CALIFORNIA FISH AND GAME

"Conservation of Wildlife Through Education"

CDFW Photo by Becky Pierce

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California Fish and Game

Contents

Notes from the Editor

Volume 100, published in the centennial year of *California Fish and Game*, has been completed. This effort, to commemorate the 100th year of publication of California's longest running, continuously published scientific journal, was the result of the efforts of many individuals, including researchers, corresponding editors, and reviewers.

The centennial volume, which consisted of four special issues each addressing a particular aspect of fish and wildlife conservation, was the largest ever published by the California Department of Fish and Wildlife. Publication began in 1914 under the California Division of Wildlife, and continued for many decades under the California Department of Fish and Game (CDFG). Legislation implemented in 2013 resulted in the renaming CDFG, which became the California Department of Fish and Wildlife (CDFW). One hundred years from now we cannot predict what CDFW will be called, but we can hope that the support for its journal, *California Fish and Game*, will remain strong.

Volume 100 consisted of 758 total pages, which were nearly evenly distributed among the four special issues. The Special Plant Issue (100[1]) contained 14 papers, as did the Special Wildlife and Special Fisheries issues (100[3] and 100[4], respectively), while the Special Marine Issue (100[2]) contained 12 papers. These papers were produced collectively by 123 individual authors, and 86 individuals, each an expert in the subject matter they were asked to comment on, provided peer reviews. These reviewers represented academic institutions, resource management agencies, non-governmental organizations, or consulting organizations.

Governor Jerry Brown introduced volume 100, the Special Native Plant Issue, and emphasized that, "Stewardship—the idea of holding our fish, wildlife and natural resources in trust and passing them along in a better state to future generations—must be our fundamental ethic" and that "California's roots run deep in science, wildlife management and conservation." Additional introductory remarks were provided jointly by CDFW Director Charlton (Chuck) Bonham and Dan Gluesenkamp, Executive Director of the California Native Plant Society. Bonham and Gluesenkamp emphasized that, "As we learn more about why California is special, not just for us but for the whole planet, we strengthen our pledge to dedicate our minds, our hands and our hearts to conserving it."

The Special Marine Issue was introduced by Michael Sutton, President of the California Fish and Game Commission. In his remarks, Sutton noted that, "In this time of rapidly changing media, it is a testament to the quality of this publication that it has survived and continues to thrive into its second century." Director Bonham teamed with Francisco Werner, Director of the Southwest Fisheries Science Center, and provided additional introductory material. Bonham and Werner noted that, in particular, "Based on what we achieved in the previous 100 years, there is every reason to believe, that working together as we have in the past, we will continue to provide the necessary science, which will result in the best management advice and ultimately in a healthy California Current Ecosystem supporting our human coastal communities."

       The Special Wildlife Issue was introduced by Anthony Rendon, Chair of the Assembly Water, Parks and Wildlife Committee. In his remarks, Rendon noted that, "The work of scientists at the Department of Fish and Wildlife and elsewhere has helped guide decisions and the direction of natural resource conservation and management programs for more than a century." Director Bonham teamed with Terry Bowyer, of Idaho State University, in a follow-up to Rendon's comments. In their remarks, Bonham and Bowyer challenged the current contributors and readers of the journal, and "... all those who may follow in their footsteps, ... to never stop seeking to understand and manage the many current challenges—as well as those not yet imagined—that wildlife and wildlife habitat in California and the world face." That is a daunting, but necessary challenge, and one that I am optimistic that *California Fish and Game* will play a role in achieving.

       Fran Pavley, Chair of the Senate Natural Resources and Water Committee, provided an introduction to the Special Fisheries Issue. Senator Pavley's remarks were timely, noting that, "California has lost approximately 95 percent of its wetlands to development. All but one of our major rivers has been dammed, thus blocking the natural passage of anadromous fish to their historic spawning streams. The diversion of water from natural drainages ... has had tremendous adverse effects on California's native aquatic organisms." In their introduction to the Special Fisheries Issue, and in the midst of the California's ongoing and historic drought, Director Bonham and Phil Pister, retired CDFW fisheries biologist, described the evolution of fisheries management in California, and noted that adaptive management will always be an important component of conservation efforts.

       The Centennial Volume of *California Fish and Game* truly was a team effort, with corresponding editors for each of the four disciplines featured in Volume 100 handling solicitation of papers, the peer-review process, decision making, and initial copy editing. Cherilyn Burton was responsible for the Special Native Plants Issue, Pete Kalvass and Ian Taniguchi processed all of the papers for the Special Marine Issue, and Kevin Schaefer, Roger Bloom, and Rob Titus served as corresponding editors for the Special Fisheries Issue. Additionally, guest editors Scott Osborn, Jeff Villepique, and Jack Connelly were responsible for handling the peer-review process for several papers included in the Special Wildlife Issue. Finally, I want to call special attention to the efforts of Debra Hamilton, from the Office of Communications, Education, and Outreach, who played pivotal roles in the publication of Volume 100 by ensuring that all aspects of production—importing manuscript files, preparing page proofs, correcting page proofs, and the posting and printing of final copy—were handled. Here's to another century of publication of *California Fish and Game*.

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The decline of native freshwater mussels (Bivalvia: Unionoida) in California as determined from historical and current surveys

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Freshwater mussels are increasingly recognized as important components of aquatic ecosystems but paradoxically are one of the most critically imperiled faunal groups in North America. In California the conservation status of all three native genera had not been comprehensively evaluated in over 30 years. We determined the current distribution of freshwater mussels in California by resurveying historical sites of known occurrences and evaluating the relative change between historical and contemporary surveys. A total of 450 historical records were compiled and represented 116 unique, locatable sites. Nearly 70% of the historical sites were resurveyed, and freshwater mussels were found at 47% of the resurveyed sites. Of the three mussel genera (*Anodonta*, *Gonidea* and *Margaritifera*) known from California, *Anodonta* was historically the most commonly observed genus, but was only found at 33% of the resurveyed sites. Although *Margaritifera* and *Gonidea* were historically found at fewer sites than *Anodonta*, they were extant at 65% and 55% of the resurveyed sites, respectively. Mussel losses were especially apparent in southern California, with mussels extirpated from 13 of 14 resurveyed sites. The absence of mussels from many historical sites, especially in southern California, parallels the on-going decline of freshwater mussel populations nationally.

Keywords: *Anodonta,* California, freshwater mussels, *Gonidea angulata*, historical and current distribution, *Margaritifera falcata*

The native aquatic molluscan fauna of North America is extremely diverse relative to other continents, and over 60% of the world's known species of freshwater mussels (Bivalvia: Unionoida) occur there (Master et al. 1998).   The decline of this fauna, especially in the eastern United States where the majority of species are found, has been well documented over the past two decades (Williams et al. 1993, Bogan 1993, Lydeard et al. 2004, Wilcove and Master 2005, Haag 2012). The degradation of freshwater environments (water diversions, loss of riparian vegetation, mining, road building, competition with invasive species, and climate change), a ubiquitous worldwide phenomenon, has been implicated in the loss of many aquatic species (Bogan 1993, Williams et al. 1993, Malmqvist and Rundle 2002, Hastie et al. 2003, Hovingh 2004, Lydeard et al. 2004, Strayer et al. 2004, Helmstetler and Cowles 2008, Regnier et al. 2009, Black et al. 2010, Strayer 2010). As a result, freshwater mussels have suffered precipitous declines in abundance and distribution and are considered, together with freshwater gastropods (Johnson et al. 2013), to be the most imperiled faunal group in North America, with about 71% of the 297 known species considered endangered, threatened, or of special concern (Williams et al. 1993, Lydeard et al. 2004, Wilcove and Master 2005). An additional 20 species (7%) of the fauna are considered extinct. As the vast majority of the freshwater mussel diversity in the United States occurs east of the Rocky Mountains, it is not surprising that there has been little focus on western species. Historically it was thought that only nine freshwater mussel species occurred west of the Rocky Mountains, but recent genetic evidence (e.g., Mock et al. 2010) suggests that the western mussel fauna may be more diverse than previously thought, and many taxonomic issues (e.g., species-level designations) remain unresolved. For example, in the previously single genus *Anodonta* there is genetic support to suggest that three distinct genera are present in the western United States, and that six distinct clades exist among those genera (Chong et al. 2008). The distribution of the clades conforms to major western river basins (Mock et al. 2010) and not necessarily to previous taxonomic designations. The two other genera of western freshwater mussels, *Margaritifera* and *Gonidea*, lack this genetic diversity (Mock et al. 2013), and their taxonomic positions remain congruent with historical and current taxonomic designations.

Mollusks are one of the better surveyed invertebrate groups largely because of the interest of shell collectors beginning in the 18th century (Wright 1897). Exploratory expeditions to the western frontier began soon after Lewis and Clark arrived in the Pacific Northwest in 1805. The English botanist Thomas Nuttall was the first to secure specimens of freshwater mussels from west of the Rocky Mountains. Nuttall later gave the specimens to Isaac Lea in Philadelphia, and Lea was the first to describe new species of freshwater mussels from the western United States, including the California floater, *Anodonta californiensis* (Lea 1852); western floater, *Anodonta kennerlyi* (Lea 1860); winged floater, *Anodonta nuttalliana* (Lea 1838); Oregon floater, *Anodonta oregonensis* (Lea 1838); and western ridged mussel, *Gonidea angulata* (Lea 1838). The western pearlshell, *Margaritifera falcata* (Gould 1850), Yukon floater, *Anodonta beringiana* (Middendorff 1851), and *Anodonta dejecta* (Lewis 1875) were also described in this period.   After Lewis (1875) described *A. dejecta*, all of the currently recognized western freshwater mussel species with affinities to California had been described.

Despite the effort of early conchologists, information on western mussel populations has remained sparse and fragmented. The only synopsis of freshwater mussels in the state of California was published in 1981, and included general information on trends in abundance and distribution (Taylor 1981). In this assessment, Taylor considered the historical ranges

and current status of four species of freshwater mussels known to occur in California including *A. californiensis, A. wahlamatensis*, *G. angulata,* and *M. falcata*. Taylor noted *A. californiensis* historically ranged from southern British Columbia to northernmost Baja California and was likely extinct from most of the Central Valley and southern California; *A. wahlamatensis* historically ranged from central California to the Columbia River along the Oregon-Washington border, and was probably extirpated from most of its original range; *G. angulata* historically ranged from southern British Columbia to southern California and east to southern Idaho and northern Nevada, and was likely extirpated in most of its original range in California; and *M. falcata* historically ranged from southern Alaska to central California and eastward to western Montana, western Wyoming and northern Utah, and was probably extinct in the San Lorenzo River in California. Status of a fifth species, *A. oregonensis*, though mentioned as occurring in California by Taylor, was not assessed in the 1981 publication. An additional species, *A. dejecta,* historically known from California (Ingram 1948), was not included in Taylor's checklist. Subsequent to Taylor's checklist, *A. wahlamatensis* was placed in synonymy with *A. nuttalliana* (Williams et al. 1993).

Despite a number of ecological and distributional studies over the past decade regarding California freshwater mussels (Howard and Cuffey 2003, Howard 2004, Brim Box et al. 2005, Howard et al. 2005, Howard and Cuffey 2006a, 2006b; Spring Rivers 2007, ENTRIX 2007, Howard 2008, Howard 2010) knowledge of the distribution and conservation status of freshwater mussels in the state remains wanting. To provide a better understanding of freshwater mussel distribution in California, we compiled historical and spatial observations from museum specimens and published records. Using this information, we identified and surveyed a majority of known historical sites to better understand the current status and distribution of freshwater mussels in California.

Materials and Methods

Historical data collection.—We compiled historical observational data of freshwater mussels found in California freshwater systems from literature, museum collections, and personal communications. For this study, we define historical records as those recorded or collected before 1995; recent records are defined as post-1995. Bivalve collections at the California Academy of Sciences (CAS) in San Francisco, the Academy of Natural Sciences in Philadelphia (ANSP), and the United States National Museum (USNM) in Washington, D.C. (Smithsonian), were physically inventoried. This entailed searching the museum collections containing freshwater mussel shells, affirming identifications and recording accounts of all specimens documented from California.

We reviewed the published (Appendix I) and gray literature to obtain records for freshwater mussels from California. In addition, the USFS Freshwater Mollusk Database at Utah State University was queried to obtain published and unpublished records of freshwater mussel occurrences in California. This database contains over 1,000 records of historical occurrences of bivalves in the western United States, dating back to the 1830s.

Field survey – historical sites.—We categorized historical records by specificity of the site (i.e., how well the historical information described the site locality). Many records did not provide the information needed to locate historical sites. For example, many historical records list only a river or a county. Field surveys were designed to resurvey as

many historical sites as possible and to visit river systems where mussels were historically found to ensure representative coverage of all major river systems in California.

In the summers of 2008 and 2009 historical freshwater mussels sites were surveyed. We used timed searches, which are effective for detecting the majority of mussel species present at a site (Strayer and Smith 2003). All sites were surveyed by snorkeling or scuba diving, and by direct observation in shallow areas. At each site, we attempted to check habitats where mussels could occur, including stream banks and channel substrate, root and sedge mats, rock crevices, under woody debris (logs), and within aquatic vegetation. Each site was surveyed until no new species were found or potential habitats where freshwater mussels could occur were searched. A minimum of one-person hour was spent at each site. Despite current studies suggesting that one hour is not enough time to discover rare freshwater mussel species (Metcalf-Smith et al. 2000, Tiemann et al. 2009), timed searches are effective for detecting the majority of freshwater mussel species present at a site (Miller and Payne 1993, Strayer et al. 1997, Vaughn et al. 1997, Strayer 1999, Strayer and Smith 2003). The objective of our survey was to detect the presence of freshwater mussel species at a site, and therefore timed searches are considered an appropriate method.

In addition to our field surveys, we compiled recent records of freshwater mussel occurrences from previous field surveys (e.g., Brim Box et al. 2005; Howard 2008, 2010) and from a freshwater database compiled by The Xerces Society (2014). We included these records as current if they corresponded to historical sites.

RESULTS

Historical data.—A total of 450 historical records were compiled from museum collections, and published and unpublished records. These records include drainages in California ranging from the southernmost part of the state to the Oregon border (Table 1, Figure 1). The historical records describe varying levels of specificity in site locations: some detail specific site localities (where sites can be located), others list rivers, and others only counties or simply "California".

TABLE 1.—Museum and published sources documenting historical occurrences and the level of precision of those locations for freshwater mussels in California, USA.

Historical source	CAS	USNM	ANSP	Published reports
Specific site locality	116	35	15	76
River	18	31	15	64
General site locality	26	33	7	14
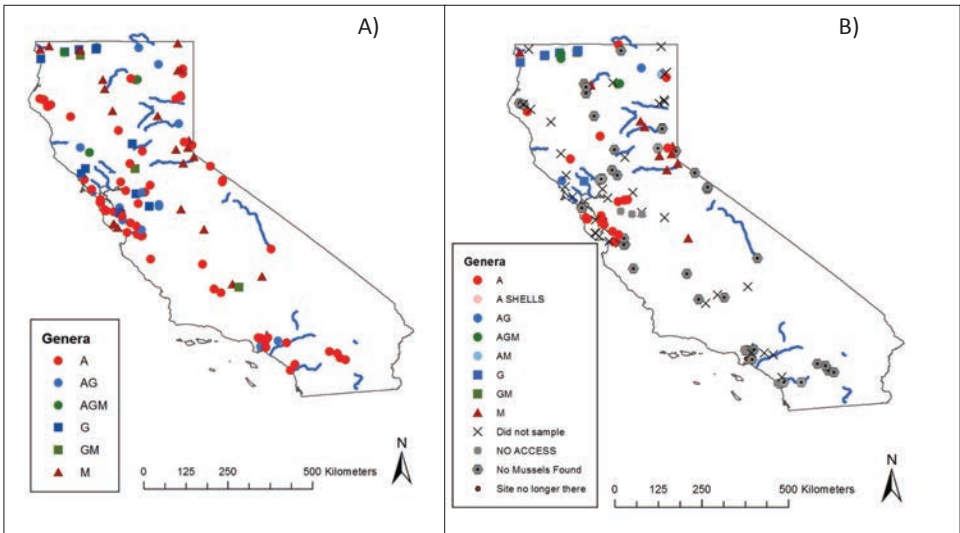
Figure 1.—Panel (A) Distribution of 116 historical locations of freshwater mussels in California. Colored symbols represent genera found at sites as follows: A=*Anodonta* spp.; AG = *Anodonta* spp. and *Gonidea angulata*; AGM = *Anodonta* spp., *G. angulata* and *Margaritifera falcata*; G = *G. angulata*; GM = *G. angulata* and *M. falcata*; M = *M. falcata*. Blue lines represent 24 additional rivers where mussels were historically found but where specific site localities were not recorded. Panel (B) Distribution of current locations of freshwater mussels in California based on surveys of 80 of 116 historical sites and 16 of 24 historical water bodies. Colored symbols represent species found at a site, and gray symbols with a center dot are sites where no mussels were found.

Of the three freshwater genera found in California, *Anodonta* was the most commonly observed or collected, historically constituting 64% (*n*=287) of the historical records; *Gonidea* were included in 20% of the records (*n*=88); and *Margaritifera* in 16% (*n*=75).

The oldest museum specimens we found date back to the 1800s. These include *M. falcata* found on May 17, 1877 in the McCloud River, Shasta County; *A. nuttalliana* dated 1877 from an unknown location in the Sierra Valley, Plumas County, and in 1892 from Mountain Lake in the Presidio in San Francisco, San Francisco County; *A. oregonensis* from the Pajaro River dated 1892, San Benito and Santa Clara counties; and *G. angulata* dated 1891 near Healdsburg, and in 1897 from the Russian River near Forestville (both in Sonoma County). Many of the museum specimens did not include specific collection dates or information but are likely very old (i.e., 19th century) based on the condition of tags, handwriting and shell preparation (tying shells with string). The oldest published California record is listed by Gould (1856), who described *M. falcata* as occurring in the Sacramento River in 1850.

