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Cover Photograph: Banded Rock Rattlesnake (*Crotalus lepidus klauberi*). (Photographed by Ricardo Palacios Aguilar).

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NOTES

ASPIDOSCELIS NEOTESSELATUS (COLORADO CHECKERED WHIPTAIL): DIETARY OBSERVATIONS AND BIOLOGY IN THE NORTHERN PART OF THE RANGE

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***Abstract*.—Triploid parthenogenetic *Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) is endemic to southeastern Colorado and has one of the smallest natural continental distributions of a species in the genus *Aspidoscelis*. Further, it is a species of conservation concern in the state. Recent investigations of *A. neotesselatus* in the 55,000-ha Fort Carson military installation (mostly in Pueblo County, Colorado) have generated a wide number of studies relevant to mitigation of military training activities on habitats occupied by this vulnerable species. Surveys of *A. neotesselatus* in metropolitan Denver (Denver and Adams counties) assessed the distribution of introduced arrays of *A. neotesselatus*. Together, these projects involved numerous investigators who collectively spent hundreds of hours in the field systematically studying a variety of biological attributes of this all-female species based on capture-release or binocular-aided observation methodologies. Despite the extensive studies involving this species, the diversity of prey consumed in more northerly parts of the range has receive no attention. This report describes photographically documented instances of prey capture by *A. neotesselatus* in the northern part of its natural range as well as in an area where the species is introduced. We observed *A. neotesselatus* predation of an adult cicada, an adult noctuid moth, large larval lepidopterans, and adult orthopterans. Historically, studies of diploid parthenogenetic *Aspidoscelis tesselatus* (Common Checkered Whiptail) and triploid parthenogenetic *A. neotesselatus* (Colorado Checkered Whiptail) in Colorado have used large samples of preserved specimens. This study demonstrated how useful information pertinent to the conservation of this species can be obtained in the absence of specimen collection.**

Key Words.—Colorado; feeding; introduced species; prey capture; whiptail lizards

Recent publications based on intensive field investigations have contributed to clarification of many aspects of the biology and conservation status of triploid parthenogenetic *Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) in the extreme northern part of its distribution in Colorado. Several of these reports were focused on controlled access sites in the approximately 55,000-ha U.S. Army Fort Carson (FC) military installation, which encompasses parts of El Paso, Fremont, and Pueblo counties, Colorado (Fig. 1). These publications addressed demographics (Aubry et al. 2019), competing reproductive and physiological investments (Aubry et al. 2020), variations in steroid hormones, energetic state, and immunocompetence across reproductive contexts (Hudson et al. 2020), age dependent search behavior (Kusaka et al. in press), and habitat-dependent search behavior (Utsumi et al. 2020). Although it seemed that the approximate northern limits of *A. neotesselatus* had been documented along Fountain Creek in El Paso County (Fig. 1) by Taylor et al. (2015a, 2016), Livo et al. (2019) reported introduced arrays of the species that are now well-established in metropolitan Denver (MD) along a 4-km stretch of the South Platte River and vicinity in Adams and Denver counties. This new area reported for the species, which is within a heavily industrialized area in sight of downtown Denver, represents an approximately 125 km northern range extension from the Fountain Creek site in El Paso County (Fig. 1). This species is also established at a distant site in Grant County, Washington (Weaver et al. 2011).

Importantly, the aforementioned studies have provided information that will help mitigate the effects of military training activities on substantial parts of the habitat occupied by *A. neotesselatus* in FC and throughout its natural range, and the studies were done without sacrificing lizards. It is noteworthy that Colorado Checkered Whiptail has one of the smallest natural continental distributions of a species in the genus *Aspidoscelis*, which includes published documentation of parts of only seven counties, all in southeastern Colorado (i.e., Crowley, El Paso, Fremont, Las Animas, Otero, Pueblo, and Teller). Moreover, with few exceptions

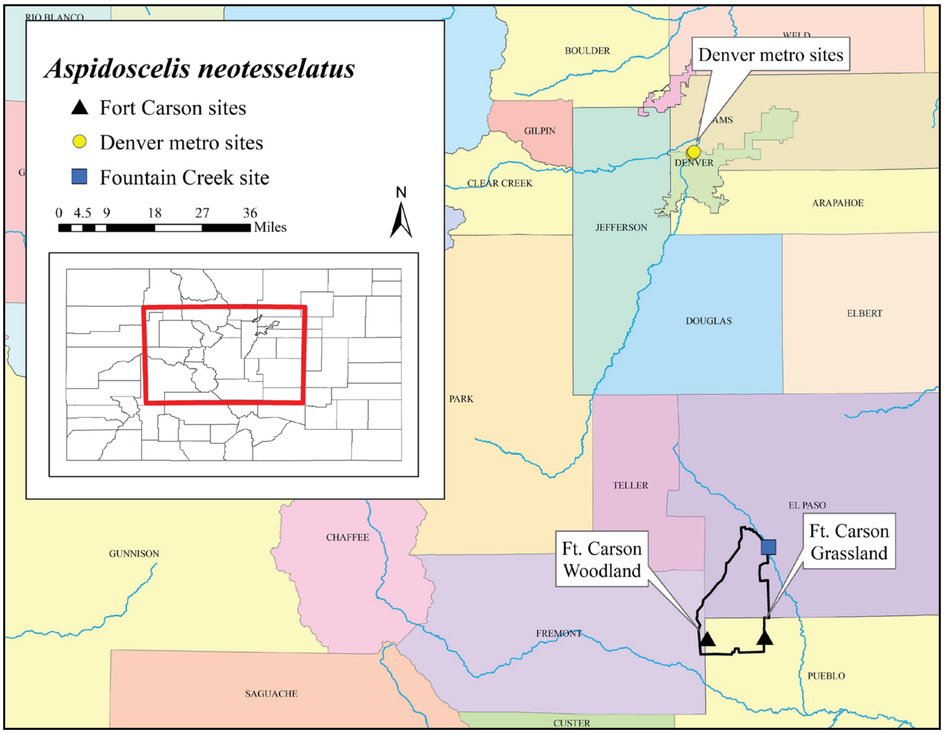

Figure 1. Aspects of the distribution of *Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) in Colorado: general area of the state under consideration (red rectangle); two sites of prey capture in Pueblo County (black triangles); U.S. Army Fort Carson military installation (black outline); northernmost natural distribution record at Fountain Creek, El Paso County (blue square); and recently discovered arrays in metropolitan Denver and Adams and Denver counties (yellow circles).

this distribution area is entirely contained within areas of Colorado which are intensively used and/or altered by humans, including the U.S. Army training area in the 95,464-ha Pinon Canyon Maneuver Site (PCMS), in the 55,000-ha FC military installation, in several cities such as La Junta and Pueblo, and in MD (Walker et al. 1997; Taylor et al. 2006, 2015a; Aubry et al. 2019; Livo et al. 2019).

