclear genetic cluster assignment, several incorrect field assignments were apparent (Table 2). This was especially true for field assignments of the large-bodied long-eared chipmunk and shadow chipmunk wherein 6.5% (12 of 185) of field-assigned long-eared chipmunks were genetically identified as shadow chipmunks and a full 30% (28 of 93) of field-assigned shadow chipmunks were genetically identified as long-eared chipmunks. The small-bodied species (yellow-pine chipmunks and lodgepole chipmunks) were also occasionally confused in the field with 1 of 70 (1.4%) yellow-pine chipmunks being mistaken for lodgepole chipmunks and 8 of 68 (11.8%) field-assigned lodgepole chipmunks being genetically identified as yellow-pine chipmunks.

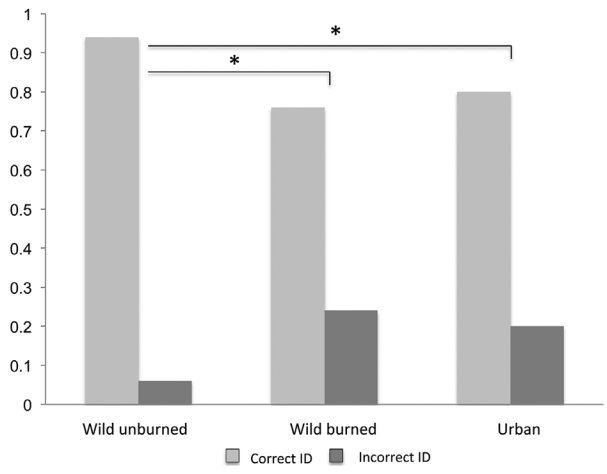

Figure 4. Proportion of chipmunk individuals (ID) in the Lake Tahoe Basin, USA, 2009–2010, that were correctly (light gray) and incorrectly (dark gray) identified to species in the field at sites with varying levels of disturbance ranging from wild unburned to wild burned and urbanized sites. Asterisks indicate that wild unburned sites had statistically lower rates of misidentification than sites that had been recently burned or were urbanized. The latter 2 categories were not statistically different from one another.

Overall, there was concordance among nuclear sequence data, mitochondrial sequence data, and microsatellite genotypes. Of the 416 individuals included in the microsatellite analysis, 87 of them were sequenced for cyt *b* and all but 2

showed concordance between their mtDNA and nuclear microsatellite assignment, or in the case of those individuals whose genotypes were composed of the markers of multiple species (admixed individuals), their predominant genotypic class. Likewise, of the 416 individuals included in the microsatellite analysis, 69 were sequenced at the *Zp2* locus, which agreed with the nuclear genotype in all cases, and in the case of hybrids, the dominant genotypic class (Fig. S1, available online in Supporting Information).

We found limited evidence of hybridization in the dataset with 11 individuals having q values <0.90 for any 1 genetic or taxonomic cluster. The 90% credibility intervals for these individuals were wide for the predominant genetic cluster to which they were assigned and included 0 for any other genetic cluster. With such wide credibility intervals, our evidence for hybridization was limited, nonetheless, we report these admixed individuals as potential hybrids (Table 2). Further corroborating that hybridization may at least occasionally occur between chipmunks in the Tahoe Basin was our evidence of mitochondrial mismatch with both field and nuclear microsatellite assignment of 2 individuals. Two individuals assigned as shadow chipmunks in the field had q values of 0.97 and 0.99 for the shadow chipmunk nuclear genetic cluster. However, both individuals had mtDNA haplotypes that were well-nested in the long-eared chipmunk clade (Table 2 and Fig. 2), clearly supporting hybrid ancestry of these individuals. Of the 11 individuals with admixed genomes ($q < 0.90$ for any 1 group), 6 had $q = 0.6$–0.88 for the genetic cluster to which they were field assigned. The other 5 admixed individuals always had at least some genetic affinity to the group to which they were identified in the field ($q = 0.14$–0.22), although their predominant genetic assignment was to another species' genetic cluster. Finally, we found at least 1 example of every possible species pair in our set of putative hybrid individuals, but 6 of 11 were between long-eared chipmunk and shadow chipmunk. Interestingly, in 5 of the 9 admixed individuals that were captured multiple times, field crews noted difficulty in identification and even alternated in species assignments across capture events.

Based on the genetic assignment of individuals and eliminating the 11 individuals with admixed nuclear genotypes, plotting of coordinate 1 versus coordinate 2 of the PCoA shows relative diversity and divergence among the species we examined (Fig. 3). Despite their phenotypic similarity and propensity for mis-assignment in the field, long-eared chipmunks and shadow chipmunks are genetically distinct with an F_{ST} of 0.179, although all species in this study were fairly highly differentiated with F_{ST} ranging from a low of 0.176 between yellow-pine chipmunk and lodgepole chipmunk to a high of 0.211 between long-eared chipmunk and lodgepole chipmunk (Fig. 3 inset).

Incorrect Field Assignments in Wild Versus Disturbed Sites

The overall rate of incorrect field assignments across all species and sites was 13.7% (57 of 416). However, in comparing the proportion of incorrect assignments across site types, we found that field errors were not evenly distributed among relatively undisturbed wildlands and disturbed (i.e., burned, urbanized) sites (overall $\chi^2 = 20.58$, $P < 0.001$; Fig. 4). Specifically, undisturbed wildlands had the lowest rate of incorrect assignments (5.9%; 11 of 188 individuals misidentified), whereas recently burned wildlands had higher rates (23.8%; 20 of 84; $\chi^2 = 13.15$, $P = 0.001$). Likewise, urbanized sites had higher rates of incorrect assignments (20%; 23 of 115; $\chi^2 = 11.89$, $P = 0.003$) than undisturbed wildlands. Urbanized and burned wildland sites did not differ from one another ($\chi^2 = 0.41$, $P = 0.815$).