Unfortunately, many museum tags did not contain specific locations or even county information. Of the total 450 historical records, only 242 provided enough information to locate the historical sites. Examples of historical records with adequate details to locate sites include CAS collections from Scott River at Kelsey Creek where *M. falcata* and *G. angulata* were found in 1924. Other examples of sites that could be located are those such as Clear Lake in Lake County, or Stow Lake in San Francisco's Golden Gate Park, San Francisco County.

We found that multiple observations or collections were often made from individual sites; therefore, these 242 records constitute a total of 116 unique sites from 80 ponds, lakes, creeks, rivers or reservoirs in California (Figure 1, Appendix II). For example, there are 18 records from Clear Lake over a period of >100 years — dating from 1870 to 1981. Therefore, we considered these 18 records as one site. Alternatively, it was possible to locate multiple locations on a particular creek or river as individual sites, and in these cases those sites were treated as separate entities. For example, five sites were identified from Coyote Creek in Santa Clara County. Of particular note are seven museum lots from the Smithsonian and CAS where *A. nuttalliana*, *A. oregonensis* and *A. californiensis* were collected from the now dry Tulare Lake in Kings County, which was drained in the 1930s. Unfortunately the Tulare Lake shells do not have dates associated with them.

In addition to the 242 records with specific site information, 128 (of the total 450 historical records) records provided enough information to identify specific rivers or water bodies from which the specimens were collected. Appendix II lists the 104 rivers, lakes, reservoirs and other water bodies where freshwater mussels were historically found in the state (80 which constitute unique site localities and 24 which include only river names), and Figure 1 maps the historical compared to current distributions.

The remaining historical records (*n*=80) provide only general information such as counties, locations such as "Borrego Springs, California from park naturalist" or "Central Valley, in the larger, slow streams only, as far south as the northern San Joaquin Valley" or simply list the state of California.

Field surveys of historical sites.—We attempted to survey as many historical sites and rivers as possible. Of the 116 historical sites with specific locality information, we surveyed or obtained recent information for a total of 80 sites (69%) (Figure 1). Of these sites, live mussels were found at 30 sites (38%), and shells only were found at one site. Five of the 80 sites we visited were inaccessible, such as Silverlake Reservoir in Los Angeles County; two lakes were dry (Owens Lake and Tulare Lake, Inyo and Kings counties, respectively); and one stream (Ballona Creek, Los Angeles County) had been moved from its historical location.

We attempted to sample 54 of the 80 sites where the genus *Anodonta* historically occurred, but could not access four sites, found one site no longer at the historical location, and two sites were dry (Table 2). Of the 47 sites we did survey, live *Anodonta* were found at 19 sites (40%) and shells only at one site. Since recent studies have found that genetic

TABLE 2.—Number of historical sites surveyed and results by genus. Parenthesis indicates where only shells were found. Composition change reflects shift in genus at sites (A to G = *Anodonta* to *Gonidea*; G to A = *Gonidea* to *Anodonta*; M to A = *Margaritifera* to *Anodonta* and M to G = *Margaritifera* to *Gonidea*.

Current status of historical sites	Anodonta	Gonidea	Margaritifera
Total historical sites	80	31	31
Historical sites surveyed	47	26	22
No access to sites	7	3	0
Sites where genus was found	19 (1)	12	13
Number of sites now vacant	25	9	6
Number of sites where genus changed	2 (A to G)	5 (G to A)	1 (M to A)
			2 (M to G)

subdivisions are incongruent with current taxonomic designations in western *Anodonta* (Chong et al. 2008), we identified *Anodonta* only to the genus level. We sampled 22 of the 31 sites where *M. falcata* historically occurred, and live *M. falcata* were found at 13 of those sites (59%) (Table 2). Twenty six of the 31 sites where *G. angulata* historically occurred were surveyed and live *G. angulata* were found at 12 sites (46%) (Table 2). We surveyed five sites where all three genera of mussels were historically documented and found all three genera at two of those sites—both located in the Pit River in Shasta County.

At a number of sites the genus of mussel found in the current survey was not the genus found in the historical surveys (Table 2). For example, *Anodonta* were found at a total of 19 sites in the current survey, and at six of these sites *Anodonta* were not recorded from the historical surveys. Similarly, we found *Gonidea* at 12 historical sites and at four additional sites where it was not historically recorded (Table 2).

In addition to the historical sites that could be spatially located, we also surveyed 16 additional rivers where historical mussel records existed, but specific site information did not (Appendix II). We were unable to visit eight other rivers where general historical information existed. Where possible, multiple sites were surveyed within these 16 additional river systems. Live freshwater mussels were found in 12 (75%) of these river systems. In general, when mussels were found, individuals were widely dispersed and rarely found in dense beds. Five sites are noted exceptions: three sites on the main stem Klamath River (Siskiyou County), one site on the upper Pit River (Modoc County), where thousands of *G. angulata* individuals were densely packed near the channel banks; and one site on the South Fork Eel River in Mendocino County, where thousands of *Anodonta* spp. and *M. falcata* were found in a 100-meter-long meander bend.

Although 15 (13%) historical sites were surveyed in southern California, only one site contained live mussels. Live *Anodonta* spp. were found in the Bishop Creek Canal, a diversion of the Owens River in Inyo County.

Discussion

It is clear from museum records and published literature that freshwater mussels historically occurred throughout California. Given that multiple records were found from a wide variety of California sites and river systems, we suspect that in many cases mussels may have been extremely locally abundant at some sites. For example, there are numerous records for Clear Lake over a period of 100 years, and a similar number of records exist for the San Joaquin and Sacramento rivers over a period of 80 years. Early collectors were unlikely to have been snorkeling or scuba diving, and we therefore assume these collections or observations were made from the shore, and that mussels were conspicuous and visible in great numbers. In addition, many museum records contain numerous (e.g., 50) shells collected during a single visit.

Based on our survey of historical sites and multiple drainages throughout California, it appears that all three genera have undergone range restrictions within the state as compared to their historical distributions. This conclusion is consistent with Taylor's (1981) earlier observations for California, and with observations made on the conservation status of mussels found in other western states (Hovingh 2004). *Anodonta*, in particular, appears to be restricted to many fewer water bodies, and with far fewer individuals present at a site, as compared to historical records. This observation is consistent with the conservation status

some species in this genus have been given in California. For example, populations of *A. californiensis* are considered critically imperiled in southern California (Xerces Society 2014) and *A. californiensis* is a Sensitive Species on multiple national forests in California. The decline of freshwater mussels has been well established with causes linked to degradation of freshwater environments (Bogan 1993, Lydeard et al. 2004, Vaughn 2010, Strayer and Malcom 2012). In California, native fish species have suffered severe declines (Williams et al. 1985, Moyle 2002) with over 80% at risk of extinction (Moyle et al. 2011; 2013). Since fish serve as hosts for larval freshwater mussels, this degree of imperilment of fishes has the potential to depress mussel recruitment and hasten declines.

It appears that mussels have been extirpated from multiple historical sites in southern California. In our study, mussels were only found at one site, and earlier researchers (Taylor 1981, Coney 1993) also noted the disappearance of mussels from this part of California. Coney (1993), in particular, reached the conclusion that after eight years of searching for freshwater mussels, they were "...undoubtedly extirpated from all of Southern California." Our results demonstrate that historical data can play an important role in determining long-term trends in freshwater mussel distributions within defined geographic areas. Because mussels are well represented in museum collections and historical literature, their occurrence and distribution have been documented almost from the time of mass European colonization of the western United States. A comparison of these historical records to current distributions suggests freshwater mussel declines in California parallel those occurring nationally. To further our understanding of the status of freshwater mussels in California, future research should focus on resurveying the remaining sites and rivers in the state where freshwater mussels were historically found.

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APPENDIX I: PUBLISHED REFERENCES USED TO GATHER INFORMATION ON THE HISTORICAL OCCURRENCES OF FRESHWATER MUSSELS IN CALIFORNIA

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Appendix II.—Number of Historical Locatable Sites by Water Body and Genera Found Historically and Currently in Those California Lakes, Rivers and Creeks

Where historical site equals 0, historical records refer only to the listed water body, not unique locations. Abbreviations for genera are as follows: A = *Anodonta* spp. G = *Gonidea angulata*, and M = *Margaritifera falcata*. Investigators recently have found that genetic subdivisions are incongruent with current taxonomic designations in western *Anodonta* (Chong et al. 2008); hence, we identified *Anodonta* only to the level of genus.

Water Body	Number of historical locatable sites	Genera found historically	Genera found currently
Alameda Creek	1	A	A
Arroyo Seco River	0	A	Not sampled
Ballona Creek	1	A, G	Site eliminated[a]
Big River	0	M	Not sampled
Blue Lake, Lassen Co.	1	A	A
Bridgeport Reservoir	1	A	None
Buena Vista Lake	1	A	Not sampled
Cedar Creek	1	M	Not sampled
Cerritos Lake	1	A	None
Chino Creek	2	A, G	Not sampled
Clear Lake, Lake Co.	1	A, G, M	A
Clear Lake, Modoc	1	A	Not sampled
Coyote Creek	5	A, G	A
Crystal Springs Reservoir	1	A	A
Delta Mendota Canal	1	A	No access
Donner Lake	1	A	A
Dry Creek, Yuba Co.	1	A	Not sampled
Dry Creek, Stanislaus Co.	1	A, G	Not sampled
East Branch North Fork Feather	1	M	M
Eel River	4	A, G, M	A, M
East Lake Park, Los Angeles	1	A	None
Elysian Park, Los Angeles	1	A	None
Feather River	2	A, G	M
Goose Lake	1	M	Not sampled
Guadalupe River	1	A, G	Not sampled
Irrigation ditch – Buttonwillow	1	A	None
Irrigation Ditch – Knights landing	1	A	M
Kern River	1	G, M	None
Klamath River	5	A, G, M	G, M
Lagunitas Creek	0	A	A, M
Lake Merced	1	A	A (Shells)
Long Valley Creek	1	A	Not sampled
Los Angeles River	0	A, G	None[b]

APPENDIX II.—Continued

Water Body	Number of historical locatable sites	Genera found historically	Genera found currently
Lost River	0	A, G	A
McCloud River	0	M	A, M
Merced River	1	M	M
Middle Fork American River	1	M	A
Middle Fork Feather River	0	A	M
Middle River	1	G	Not sampled
Mill Creek	1	M	M
Mojave River	0	A	Not sampled
Mountain Lake	1	A	None
Napa River	0	A	G
New River	0	A	Not sampled
Nicasio Lake	1	A	Not sampled
North Fork Feather	0	M	M
North Fork Mokelumne	1	A	M
Owens Lake	1	A	Dry lake
Owens River	0	A	A
Pacheco Creek	1	A, G	None
Pajaro River	0	A, G, M	A
Patricks Creek	1	M	Not sampled
Petaluma Creek	0	A	Not sampled
Pit River	4	A, G, M	A, G, M
Putah Creek	0	A, G	None
Quinto Creek	1	A	Not Sampled
Rio Hondo	1	A	Not Sampled
Rush Creek	0	A	Not Sampled
Russian River	2	G	A, G
Sacramento River	5	A, G, M	A, G, M
Salinas River	1	A	None
Salmon Creek	1	A	Not sampled
Salton Sea	1	A	None
San Benito	1	A	None
San Bernardino Creek	0	A	Not sampled
San Francisquito Creek	1	A	Not sampled
San Joaquin River	4	A, G, M	A, M
San Lorenzo River	3	M	Not sampled
San Luis Rey River	0	A	None
Santa Ana River	0	A, G	None
Santa Ana Creek – tributary to Pajaro River	1	A	Not sampled
Santa Margarita River	2	A	NONE

APPENDIX II.—Continued

Water Body	Number of historical locatable sites	Genera found historically	Genera found currently
Savannah Pond – Los Angeles	1	A	None
Scott River	2	G, M	A, G, M
Secret Creek	1	A	Not sampled
Sellick's Springs	1	A	Not sampled
Shasta Lake	1	A, M	None
Shasta River	2	A, G	G, M
Silver Fork South Fork American River	1	M	M
Silverlake Reservoir	1	A	No access
Smith Reservoir	1	A	Not sampled
Smith River	0	M	M
Soap Lake	1	A	A
South Fork American	0	M	M
South Fork Eel River	2	A	A, M
South Fork Kern River	1	M	Not sampled
South Fork Pit River	2	M	A, M
South Walker River	1	A	None
Spanish Creek	1	M	M
Stow Lake	1	A	None
Susan River	0	A	M
Tequesquite Creek	1	A	Not sampled
Topaz Lake	1	A	None
Truckee River	3	A, M	M
Tulare Lake	1	A	Dry lake
Tule Lake	1	A, G	None
Tuolumne River	2	A, G	M
Union Creek	1	A	Not sampled
Upper Blue Lake, Lake County	1	A, G	Not sampled
Upper Spring Lake	0	A	A
Upper Truckee River	1	M	M
Whitewater River	3	A	None
Willow Creek	1	A	A
Yuba River	0	A, M	M

[a] Site no longer located in area described historically
[b] No mussels present per Coney (1993)

Comparison of selected population characteristics of adult Chinook salmon during upstream passage through a resistance board weir and during carcass surveys

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We compared population characteristics of adult Chinook salmon (*Oncorhynchus tshawytscha*) during 2003–2006 in the lower Stanislaus River, Stanislaus County, California, by counting and measuring live fish moving past a resistance board weir and dead fish counted and measured by the California Department of Fish and Wildlife (CDFW) during annual carcass surveys. The comparison of annual escapement was extended to 2007–2009 by including unpublished data. Although annual salmon passage counts at the weir were significantly correlated with estimates of carcass survey escapement, size estimates of live fish passing the weir were smaller on average than dead fish measured during carcass surveys. Sex ratios also differed for fish counted at the weir compared to those counted during carcass surveys. In general, females outnumbered males in both datasets, except in 2004 when more males than females were counted at the weir. Ratios of clipped to unclipped adipose fins differed significantly between fish from the weir and from the carcass surveys during 2005–2006, but not during 2004. These results suggest that population characteristics of adult salmon returning to the Stanislaus River may be better represented by the relatively high numbers of live fish examined during their concentrated passage through the weir than by the lower numbers of widely dispersed dead fish examined during carcass surveys.

Key words: Central Valley, Chinook salmon, *Oncorhynchus tshawytscha*, resistance board weir, carcass survey, annual escapement

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Accurate measures of salmonid escapement are critically important to fisheries managers for regulating fishing seasons, monitoring habitat enhancement programs, and supporting the reestablishment of suppressed populations (e.g., Hatch et al. 1998, Dauble and Mueller 2000, Merz and Merz 2004, Keefer et al. 2005, Gallagher et al. 2010). Escapement of adult Pacific salmon (*Oncorhynchus* spp.) can be estimated with a variety of

techniques. In California's Central Valley, traditional methods for estimating Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) escapement include visual counts of live fish (Clark 1929, Fry 1961, Hillborn et al. 1999), live trapping (Whelan et al. 1989), carcass mark-recapture surveys (Cousens et al. 1982, Shardlow et al. 1987, Boydstun 1994, Law 1994, Crawford et al. 2007), redd surveys (Gallagher and Gallagher 2005, Courbois et al. 2008), and hatchery counts (Brown et al. 1994, Mills and Fisher 1994, Williams 2006).

Despite the widespread use of traditional survey methods, they are inherently variable and inaccurate, resulting in uncertainty when making temporal or spatial comparisons of escapement estimates. For example, sampling bias is well documented for carcass surveys (Sykes and Botsford 1986, Rajwani and Schwarz 1997, Zhou 2002, Miyakoshi et al. 2003, Murdoch et al. 2009, Murdoch et al. 2010) due to difficult-to-satisfy assumptions when computing estimates. Furthermore, steelhead are iteroparous (multiple reproductive cycles over the course of an individual's lifetime), making traditional survey methods inappropriate for estimating escapement (Evans and Beaty 2004, Narum et al. 2008). Surveyor bias in identifying redds and superimposition of redds are also known to affect the accuracy of escapement estimates based on redd counts (Fukushima et al. 1998, Dunham and Rieman 2001). Adult escapement estimates from hatchery counts are also problematic because hatcheries are typically located at or near the upper extent of salmonid spawning areas, and the counts are strongly influenced by proportions of naturally produced (natural) versus hatchery fish (Fleming and Gross 1993, Banks et al. 2000).

Technological advances in recent years have allowed development of new and improved methods to estimate escapement and overcome some of the challenges associated with traditional survey techniques**.** Contemporary methods include video monitoring (Hatch et al. 1994, Davies et al. 2007, Killam 2008, Palmer et al. 2008) and electronic counters (Shardlow and Hyatt 2004, Tiffan et al. 2004, Garcia de Leaniz et al. 2006, Santos et al. 2008). Often, video monitoring and electronic counter systems require discrete passage areas to adequately detect fish movement. In these instances, passage can be constrained by natural channel features or artificial structures (e.g., fish ladders or weirs) to constrict passage and guide fish past monitoring equipment. As a result, advancements in weir design and applications have greatly increased the efficacy of these remote monitoring systems.

Historically, fish weirs were designed as fixed or rigid structures (Anderson and McDonald 1978, Baxter 1982, Hill 1991) that directed fish into a more confined area for sampling or collection (Gobalet and Wake 2000). Rigid picket weirs have been used for many years and work well in smaller streams with relatively low flow and debris levels; however, in larger river systems, they are prone to failure due to fluctuating flows and high debris loads. Subsequent repair and replacement costs are expensive and time-consuming, and data lost during downtimes are irreplaceable. A design variant, the resistance board weir (RBW), has received significant use over the past few decades, primarily in Alaska (e.g., Wiswar 1997, Harper and Watry 2001, Gates and Harper 2003). Rigid weirs and RBWs share the same fundamental concept, but a flexible design allows the RBW to operate under a broader range of river conditions. Under high water pressure, an RBW is designed to collapse, whereby its panels are forced down to lay on the river bottom, effectively allowing high flow and debris to freely pass over it. After river flows subside, the panels can be reset and quickly restored to operation.