Feeding strategy studies by Utsumi et al. (2020) and Kusaka et al. (in press) were only the second and third reports on any aspect of food acquisition in the species but did not include observations on either capture of prey or the food choices of *A. neotesselatus*. Paulissen et al. (1993) provided the only report of diet composition in this Colorado endemic lizard. The study included data from sites of syntopy with diploid parthenogenetic *A. tesselatus* (Common Checkered Whiptail), the maternal progenitor of the triploid species, as well as sites of occurrence allopatric to other teiid species in Colorado. Published prior to the description of *A. neotesselatus* by Walker et al. (1997), Paulissen et al. (1993) compared stomach contents from preserved specimens in what was then recognized as diploid and triploid clones of the *A. tesselatus* complex (Parker and Selander 1976; Walker et al. 1995). In addition to the foregoing review of recent research activities on *A. neotesselatus*, this report adds the first observations of prey capture events for juveniles and adults of the species. These captures of prey in *A. neotesselatus*, with emphasis on the ingestion of large insect larvae and flight-capable insects, were photographically recorded in FC and in MD. Not only are the seizure and ingestion phases of feeding rarely observed in food studies, some of the events reported herein also involved unusual prey based on the dietary list published for *A. neotesselatus* by Paulissen et al. (1993).

The nomenclatural status of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselatus*), referred to as *A. neotesselata* in many publications following the erroneous emendation by Reeder et al. (2002), was technically clarified by Tucker et al. (2016). Based on Article 30.1.4.2 International Code of Zoological Nomenclature in 1999, the name *Aspidoscelis* must be treated as grammatically masculine rather than feminine as presumed by Reeder et al. (2002). This clarification also impacted the suffixes of specific epithets of the maternal progenitor of *A. neotesselatus* (diploid normally parthenogenetic *A. tesselata* was returned to *A. tesselatus*) and paternal progenitor (gonochoristic *A. sexlineata* was returned to *A. sexlineatus*). We use the term array for local groups of parthenogenetic *A. tesselatus* and *A. neotesselatus* (e.g., Cordes and Walker 2006; Walker et al. 2012; Taylor et al. 2015b; Livo et al. 2019). We reserve the term population for groups of males and females of gonochoristic (= bisexual) species such as *A. sexlineatus viridis* (Prairie Racerunner).

The foraging and prey capture events in FC were rare observations during other research objectives that employed field data collection, lab assays, and statistical

Figure 2. Second year juvenile *Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) of pattern class A (estimated < 60 mm snout-vent length) foraging in thick ground litter; photographed 25 June 2019 at a woodland study site TA55 in U.S. Army Fort Carson military installation, Pueblo County, Colorado. (Photographed by Carina Kusaka).

modeling to better inform *A. neotesselatus* conservation concerns. Many of these activities were parts of a larger project in FC led by LMA of Colorado State University on the demography and physiology of *A. neotesselatus*. Binoculars permitted collection of data for statistical analyses of search behaviors in lizards of different size classes from distances that would not distract the lizards from normal activities. Other field activities were led by LJL to access the extent of the distribution and impact of the newly discovered arrays of *A. neotesselatus* in Adams and Denver counties. Neither *A. tesselatus* nor *A. sexlineatus* were syntopic with *A. neotesselatus* at any of the study sites in FC, although *A. sexlineatus* was syntopic with *A. neotesselatus* in parts of Adams and Denver counties.

We opportunistically photographed lizards to ascertain their pattern class affiliation and document unusual prey captures; we did not capture any of the lizards described in this paper. We surmised that photographed lizards from FC, based on Walker et al. (1997, 2012), Taylor et al. (2015b), and Aubry et al. (2019), were from arrays of *A. neotesselatus* pattern class A (Fig. 2–3), whereas both pattern classes A (Fig. 4) and B (Fig. 5) were photographed in Denver County (Livo et al. 2019). Observations in FC in May through July revealed that individuals of *A. neotesselatus*, under favorable environmental conditions, typically begin to emerge from overnight retreats by 0800–0830 (Mountain Daylight Time), usually bask to elevate body temperature, and then typically forage with intermittent basking until 1100–1130. On 25 June 2019 at 1015, we photographed an example of foraging by a second-year subadult lizard (Fig. 2). We identified it as an individual of pattern class A of Colorado Checkered Whiptail based on the dorsal pattern of six complete pale-colored primary stripes, a series of pale-colored vertebral components rather than

Figure 3. Two *Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) in the U.S. Army Fort Carson military installation, Pueblo County Colorado. (A) A near maximum sized adult with a problematic dorsolateral color pattern for pattern class A (estimated > 92 mm snout-vent length [SVL]) with a large Putnam's Cicada (*Platypedia putnami*, family Cicadidae); photographed 28 May 2018 at a woodland study site TA55. (Photographed by Maria Eifler). (B) Adult of pattern class A (estimated > 80 mm SVL), based on six persistent primary stripes and absence of a complete vertebral line, with a moderately large Miller Moth (*Euxoa auxiliaris*, family Noctuidae); photographed 9 June 2019 at the grassland study site. (Photographed by Carina Kusaka).

a complete line between the paravertebral stripes, and a boldly striped tail. The lizard had created and then focused on a small, cleared area in the extensive ground litter in searching for prey. It was photographed at a woodland site designated Training Area (TA) 55 in FC in Pueblo County (see Aubry et al. 2020; Fig. 1). Additional instances of foraging and feeding were observed in lizards from a distance as they searched for prey either on relatively barren substrate (e.g., Fig. 3) or sorting through deep accumulations of ground litter (e.g., Figs. 2, 3).

On 28 May 2018 at approximately 1100, we encountered an adult lizard with a color pattern not previously reported for *A. neotesselatus* pattern class A. It appeared to be at or near the maximum body size for an adult of *A. neotesselatus*. The exposed left side of the body of the lizard has alternating black and gray-white vertical bars and no evidence of a lateral stripe (Fig. 3A). Such ontogenetic modifications are more characteristic of pattern class C of diploid *A. tesselatus* (Walker et al. 1997, 2019), but possibly could also occur in large (i.e., very old) adults of *A. neotesselatus* pattern class B (Walker et al. 1997, 2012; Taylor et al. 2015b). The lizard was observed at a woodland site designated TA 55 (Fig. 1), which we plotted in Pueblo County using Google Earth (also see photograph in Aubry et al. 2019; Fig. 2). It was observed under a tree branch in a sandy area essentially devoid of ground litter with an unusually large prey item in its jaws. It was later determined that the large adult of *A. neotesselatus* had captured an individual of Putnam's Cicada (*Platypedia putnami*). It likely represented what is at or near the maximum-sized prey that could be consumed by even the largest adult *A. neotesselatus*.