DISCUSSION

We show that although the majority of field identifications of chipmunk species are reliable, one species pair in particular, long-eared chipmunk and shadow chipmunk, presented consistent difficulty for field crews. This is particularly problematic because our rates of misidentification differed between disturbed and relatively undisturbed sites. Specifically, rates of misidentification in disturbed sites were >3 times higher than relatively undisturbed sites. Misidentifications were not restricted to particular field crews, sites, or years but rather spanned many observers across multiple years and locations. Misidentifications in disturbed landscapes are additionally concerning because it is already expected that disturbance is influencing species occurrences in these areas. These distributional changes are not unique to chipmunks nor the Lake Tahoe Basin, and therefore need to be considered across all mammalian surveys.

Although the bias in misidentification in disturbed sites was surprising, it nonetheless could have resulted in an underestimation of the influence of disturbance on shadow chipmunks and lodgepole chipmunks. If this misidentification error is common, then this might indicate the decline observed in shadow chipmunks (Hall 1995, Moritz et al. 2008) has actually been underestimated. Although rates of misidentification among species of small mammals are poorly documented, the conservation challenge posed by misidentification between relatively common and uncommon or imperiled species are of general concern (Metcalf et al. 2007, Burbidge et al. 2011). Additionally, false positives, and the subsequent overestimation of a population may result in other problems, such as an overly optimistic view of colonization, and species resiliency (Molinari-Jobin et al. 2011).

Our observed rates of misidentification in disturbed habitats could be in part the result of the long-eared chipmunk shifting its habitat use in disturbed sites, and specifically, that this generalist may have broadened its habitat use to areas that crews more typically associated with shadow chipmunks. Even subtle ecological differences among co-occurring members of the same guild can lead to differences in response to ecological change, leaving habitat specialist species less able to recover from population decline and habitat change, whereas the generalist species rebound more quickly (Janecka et al. 2016). An increase in abundance of generalist species in post-burn small mammal communities has been documented (Zwolak and Foresman 2007), although few studies have focused on shifts in post-burn habitat use or the mechanisms underlying post-burn

changes in abundance (Zwolak et al. 2012). As with changes in habitat use with fire disturbance, we have limited understanding of how urbanization affects forest mammal communities of western North America, although dramatic shifts in small-mammal communities are associated with urbanization elsewhere (Gomes et al. 2011, Wells et al. 2014). In general, disturbed habitats are expected to have altered forage resources and rates of predation, and reduced habitat complexity (Amacher et al. 2008), all potentially contributing to changes in habitat use. The underlying source of high rates of misidentification we have identified in disturbed sites warrants further investigation, especially if they are partly due to ecological shifts in habitat use.

Our genetic analyses suggest that field identifications may further be complicated by occasional hybridization between chipmunks in the Tahoe Basin. Although the phenotypic effects of hybridization between these particular species are not known, hybridization may have some phenotypic effect. Indeed, in 5 of 9 admixed individuals that were captured on multiple occasions, field crews noted difficulty in species assignment and even changed assignments in subsequent capture events, which suggests hybrids may have had unusual phenotypes.

Nearly half the cases of hybrid ancestry found in our analyses were between the long-eared chipmunk and shadow chipmunk. Not only were these the species most commonly mistaken for one another, but this evidence of hybridization suggests that similarity in body size may play a role in mate choice decisions in these species (Shurtliff 2013). Further, our evidence of long-eared chipmunk mtDNA introgression into an otherwise seemingly pure shadow chipmunk nuclear genetic background is entirely consistent with the extensive evidence of hybridization and mitochondrial capture in many species of chipmunks (Sullivan et al. 2014). Under certain demographic scenarios or selective environments, the type of early stage capture we have documented can rise in frequency and spread spatially. Our evidence thus far does not suggest that hybridization is having a profound impact on the genetic composition of chipmunks in the Tahoe Basin. Nonetheless, our data lend support to growing evidence from several well-documented chipmunk hybrid zones (Good et al. 2003, 2008; Hird and Sullivan 2009; Reid et al. 2010) and genus-wide evidence of mitochondrial capture (Sullivan et al. 2014) that hybridization may be more common in this genus than once thought.

Assessing trends in wildlife populations is fundamental to conservation science and land management. Biotic inventories yield baseline data on community composition and structure; however, incorrect field identifications can influence estimates of the distribution and abundance of species in particular communities, and thus, downstream management decisions (Hall 1995, Coppeto et al. 2006, Wilson et al. 2008). In particular even moderate levels of false positives can lead to substantial overestimation of populations (Tyre et al. 2003), stressing the need for accurate species identifications. For this reason field keys, especially for difficult to distinguish species, those hybridizing, and those in disturbed habitats need to be informed by genetic data.

MANAGEMENT IMPLICATIONS

Field surveys that include chipmunk species must avoid using typical habitat as a potential species identifier because chipmunk species are shifting their ranges and associations because of global change. A genetic approach to species identification is the most reliable method for identifying chipmunks in field surveys. All small-mammal inventories, especially those that include chipmunks or other hybridizing species, and those being conducted in disturbed sites may benefit from: 1) use of molecular tools to corroborate field identifications in at least a subset of samples; 2) vouchering and genotyping of representative specimens to fully document phenotypic variation at field sites from which new field crews can be trained; and 3) continual revision of field keys as local phenotypic and molecular data become available.

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