Resistance board weir technology was originally developed in 1986 by Daishin Kogyo Co., Ltd. (Tobin 1994), and has been used only recently in California. The RBW

uses the hydrodynamic force of flow against boards set to create resistance and lift to elevate integrated polyvinyl chloride (PVC) panels above the water surface, creating a fence-like barrier across the channel. As with most fish structures, passage is restricted to allow for species identification, enumeration, live trapping and sampling and, in some instances, to completely impede passage. Although recent technologies have increased the application of RBWs for monitoring fish stocks (e.g., Anderson et al. 2007, Zimmerman and Zabkar 2007), we are not aware of any published reports that compared RBW accuracy with those of more traditional methodologies for estimating adult spawning escapement or characterizing their population structure.

The purpose of this paper was to determine if population characteristics of adult Chinook salmon measured as they passed through an RBW were similar to those measured by the California Department of Fish & Wildlife (CDFW) during carcass surveys. Specifically, we compared selected measurements of salmon—i.e., escapement estimate, fork length (FL), sex ratio, and adipose fin clip ratio—as they returned during fall and early winter to spawn in the Stanislaus River.

Materials and Methods

Study area.—The snow-fed Stanislaus River is one of three major east-side tributaries of the lower San Joaquin River system in California. Headwaters originate in Alpine and Tuolumne counties at an elevation of 3,675 m and drain approximately 240,000 ha of the western slope of the Sierra Nevada (Kondolf et al. 2001). The Stanislaus River flows in a westerly direction to its confluence with the San Joaquin River (elevation, 30.5 m), approximately 14.5 km west of Ripon in Stanislaus County. Goodwin Dam (37º 51' N, 120º 37' W), located at river km (rkm) 93.9 (measured from the confluence of the Stanislaus and San Joaquin rivers), is the upstream migration barrier to anadromous fish and demarks the upstream extent of the lower Stanislaus River (Figure 1).
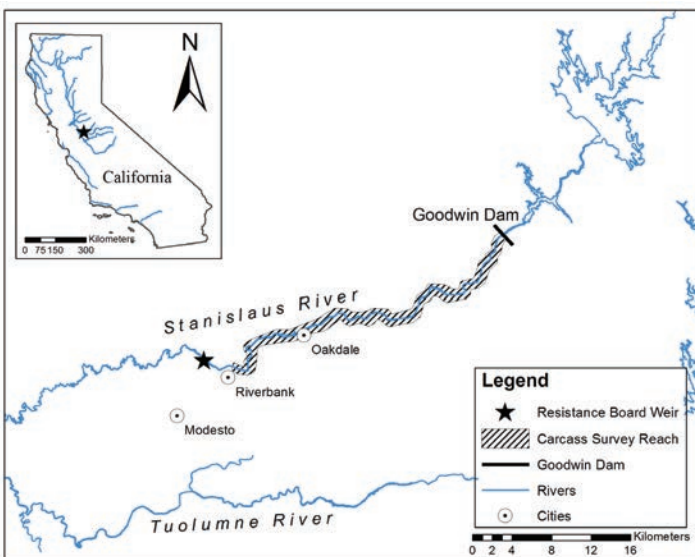

Figure 1.—Map of the study area showing locations of the resistance board weir at river km 50.6 (37° 44' N, 120° 58' W) on the Stanislaus River, California, and the reach where carcass surveys are conducted.

Historically, steelhead and several races of Chinook salmon inhabited the Stanislaus River watershed, including fall, late-fall, and spring runs (Yoshiyama et al. 2000). According to Fry (1961), approximately 35,000 adult fall-run Chinook salmon migrated up the Stanislaus River in 1953. The fall-run still predominates even though total adult escapement is only a fraction of its original abundance.

Site selection.—Site characteristics to consider for RBW operation include flow, velocity, water depth, channel width, substrate composition, channel profile, and seasonal timing of high water events (Larson 2001, Anderson et al. 2007, Zimmerman and Zabkar 2007). In general, laminar flows with slow to moderate water velocity, depths less than 1 m during normal flows, and substrates dominated by coarse gravel or cobble are ideal for RBW operation (Tobin 1994). During the present study, water depth in the 32 m-wide channel of the Stanislaus River ranged from 0 m to 1 m during normal flows. This locality was characterized by a relatively uniform (flat) river bottom dominated by sand and gravel, which allowed proper anchoring and sealing of the RBW to prevent uncounted fish escapement. Both banks had gradual slopes, enabling water to inundate the floodplain during high flow events and effectively reduce water velocities at the RBW.

Construction and installation.—Construction and installation of the RBW followed general techniques described by Tobin (1994) and Stewart (2002, 2003). Floating resistance board panels (0.91 m × 6.10 m) were constructed from electrical grade schedule 40 polyvinyl chloride (PVC) pipe (2.54 cm x 6.10 m) and 1.27-cm-thick ultra-high molecular weight polyethylene (UHMW). Modifications to general construction techniques detailed in Stewart (2002) were as follows: design and installation of a PVC "cap" to allow for recreational boat passage and to protect the RBW panels from damage; 3.18-cm stainless steel hose clamps were used as retaining sleeves instead of PVC to add stability to each panel; 3.81-cm-thick insulating sheet styrofoam was added to each resistance board to increase panel buoyancy; bulkheads were constructed from 2.54-cm square aluminum tubing and PVC pipe (2.54 cm) instead of wood to increase structural strength and RBW longevity; and ripped-in-half acrylonitrile butadiene styrene (ABS) plastic (7.62 cm) was placed over the substrate rail cable to reduce potential injuries to fish. We used stainless steel or aluminum hardware throughout in an effort to reduce corrosion.

Resistance board weir construction required four people to complete in approximately 8 weeks. Annual site installation and removal required 4–6 people and approximately 2 days. General in-season maintenance and trapping required two people for 1–4 hrs/day. Maintenance included cleaning the RBW and downloading passage data. We operated the RBW each season (late September to early January) from 2003 to 2007 to capture the fall-run Chinook salmon migration.

We designed and installed a trap (1.52 m high x 1.52 m wide x 4.88 m long) to periodically collect live fish each season, obtain biological samples (e.g., scales and tissue), and validate passive counts. The live-trap frame was constructed from 7.62-cm aluminum channel and tubing into which we drilled 2.54-cm diameter holes spaced 6.67 cm apart on center and fitted with 2.54-cm galvanized electrical conduit.

Monitoring technology.—The 32-m wide RBW was coupled with a passive monitoring system that used infrared detection and digital image technology (RiverWatcher, Vaki Aquaculture Systems, Ltd., Kopavogur, Iceland) to record fish as they passed the RBW. The system was composed of a pair of infrared scanner plates (20 cm × 60 cm, spaced 30-cm apart), an underwater color digital camera, and a computer (PC) to run the software program

and store collected data. Each scanner plate had two vertical rows containing 96 infrared diodes. As an object moved through the scanner, it obstructed the infrared light beams and a silhouette of the object was generated. After the PC sensed that an object had broken the scanner plane, the digital camera was triggered to record the silhouette and capture up to five digital photographs. Date, time, direction of travel (upstream or downstream), maximum body depth (mm), and water temperature were also recorded. Maximum fish body depth was used to calculate total length (TL) using a length:depth ratio of 4.2:1 for Chinook salmon; this ratio is an average for all Chinook salmon trapped and handled at the RBW over the sampling period (Cramer Fish Sciences, unpublished data), and possibly overestimates the lengths of females and underestimates the lengths of males (Mesick et al. 2009). Total length was then converted to fork length (FL) with conversion equations provided by Conrad and Gutmann (1996). Data collection and live fish handling methods complied with all applicable state and federal permitting requirements.

The monitoring system operated continuously following installation each season. The scanner was positioned at the rear entrance and the camera on the side of the trap to record fish as they swam past the RBW. A clear acrylic panel (1.27-cm thick) was used to create a viewing window for the camera to capture images. White acrylic (1.27-cm thick) was used as a background to photograph fish as they passed through the trap. White light-emitting diodes (LEDs) illuminated the viewing window at night to capture clear digital images (Anderson et al. 2007).

Two 0.61-m × 0.91-m photovoltaic panels mounted to a 6.10-m-tall stainless steel pole (to reduce shading from riparian vegetation) were used to power the system. Panels were connected to a 20A/12V photovoltaic system controller (MorningStar Corporation, Model SS-20L), which were used to charge a bank of eight 6V deep-cycle batteries (Trojan Battery Company, Model T-125 6V), two sets of four batteries joined in a series, and then joined in parallel to create a 12V DC power source.

Statistical analyses.—Annual counts of Chinook salmon passing the RBW during 2003–2009 were compared with estimates of spawning escapement derived from the CDFW carcass surveys. Summary counts of salmon passage from 2007 to 2009 were obtained from FishBio (Oakdale, California), a firm that took over operation of the RBW in 2007 (FishBio 2013). Escapement estimates from carcass surveys during the same time period were retrieved from GrandTab (CDFG 2013), a database maintained by the CDFW. Other data from the carcass surveys (i.e., fish lengths, sex ratios, and adipose fin presence) were obtained from Guignard (2004, 2005, 2007a, 2007b).

All statistical tests were performed with SAS version 9.2 (SAS Institute Inc. 2009). Relationships between total fish counts from the RBW and escapement estimates from carcass surveys were assessed using Pearson product-moment correlation analysis. Mean FL of salmon measured at the RBW and during carcass surveys were compared with two-way analysis of variance (ANOVA), where "method" (RBW and carcass survey) and "year" (2003–2006) were categorical variables representing the main effects. Length-frequency distributions were compared between the two methods within years using the Kolmogorov-Smirnov two-sample test. Sex ratios (males versus females) and adipose fin clips (present versus absent) were also compared between the two methods within years by using the chi-square (X^2) test for homogeneity. Unless specified otherwise, the level of significance for rejecting null hypotheses of statistical tests was α=0.05.

RESULTS

Annual counts of adult Chinook salmon moving upstream past the RBW during 2003–2009 were significantly correlated with annual escapement estimates computed by CDFW from carcass surveys ($r_s = 0.802$, $P = 0.0300$; Figure 2). In general, as counts of live salmon passing the RBW increased, so did the counts of salmon carcasses several days or weeks later in upstream locations surveyed by CDFW.
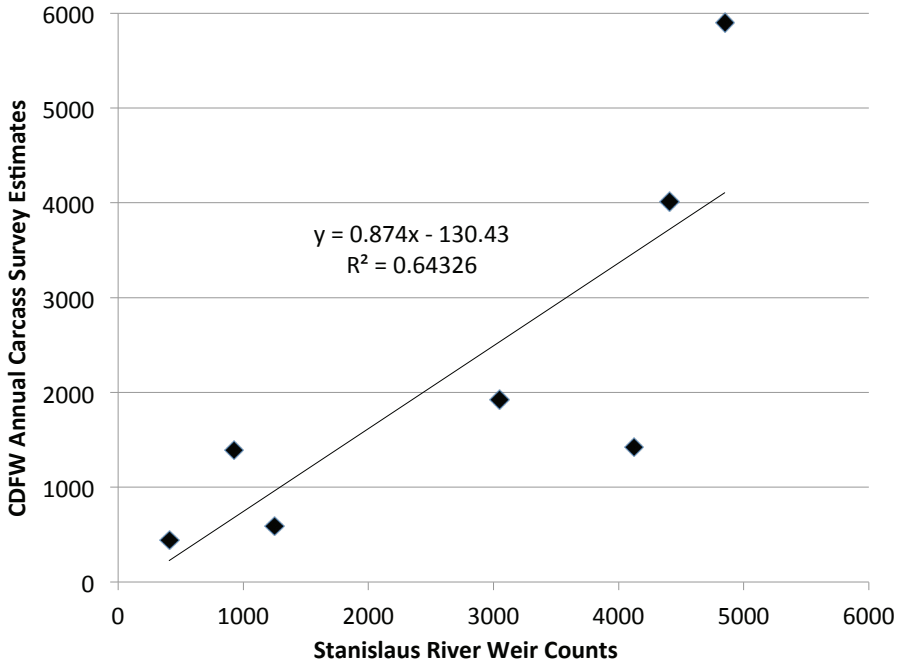

FIGURE 2.—Relation between Chinook salmon escapement estimated from resistance board weir counts and from carcass survey counts on the Stanislaus River, California, 2003–2009.

During 2003–2006, length-frequency distributions of live fish passing the RBW were significantly different from length-frequency distributions of dead fish recovered during carcass surveys (Figure 3; Kolmogorov-Smirnov two-sample test of FL measurements in 2003, $D = 0.444$; in 2004, $D = 0.519$; in 2005, $D = 0.417$; and, in 2006, $D = 0.247$; for all years, $P < 0.0001$). According to two-way ANOVA, mean FLs exhibited significant method*year interaction (Table 1). As a result, we computed separate one-way ANOVAs within each year to compare mean FLs of fish from the two methods. On average, live fish passing the RBW were significantly shorter than dead fish recovered during carcass surveys for each of the four years: in 2003, $F_{1,14632} = 1,146.00$; in 2004, $F_{1,14632} = 1,299.72$; in 2005, $F_{1,14632} = 258.23$; and in 2006, $F_{1,14632} = 34.97$; for all years, $P < 0.0001$.
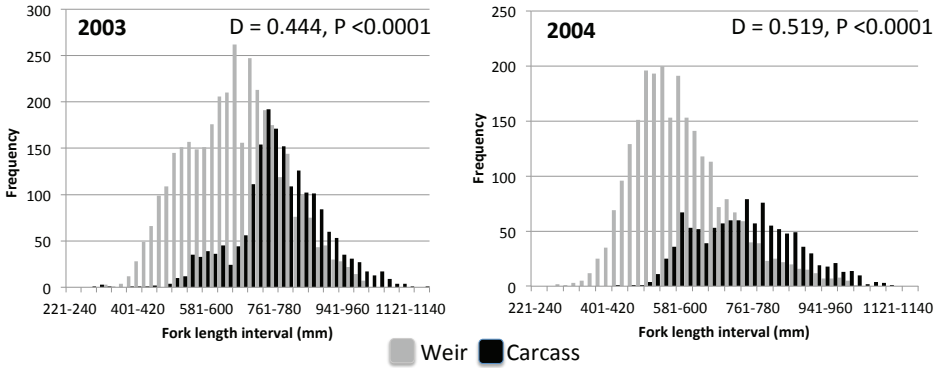
FIGURE 3.—Length frequency distributions of Chinook salmon measured at the resistance board weir and during carcass surveys on the Stanislaus River, California, 2003–2006.

TABLE 1.—Results of two-way analysis of variance for mean fork lengths of adult Chinook salmon measured by two "methods" (resistance board weir and carcass survey) over four "years" (2003, 2004, 2005, and 2006) on the Stanislaus River, California.

Source	*df*	Mean square	*F*-statistic	*P*-value
Model	7	8,663,258.00	548.50	<0.0001
Method	1	20,928,848.03	1,325.08	<0.0001
Year	3	2,824,839.60	178.85	<0.0001
Method*Year	3	886,210.14	56.11	<0.0001
Error	14,632	15,794.40		

Sex ratios differed significantly between live fish counted at the RBW and dead fish recovered during carcass surveys (in 2004, X^2_1 = 186.0, P <0.0001; in 2005, X^2_1 = 22.2, P <0.0001; in 2006, X^2_1 = 12.2, P = 0.0005; Figure 4). With one exception, females predominated over males at the RBW and during carcass surveys. The exception occurred at the RBW in 2004 when a larger proportion of the population consisted of males (67%) rather than females (33%). During each of the remaining three years, higher percentages of males were documented at the RBW (41%–67%) than during carcass surveys (29%–40%).
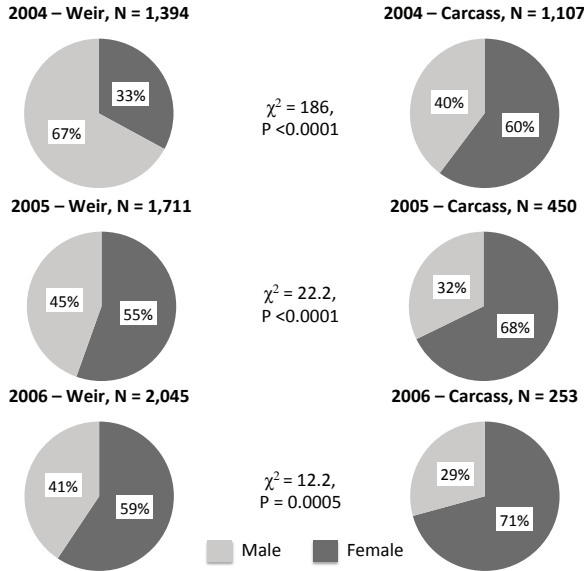
2004 – Weir, N = 1,394   **2004 – Carcass, N = 1,107**

$\chi^2 = 186$,
P <0.0001

2005 – Weir, N = 1,711   **2005 – Carcass, N = 450**

$\chi^2 = 22.2$,
P <0.0001

2006 – Weir, N = 2,045   **2006 – Carcass, N = 253**

$\chi^2 = 12.2$,
P = 0.0005

Male   Female

FIGURE 4.—Sex ratios of Chinook salmon measured at the RBW and during carcass surveys on the Stanislaus River, California, 2004–2006.