On 9 June 2019 at approximately 1035, we encountered a prey-capture event involving an adult *A. neotesselatus* with six unfragmented primary dorsal stripes typical of pattern class A (Walker et al. 1997). The lizard was observed at the grassland site in Pueblo County designated TA48 (see habitat photograph in Aubry et al 2019, Fig. 2; Fig. 1 this study). Although the area was characterized as a predominantly grassland site in the study of habitat-dependent search behavior in *A. neotesselatus* (Utsumi et al. 2020), towards the edge of the plot was a mixed assemblage of One-seed Juniper (*Juniperus monosperma*) and Pinyon Pines (*Pinus edulis*). The lizard was observed in a thick layer of woody debris that had accumulated under the canopy of a large One-seed Juniper (Fig. 3B) with a winged insect in its jaws. The lizard remained stationary with an eye trained on the observer. Individual *A. neotesselatus* often can be closely approached by stealth, thus the observer saw that the lizard continued to chew on and orally manipulate the insect before it was swallowed. The prey was subsequently identified as a Miller Moth (*Euxoa auxiliaris*) in the family Noctuidae, members of which often achieve what some observers consider a ubiquitous and noxious presence in Colorado in spring and summer, especially after mild winters (see Colorado State University Extension fact sheet 5.597).

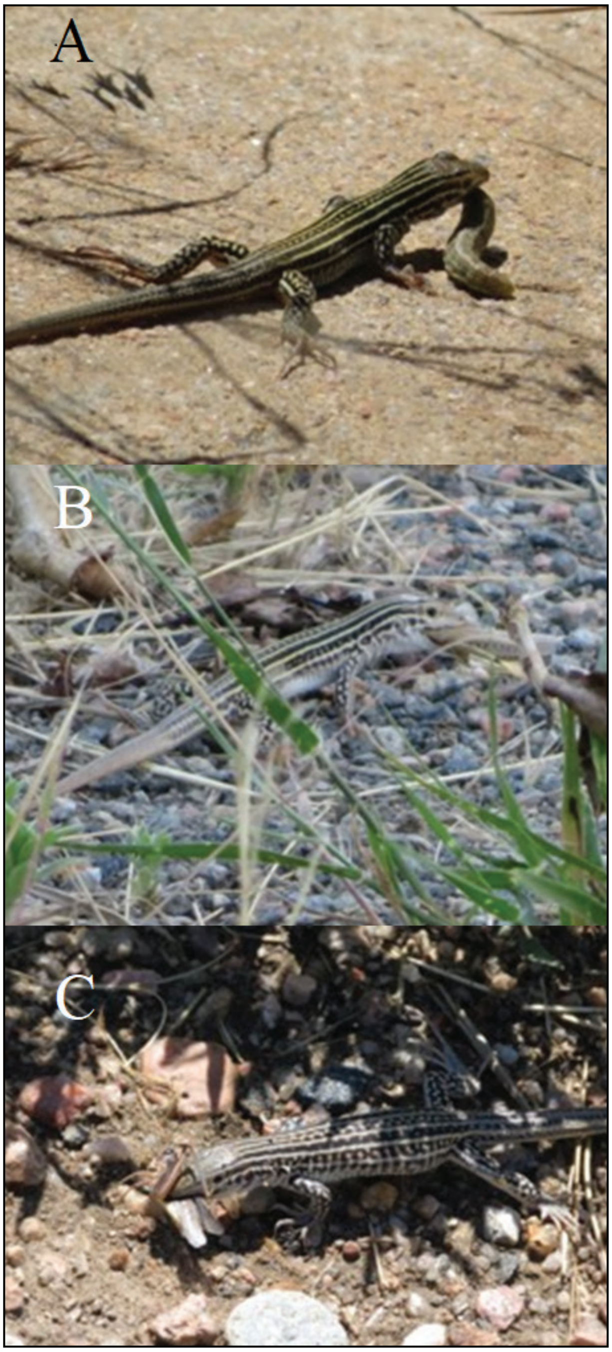

Figure 4. Second year juvenile *Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) from an introduced array in Denver County, Colorado. (A) Individual of pattern class A (estimated > 55 mm snout-vent length [SVL]), based on the dorsal pattern, with a large larval lepidopteran; photographed 1 June 2018. (B) Individual of pattern class A (estimated > 50 mm SVL), based on the dorsal pattern, with an adult orthopteran; photographed 29 June 2019. (C) Individual of pattern class A (estimated > 65 mm SVL), based on the dorsal pattern, with an adult orthopteran; photographed 21 July 2019. (Photographed by Lauren J. Livo).

We observed and photographed four prey-capture events for *A. neotesselatus* in the recently discovered

Figure 5. A third or fourth year adult *Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) of pattern class B (estimated > 75 mm SVL), based on zig-zag continuous vertebral line, with a giant lepidopteran larva; photographed 12 August 2019 from an introduced array in Adams County, Colorado. (Photographed by Lauren J. Livo).

arrays in MD including parts of Denver and Adams counties (Fig. 1). On 1 June 2018 at 0909, we encountered a second season juvenile in Denver County with the head of a large larval lepidopteran in its jaws. The lizard was initially encountered on an open slope with scattered grass. It dropped the insect at least twice before picking it up and beginning to ingest it (Fig. 4A). On 29 June 2019 at 1052, we encountered another second season juvenile with a lengthy regenerated tail in Denver County, along the edge of a level gravel path with a partly (and then more fully) ingested orthopteran prey (Fig. 4B). On 21 July 2019, we observed a third second season juvenile in Denver County, struggling with a grasshopper on the open ground near weedy plants (Fig. 4C); the lizard pressed the grasshopper into the ground and adjusted the insect in a more headfirst position and then finished consuming it within about a minute. On 12 August 2019 at 1213, we encountered a third or fourth season adult of pattern class B in Adams County; the lizard was clasping the head of a large larval lepidopteran in its jaws. Over the approximately 3 min of observation, on two occasions the lizard dropped the caterpillar, adjusted its position, and resumed its efforts to consume it (Fig. 5).

Individual *Aspidoscelis neotesselatus* are sensitive to differences in habitat types while foraging. In a study on FC taking place on two habitat types, foraging adult *A. neotesselatus* differed in movement patterns, with longer first passage times observed in shrub grassland compared to Pinyon Pine–Juniper woodland, correlating with percentage ground cover and negatively correlating with tree cover (Utsumi et al. 2020). In addition, step length and path length were shorter at the shrub grassland site (Utsumi et al. 2020). Kusaka et al. (in press) found significant differences between search behaviors in adults and juveniles of *A. neotesselatus* that would influence habitat selection and reduce intraspecific competition. Adults moved greater distances, made use of larger areas, and had longer step-lengths than juveniles. Adults and juveniles also differed in habitat use when foraging. Adults were found more frequently in the open and in association with Mountain Mahogany (*Cercocarpus montanus*), while juveniles spent more time in deadwood, grass, and One-seed Juniper. Regardless of body size, however, we observed that lizards typically ingested numerous small prey organisms rather than large prey.

Diet-based studies have revealed that both diploid *A. tesselatus* and triploid parthenogenetic *A. neotesselatus* are opportunistic predators, feeding mainly on a variety of arthropods (Paulissen et al. 1993; this study). The stomach contents analysis of preserved specimens of *A. neotesselatus* from several sites in southeastern Colorado revealed a pattern of consumption of either grasshoppers or termites depending on the habitat and season sampled. Some mature cicadas are too large to be consumed by other than one of the largest adults of *A. neotesselatus*. Moreover, capture of this homopteran would most likely be possible only if one should become available by accidental grounding or at emergence and then attract a forging lizard before taking flight. Based on observations by JMW in Ninemile Valley of the Purgatoire River at Higbee, Otero County, capture of grasshoppers by both *A. tesselatus* and *A. neotesselatus*, and reported herein by the latter species, is an energy-intensive activity that likely succeeds because of the explosive seasonal density of several species of orthopterans in southeastern Colorado.

Based on samples of lizards from Otero and Pueblo counties (Paulissen et al. 1993), capture of adult lepidopterans is a rare occurrence for both diploid *A. tesselatus* (which does not occur in the FC study area), and triploid *A. neotesselatus*, which is widely distributed in FC (Aubry et al. 2019; Utsumi et al. 2020). We found that capture of sizable, calorie-rich moths by this whiptail species probably is an expected consequence of the seasonal abundance of this noctuid in southeastern Colorado in recent years. Miller Moths tend to be most abundant after a mild winter as occurred in southeastern Colorado in 2017–2018. As such, they are also often found in great numbers, either stationary or crawling about on the ground, which would periodically make them a readily available food source for *A. neotesselatus*, assuming they are palatable.

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LITERATURE CITED

Aubry, L.M., D. Eifler, K. Utsumi, and S.S. French. 2019. Demographic assessment of the triploid parthenogenetic lizard *Aspidoscelis neotesselatus* at the northern edge of its range. Herpetological Conservation and Biology 14:411–419.

Aubry, L.M., S.B. Hudson, B.M. Kleuver, A.C. Webb, and S.S. French. 2020. Competing reproductive and physiological investments in an all-female lizard, the Colorado Checkered Whiptail. Evolutionary Ecology 33:1–18.

Cordes, J.E., and J.M. Walker. 2006. Evolutionary and systematic implications of skin histocompatibility among parthenogenetic teiid lizards: three color pattern classes of *Aspidoscelis dixoni* and one of *Aspidoscelis tesselata*. Copeia 2006:14–26.

Hudson, S.B., B.M. Kleuver, A.C. Webb, and S.S. French. 2020. Steroid hormones, energetic state, and immunocompetence vary across reproductive contexts in a parthenogenetic lizard. General Comparative Endocrinology 288:113372.

Kusaka, C., K. Utsumi, C. Staley, R. Pedersen, J. Valdiva, E. Liu, H. Caracalas, H. Reynolds, M.A. Eifler, and D.A. Eifler. In press. Age dependent search behavior in the Colorado Checkered Whiptail (*Aspidoscelis neotesselatus*). Western North American Naturalist.

Livo, L.J., T.L. Wilcox, and H.L. Taylor. 2019. Established arrays of triploid, parthenogenetic *Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) in Denver and Adams counties, Colorado: evidence of untapped ecological potential. Herpetological Review 50:690–694.

Parker, E.D., Jr., and R.K. Selander. 1976. The organization of genetic diversity in the parthenogenetic lizard *Cnemidophorus tesselatus*. Genetics 84:791–805.

Paulissen, M.A., J.M. Walker, J.E. Cordes, and H.L. Taylor. 1993. Diet of diploid and triploid populations of parthenogenetic whiptails lizards of the *Cnemidophorus tesselatus* complex (Teiidae) in southeastern Colorado. Southwestern Naturalist 38:377–381.

Reeder, T.W., C.J. Cole, and H.C. Dessauer. 2002. Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. American Museum Novitates 3365:1–61.

Taylor, H.L., B.A. Dole, and J.M. Walker. 2006. Proximate causes of a phylogenetic constraint on clutch size in parthenogenetic *Aspidoscelis neotesselata* (Squamata: Teiidae) and range expansion opportunities provided by hybridity. Journal of Herpetology 40:294–304.

Taylor, H.L., L.J. Livo, D.J. Martin, W.R. Maynard, A. Estep, R. Clawges, D. Roth, J. Kellner, and T. Jackson. 2015a. New northern distribution records for pattern classes A, B, and D of *Aspidoscelis neotesselata* (Colorado Checkered Whiptail) in Colorado, and biogeographic sources of northern colonists. Herpetological Review 46:312–319.

Taylor, H.L., A.J. Wilmes, L.K. Garey, C.E. Montgomery, L.J. Livo, and J.M. Walker. 2016. Rare color pattern misfits in indigenous arrays of parthenogenetic *Aspidoscelis neotesselata* (Colorado Checkered Whiptail). Herpetological Review 47:561–568.

Taylor, H.L., J.M. Walker, C.J. Cole, and H.C. Dessauer. 2015b. Morphological divergence and genetic variation in the triploid parthenogenetic teiid lizard, *Aspidoscelis neotesselata*. Journal of Herpetology 49:491–501.

Tucker, D.B., G.R. Colli, L.G. Giugliano, S.B. Hedges, C.R. Hendry, E.M. Lemmon, A.R. Lemmon, J.W. Sites, Jr., and R.A. Pyron. 2016. Methodological congruence in phylogenomic analyses with morphological support for teiid lizards (Sauria: Teiidae). Molecular Phylogenetics and Evolution 103:75–84.

Utsumi, K., C. Kusaka, R. Pedersen, C. Staley, L. Dunlap, S.G. Smith, M.A. Eifler, and D.A. Eifler. 2020. Habitat-dependent search behavior in the Colorado Checkered Whiptail (*Aspidoscelis neotesselata*). Western North American Naturalist 80:11–18.

Walker, J.M., J.E. Cordes, and H.L. Taylor. 1997. Parthenogenetic *Cnemidophorus tesselatus* complex (Sauria: Teiidae): a neotype for. *C. tesselatus* (Say, 1823), redescription of the taxon, and description of a new triploid parthenogenetic species. Herpetologica 53:233–259.

Walker, J.M., C.E. Montgomery, J.E. Cordes, and M. Mangan. 2019. Morphological variation, habitat, and conservation status of parthenogenetic *Aspidoscelis tesselatus* pattern class C in the canyonlands of southeastern Colorado, USA. Herpetological Conservation and Biology 14:119–131.

Walker, J.M., H.L. Taylor, and J.E. Cordes. 1995. Parthenogenetic *Cnemidophorus tesselatus* complex at Higbee, Colorado: resolution of 30 years of controversy. Copeia 1995:650–658.

Walker, J.M., H.L. Taylor, G.J. Manning, J.E. Cordes, C.E. Montgomery, L.J. Livo, S. Keefer, and C. Loeffler. 2012. Michelle's lizard: identity, relationships, and ecological status of an array of parthenogenetic lizards (genus *Aspidoscelis*: Squamata: Teiidae) in Colorado, USA. Herpetological Conservation and Biology 7:227–248.

Weaver, R.E., A.P. O'Connor, J.L. Wallace, J.M. King, and J.M. Walker. 2011. Discovery of the parthenogenetic Colorado Checkered Whiptail, *Aspidoscelis neotesselata* (Squamata: Teiidae) in Washington State. Northwestern Naturalist 92:233–236.