Chinook salmon with unclipped adipose fins greatly predominated over salmon with clipped adipose fins at both the RBW and during carcass surveys (Figure 5). Excluding

2004 – Weir, N = 1,706   **2004 – Carcass, N = 1,107**

$\chi^2 = 0.419$,
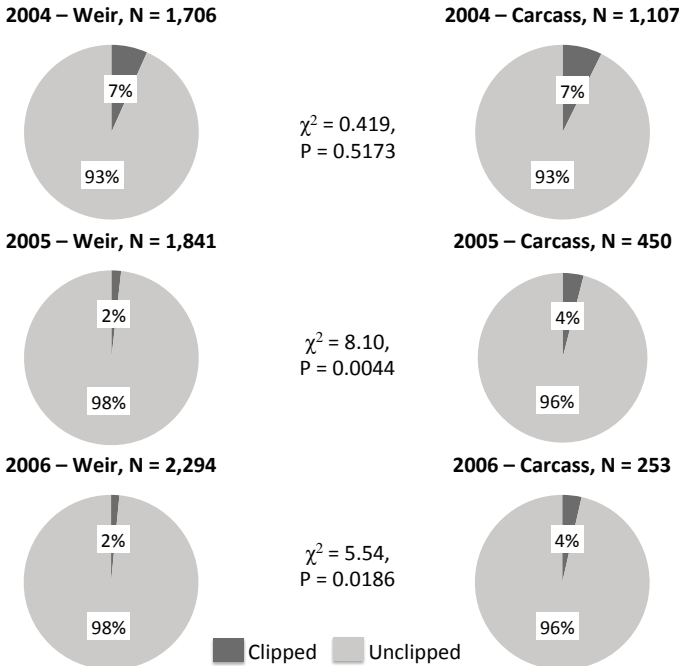P = 0.5173

FIGURE 5.—Clipped to unclipped adipose fin ratios of Chinook salmon measured at the RBW and during carcass surveys on the Stanislaus River, California, 2004–2006.

2005 – Weir, N = 1,841   **2005 – Carcass, N = 450**

$\chi^2 = 8.10$,
P = 0.0044

2006 – Weir, N = 2,294   **2006 – Carcass, N = 253**

$\chi^2 = 5.54$,
P = 0.0186

Clipped   Unclipped

2004 when the comparison was not significant ($X^2_1 = 0.419$, $P = 0.5173$), lower proportions of fin-clipped fish were encountered at the RBW than during carcass surveys (in 2005, $X^2_1 = 8.10$, $P = 0.0044$; in 2006, $X^2_1 = 5.54$, $P = 0.0186$).

DISCUSSION

Since 1953, the CDFW has documented escapement of Chinook salmon on the Stanislaus River by conducting carcass surveys over a 40-km reach from Goodwin Dam (37º 51' N, 120º 37' W), downstream to Riverbank (37º 44' N, 120º 56' W) (Guignard 2004, 2005, 2007a, 2007b). These surveys typically began in October and continued through December or early January, depending on fish abundance and river flow conditions (Mesick et al. 2009). Estimates of escapement were usually generated using the Schaefer and Jolly-Seber mark-recapture methods, whereas the Peterson mark-recapture method was used whenever carcass numbers were low (Mesick et al. 2009). The escapement estimate judged to be most accurate based on the number of carcasses tagged and recovered was then reported by CDFW in their GrandTab file (Mesick et al. 2009).

Although the database for Chinook salmon escapement in the Stanislaus River extends back roughly 60 years, the accuracy of estimates generated by carcass surveys has not been critically assessed (CDFG 2013). Nevertheless, in an effort to improve escapement estimates, carcass mark-recapture methods have been coupled with live visual counts and redd surveys (Guignard 2004, 2005, 2007a, 2007b), but even these methods require major assumptions that have not been tested (for partial listings of assumptions, see Duffy 2005).

The present study provided an opportunity to compare selected population characteristics generated at the lower Stanislaus River RBW with those derived from carcass surveys. Available evidence suggests that nearly all fish are detected when they pass through a properly operating RBW. Fewings (1994) tested the RiverWatcher in Iceland and found it to be 98.9% accurate, whereas Eatherley et al. (2005) reported the RiverWatcher to be 100% accurate when counting returns of Atlantic salmon (*Salmo salar*) in a Scottish river. According to Shardlow and Hyatt (2004), accuracy of the RiverWatcher exceeded 95% when migration rates of adult Pacific salmon were <500 fish/hour. To our knowledge, migration rates in the lower Stanislaus River never approached that level (maximum fish count, 764 fish/day; Pyper et al. 2006). During the 2004 trapping season, Pyper et al. (2006) determined that average detection probability of the lower Stanislaus River RBW was 97% (95% confidence interval, 89%–105%), suggesting a slight undercount of fish. Nevertheless, the significant correlation between annual fish counts at the RBW and escapement estimates determined from the CDFW carcass surveys over a seven-year period (2003–2009) suggests a strong association between these two methods (Figure 2).

Comparisons of Chinook salmon length frequencies derived from the RBW and the carcass surveys indicated significant differences between these two methods. In general, the RBW yielded smaller fish than did the carcass surveys (Figure 3). Zhou (2002) determined that carcass recovery rates increased as fish size increased and as stream flow decreased. According to Zhou (2002), it makes intuitive sense for a carcass recovery rate to be size-dependent. Small carcasses are more likely to be consumed or carried away by scavengers, are more difficult for surveyors to detect, and are more readily washed away. Thus, it is probable that the CDFW carcass surveys were biased towards large-bodied fish, which would explain the larger average sizes of salmon measured during the carcass surveys.

Some populations of Pacific salmon are known to display persistent and often extreme sex ratio biases (Olsen et al. 2006). O'Brien (2006) reported the sex ratio of Chinook salmon passing a RBW in the Gisasa River, Alaska, as 67% males and 33% females. Gewin (2006) found nearly the same sex ratio for fish passing a RBW on the East Fork of the Andreafsky River, Alaska. In Cottonwood Creek, a tributary of the Sacramento River in California, results from carcass surveys by Austing and Null (2012) indicated a male:female ratio for hatchery-origin Chinook salmon of nearly 7:1 whereas the ratio for natural fish was nearly 1:1. By comparison, females generally outnumbered males at both the RBW and during carcass surveys (Figure 4), except in 2004 when males were roughly twice as numerous as females at the RBW. Nevertheless, the generally lower ratios of males to females are consistent with the notion that some genetic males in Central Valley rivers, including the Stanislaus River, have undergone sex reversal and have the appearance of females, as suggested by Williamson and May (2002, 2005). Although less numerous than females, higher percentages of male Chinook salmon were documented from the RBW (41%–67%) than during carcass surveys (29%–40%). Murdoch et al. (2009, 2010) recently demonstrated that carcass drift often differs between male and female Chinook salmon due to differences in post-spawning behavior (the redd-guarding behavior of females results in fidelity to their redds; by comparison, males are not known to display redd-guarding behavior). Moreover, dying males slowly drift downstream, with smaller males usually drifting longer distances than larger males (Murdoch et al. 2010). By drifting farther downstream, small males increase their exposure to potential scavengers or simply become less detectable as a result of drifting into logjams (Murdoch et al. 2010) or deep-water habitats. A systematic bias associated with poor detection rates of smaller males during carcass surveys could account for the somewhat higher percentages of males documented during upstream passage at the RBW.

Even though not statistically different in 2004, lower proportions of fin-clipped individuals were recorded during 2005 and 2006 among live fish passing the RBW than among dead fish recovered in carcass surveys (Figure 5). We found that high turbidity, heavy loads of floating debris, and simultaneous passage by several salmon adversely affected detection of morphological features such as presence or absence of an adipose fin in camera images taken at the RBW. We are not aware, however, if a reduction in detection probability would lead to an increase in false positives (i.e., that a missing adipose fin would be incorrectly scored as being present).

In conclusion, our results suggest that population characteristics of adult Chinook salmon can be more accurately quantified by using a strategically positioned RBW than by conducting manpower-intensive carcass surveys. Continued improvements in image recording, image processing, and computer analysis programs should further enhance the accuracy of automated imaging procedures employed at RBWs for fish species and sex ratio identification, and fish size measurements (Pippy et al. 1997, Hatch et al. 1998, Cadrin and Friedland 1999, Merz and Merz 2004). In addition, RBWs offer more versatility, and can be used in other applications such as segregating different runs of fish or blocking fish entry into a protected watershed.

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Managing monarch butterfly overwintering groves: making room among the eucalyptus

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Proper management and conservation of the coastal California overwintering sites used by western monarch butterflies *(Danaus plexippus L.)* is critical for continued use of these sites by monarchs. Many management efforts are currently concentrating on eucalyptus-only sites because of the prevailing notion that monarchs "prefer" eucalyptus over native tree species. Herein, we test the "eucalyptus preference" hypothesis with data from five overwintering sites comprised of blue gum eucalyptus (*Eucalyptus globulus*) and at least one other native tree species from fall 2009 to spring 2012. We found that when monarchs clustered disproportionately on a tree species relative to its availability, they clustered significantly more than expected on native trees and significantly less than expected on eucalyptus. Also, in years when the overwintering population was highest, monarchs clustered disproportionately on native conifers, and they often switched from clustering on eucalyptus in the early winter to native conifers in the middle or late winter. Our results suggest that overwintering groves should be managed to include a mixture of tree species.

Key words: monarch, *Danaus plexippus*, eucalyptus, habitat preference, overwintering, Monterey cypress, Monterey pine

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Each fall, monarch butterflies (*Danaus plexippus* L.) in western North America migrate long distances to specific groves of trees on the California coast where they gather in large clusters for the winter (Williams et al. 1942, Urquhart and Urquhart 1977). Based on population estimates derived from annual surveys at these sites, it is inferred that the western population has declined by 90% since 1997 (Stevens and Frey 2004, Xerces Society 2013). The two main drivers behind this decline are hypothesized to be the loss of breeding habitat (milkweed patches) in the interior western and southwestern United States, and the loss or degradation of overwintering habitat (tree groves). From 1990 to 1998, there was a 12% decline in available overwintering habitat for monarchs in California (Meade 1999,

Frey and Schaffner 2004). That trend is expected to continue, given that there has been no management policy put in place to stop or reverse the decline. In addition to direct loss, overwintering sites can become unsuitable for monarchs through tree cutting and removal, senescence, tree fall, disease, parasitism, or herbivory (Leong et al. 1991, Weiss et al. 1991, Fallon and Jepsen 2013).

A suitable overwintering site is comprised of a grove of trees that produce a microclimate with a narrow set of values across several parameters. Suitable grove conditions include temperatures that are above freezing (Calvert et al. 1983) but not too warm (Alonso-Mejia et al. 1997), low light intensity and solar radiation with high water vapor pressure (Leong et al. 1991), wind speeds lower than 2 m/s (Leong 1990), and access to fresh water, sometimes via streams or puddles but often in the form of fog drip or morning dew (Tuskes and Brower 1978). The microclimate within an overwintering grove is impacted by landscape-level factors and by the local configuration and characteristics of trees at the site. Canopy height and density, branch configuration, and type of foliage will determine the microclimate and influence if, or where, monarchs cluster. These characteristics may vary considerably depending on tree species. Therefore, monarchs may cluster on different tree species under different climatic conditions.

At California overwintering sites, monarchs have been recorded clustering on a variety of native and non-native trees, primarily blue gum eucalyptus (*Eucalyptus globulus*), Monterey pine (*Pinus radiata*), Monterey cypress (*Hesperocyparis macrocarpa*), and coast redwood (*Sequoia sempervirens*). Historical observations suggest that monarchs clustered primarily on native conifers, particularly Monterey pine (Riley and Bush 1881, 1882; Shepardson 1914). The introduction of eucalyptus in the mid-nineteenth century, however, changed the landscape of coastal California. In southern California, which lacked the coniferous forests of the central and northern coast, eucalyptus became widespread on the landscape as groves were planted for lumber and shade (Groenendaal 1983, Santos 1997). In central California, blue gum eucalyptus was planted extensively while coastal areas forested with Monterey pine were concurrently harvested (Jones and Stokes 1994).

Monarchs currently cluster almost exclusively on eucalyptus in the southern portion of their overwintering range in California (i.e., Santa Barbara, Ventura, Los Angeles, Orange, and San Diego counties). Overall, monarchs use eucalyptus at 75% of California's overwintering sites (Frey and Schaffner 2004), an observation that might lead one to conclude that monarchs "prefer eucalyptus", and in fact, this has become "common knowledge." Some monarch management plans go as far as advocating for conservation and management efforts exclusively at eucalyptus-only overwintering sites (Sakai and Calvert 1991), while others recommend planting more eucalyptus (Oberhauser et al. 2009).

Monarch preference for tree species has never been formally tested, partially because it is not possible to test for preference at groves comprised only of eucalyptus. It is only possible to establish preference if alternate resources are available, and if utilization is measured relative to resource availability. Our purpose is to examine monarch tree use at sites with multiple available tree species, and determine whether monarchs prefer eucalyptus or if they merely use it in proportion to its availability. If monarchs do not prefer eucalyptus it would suggest that monarchs use eucalyptus at sites that have suitable microclimates regardless of the tree species present: if they are not preferential of the tree, then they must be preferential of the site. Such a paradigm shift would move us from managing and restoring eucalyptus towards managing and restoring overwintering sites.

Materials and Methods

We counted the number of clustering monarchs at five overwintering sites during the overwintering period from fall 2009 to spring 2012. Our weekly monitoring also included information on tree species used, and we examined these data in the context of availability of different species of trees.

Study sites.—All sites were well-known climax overwintering sites, i.e., overwintering sites occupied by monarchs for the entire season (Leong et al. 2004). Monarchs were present throughout the entire overwintering season during every year of the study. Sites were selected from among all known climax sites because the groves contained multiple tree species.

Pacific Grove Monarch Sanctuary (36° 37' N, 121° 55' W) is located in Pacific Grove, California, on the south edge of Monterey Bay, Monterey County. The 1.1-ha site consists of *E. globulus* on the south edge and southeast corner, *P. radiata* and *H. macrocarpa* throughout the rest of the property, coast live oak (*Quercus agrifolia*) in the understory, and several non-native ornamental trees and shrubs. The Big Sur private property site (36° 07' N, 121° 38' W) is located on the Big Sur coast in Monterey County. Monarchs cluster on a 1-ha parcel containing groves of *E. globulus, H. macrocarpa, P. radiata,* and *S. sempervirens*. The site also contains landscaped gardens with plantings of non-native shrubs and flower gardens. Morro Bay Golf Course (35° 21' N, 120° 50' W) is located in Morro Bay, San Luis Obispo County. Total area of the two groves at this site is 4 ha. These groves are comprised mainly of *E. globulus* with *P. radiata* along the outer edges, and little to no understory vegetation. Pismo Beach Monarch Grove (35° 07' N, 120° 37' W) is located adjacent to the Pismo State Beach North Beach Campground in Pismo Beach, San Luis Obispo County. The 1.2-ha overwintering site is comprised of a large *E. globulus* grove with some *P. radiata* and *H. macrocarpa* scattered along the northeast edge. A creek flows along the north edge of the site, which is lined with arroyo willow (*Salix lasiolepis*). There is minimal understory. Oceano Campground (35° 07' N, 120° 37' W) is located within the Pismo State Beach Oceano Campground in Oceano, San Luis Obispo County. The 0.7-ha overwintering site is within the 26-ha campground, and is comprised mainly of *P. radiata* with some cultivated Torrey pine (*Pinus torreyana*), and a small stand of *E. globulus*. There is extensive understory of native and non-native shrubs and forbs.

Monarch overwintering surveys.—Surveys were conducted weekly at each of the five sites from mid-October through mid-March, or until monarchs dispersed from the site in spring. During the 2009–10 season, surveys began in November at all sites except Pacific Grove, which began in October, and ended at all sites in February. During the 2010–11 season, all sites were surveyed from October through March. During the 2011–12 season, all sites were surveyed from October through February. The number of clustered monarchs was estimated using a standardized method (described in Frey et al. 1992). The total number of monarchs estimated clustering on each tree species during each visit was recorded. The average number of monarchs estimated clustering on each tree species per month per site was also calculated, and was used as a metric for tree utilization.

Canopy cover measurements.—Canopy cover was measured at the five sites in summer 2012. All tree species used by monarchs at the sites were evergreens and, thus, were leafed out year-round. At each overwintering site, a polygon that encapsulated all trees that had been used by the monarchs over the last 10 years was mapped, thereby enclosing the

largest area of known use (Hamilton et al. 2002, Frey et al. 2003, Frey et al. 2004, Griffiths and Thorngate 2008, Griffiths 2009). These polygons were overlaid with a 20-m grid, and at the corners of each grid square a densiometer was used to estimate canopy cover. Only canopy above 3 m was considered, as monarchs have rarely been recorded clustering below that height at these sites in the last decade (Hamilton et al. 2002, Frey et al. 2003, Frey et al. 2004, Griffiths and Thorngate 2008, Griffiths 2009). We then used these data to calculate the proportion of total canopy cover of each tree species at each site. The proportion that each tree species contributed to the total canopy cover was used as a metric for tree species availability.

Statistical analyses.—Tree use was analyzed using chi-square tests, which tested whether monarchs were using trees in proportion to their availability (Sokal and Rohlf 1995). The predicted use reflective of availability (expected cluster values referenced below), was calculated by taking the total observed counts and distributing them across tree species based on the relative canopy cover of each tree species. We used R 2.15.3 (R Core Team 2013) to conduct three chi-squared goodness-of-fit tests and compared (1) the average monthly observed vs. expected monarchs clustering on eucalyptus or native conifers; (2) observed vs. expected monarch numbers during maximum occupancy (highest population size) of that site during that overwintering season; and (3) observed vs. expected monarch numbers for mid-season (closest to December 31) surveys. A sign test of the significant chi-square results was used to determine if monarchs clustered significantly more than expected on eucalyptus or on native trees (Sokal and Rohlf 1995). Because multiple counts were done at each site in the same seasons, we used a repeated measures ANOVA (Gotelli and Ellison 2004) using JMP 10.0 (SAS Institute Inc. 2012) to test for effects of tree species, site, month, and year on the number of clustering monarchs. Monthly monarch cluster averages were cube-root transformed to more closely approximate normality.

RESULTS

Canopy cover varied greatly between sites (Table 1). Only *E. globulus* and *P. radiata* were present at every site we sampled. *E. globulus* canopy cover ranged from 15.3% at Oceano Campground to 97.4% at Morro Bay Golf Course. *P. radiata* canopy cover ranged from 1.1% canopy cover at Big Sur private property to 84.2% at Oceano Campground.

TABLE 1.— Canopy cover proportions by tree species at five monarch butterfly *(Danaus plexippus)* overwintering sites from 2009 – 2012 in Monterey and San Luis Obispo counties, California.