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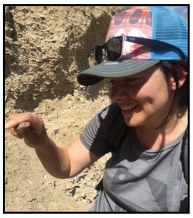

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NOTES

ATYPICAL HABITAT USE BY THE THREATENED ALAMEDA WHIPSNAKE IN THE EASTERN BAY AREA OF CALIFORNIA

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***Abstract*.—The Alameda Whipsnake (*Masticophis lateralis euryxanthus*) has been considered a chaparral-associated species by several researchers. Observations over the last two decades have included reports of atypical habitat use, suggesting that the species and subspecies has a higher level of plasticity in habitat use than has been believed previously. We found numerous Alameda Whipsnakes using habitat that has heretofore been considered atypical, including extensive Oak Woodlands and olive orchards. It appears that vegetative structure may be a more critical component of suitable habitat for the Alameda Whipsnake than the type of plant species.**

Key Words.—association; chaparral; declining; *Masticophis lateralis euryxanthus*; management; structure

Early descriptions of habitat use of the California Whipsnake (*Masticophis lateralis*) were scant and lacked detail. Hallowell (1853) described habitat associations as adjacent to aquatic sites in California. Van Denburgh (1897) only described the species as a good climber, suggesting that the species was found around vegetative structure and cover within the landscape. Grinnell and Grinnell (1907), and Grinnell and Camp (1917) gave further detail on the habitat types, which were described as brushy places, and Chaparral. References to habitat have invariably focused on chaparral habitats for 160 y following the species description (Ortenburger 1928; Stebbins 1954; Pickwell 1972; Stebbins and McGinnis 2018). Subsequent to the split of *M. lateralis* into two distinct subspecies, the Chaparral Whipsnake (*M. l. lateralis*) and Alameda Whipsnake (*M. l. euryxanthus*) by Riemer (1954), *M. l. euryxanthus* was recognized as declining and was listed as threatened by the California Department of Fish and Wildlife in 1971, and in 1991, by the U.S. Fish and Wildlife Service (USFWS 1994).

Special-status species listing of *M. l. euryxanthus* prompted some researchers to focus their investigations, including specific studies on habitat use. Swaim and McGinnis (1992) defined habitat use as strongly associated with Chaparral habitat; however, Alvarez et al. (2005) summarized 129 observations of atypical habitat use and suggested that the subspecies was not necessarily obligated to Chaparral habitat, but instead used Chaparral as well as adjacent habitats. Swaim and McGinnis (1992) considered *M. l. euryxanthus* use of slope as limited to specific aspects. Alvarez (2006), however, considered aspect use more flexible than that reported by Swaim and McGinnis (1992). Herein, we describe a previously unreported habitat type used by *M. l. euryxanthus*, and further support the contention of Alvarez (2006) that all slope aspects are likely used by this threatened subspecies.

We conducted herpetofaunal surveys at Mt. Wanda, on the John Muir National Historic Site, Martinez, California, in 2018. The site was comprised of non-native annual grasslands, Blue Oak (*Quercus douglasii*) woodland, including small patches of ornamental trees (e.g., eucalyptus, *Eucalyptus* sp., and olive, *Olea* sp.), and two very small patches (total < 0.4 ha) of Coastal Sagebrush Scrub. To effectively sample the site and determine species richness, sampling locations were set up in all available habitat types (Fig. 1). We installed, 10 drift fence lines, each with four funnel traps (two on either

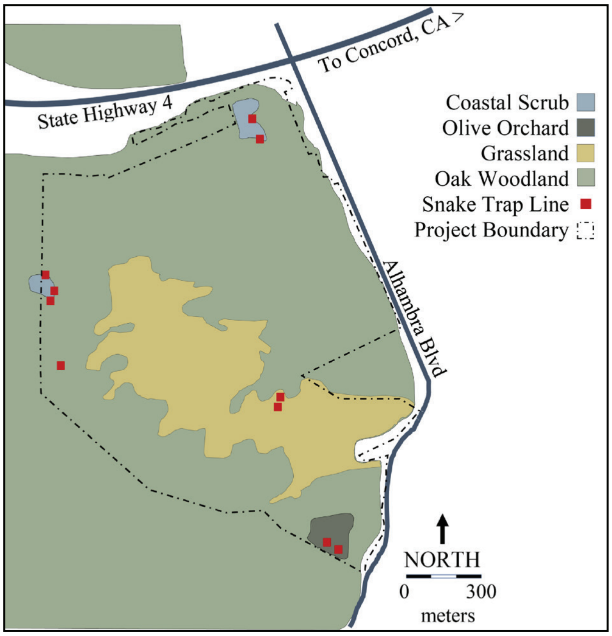

FIGURE 1. A schematic representation of the general habitat types and locations of trapping arrays for reptiles, including the Alameda Whipsnake (*Masticophis lateralis euryxanthus*) in 2018 at Mt. Wanda, John Muir Historic Site, Martinez, California.

Table 1. The number of captures (n) of herpetofauna during trapping at 10 locations at Mt. Wanda, John Muir Historic Site, Martinez, California, in 2018. Habitat types defined as CS = Coastal Scrub, GR = Grassland, OW = Oak Woodland, OO = Olive Orchard.

Species	n	Habitat types
AMPHIBIANS		
Salamandridae		
California Newt (*Taricha torosa*)	13	CS, OW, OO
Plethodontidae		
Arboreal Salamander (*Aneides lugubris*)	21	CS, GR, OW
Ensatina Salamander (*Ensatina eschscholtzii*)	2	CS, GR
California Slender Salamander (*Batrachoseps attenuates*)	6	GR, OW, OO
Hylidae		
Pacific Treefrog (*Hyliola regilla*)	17	CS, GR, OW
REPTILES		
Phrynosomatidae		
Western Fence Lizard (*Sceloporus occidentalis*)	249	CS, GR, OW, OO
Scincidae		
Western Skink (*Plestiodon skiltonianus*)	87	CS, GR, OW, OO
Anguidae		
Southern Alligator Lizard (*Elgaria multicarinata*)	26	CS, GR, OW
Colubridae		
Ring-necked Snake (*Diadophis punctatus*)	7	GR, OW
Alameda Whipsnake (*Masticophis lateralis euryxanthus*)	34	CS, OO
Gopher Snake (*Pituophis catenifer*)	22	CS, GR, OW, OO
Common Kingsnake (*Lampropeltis getula*)	10	CS, GR
California Night Snake (*Hypsiglena torquata*)	2	CS
BIRDS		
Troglodytidae		
Bewick’s Wren (*Thryomanes bewickii*)	3	CS, GR, OW
MAMMALS		
Soricidae		
Ornate Shrew (*Sorex ornatus*)	2	OW
Muridae		
Western Harvest Mouse (*Reithrodontomys megalotis*)	27	CS, GR, OW, OO
House Mouse (*Mus musculus*)	9	CS, GR, OW
Cricetidae		
Deer Mouse (*Peromyscus maniculatus*)	47	CS, GR, OW, OO
Brush Mouse (*Peromyscus boylii*)	75	CS, GR, OW
Pinyon Mouse (*Peromyscus truei*)	35	CS, GR, OO
California Mouse (*Peromyscus californicus*)	18	CS, GR, OO
California Pocket Mouse (*Chaetodipus californicus*)	6	CS
California Meadow Vole (*Microtus californicus*)	66	CS, GR, OW, OO
Unknown Mouse (cricetidae)	1	CS
Geomyidae		
Botta’s Pocket Gopher (*Thomomys bottae*)	3	CS, OW

end). The funnel traps were a modified style of the Fitch Trap (1951) and were checked daily. All specimens were removed, processed (i.e., weighed, measured, marked) and released at the site of capture.

While searching the site, we collected four species of amphibian from the families Salamandridae and Plethodontidae; four species of lizard from the families Phrynosomatidae, Scincidae, and Anguidae; and three species of snake from the family Colubridae (Table 1). Among the colubrid snakes collected, we captured *M. l. euryxanthus* at three locations (Table 1). Two sites were in the ecotone between two small, isolated patches of

Figure 2. Representative photograph of the historic olive (*Olea* sp.) orchard at Martinez, California, that was used by at least eight Alameda Whipsnakes (*Masticophis lateralis euyxanthus*) in 2018. (Photographed by Angel Sprague).

Coastal Scrub (0.04 and 0.36 ha) and extensive Blue Oak woodlands, where we captured 16 individuals (65% of captured whipsnakes). A third site was a 1.3 ha historic olive orchard on an eastern-aspect slope, where we captured nine individuals (35% of captured whipsnakes). The olive orchard was comprised of regularly spaced olive trees on relatively bare substrate (Fig. 2). Widely spaced patches (1–2 m^2) of low growing (< 1 m tall) Buck Brush (*Ceonothus cuneatus*) were also growing on the edges of the olive orchard. The orchard was generally surrounded on the north and west by an extensive stand of California Bay (*Umbellularia californica*), on the south by a large woodland of Coast Live Oak (*Q. agrifolia*), and on the east by ungrazed, non-native annual grassland.

Masticophis l. euryxanthus that we released after data collection at these three sites regularly retreated by rapidly climbing adjacent, low growing shrubs, and then ultimately climbing into the intersecting canopy of olive trees or adjacent oaks (*Quercus* spp.; Fig. 3). We suspect that the olive orchard appeared structurally similar to oak woodlands with woody understory (i.e., partially closed canopy with bare ground substrate and/or various lower-level shrubs) and represented structure preferred by this subspecies (Ortenburger 1928; Stebbins 1954; Pickwell 1972; Stebbins and McGinnis 2018). Numerous researchers suggest that *M. lateralis* seeks an escape route that uses its semi-arboreal ability (Grinnell and Grinnell 1907; Ortenburger 1928; Stebbins 1954). The olive orchard on the Mt. Wanda site that *M. l. euryxanthus* used appeared to have a high level of habitat suitability: food (i.e., three lizard species), basking sites (olive tree canopy), retreat and cover sites (structure of vegetation, structure type), and seasonal retreat sites (rodent burrows). Although a small (0.7 ha) historic olive orchard on an eastern slope typically would not be considered suitable habitat for this subspecies, it is likely the structure, rather than the vegetation type, added to or created the suitability. Alternatively, this snake may have a greater level of habitat plasticity then previously suspected. In either case, we were able to document the use of the olive tree orchard by at least 10 individual adult *M. l. euryxanthus*, along with other snake species.

We were also able to document that *M. l. euryxanthus* was capable of using extremely small patches of Coastal Scrub habitat that were completely surrounded by extensive Blue Oak woodland. We trapped 12 adult snakes adjacent to the larger of the two small patches (i.e., 0.36 ha) of Coastal Scrub. This patch was smaller than the smallest home range reported for a single male *M. l. euryxanthus* (1.9 ha; Swain 1994) indicating that the snakes were very likely using surrounding habitat with some level of regularity. This would strongly suggest that the protection of habitats adjacent to Chaparral and/or scrub may be critical in protecting the species.

A greater understanding of habitat components and their use may play a role in the successful management of declining species. Land managers and regulators considering actions affecting habitat within the suspected range of *M. l. euryxanthus* should consider any vegetation

Figure 3. A 1.3 m long Alameda Whipsnake (*Masticophis lateralis euyxanthus*) in a Blue Oak (*Quercus douglasii*) on Mt. Wanda, John Muir Historic Site, Martinez, California, in 2018. (Photographed by Kelly A. Davidson).

type that is structurally similar to Chaparral as potential habitat for the species. The structure of orchards, ornamental gardens, and residential landscapes, especially those adjacent to occupied natural areas, may provide habitat for this threatened snake, and careful attention should be used when managing such sites in the range of *M. l. euryxanthus.*

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Literature Cited

Alvarez, J.A., M.A, Shea, and A.C. Murphy. 2005. A compilation of observations of Alameda Whipsnakes outside of typical habitat. Transactions of the Western Section of The Wildlife Society 41:21–25.

Alvarez, J.A. 2006. *Masticophis lateralis euryxanthus* (Alameda Whipsnake) habitat. Herpetological Review 37:233.

California Department of Fish and Game. 1987. Results of five-year reviews of 113 California threatened and endangered species. Non-Game Heritage Program, Sacramento, California.

Fitch, H.S. 1951. A simplified type of funnel trap for reptiles. Herpetologica 7:77–80.

Grinnell, J., and C.L. Camp. 1917. A distributional list of the amphibians and reptiles of California. University of California Publications in Zoology 17:127–208.

Grinnell, J., and H.W. Grinnell. 1907. Reptiles of Los Angeles County, California. Bulletin of Throop Polytechnic Institute 35:1–65.

Hallowell, E. 1853. On some new reptiles from California. Proceedings of the National Academy of Sciences 6:236–238.

Ortenburger, A.I. 1928. Whipsnakes and racers. Plimpton Press, Norwood, Massachusetts, USA.

Pickwell, G. 1972. Amphibians and Reptiles of the Pacific States. Dover Publications, New York, New York, USA.

Riemer, W.J. 1954. A new subspecies of the snake *Masticophis lateralis* from California. Copeia 1954:45–48.

Stebbins, R.C. 1954. A Field Guide to Amphibians and Reptiles of Western North America. McGraw Hill, New York, New York, USA.

Stebbins, R.C. 1985. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Publishing Company, Boston, Massachusetts, USA.

Stebbins, R.C., and S.M. McGinnis. 2018. Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Harcourt Publishing Company, Boston, Massachusetts, USA.

Swaim, K.E., and S.M. McGinnis. 1992. Habitat associations of the Alameda Whipsnake. Transactions of the Western Section of The Wildlife Society 28:107–111.

Swaim, K.E. 1994. Aspects of the ecology of the Alameda Whipsnake *Masticophis lateralis euryxanthus.* M.S. Thesis, California State University, Hayward, California. 140 p.