Site	Tree Species				
	Blue gum eucalyptus	Monterey pine	Monterey cypress	Coast redwood	Other
Pacific Grove Monarch Sanctuary	0.425	0.345	0.220	-	0.010
Big Sur private property	0.449	0.011	0.447	0.091	0.002
Morro Bay Golf Course	0.974	0.026	-	-	-
Pismo Beach Campground	0.762	0.035	0.108	-	0.095
Oceano Campground	0.153	0.842	-	-	0.005

Monarch abundance varied widely among sites and among years (Figure 1). The fewest monarchs were present in 2009–2010. At all sites except Big Sur, there were more monarchs present during 2010–2011 than during 2009–2010. There were more monarchs present at all sites during 2011–2012 than in any other overwintering season of our study. Likewise, the proportion of monarchs clustering on eucalyptus vs. native trees varied among sites and among years (Figure 1). In most years and at most sites, monarchs did not even cluster in the same proportions on eucalyptus throughout one season, indicating that some monarchs moved, or that monarchs switched tree species. At three sites in at least one year monarchs clustered on eucalyptus near the beginning of the season but switched to native conifers in the middle or at the end of the season (Figure 1).
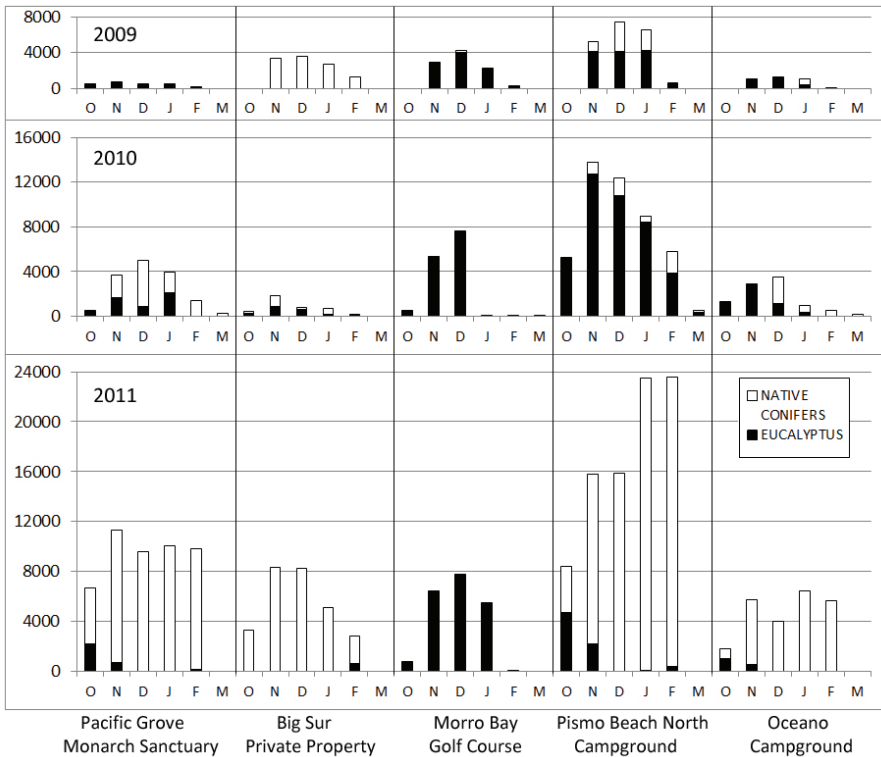
FIGURE 1.—Number of monarch butterflies *(Danaus plexippus)* present and tree usage at five overwintering sites in Monterey and San Luis Obispo counties, California, during three winters from 2009 to 2012. Site names are listed across the bottom. Each vertical bar represents the total number of monarchs estimated to be present at that site in that month (starting in October and ending in March of each year). Each bar is colored according to the number of monarchs clustering on blue gum eucalyptus (filled) or native conifers (un-filled) such as Monterey pine, Monterey cypress, and coast redwood.

In all three years and at all five sites, the chi-square values were significant (X^2 values ranged from 13.27–233530.72, $P < 0.001$ in all cases), indicating that monarchs were not clustering on tree species in proportion to canopy availability over the course of a season, during maximum site occupancy, or during the middle of the overwintering season. Sign tests for each of the three years were not significant, indicating that monarchs did not show

Table 2.—Sign test results for tree species utilization by monarch butterflies *(Danaus plexippus)* relative to tree species availability across three years and five California overwintering sites in Monterey and San Luis Obispo counties, California, 2009 – 2012. Site-year cases where a chi-square test showed that monarchs clustered significantly more than expected on eucalyptus are labeled as "+". They are labeled as "-" when a chi-square test indicated that monarchs clustered significantly less than expected on eucalyptus. One analysis was done over the course of the whole season using monthly count averages, one analysis was done on population counts at maximum seasonal occupancy, and the third was done on population counts closest to the middle of the season (31 December). *P*-values for all three tests were non-significant, indicating no overall tree species preference even though the chi-squared test showed that trees species were not used relative to their availability.

Site	Year	Whole season	Max Occupancy	Mid-season
Pacific Grove Monarch Sanctuary	2009–10	+	+	-
	2010–11	-	-	-
	2011–12	-	-	-
Big Sur private property	2009–10	-	-	-
	2010–11	+	+	-
	2011–12	-	-	-
Morro Bay Golf Course	2009–10	-	-	+
	2010–11	+	+	+
	2011–12	+	+	+
Pismo Beach Campground	2009–10	-	-	-
	2010–11	+	+	+
	2011–12	-	-	-
Oceano Campground	2009–10	+	+	+
	2010–11	+	+	-
	2011–12	-	-	-
	Total +	7	7	5
	Total -	8	8	10
	P-value	1.00	1.00	0.30

a preference for eucalyptus or native conifers (Table 2). Nevertheless, monarchs clustered more than expected on native trees more than 50% of the time (8 out of 15 times on a seasonal level, 8 out of 15 times at peak occupancy, and 10 out of 15 times during mid-season).

Repeated measures ANOVA showed that the average number of monarchs present at all sites was significantly higher during 2011–12 ($F_{2,12}$ = 4.73, P = 0.013). The average number clustering on native trees was also significantly higher during 2011–12 ($F_{2,12}$ = 9.24, P < 0.001). During the 2011–12 season, monarchs clustered significantly more than expected on conifers in every month of the winter (October through February) at three of five sites (Pacific Grove Monarch Sanctuary, Big Sur Private Property, and Pismo Beach North Campground), and clustered significantly more than expected on conifers at Oceano

Campground from November through February (Figure 1). Therefore monarchs clustered disproportionately more on native conifers in 2011–12 earlier and for more consecutive months than during 2009–10 and 2010–11.

<center>DISCUSSION</center>

Among our study areas, monarchs did not exhibit an overall preference for eucalyptus across sites and years during the middle of the season, at maximum site occupancy, or during the overwintering season as a whole. These results force us to reject the "eucalyptus tree preference" hypothesis. Additionally, monarchs exhibited tree switching, moving from clustering predominantly on eucalyptus to clustering predominantly on native trees over the course of the season. They also clustered significantly more than expected on native trees at mid-winter in 10 out of 15 site-year combinations. This indicates that monarchs may prefer different tree species under different microclimate conditions.

A weakness when examining tree use across an entire season is that such an approach includes all of the conditions that monarchs experienced at a site within one winter and ignores fine-scale weather variations. Previous studies have shown that monarchs move between trees in response to changing microclimate (Leong et al. 1991, Frey et al. 1992); therefore it is important to record clustering behavior in a variety of weather conditions. It is possible that monarchs show a different tree species preference when microclimate conditions are the least favorable, and this is the reason that we examined tree use during mid-season, when winter storms are more frequent, temperatures are lower, and wind speeds are higher (NCDC 2012). Indeed, monarchs clustered in a different pattern during the mid-season counts than during the whole-season and maximum occupancy counts: they clustered significantly more than expected on native trees in a majority of years at all sites except one. It should be noted, however, that this site (Morro Bay Golf Course) is our weakest test of the preference hypothesis because it is 97% eucalyptus; the other four sites range from 15–76% eucalyptus.

Monarchs select overwintering sites based on a narrow set of microclimate parameters (Tuskes and Brower 1978, Calvert et al. 1983, Leong 1990, Leong et al. 1991, Anderson and Brower 1996). Our results show that monarchs utilize multiple tree species during a single season and within single groves. We propose that different trees result in different microclimates because they have varying heights, foliage density, and structure, and suggest that it is possible that monarchs shift among tree species in response to changes in ambient conditions. At three of the five sites, and at one or more sites in all three years, monarchs switched from clustering predominantly on eucalyptus to clustering predominantly on native trees in the middle of the season. In most site-year cases where monarchs exhibited tree switching, they clustered more than expected on eucalyptus at the beginning of the season (except in 2011–12, see below), and then clustered more than expected on native trees during mid- and late season. We hypothesize that when the weather is most inclement, monarchs will shift from eucalyptus to native conifers. This could be tested by carefully measuring microclimate conditions in overwintering groves and correlating monarch movement with shifting weather. More study is needed to determine exactly what conditions prompt monarchs to switch tree species, and whether there are circumstances under which they will use native trees to the exclusion of eucalyptus.

Interestingly, when the annual overwintering population was at its highest (in 2011–12) during the three years of this study, monarchs clustered significantly more on native trees, and did so earlier in the season and for a greater length of time. Tree switching occurred in 2011–12 at only two sites (Pismo North Beach Campground and Oceano Campground), whereas at the other three sites monarchs clustered predominantly on native trees from the start of that season. Only at Oceano Campground did monarchs cluster disproportionately on eucalyptus at the start of that season; at Pismo North Beach Campground they clustered on eucalyptus in proportion to its availability. It seems that the size of the overwintering population may influence how and where monarchs cluster. Our results indicate that when more monarchs are present, they may cluster preferentially on conifers.

Groves comprised entirely of eucalyptus may not be optimal for monarchs when compared with mixed-species groves because monarchs would not be able to respond to local conditions available across different tree species. Our data show that monarchs moved off of eucalyptus and on to conifers in December and January, and that monarchs clustered disproportionately more on conifers during the mid-winter (December 31) when the climate is most unstable. At a eucalyptus-only site, monarchs would not be able to take advantage of the more favorable microclimate offered by conifers. This could cause monarchs to leave eucalyptus-only sites, or could even result in increased mortality from winter storms.

Our data lead us to recommend that land managers with eucalyptus-only overwintering groves on their properties manage for monarch butterflies by creating and maintaining appropriate tree species diversity within the overwintering grove. At overwintering sites located on the central coast of California north of Santa Barbara County, planting native conifers such as *P. radiata* and *H. macrocarpa* would be appropriate where trees have fallen or have been removed, or are likely to be removed. This recommendation would not be appropriate for Southern California since we have not evaluated data from that region and because the native conifers are not suited to that climatic region. Management must be long-term and far-sighted. Newly planted trees will probably not be large enough to provide clustering habitat for at least 10 years. Therefore, it is best to anticipate where future trees will be desirable and manage proactively rather than reactively. If we are to successfully manage overwintering sites, we must do so in a manner that provides the proper climactic parameters that monarchs need, such as filtered sunlight, available water, and wind speeds below 2 m/s. We must determine the most challenging conditions that monarchs experience while overwintering, and what microhabitats and trees they use under those circumstances. Only then can we craft management practices that will conserve and protect the habitat that is so critical to the monarch's continued survival.

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Feeding and spatial ecology of mountain lions in the Mendocino National Forest, California

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Between 2010 and 2012, we studied the feeding and spatial ecology of mountain lions (*Puma concolor*) in the Mendocino National Forest, California, a single-ungulate system in which their main prey were black-tailed deer (*Odocoileus hemionus columbianus*). Mountain lions displayed relatively high ungulate kill rates ($\bar{x}$ = 1.07 ungulates/week, and $\bar{x}$ = 5.78 kg/day), and also displayed individual variation in diet composition. The majority (77.6%) of deer ≥1 year old killed by mountain lions were in fair or better condition despite possible observed selection towards deer in older age classes (≥9 years old). Analyses of hunting behavior indicated that prey types were killed in varying proportions among different time periods, with fawns more frequently killed during diurnal hours. We also found differences in habitat characteristics between kill sites and subsequent feeding sites, with feeding sites lower in elevation, flatter in slope, and with greater canopy density. Individual 95% fixed kernel home ranges varied between 102 and 614 km². Estimated population densities of mountain lions including known kittens were comparatively low (0.68 mountain lions/100 km²).

Mountain lions are the most widely distributed carnivore in the western hemisphere (Sunquist and Sunquist 2002), and across their distribution they exhibit localized approaches in foraging behavior and spatial use (Murphy and Ruth 2010, Hornocker and Negri 2010, Elbroch and Wittmer 2012). For example, high prey biomass and the lack of large mammalian competitors in steppe habitats in Chilean Patagonia result in frequent use of open habitats that are largely avoided in North America (Beier 2012, Elbroch and Wittmer 2012, Wilmers et al. 2013). More broadly, diet composition varies among ecosystems depending upon prey assemblages and prey densities and abundances (Murphy and Ruth 2010). In order to understand mountain lion ecology it is therefore important to understand distinct strategies for and adaptations to unique ecosystems and thus the ecology of local populations.

The feeding ecology of mountain lions has been studied intensively due, in part, to broad interest in their effects on local prey populations including game species. Nevertheless, there remain aspects of its feeding ecology that are under-studied or unknown. For example, ungulates are the main prey of mountain lions in terms of biomass (Hornocker 1970, Knopff 2010, Ruth and Murphy 2010). However, kill rate estimates have shown large variation among studies, and there is debate as to whether these differences are attributable to environmental conditions, including prey species, or methodological differences, either in the field or in statistical analyses (Knopff et al. 2010, Ruth and Murphy 2010, Elbroch et al. 2014). Also, studies using scat analyses indicate that smaller vertebrates are a frequent component of their diet, although their importance in terms of biomass remains debated (Murphy and Ruth 2010, Bacon et al. 2011). Previous research has also shown that individual mountain lions specialize in their selection of prey (Ross et al. 1997, Elbroch and Wittmer 2013a), which in turn may have significant implications for modeling predator-prey dynamics, particularly when evaluating the effects of predation on rare prey (Wittmer et al. 2014).

Understanding space use of mountain lions is also important to determine the effect of mountain lions on prey species. In particular, home range size and overlap among resident mountain lions determine population density, and therefore affect mountain lion predation on local prey populations. Home range size and use, however, vary among ecosystems based on prey availability and distributions (Grigione et al. 2002, Elbroch and Wittmer 2012), as well as the energetic demands of individual mountain lions (e.g., sex class, pregnancy, and age; Logan and Sweanor 2001, Grigione et al. 2002). In general, mountain lion home ranges are smaller and mountain lion population densities are higher in areas of high quality habitats (i.e., with high prey density; Logan and Sweanor 2001, Grigione et al. 2002, Shaw 2010).

In 2010, we initiated a study in the Mendocino National Forest, California, in order to further our understanding of the feeding and spatial ecology of mountain lions in the area. The Mendocino National Forest is an important public hunting area for black-tailed deer in California, and our goal was to evaluate the impact of mountain lion predation on black-tailed deer (*Odocoileus hemionus columbianus*). Particular objectives were to: (1) determine mountain lion diet composition and kill rates; (2) evaluate age-distribution and

condition of ungulate prey; (3) further understand the cryptic hunting behaviors of mountain lions; and (4) quantify home range sizes and the density of the mountain lion population.

MATERIALS AND METHODS

Study area.—We conducted our study in and adjacent to the Mendocino National Forest, California, from June 2010 to November 2012. The Mendocino National Forest is considered one of the premier public hunting areas for black-tailed deer in California. An established network of dirt roads provides ready access and the area is close to major urban areas including the cities of Sacramento, San Francisco, and San Jose. Our mountain lion study was part of a much larger study aimed at quantifying the population dynamics of black-tailed deer in the area (Marescot et al. in press).

The study area encompassed approximately 1,000 km^2 and included portions of Mendocino, Tehama, Glenn, and Lake Counties (39° 42' N, 122° 55' W; Figure 1). Elevations in the study area ranged from 396 to 2,466 m, with moderately rolling terrain at lower elevations and moderately steep, mountainous terrain at higher elevations. Climate varied seasonally, with mean daily temperatures ranging from -1°C to 24°C and extreme temperatures ranging from -2°C to 45.5°C (NOAA-Mendocino Pass, CA Weather Station; http://www.ncdc.noaa.gov/cdo-web/). Mean annual precipitation averaged 132 cm; the majority of precipitation occurred from December through March with only trace precipitation from May through September (NOAA-Ukiah Municipal Airport, CA Weather Station; http://www.ncdc.noaa.gov/cdo-web/). Below 1,000 m precipitation was predominantly in the form of rain, while at higher elevations, snow was common.
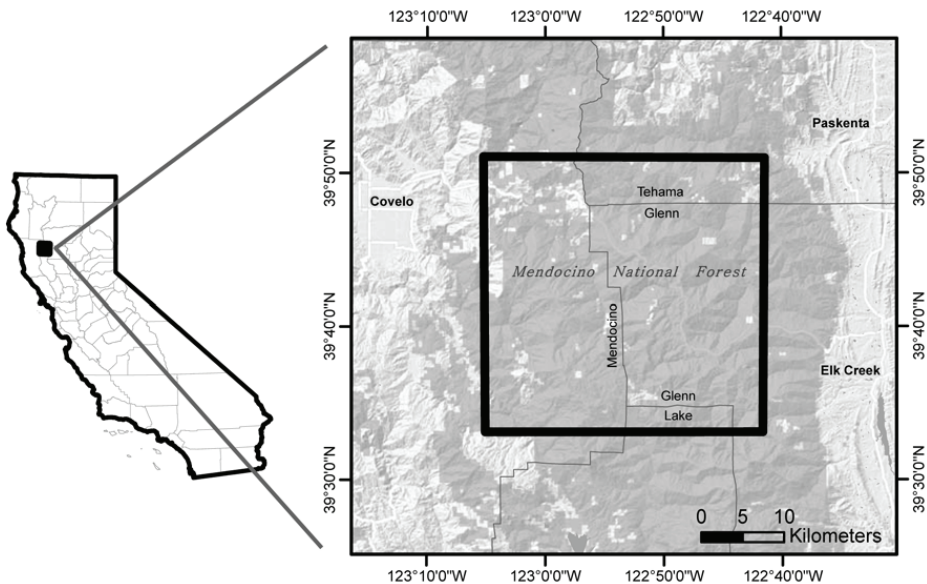

FIGURE 1.—Location of the study area, which included Mendocino National Forest and adjacent private lands, from 2010–2012. The study area is outlined by the thick black line, within the greater context of the North Coast Range and California.