U.S. Fish and Wildlife Service. 2002. Draft recovery plan for Chaparral and scrub community species east of San Francisco Bay, California. Portland, Oregon, USA. 312 p.

U.S. Fish and Wildlife Service. 1994. Endangered and threatened wildlife and plants; proposed endangered status for the Callippe Silverspot Butterfly, Behren's Silverspot Butterfly and the Alameda Whipsnake from northern and central California. Federal Register 59:5377–5384.

Van Denburgh, J. 1897. The reptiles of the Pacific Coast and Great Basin. Occasional Papers of the California Academy of Sciences 5:1–236.

Jeff A. Alvarez is a Herpetologist who has specialized in California reptiles and amphibians for over 30 y. He has worked with California Red-legged Frogs (*Rana draytonii*), California Tiger Salamanders (*Ambystoma californiense*), Western Pond Turtles, (*Actinemys marmorata*) and Alameda Whipsnakes (*Masticophis lateralis euyxanthus*) for much of his career. His focus is on the conservation and natural history of herpetofauna, survey techniques development, and conducting peer-level special-status species workshops. (Photographed by Sarah Foster).

Kelly Davidson has been employed as the District Biologist for Mt. View Sanitary District. Martinez, California, since 2010. She manages 160 ac of wetlands in the eastern San Francisco Bay Area, which provides habitat for several special-status species including the Salt Marsh Harvest Mouse (*Reithrodontomys raviventris*), Western Pond Turtle (*Actinemys marmorata*), California Black Rail (*Laterallus jamaicensis*), and others. She holds a M.S. in Education from California State University, East Bay, and a M.S. in Natural Resources from Oregon State University, Corvallis, where she studied the use of artificial habitats by Western Pond Turtles in California. (Photographed by Kelly A. Davidson).

Fernando Villalba attended the University of California, Davis, where he received a B.S. in Wildlife Biology and a M.S. in Native American Studies. He has worked in many roles with the U.S. National Park Service including as a Biologist for 10 y, and more recently as the Regional Youth and Volunteer Programs Manager. Fernando is also a contributor to the Botanical Phenology Project and co-authored the California Phenology Project Plant Monitoring Protocol. (Photographed by Kelly A. Davidson).

Denise Amador is a Field Scientist with a demonstrated history of working with native vegetation and wildlife on public land. She is interested in restoration ecology, population ecology, and the conservation of endangered species. (Photographed by Angel Sprague).

Angel Sprague is a Wildlife Biologist currently researching Alameda Whipsnake populations in the San Francisco Bay Area. She received her B.S. in Conservation Biology from California State University, Sacramento, and her M.S. in Wildlife Biology from Fort Hays State University, Kansas. She has also studied federally listed as threatened Northern Myotis (*Myotis septentrionalis*) in the midwestern prairie and the Desert Tortoise (*Gopherus agassizii*) in the desert Southwest. She hopes to continue researching population dynamics, and the conservation and climate change impacts of threatened and endangered species. (Photographed by Denise Amador).

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Notes

A New Insular Population of Arboreal Salamander (*Aneides lugubris*) in the San Francisco Bay

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Abstract.—**The origin of island populations of herpetofauna is often unclear for some species. Successful colonization events are rare, and likely stochastic, but establishment does occur if current site conditions are suitable. We detected a breeding population of Arboreal Salamanders (*Aneides lugubris*) on a small rock island in the San Francisco Bay. The origin of this population is unknown, but it appears to be thriving amid anthropogenic structures and an altered landscape.**

Key Words.—colonization; island; population; rafting; reproducing

The range of some amphibian species can be enigmatic and may appear random, such as in the slender salamander (*Batrachoceps*) species complex of the southern Sierra Nevada (Sweet 2019). Species distributions may be patchy, with large gaps between disjunct and isolated populations of a single species complex, such as the Columbia Spotted Frog (*Rana luteiventris*; McGinnis and Stebbins 2018). Such population distributions may result from range contractions or colonization events over time (Tyler 1991; Marsh and Trenham 2001). Population isolation is known in the Arboreal Salamander (*Aneides lugubris*), which is found in three distinct, isolated, foothill populations on the California mainland (Sierra Nevada, North Coast Range, and South Coast Range), and are also one of the three amphibians (with the Garden Slender Salamander, *B. major*, and the Channel Islands Slender Salamander, *B. pacificus*) in California that occur on oceanic islands (Van Denburgh 1905; Anderson 1960; Banta and Morafka 1966; McGinnis and Stebbins 2018). It is found on Coronado Island, Baja California, Mexico (Grismer 2002), Catalina Island, Los Angeles County, California, and Año Nuevo Island, Santa Cruz County, California (McGinnis and Stebbins 2018), and North Farallon Island, San Francisco County, California (VanDenburgh and Slevin 1914; Lee et al. 2012). Arboreal Salamanders are also on islands in the San Francisco Bay including Angel Island, Marin County, Red Rock Island (at the convergence of San Francisco, Marin, and Contra Costa counties), and Brooks Island, Contra Costa County (Anderson 1960).

Storer (1925) and Schoenherr (2007) postulated that populations of Arboreal Salamanders on North Farallon Island originated from the mainland of the central coast, south of the Salinas River. Anderson (1960), studying the Arboreal Salamander on islands in the San Francisco Bay, believed that they either originated from surrounding mainland populations and colonized islands through rafting, or were remnant populations from approximately 10,000 years prior, when the bay was an inland valley and salamander populations were likely contiguous throughout the region. More recently, genetic work by Reilly et al. (2015) appeared to support the contention that populations of Arboreal Salamanders from North Farallon Island originated from mainland populations in Marin County, which they suggested may have been historically connected through a land bridge. Here we report on a new insular population of Arboreal Salamanders on a small rock island, East Brother Island, in the San Francisco Bay, Contra Costa County, California.

East Brother Island is a very small (0.3 ha) rocky island located 0.34 km west of Point San Pablo, Contra Costa County (Fig. 1; 39.962582°N, -121.433271°W). Historically, the island was a solid bedrock protrusion from the bay (similar to the adjacent West Brother Island)

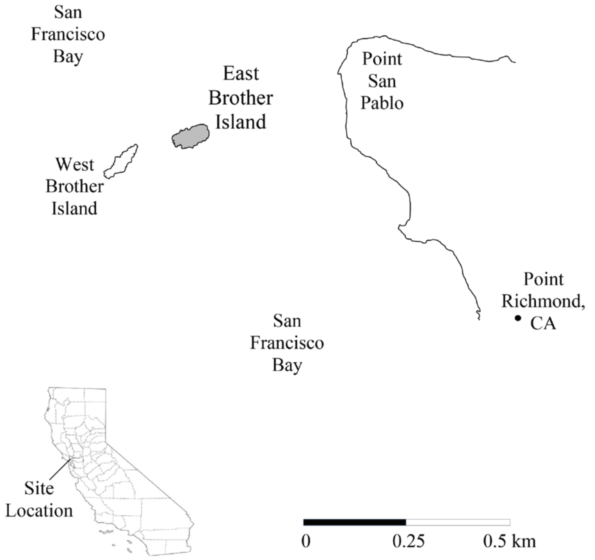

Figure 1. General location of East Brother Island, in northwest San Francisco Bay, relative to the Contra Costa County coast (Point San Pablo), California.