Major habitat types based on the California Wildlife Habitat Relationships categories (Mayer and Laundenslayer 1988) changed with elevation, and included (in order of increasing elevation): blue oak (*Quercus douglasii*) woodland, annual grassland, montane hardwood conifer, Douglas fir (*Pseudotsuga menziesii*), mixed chaparral, montane hardwood, ponderosa pine (*Pinus ponderosa*), Klamath mixed conifer, montane riparian, and montane chaparral. Black-tailed deer were the most common large ungulate in the area. Other ungulates present include non-native wild pigs (*Sus scrofa*), tule elk (*Cervus elaphus nannodes*), and domestic cattle (*Bos taurus*), all of which occurred at very low densities. Competitors and scavengers noted at mountain lion kills included black bears (*Ursus americanus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), turkey vultures (*Cathartes aura*), and common ravens (*Corvus corvax*) (Allen et al. 2014a).

Animal captures.—Between June 2010 and November 2012, we captured mountain lions using trained hounds and box traps. Upon capture, mountain lions were anesthetized with Telazol® (tiletamine HCl and zolazepam HCl; Fort Dodge Animal Health, Fort Dodge, IA). Ketamine HCL (Ketaset®, Fort Dodge Animal Health, Fort Dodge, IA) was administered as needed to maintain anesthesia during processing. Once anesthetized, we determined the sex and then weighed, measured, and fitted each with an ear tag and a combined ARGOS satellite GPS/radio telemetry collar (Lotek 7000SAW, New Market, Ontario, Canada). We used measurements of gum-line recession to determine the age of captured mountain lions (Laundre et al. 2000), and classified them as subadults (<3 years) or adults (≥3 years). All capture methods were approved by an independent Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341 and 16886), and by the Wildlife Investigations Laboratory of the California Department of Fish and Wildlife.

Collar programming and field methods.—We programmed collars to acquire GPS locations at 2-hr intervals, and downloaded location data via satellite every 3 days. We then displayed location data in ArcGIS 3.2 (ESRI, Redlands, CA) to visually identify clusters of GPS points and thus potential kill sites. In this study we defined GPS clusters as ≥5 locations (or a minimum of 8 hours between first and last locations) within 150 m of each other that contained at least one crepuscular or nocturnal location (Elbroch and Wittmer 2013a), and we attempted to visit every GPS cluster for each individual puma. We performed field investigations after downloads of Argos-relayed GPS locations and used handheld GPS units (Garnim 60csx) to locate possible prey remains.

We used the state of decay and locations of bite marks on prey carcasses to assess whether the prey had been killed or whether the mountain lion had been scavenging. We classified prey species through skeletal features and external characteristics (hair and pelage, or feathers). At each feeding site (and a subset of kill sites—see below) we recorded the elevation, overhead tree species, and determined the primary microhabitat type within a circle with diameter 20 m^2 and the carcass at its center, based on descriptions of Mayer and Laundenslayer (1988). We then used a concave spherical densiometer to measure the canopy cover and a clinometer to measure the slope of the feeding site.

We estimated the age of black-tailed deer killed by mountain lions to the closest month for individuals <1 year old based upon field observations and the assumption that fawns were born on June 16th of each year. We estimated the age of black-tailed deer for individuals 1–2.5 years old using tooth irruption patterns (Heffelfinger 2010), and for individuals >2.5 years old by cementum annuli analysis (Low and Cowan 1963; Matson's

Laboratory, Milltown, MT). We determined condition for adult black-tailed deer from the color and consistency of the bone marrow (Hornocker 1970), differentiating 4 categories: poor (red or red and pink marrow), fair (pink marrow), good (pink and white marrow), and excellent (white marrow). We estimated prey weights based on published literature: for deer, we used monthly sex-specific weights for fawns, and annual sex-specific weights for adults based on data from Sitka black-tailed deer (*O. h. sitkensis*; Parker et al. 1993); for other mammal species we used the mean weights described in Jameson and Peeters (2004), and for bird species we used the mean weights described in Sibley (2005).

Statistical analyses.—We used program *R* version 3.0.0 (R Core Team 2013) for our statistical analyses, except where noted. Following *R* guidelines (R Core Team 2013), we cite associated packages used in the analyses. In each statistical test, we considered $P \leq 0.05$ to be statistically significant.

We determined the frequency of occurrence for each species in the diet of mountain lions through prey remains found at GPS clusters. We determined kill rates for each individual mountain lion for the entire time each had a functional GPS collar, with the duration of monitoring periods shown in Table 1. We calculated kill rates in terms of both number of individuals killed (animals/week) and biomass (kg/day) for each collared mountain lion. We calculated both types of kill rate for all prey items, and then separately for ungulates, with the number of ungulates killed per week allowing for comparison to previous studies of mountain lion kill rates (summarized in Table 1 of Knopff et al. 2010).

TABLE 1.—The kill rates and percent of diet made up of non-ungulates for mountain lions monitored during the study in the Mendocino National Forest, California, 2010–2012. The duration of the monitoring period for each mountain lion is shown in days. The percent of diet made up of non-ungulates was calculated by occurrence of individual animals over the course of the entire monitoring period. Kill rates were calculated for all prey species and just ungulates for GPS clusters of ≥8 hours, with kill rates of mass calculated as kg/day and kill rates of number of individuals calculated as animals/week.

| | | | Kill Rates | | | |
| | | | All Prey | | Ungulates | |
ID	Monitoring Period (days)	Percent of Non-ungulates in Diet	Mass (kg/day)	Individuals (animals/week)	Mass (kg/day)	Individuals (animals/week)
F1	477	21.1%	4.78	1.12	4.68	0.88
F17	328	8.9%	5.82	1.20	5.81	1.09
F19	202	20.0%	4.37	0.87	4.34	0.69
F23	186	44.7%	5.27	1.81	4.77	0.98
F43	209	8.1%	10.27	2.08	10.26	1.91
M33	386	5.7%	6.84	1.29	6.71	1.20
M36	83	43.8%	4.37	1.35	3.92	0.76

We hypothesized that individual mountain lions would vary in the proportion of non-ungulate prey in their diet. For each individual mountain lion we categorized each animal killed as ungulate or non-ungulate, and then used a chi-square test with a 7x2 contingency table (Sokal and Rohlf 1987) to test for differences in the proportion of the two prey types among individual mountain lions. For our analyses of age and condition of deer killed by

mountain lions we only used kills where we found teeth (irruption $n = 34$, cementum annuli $n = 38$) and long-bones ($n = 89$) needed to determine these variables. We hypothesized that male and female black-tailed deer would be killed at different ages because in hunted populations with male-only harvest restrictions, there may be fewer male deer available in the old age class than sub-adult or prime age classes. Because of a low sample size in some classes, we used a Fisher's exact test (Sokal and Rohlf 1987) to test our hypothesis, with categories of sub-adults (1–2.5 years old), prime age (3–8 years old), and old ($\geq$9 years old) for deer of each sex.

We defined the time of kill for each prey carcass using the hour of the first waypoint at each mountain lion GPS cluster, 12 values available (0000, 0200, 0400, 0600, 0800, 1000, 1200, 1400, 1600, 1800, 2000, 2200). We then grouped times into 3 categories: nocturnal, diurnal, and crepuscular (times within 1 hour of sunrise and sunset), based on daily local sunrise and sunset times. We hypothesized that because mountain lions display specialization in their prey killed (Ross et al. 1997, Elbroch and Wittmer 2013a) and the timing of their feeding bouts (Pierce et al. 1998), that individual mountain lions might also vary in the times they hunt and kill prey. For each individual mountain lion we categorized each kill by time period, and used a Fisher's exact test to test for variation among individual mountain lions. We next split prey into 3 types: adult deer ($\geq$1 year), fawns (<1 year old), and non-ungulate prey. Because mountain lions are primarily nocturnal hunters (Currier 1983, Pierce et al. 1998, Sweanor et al. 2008), we expected that each prey type would be killed in higher proportions during the night, and hypothesized that prey types would not vary in their proportions among time periods. We categorized each kill by prey type and the categories of times of kill and used a chi-square test with a 2x3 contingency table (Sokal and Rohlf 1987) to test our hypothesis. We used a post-hoc Bonferroni test to determine where significant differences occurred.

On 13 occasions we determined the location where mountain lions killed black-tailed deer and compared their characteristics to matched, subsequent feeding sites. To find the kill site we followed the trails of mountain lions, backwards from the feeding site, to the point where the deer's tracks ended and the deer first hit the ground. At kill sites we recorded elevation, primary habitat type, overhead tree, canopy cover, and slope, following the same procedures as at feeding sites. We hypothesized feeding sites would be different from kill sites because mountain lions would choose concealment to feed (Murphy and Ruth 2010). We hypothesized that mountain lions would drag deer downhill (lower elevation) due to the mass of the deer and to flatter areas (less slope) for ease of feeding, while also choosing areas of high canopy cover to limit detection by avian scavengers (Elbroch and Wittmer 2013b). We first tested each variable (elevation, slope, and canopy cover) for normality with a Shapiro-Wilk normality test, and then tested for variance equality with a Levene's test (Sokal and Rohlf 1987). We then used a two-tailed Student's *t*-test with equal variances (Sokal and Rohlf 1987) to test for differences between kill and feeding sites for each variable.

We estimated home ranges of mountains lions for the total time they wore GPS collars in our study area using the fixed bivariate kernel method (Worton 1989). We first translated location data into R spatial data using the sp package (Pebesma and Bivand 2005, Bivand et al. 2008) and then used the adehabitatHR package (Calenge 2006) to estimate 95% kernel home ranges for each lion. We determined the kernel smoothing factor (h) using least squares cross validation (Seaman and Powell 1996).

We calculated a minimum population density following methods outlined in Elbroch and Wittmer (2012) and Rinehart et al. (2014). We employed a density estimate for August–October 2011 using overlapping home ranges for that 3-month period. We based our minimum population estimate on our 402 km² 'trapping area' (Rinehart et al. 2014), an area in which we believe we had captured every resident mountain lion (based on the methods used in Smallwood and Fitzhugh [1993] we did not find any mountain lion tracks in the area that could not be accounted for by mountain lions wearing GPS collars). Using ArcGIS 9.3 we created 95% kernel home ranges for the 3-month period for each mountain lion by sex and age; we then summed the proportion of their overlapping home ranges within the trapping area (using Hawth's tools and ArcGIS 9.3) to determine the density of adult resident mountain lions for each sex, and then overall for mountain lions (including juveniles and kittens) in the study area. To avoid bias associated with scaling a density to a different spatial extent than that of the study area, we then reported densities per 402 km² (Rinehart et al. 2014). With the understanding that we would negatively bias results by scaling down the population density, we also present densities per 100 km² for comparison with other studies.

RESULTS

Kill rate and diet composition.—We captured 7 mountain lions (5 females, 2 males) and monitored each mountain lion for $\bar{x} = 9.07 \pm 4.79$ *SD* months (Table 1). We conducted field investigations of 598 out of 609 identified GPS clusters, and we investigated the ARGOS-relayed GPS clusters within $\bar{x} = 6.78 \pm 8.18$ *SD* (range 0–60) days after the mountain lion left the kill.
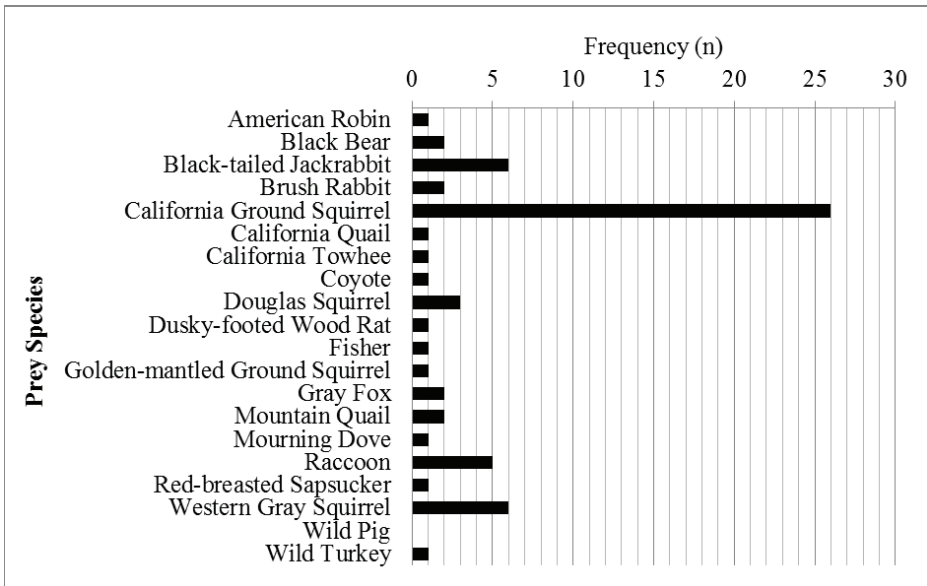

FIGURE 2.—The frequency of occurrence for each non-ungulate prey species we documented mountain lions eating during the study in the Mendocino National Forest, California, 2010–2012.

We identified 352 mountain lion kills, including 288 black-tailed deer, 2 black bears, and 62 small-to-medium sized vertebrates (Figure 2), as well as 4 acts of mountain lion scavenging. Kill rates for all prey species were $\bar{x} = 1.39$ (*95% CI* = 1.07-1.70) animals/ week, and $\bar{x} = 5.96$ (*95% CI* = 4.40-7.51) kg/day (Table 1). Kill rates for ungulates were $\bar{x} = 1.07$ (*95% CI* = 0.77-1.38) ungulates/week, and $\bar{x} = 5.78$ (*95% CI* = 4.16-7.40) kg/day (Table 1). Black-tailed deer contributed 98.6% of prey biomass and 74.4% of deer killed by mountain lions were ≥ 1 year old.

Hunting and feeding behavior.—Our chi-square analysis revealed a significant difference among individual mountain lions in the proportion of non-ungulate prey in their diet ($X^2_6 = 45.03$, $P < 0.0001$) (Table 1). Our analysis revealed a sex-specific difference in the proportion of deer killed in different age classes ($P_2 = 0.0378$) (Figure 3), with more females in the old age class than prime age class. The condition of black-tailed deer ≥ 1 year old killed varied, with 12.4% of individuals in excellent condition, 32.6% in good condition, 32.6% in fair condition, and 22.4% in poor condition.
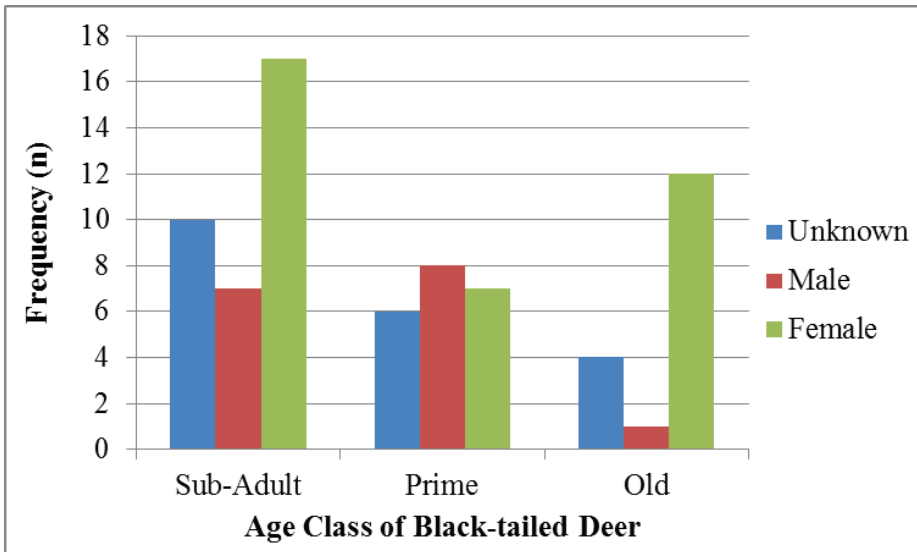

Figure 3.—The frequency of black-tailed deer killed by mountain lions among age and sex classes. Male, female, and unknown deer are shown by class, with sub-adult representing deer 1–2.5 years old, prime representing deer 3–8 years old, and old representing deer 9–22 years old. Sub-adult deer were aged using teeth irruption, while prime and old deer were aged using cementum annuli analysis. Mendocino National Forest, California, 2010–2012.

Our chi-square analyses did not reveal a significant difference among individual mountain lions in the time periods kills were made ($X^2_{12} = 11.43$, $P = 0.4927$), but did reveal significant differences in the time of kills for different prey types ($X^2_4 = 12.82$, $P = 0.0122$, Figure 4). Our post-hoc analyses revealed fawns were more likely to be killed in diurnal periods ($X^2_2 = 10.18$, $P = 0.0061$), while non-ungulate prey were more frequently killed during nocturnal periods but were marginally insignificant ($P = 0.0705$).
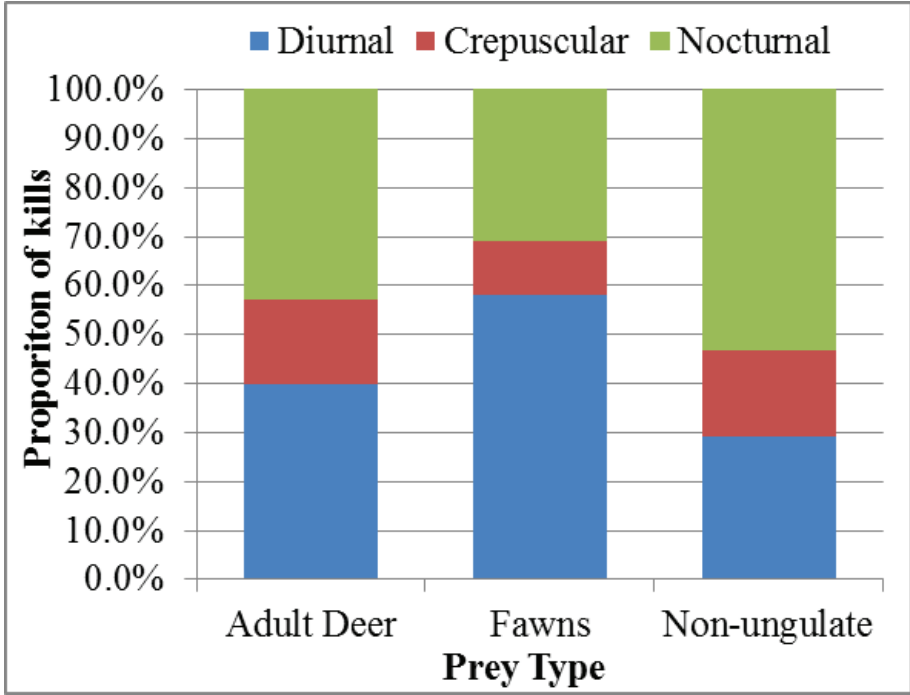
Figure 4.—The proportion of kills made by mountain lions for each prey type by time period. The time periods were grouped into 3 categories: nocturnal, diurnal, and crepuscular (within 1 hour of sunrise or sunset). Mendocino National Forest, California, 2010–2012.

Based on our 13 detailed site investigations, black-tailed deer were dragged $\bar{x} =$ 21.7m $\pm$ 4.28 *SE* from the kill site to the feeding site. Approximately 40% of the feeding sites had different primary habitats and overhead tree species than the kill sites. The elevation at feeding sites was significantly lower than at kill sites ($P_{12} = 0.0325$), with feeding sites $\bar{x} =$ 5.77m $\pm$ 2.39 *SE* lower in elevation than kill sites. The slope at feeding sites was significantly flatter than at kill sites ($P_{12} = 0.0174$), with feeding sites $\bar{x} = 13.54° \pm 5.02$ *SE* flatter in slope than kill sites. The canopy cover at feeding sites was significantly more dense than at kill sites ($P_{12} = 0.0101$), with the canopy cover of feeding sites $\bar{x} = 29.4\% \pm 10.2$ *SE* more dense than kill sites.

Home range sizes and population density.— Ninety-five percent kernel home ranges were $\bar{x} = 266 \pm 116$ km^2 for 4 adult females, 102 km^2 for 1 subadult female, 348 km^2 for 1 adult male, and 142 km^2 for 1 subadult male (Table 2). We calculated a snapshot, minimum population density of 1.74/402 km^2 (0.43/100 km^2) for adult female mountain lions and 0.49/402 km^2 (0.12/100 km^2) for adult males. Total mountain lion density in the study area including known kittens was 2.75/402 km^2 (0.68/100 km^2).

Table 2.—The characteristics and home range sizes of mountain lions in the Mendocino National Forest, California, 2010–2012. The age, age class and weight at original capture are shown, along with the number of GPS points used in the home range analyses. Home ranges (km^2) were calculated using 95% kernels for the entire time the mountain lion was collared.

ID	Age (years)	Class[a]	Weight (kg)	Number of GPS Points	95% Kernel home range km^2
F1	6.5	AF	34.6	5342	614.1
F17	1.4	SF	31.5	3695	102.4
F19	4.1	AF	33.6	1565	148.1
F23	4.2	AF	49.5	2125	158.6
F43	3.1	FG	38.1	2035	143.5
M33	7.0	AM	59.1	4255	347.8
M36	2.5	SM	48.1	971	141.8

[a]AF = Adult Female; AM = Adult Male; SF = SubadultFemale;
SM= Subadult Male; FG = Family Group

Discussion

We found relatively high ungulate kill rates, with mean kill rates of 1.07 (95% CI = 0.77–1.38) ungulates/week among the highest kill rates reported for mountain lions to date (see summary in Table 1 of Knopff et al. 2010). These results, however, may be a consequence of intensive field methods rather than an indication of true differences in the feeding ecology of mountain lions in our study area, or an effect of the smaller ungulate size in our study area (Laundre 2008, Elbroch et al. 2014). Alternatively, the high kill rates may be due to interactions with competitors, particularly black bears. Black bears are a dominant scavenger (Allen et al. 2014a), and researchers have recently hypothesized that black bear kleptoparasitism may result in increased kill rates of mountain lions (Murphy et al. 1998, Allen et al. 2014b, Elbroch et al. 2014). Allen et al. (2014b) reported that kill rates in summer and fall when black bears were active in our study area were substantially higher than kill rates in winter and spring when black bears were predominately hibernating. Elbroch et al. (2014) reported that kill rates in three study areas with different scavenger communities were all higher than predicted by energetic needs of mountain lions.

We found high non-ungulate prey diversity when compared to previous studies that used GPS cluster methods to find mountain lion kills. Individual mountain lions also varied in the amount that non-ungulate prey species contributed to their diet, lending further support to previous research showing that individual mountain lions exhibit variation in prey selection (e.g., Ross et al. 1997, Elbroch and Wittmer 2013a). GPS cluster investigations may estimate different diet composition as compared to diets determined with scat analyses (Murphy and Ruth 2010, Bacon et al. 2011), due to the difficulty of finding small prey items. However, although our study likely underestimated small prey items, it further emphasized

that studies utilizing intensive GPS investigation are capable of describing small prey in diet composition (Pitman et al. 2014). We did not record any predation on tule elk or wild pigs, and this may be due to their low density in the study area or the fact that they are recent (elk) or novel (pigs) additions to the local prey community (*sensu* Novaro et al. 2000). Wild pigs are a pest species in California, and our results suggest that managers may not be able to depend on mountain lions to slow further range extensions.

Despite the diversity of non-ungulate prey species we observed, black-tailed deer were the most important prey of mountain lions (98.6% of biomass), the majority of which (77.6%) were judged to have been in fair or better condition. The lack of deer in poor body condition killed by mountain lions in our study is similar to previous results (i.e., 80% of deer killed by mountain lions in good body condition; Pierce et al. 2000), and might be indicative of good health of the local deer population. The age structure of adult female deer killed by mountain lions, however, was skewed towards older individuals. As can be expected in a black-tailed deer population in which only males are heavily-hunted, only two male deer were killed past prime age and more females killed were in the old age class than in the prime age class. This included an individual aged 22 years old (based on cement-annuli results; Matson's Laboratory LLC, Missoula, MT), and our results may suggest increased success of killing individuals past their prime age, or a much older deer population than is common in California.

Our analyses of hunting behaviors suggest that we may need to rethink some assumptions used in previous studies. Mountain lions are predominantly active during nocturnal and crepuscular hours (Currier 1983, Pierce et al. 1998, Sweanor et al. 2008), and it has thus been generally assumed that most of their kills occur during these periods. However, our results showed variation in time of kill by prey type, but also lower proportions of prey killed during nocturnal periods than expected. For example, adult black-tailed deer were killed in similar proportions during nocturnal and diurnal time periods, while deer <1 year old were killed significantly more frequently during diurnal time periods. This suggests that mountain lions are hunting during diurnal hours as opportunities arise, especially during summer when young ungulates are available. This result is in contrast to previously published studies (Currier 1983, Pierce et al. 1998, Sweanor et al. 2008) and may have led researchers to underestimate kill rates. Additionally, many studies attempting to link predation and predation risk to habitat have used the location of prey remains (e.g. Atwood et al. 2007, Elbroch and Wittmer 2012, Apps et al. 2013). However, our results showed that the location of prey remains were different than the location of the actual kill in many respects, including primary habitat type. Kill sequences often occur over large areas, and if we inferred predation risk from habitat where prey remains were found, we would be evaluating preferences for feeding sites of mountain lions rather than habitats where deer are at risk of being killed. Future studies should take this assumption into account and attempt to define the scale of risk and locate kill sites when describing habitat-specific risks for prey.

The population density in our study area was lower than in many other studies, while observed home ranges were in the published range for mountain lions (Logan and Sweanor 2010). The reasons for the observed low population densities, however, are unclear. Hunting of mountain lions in California has been prohibited since 1972 (Torres et al. 1996) and mountain lion populations from coastal California have historically had high population densities (Roberson and Lindzey 1984). For example, Hopkins et al. (1986) reported densities of 3.6/100 km^2 in a coastal area in central California, almost 6 times higher than the densities we observed. Instead our population density was more comparable to the

lowest recorded mountain lion population densities of 0.37/100 km^2 reported by Lindzey et al. (1994) in Utah. Given the high abundance of black-tailed deer in the study area (20 deer/km^2; D. Casady, unpublished data) it is doubtful that the low mountain lion density was caused by low prey density. We speculate that low mountain lion densities were more likely a consequence of other factors such as illegal hunting or interference competition with dominant scavengers such as black bears. For example, previous studies have shown that poaching can greatly reduce mountain lion population densities (0.3-0.74/100 km^2 in areas with poaching compared to 1.55-2.89/100 km^2 in areas without poaching) (Paviolo et al. 2009). Alternatively, the usurpation of kills by bears has been reported to force solitary felids to kill deer more frequently (Krofel and Kos 2010, Krofel et al. 2012), and this may also be true of mountain lions, with lower available energy potentially resulting in low recruitment rates. Unknown factors or interplay between poaching and usurpation of kills by black bears could also account for low mountain lion densities in the study area. High ungulate kill rates together with seemingly low densities of mountain lions in our study area could have important implications for the future dynamics of black-tailed deer in the Mendocino National Forest.

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Documentation of mountain lions in Marin County, California, 2010–2013

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Prior to 2010, mountain lions (*Puma concolor*) have rarely been documented in Marin County, California. Although there are reports of sightings of mountain lions or observations of mountain lion sign, most have not been verified by photographs or physical samples. A search of museums throughout the United States (Long and Sweitzer 2001) revealed that the only specimen from Marin County appears to be a mountain lion collected in 1931 (MVZ:Mamm:47199). Gross and Fitzhugh (1985) compiled a list of 148 reports of mountain lion observations in Marin County from 1961 to 1984 based on agency records or personal communications with local residents. The majority of those accounts were visual recollections that could not be verified, and no physical or photographic documentation accompanied any of the reports. Since 1972, four depredation permits have been issued for mountain lions in Marin County, with no confirmed kills under those permits (CDFW 2014).

Of several wildlife surveys conducted in Marin County from 1990 to 2003 (Riley 1999, Fellers and Pratt 2002, Howell and Semenoff-Irving 2005, E. E. Boydston, unpublished data), verifiable mountain lion detections were obtained only in Point Reyes National Seashore in far western Marin County. These detections were 11 images collected by motion-activated cameras during 1998–2001 (Fellers and Pratt 2002) and a video clip of a mountain lion in 2003 (Fellers 2003). Additional images of mountain lions in Point Reyes National Seashore were obtained from a single motion-triggered camera that was not part of a larger survey during 2009–2010 (G. M. Fellers, USGS, unpublished data).

Beginning in 2010, we conducted a pilot study of mountain lions in Marin County using motion-triggered cameras. Our objectives were to obtain additional documentations, confirm the presence of mountain lions outside of Point Reyes National Seashore, and

determine if mountain lions had a regular presence in the county. We deployed a total of 14 digital cameras: three Cuddeback Capture (Cuddback Digital, De Pere, WI) incandescent flash cameras taking still pictures and 11 Bushnell Trophy Cam IR (Alliant Techsystems Inc., Anoka, MN) cameras set in video mode. We set unbaited cameras within four focal areas on private and public lands, with successive starting dates for the four areas as access permission was obtained from land owners or management agencies for monitoring: (1) Nicasio—01 October 2010; (2) Olema—21 January 2011; (3) the Alpine Lake region of Mount Tamalpais—26 September 2011; and (4) Bolinas—12 September 2012 (Figure 1; geographic center: 38° 00' N, 122° 41' W).
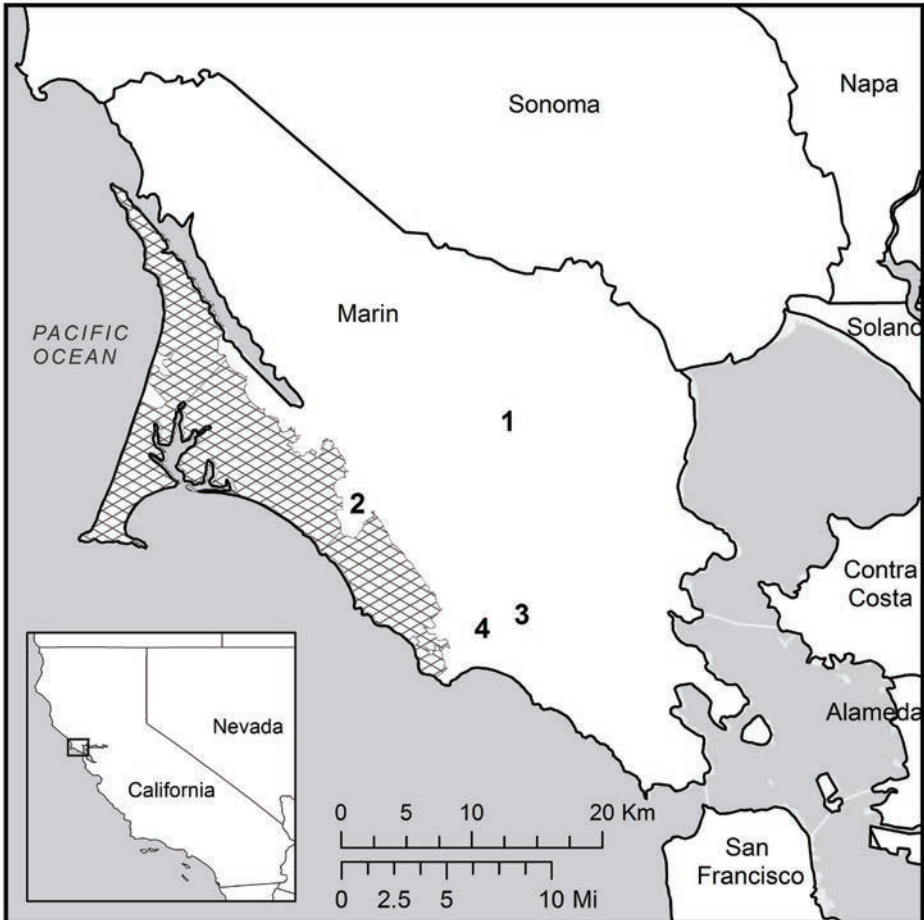

Figure 1.—From October 2010 to April 2013, motion-triggered cameras were placed at four locations in Marin County, California, which has an area of approximately 1,368 km^2 (528 mi^2). Numbers indicate the focal areas described in this paper: (1) Nicasio; (2) Olema; (3) Alpine Lake; (4) Bolinas. Other labels are nearby counties, and the cross-hatched area delineates Point Reyes National Seashore.

Within each focal area, one to four cameras were placed along unpaved fire roads or private access roads that were infrequently used by people. Cameras were placed at locations where a road narrowed due to topographical features such as a steep embankment or drop-off on one or both sides, or at an intersection with other unpaved roads or wildlife trails, with distances from 0.3 to 2 km between cameras. After a mountain lion was first detected on a trail camera in the Nicasio focal area, we set up paired cameras 3 m apart on the same side of the road or at 90° angles to obtain simultaneous or nearly simultaneous images showing different views of an animal walking by them.

We considered the focal area as the sampling unit, and grouped pictures and videos from the same focal area, at the same time of day, into detection events. We measured monitoring time as the number of calendar days per focal area, rather than estimate effort based on total numbers of cameras. To determine if one or more mountain lions were detected, we examined physical characteristics of the lion in each image (Kelly et al. 2008), and compared different views from the same detection event to build a photo-ID record. For this process, we first used images taken by paired cameras within a focal area. We then compared images across all detection events. This note reports on results of continuous camera monitoring within the four focal areas through April 2013.

In total, we obtained 122 digital images (still pictures and video clips) with mountain lions in them; no single picture or video clip showed more than one mountain lion at a time. There were 55 different detection events, with from one to six images per event, and at least 14 hours separating events. Multiple images of the same detection event always occurred within 20 minutes of each other and most were within 5 minutes. The first detection of a mountain lion in Nicasio was on 15 November 2010, 45 calendar days after placement of the first camera and prior to setting cameras in other focal areas. During 942 calendar days of monitoring in Nicasio, we obtained 24 mountain lion detection events with a median of 21 days between detections. The first mountain lion detection in Olema was on 04 March 2011 after 42 calendar days of monitoring in that area. In 830 calendar days of monitoring in Olema, there were a total of 16 detection events with a median of 30 days between events. A mountain lion was first detected in the Alpine Lake region on 21 December 2011, 86 days since initiating monitoring. After 582 days in Alpine Lake, we obtained 14 mountain lion detection events separated by a median of 22 days. In 230 days of monitoring in Bolinas, we had 1 detection event on 06 October 2012, 24 days after initiating monitoring.

The most conspicuous physical characteristic in the mountain lion images was an ocular defect that manifested as corneal cloudiness and a lack of tapetal reflection or "eyeshine" in the right eye (Figure 2A, Figure 3). This ocular defect may have been scarring of the cornea due to trauma or disease (K. Freeman, Ophthalmology for Animals, personal communication; B. D. Jansen, Arizona Game and Fish Department, personal communication; K. Krause, Serrano Animal and Bird Hospital, personal communication; S. Weldy, Serrano Animal and Bird Hospital, personal communication), and was visible in 61 images and 40 detection events. Additional physical characteristics consistently observed in detection events showing this right-eye defect included the pattern of ear notches, white flecks on the back, white patch on back of the ear, a swelling at the base of the tail in the perianal region bilateral, and sagging abdomen. Based on matching two or more of these physical characteristics, we were able to identify this same individual in a total of 46 detection events and 112 images. We refer to this animal as PC01. Other more general characteristics such as physical build and a smooth tail shape were also consistent across images of PC01. In more than half of these detection events, the penis sheath was visible, confirming PC01
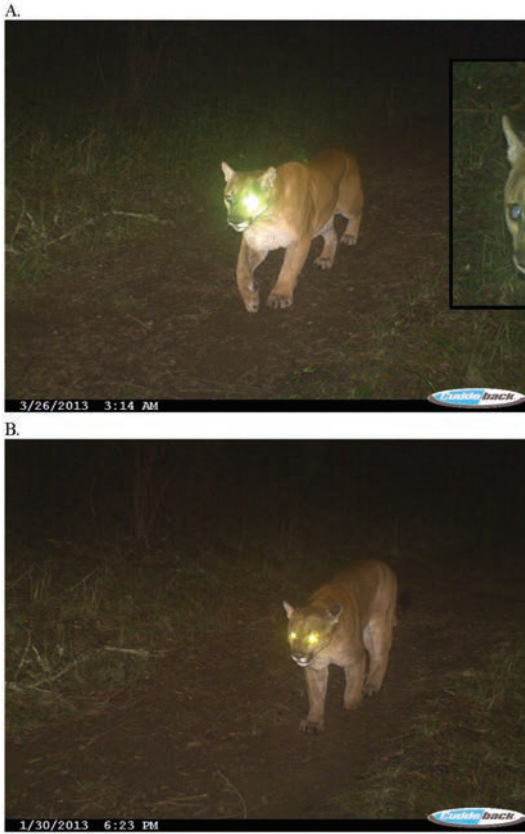
FIGURE 2.—Images from the same camera near Nicasio, Marin County, California showing differing eye shine patterns. (A) A mountain lion with an ocular defect and eyeshine registering in only the left eye was detected multiple times, including 26 March 2013 and 22 May 2011 (inset image). This mountain lion also had notches in its left ear and white shoulder flecks. (B) A mountain lion with eyeshine registering in both eyes was also detected on 30 January 2013.

FIGURE 3.—Photographic images of a mountain lion with asymmetrical eyeshine taken with a Cuddeback Capture camera near Nicasio, Marin County, California. Video clips and pictures are posted at: http://wildfelids.smugmug.com/

was a male (Montana Fish, Wildlife and Parks 2009). The 46 detections in which we could identify PC01 spanned January 2011 through April 2013. During this period, PC01 was detected in three focal areas: Nicasio, Olema, and Alpine Lake.

There were five detection events in which the mountain lion photographed did not have the identifying features of PC01, but exhibited characteristics not seen in images of PC01. Two of these events captured a mountain lion with eyeshine in both eyes. One of these events occurred on 30 January 2013 in Nicasio (Figure 2B), in which an additional image confirmed the animal in this detection event was male. The other detection occurred on 06 October 2012 in Bolinas, and was the only mountain lion detection in that focal area. The remaining detection events occurred on 12 June 2012 (two events 14 hours apart) and 29 June 2012 in the Alpine Lake area. The eyeshine pattern could not be determined in images from these three events, but all images showed an animal that appeared much leaner than PC01. Furthermore, a distinct kink in the tail at the midpoint along the length of the tail was visible in two of the events, and one of the images confirmed that the animal was a male. While there was not enough evidence to confirm these five detection events represented one or more individuals, we conclude they represented at least one mountain lion in addition to PC01.

The suitability of habitat for mountain lions in Marin County (Torres et al. 1996), the wide-ranging habits of this species (Beier et al. 2010, Dickson and Beier 2002, Pierce and Bleich 2003), and the wide distribution of mountain lions in California, including documentations in nearby counties (Ernest et al. 2003, CDFW 2014), suggested that mountain lions would occur in Marin County. Our detections of mountain lions on cameras outside of Point Reyes National Seashore add multiple verifiable confirmations to the records of their presence in this county. Further, we repeatedly documented one male mountain lion over a period of 27 months, who was consistently and uniquely identified by an ocular defect in his right eye and other physical characteristics. We also confirmed the presence of at least one other male mountain lion during the study period.

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Implications of predation by wild pigs on native vertebrates: a case study

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Following escape from a purposeful introduction on Hooper Bald in the Appalachian Mountains of North Carolina in 1912, European wild boars (*Sus scrofa*) have spread across the United States via invasions and translocations; they now occur in an estimated 44 of 50 states (for a complete review, see McCann et al. 2014). An early translocation from the North Carolina population brought wild pigs to California in 1925, where they were introduced into Monterey County by private landowners for sport hunting (Hoene 1994). From the Monterey County introduction and subsequent translocations, wild pigs spread throughout California, hybridizing with domestic pigs brought by 18th-century Spanish explorers and 19th-century immigrants to America. Vigorous hybrids now occur in 56 of 58 counties within California (Waithman et al. 1999, McCann 2012, McCann et al. 2014, CDFW 2015). Hereafter, I refer to these hybrids as wild pigs.

Wild pigs are omnivores but prefer vegetative matter, foraging heavily on the seasonal acorn mast crop in California rangelands and hardwood forests (Barrett 1982, Loggins et al. 2001, Sweitzer and Van Vuren 2002). Nonetheless, numerous wild pig diet investigations have listed vertebrate remains among stomach contents (reviewed by Ballari and Barrios-Garcia 2013). Wild pigs are known to scavenge dead vertebrates, and scavenging could explain the presence of vertebrate remains in some diet analyses, but Loggins et al. (2002) and Jolley et al. (2010) observed wild pigs actively hunting vertebrate prey. Furthermore, other investigators recently reported wild pigs as opportunistic predators of vertebrates. In California, Wilcox and Van Vuren (2009) found that 40.4% of collected pig stomachs contained vertebrate remains, including 167 individuals representing 20 species, of which 99% were mammals. In stomachs containing vertebrate prey, 61% held more than one vertebrate; one stomach contained 18 individuals of six different species (Wilcox and Van Vuren 2009). In the southeastern United States, Jolley et al. (2010) reported 64 individual reptiles and amphibians in 68 wild pig stomachs, with as many as five different species in a single stomach; one pig stomach contained 49 individual spadefoot toads (*Scaphiopus holbrookii*).

In a review of wild pig diets worldwide, Ballari and Barrios-Garcia (2013) concluded that wild pig populations in their native ranges generally consumed fewer vertebrate prey than those where wild pigs were introduced. Those authors theorized that the increased consumption of vertebrates where pigs are introduced is due to native vertebrates having evolved without pigs as predators. As members of the order Artiodactyla, wild pigs are hooved animals (ungulates), which generally are obligate herbivores. It follows that in landscapes where wild pigs are introduced, native small vertebrates would not have experienced selective pressures to avoid, escape from, or defend against ungulates. Without coevolved responses to ungulate predators, native small vertebrates are particularly vulnerable to the predatory behavior of introduced wild pigs, especially when the pigs forage in large sounders. Here I describe small vertebrates found in the stomach contents of a large wild boar after a single night of foraging within a reserve in the central Coast Range of California. Based on vertebrate prey items found among its stomach contents, and using wild pig population density estimates from studies within the reserve and from similar habitats nearby, I project the potential impacts to small vertebrates within the reserve area.

The 1300-hectare Blue Oak Ranch Reserve (BORR), one of 38 University of California Natural Reserves, is situated within the California Floristic Province between 550 and 915 meters elevation. This is an area of mixed oak woodland and grasslands, approximately 8 km east of the southern portion of San Francisco Bay in Santa Clara County, California. For a more complete site description of BORR, see Wilcox et al. (2004). On 22 September 2010, I killed a large (126 kg field-dressed) male wild pig on the reserve after it became a destructive nuisance. Immediately after dispatching the pig with a rifle, I removed the stomach and hand-sorted the contents, separating out vertebrate remains (Wilcox and Van Vuren 2009). In addition to a wide assortment of vegetable matter, including a large volume of the masticated rhizomes of cattail (*Typha latifolia*), the stomach contained 23 individual vertebrates comprising eight species (Table 1), including a gopher snake (*Pituophis catenifer*)

Table 1.—Vertebrate prey from the stomach contents of a single male wild pig (*Sus scrofa*) after one foraging event on the Blue Oak Ranch Reserve in Santa Clara County, California, and estimates of the numbers of each prey species that theoretically could be removed per foraging bout if predation rates were identical for individual wild pigs. N represents the number of individuals of each prey species found in the stomach contents described in this paper. The potential range of N (i.e., the theoretical number of prey of a particular taxon per foraging event) is the product of multiplying each prey species in the stomach by the range (lowest to highest) of pig densities estimated for Blue Oak Ranch Reserve and surrounding lands in Santa Clara County.

Common name	Scientific name	N	Potential range[a] of N
California vole	*Microtus californicus*	15	495–660
California mouse	*Peromyscus californicus*	2	66–176
Deer mouse	*Peromyscus maniculatus*	1	33–44
Western harvest mouse	*Reithrodontomys megalotis*	1	33–44
Bottae's pocket gopher	*Thomomys bottae*	1	33–44
Beechey ground squirrel	*Spermophilus beecheyi*	1	33–44
California quail	*Callipepla californica*	1	33–44
Pacific gopher snake	*Pituophis c. catenifer*	1	33–44

[a]Low density estimate (3.3/km²) from Wilcox et al. (2004); high density estimate (4.0/km²) from Sweitzer et al. (2007). A multiplier of 11 was determined from the approximate 1100 hectares of pig habitat on Blue Oak Ranch Reserve. Santa Clara County, California.

approximately 90 centimeters long. This vertebrate count exceeded the maximum quantity of any individual stomach reported by Wilcox and Van Vuren (2009), but reflected similar species composition: primarily small mammals, the majority of which were California voles (*Microtus californicus*). Because the gastric emptying rate for pigs is four to five hours (Ramonet et al. 2001), the vertebrate content of this boar's stomach likely represented a single night of foraging. The vertebrate prey of the BORR wild pig, combined with previous investigations in which multiple vertebrate species have been discovered among wild pig stomach contents (Scott and Pelton 1975, Skewes 2007, Wilcox and Van Vuren 2009, Jolley et al. 2010), suggest that predation of small vertebrates by wild pigs is not purely opportunistic, but should be considered facultative predation (*sensu* Callahan 1993).

   To understand the potential implications of this predation event, I used the prey species count from the wild pig stomach contents described above to estimate the predation potential if every wild pig on BORR consumed the same number of vertebrates in a single night of foraging (Table 1), based on estimates of wild pig densities from prior investigations conducted on BORR and nearby within Santa Clara County. This boar was killed at a time of year when wild pigs (males and females) are thought to prey on vertebrates more heavily than in other seasons (Wilcox and Van Vuren, 2009); this prey consumption estimate, therefore, may represent an upper limit. In this example, and that of Wilcox and Van Vuren (2009), the largest numbers and diversity of vertebrate prey are attributed to large solo boars; however, female wild pigs showed a high capacity for predation of small vertebrates as well, with voles forming the largest component (Wilcox and Van Vuren 2009). Females, along with juveniles of both genders, normally form the largest sounders and, thus, have the potential to be involved in large-scale predation events. Prey numbers projected in Table 1 are unlikely to be sustainable for long before local prey populations would be exhausted, or the costs of hunting unprofitably would force pigs to relocate to areas with higher prey abundance.

   California voles exhibit periodic population irruptions (Lidicker and Ostfeld 1991), providing a concentrated surplus for predators. Predation on the surplus from these periodic irruptions may explain the large number of individual voles found in some wild pig stomachs (Wilcox and Van Vuren 2009). Similarly, eastern spadefoot toads are explosive breeders (Wells 1977), briefly gathering at suitable breeding sites in large numbers. Breeding-site aggregations may account for the 49 individual eastern spadefoot toads from one stomach (representing one foraging event) reported by Jolley et al. (2010). However, the diversity of prey species in the BORR wild pig, and other pig stomachs, indicates wide-ranging foraging by wild pigs through varied habitats (Wilcox and Van Vuren 2009). This does not indicate that wild pigs key on a single species or event but, instead, merely that they are opportunistic predators. The contents of the BORR pig's stomach represented one foraging event during a season when wild pigs are hypothesized to experience a protein deficiency from an acorn-heavy diet (Barrett 1978, Belden and Frankenberger 1990, Loggins et al. 2002, Wilcox and Van Vuren 2009). Acquiring a high-protein meal coincident with a peak acorn drop makes hunting small vertebrates highly profitable, because protein is required to convert the high-starch acorn diets to stored fat for metabolic reserves (Barrett 1978).

   The ability to switch opportunistically to a local, seasonally abundant, vertebrate prey confers on wild pigs the role of generalist predator (Closs et al. 1999). As an introduced species, occupying a novel and unique role as an ungulate predator, wild pigs may realize an advantage over native carnivores that also prey on small vertebrates (Barrios-Garcia and Ballari 2012). Thus, in large numbers, wild pigs may have significant local impacts on small

vertebrates, resulting in measurable impacts on local food-web dynamics (Thompson et al. 2007), and compete with mesocarnivores dependent upon small vertebrates.

Landscapes are shaped by the evolutionary interplay of predator and prey (Hairston et al. 1960). Predation leaves detectable marks on a landscape by limiting herbivores and releasing some plant species to grow (Eisenburg 2010, Ripple and Beschta 2012). Brown et al. (1999) described fear of predation as an even stronger pressure than predation itself, because it directly affects foraging behavior of herbivores balancing their own metabolic needs with the potential to be eaten. But this "ecology of fear" is based on selective pressures relating to prey recognizing potential predators, and no such relationship has coevolved between introduced wild pigs and native small vertebrates. Some researchers have speculated that the wild pig in California is filling a niche that became available when grizzly bears (*Ursus arctos*) were extirpated from the state (Work 1993, Sweitzer and Van Vuren 2002, Grinde 2006). Native small vertebrates coevolved with grizzly bears and were likely to become prey incidentally or intentionally while grizzly bears grubbed rangelands for food (Mattson 2004a, 2004b). Wild pigs grub for food in a manner similar to grizzly bears, but no coevolution occurred in California between small vertebrates and ungulates such as wild pigs.

To better understand the role of wild pigs as novel predators, I suggest future investigators focus research on (1) dietary impacts on mesocarnivores such as bobcat (*Felis rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and raccoon (*Procyon lotor*); (2) the degree to which wild pigs fill the niche formerly occupied by grizzly bears based on the behavioral differences between the two predators and the evolved responses of small vertebrate prey; and (3) the indirect impacts of introduced wild pigs on small vertebrate populations, particularly those affected by the reduction of voles. Doing so will be challenging if wild pigs are taking on the role of mesocarnivores in terrestrial food webs, and investigations should begin where wild pig densities are highest and landscape changes are easiest to detect (Sweitzer and Van Vuren 2007).

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Chum salmon (*Oncorhynchus keta*) in the San Joaquin River, California: new record

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     Chum salmon (*Oncorhynchus keta*) are the most widely distributed and abundant in terms of total biomass of all Pacific salmon, and may have contributed up to 50 percent of the annual biomass of the seven species of Pacific salmon in the North Pacific Ocean (Salo 1991). In North America, they are found from the Sacramento River in California (Hallock and Fry 1967) northward to the Arctic shore of Alaska (Walters 1955), with a southernmost record in the USA from the San Lorenzo River near Monterey Bay, California (Behnke 2002). Chum salmon are not historically known from the San Joaquin River system (Behnke 2002, Moyle 2002).

     As part of the San Joaquin River Restoration Adult Chinook Salmon Trap and Haul effort, salmon were captured at the terminal end of irrigation canals using large, hand-held dip nets at six locations (Delta Rd., Midway Rd., Hereford Rd., Deepwell Rd., Britto Rd., and Cozzi Ave.) near Los Banos, Merced County, California. These locations were visited on a daily basis, with increased sampling in areas with barriers that blocked or severely restricted further upriver migration. Fish captured were subjected to standard handling and transportation methods (collection of biometric data and tissue samples) following standard procedures (Portz 2013).

     A single female chum salmon (Figure 1) was captured on 11 December 2013 from the Midway Road Irrigation Canal, which is hydrologically connected to the San Joaquin River via Salt Slough (120° 44' 56" E, 37° 03' 30" N). Three Chinook salmon (*Oncorhynchus tshawytscha*) also were captured during this effort (Portz 2013). The fish were transported approximately 55 kilometers in a fish haul tank and released into the San Joaquin River following processing and tissue collection. The chum salmon was verified by Don Portz, Bureau of Reclamation Fisheries and Wildlife Group and Jacque Keele,

FIGURE 1.—Female chum salmon (*Oncorhynchus keta*) captured in the Midway Road Irrigation Canal, Merced County, California, USA, on 11 December 2013. The individual was a wild female (no egg mass palpated), as indicated by the presence of an adipose fin. The fork length was 637 mm and total length was 683 mm.

Bureau of Reclamation Detections Laboratory for Exotic Species, and was identified with 100 percent similarity following Handy et al.(2011); DNA most closely matched entries from British Columbia, Canada, and Oregon, USA, as per Ratnasingham and Hebert's (2007) hierarchical placement program.

We assume that this individual is a "stray." Historical records indicate a very small run was present in the Sacramento River North during the 1950s (Hallock and Fry 1967), but no spawning has been recorded in recent decades (Moyle 2002), indicating that individuals present in the Sacramento River North and its tributaries would also be strays. To our knowledge, this is the first record of *O. keta* in the San Joaquin River and is a new record for Merced County, California (Behnke 2002, Moyle 2002).

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Copies of the following books have been received, and are available for review by interested parties. Individuals interested in preparing a formal review that will be published in *California Fish and Game* should contact the editor (Vern.Bleich@wildlife.ca.gov) with their request to do so.

ANTYPOWICH, L. 2012. A hunting we did go. True mountain adventures. Xlibris LLC, Bloomington, Indiana, USA. 213 pages. $19.95 (soft cover).

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