Figure 2. Historic conditions (circa 1893) of the East Brother Island, in northwest San Francisco Bay, California, while under the operation of the U.S. Coast Guard. Note the absence of vegetation. (Photograph courtesy of the National Archives and Records Administration).

that supported the roosting and nesting of numerous pelagic birds such as cormorants (*Phalacrocorax* spp.), pelicans (*Pelecanus* spp.), and gulls (*Larus* spp.; Perry 1984). In 1873 the island was leveled for construction of a lighthouse, fog-signal building, and associated structures, which were completed by 1874 (Perry 1984; Fig. 2). Based on a review of historic photos, East Brother Island remained largely barren during the first 100 y of the light station operation, although successive keepers generally kept personal gardens, and presumably planted ornamental plants, because mature Century Plants (*Agave americana*) appear in photographs from the early 1900s. By the 1940s, several Blue Gum (*Eucalyptus globulus*) and Monterey Cypress (*Cupressus macrocarpa*) trees had been planted, and ornamental succulents became much more widespread following the conversion of the property to a Bed and Breakfast establishment in 1980 (Perry 1984). Ground clutter, in the form of lumber and construction supplies, has been continually present throughout the history of the station due to the ongoing maintenance required to the wooden buildings on the island (Che Rodgers, pers. obs.). Today, East Brother supports a lighthouse, innkeeper residence, functioning Bed and Breakfast, and supporting infrastructure. Vegetation on the island consists of an array of ornamental plantings surrounding the lighthouse and associated buildings, a widespread cover of annual grasses and forbs, and patches of California Buckwheat (*Eriogonum fasciculatum*) around its perimeter (Fig. 3).

In Fall 2018 we conducted three separate informal surveys on the island totaling approximately 10 person hours, to determine if any herpetofauna might be present. Generally, we conducted surveys on clear, sunny days > 7 d after a previous rain. We checked every potential basking site and cover object for species that were known on nearby islands, but none were found. In the winter of

Figure 3. Structures and vegetation on East Brother Island, Contra Costa County, California, in 2019. (Photographed by Che B. Rodgers).

Figure 4. Adult and juvenile Arboreal Salamanders (*Aneides lugubris*) collected from under cover objects on East Brother Island, Contra Costa County, California, October 2019. (Photographed by Che B. Rodgers).

2018–2019, we conducted an additional, more focused, survey consisting of approximately eight person hours. We checked all potential cover objects (i.e., lumber piles, flowerpots, rocks, etc.), and we placed twenty-two 30 × 30 cm plywood cover boards around the perimeter of the island in areas with surface soils. For four weeks following their deployment, we checked coverboards opportunistically.

At three locations on the island, we found both adult and hatchling/juvenile Arboreal Salamanders under cover objects such as wood piles, terracotta pots, and flat rocks resting on soil (Fig. 4). All seven specimens we collected appeared to be healthy (i.e., no missing limbs, body condition appeared typical for the species, etc.) and were associated with what appeared to be appropriate microhabitat (Stebbins 1951; Rosenthal 1957). We found no other vertebrates under the cover boards.

The position of islands relative to prevailing currents may play a significant role in the beaching of raft materials and potential colonization. East Brother Island is in the direct line of out-going flow (at low tide) from San Pablo Bay (McGann et al. 2013) and appears to benefit from higher frequencies of intersection between raft materials and landform (Vences et al. 2003; Thiel and Haye 2006; Measey et al. 2006) than other islands in the bay. We think it likely that drifting debris that periodically washes up on the north side of the island has enabled these salamanders to colonize through rafting (See: Anderson 1960; Measey et al. 2006). If the dominant or exclusive manner in which transient colonization occurred historically (prior to the settlement of the island) was that Arboreal Salamanders did raft in on debris floating from the estuary into the bay, it is possible or probable that it took numerous events for colonization to occur. When the island consisted only of bare rock, population persistence was likely impossible for lack of microhabitat. Arboreal Salamanders benefited from later, anthropogenic alterations, such as construction of the lighthouse and associated structures, the creation of gardens, etc., that created new suitable and enduring habitat where none had previously existed. Alternatively (or concurrently), the intermittent importation of off-island soils, nursery stock, or lumber for human habitation may itself have carried individuals to the island over time (See: Storer 1925). In all likelihood, one or both factors contributed to the colonization of the island.

East Brother Island is one of only two human-occupied and/or developed islands in San Francisco Bay (along with Angel Island) known to support Arboreal Salamanders (Slevin 1928; Anderson 1960; Jeff Alvarez, pers. obs.). Some islands support California Slender Salamanders (*B. attenuates*), but not the Arboreal Salamanders (Stebbins 1951, Anderson 1960). Even islands that have had substantial soil infill and ornamental plantings (i.e., Treasure Island in San Francisco County) and/or thousands of tons of lumber transported onto them (i.e., Yerba Buena Island in San Francisco County), show no records of Arboreal Salamanders (i.e., museum specimens, iNaturalist accounts, or from our own surveys). The apparent absence of Arboreal Salamanders on some San Francisco Bay islands may result from inadequate surveys on those islands, or it may reflect surveys ill-timed to stochastic colonizing events. Conversely, the detection of Arboreal Salamanders on East Brother Island may have occurred because of high survey effort by three biologists searching a very small, open surface area. Irrespective of the origin, Arboreal Salamanders have colonized East Brother Island, and appear to be reproducing successfully. Maintaining the current lighthouse, residence for the lighthouse keeper, and all of the associated ornamental vegetation is likely critical to maintaining this newly discovered population of Arboreal Salamanders.

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LITERATURE CITED

Anderson, P.K. 1960. Ecology and evolution in island populations of salamanders in the San Francisco Bay Region. Ecological Monographs 30:359–385.

Banta, B.H., and D. Morafka. 1966. An annotated check list of the recent amphibians and reptiles inhabiting the city and county of San Francisco, California. Wasmann Journal of Biology 24:223–238.

Grismer, L.L. 2002. Amphibians and Reptiles of Baja California, including its Pacific Islands and the Islands in the Sea of Cortés. University of California Press, Los Angeles, California.

Lee, D.E., J.B Bettaso, M.L. Bond, R.W. Bradley, J.R. Tietz, and P.M. Warzybok. 2012. Growth, age at maturity, and age-specific survival of the Arboreal Salamander (*Aneides lugubris*) on Southeast Farallon Island, California. Journal of Herpetology 46:64–71.

Marsh, D.M., and P.C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15:40–49.

McGann, M., L.H. Erikson, E. Wan, C.L. Powell, and R.F. Maddocks. 2013. Distribution of biologic, anthropogenic, and volcanic constituents as a proxy for sediment transport in the San Francisco Bay coastal system. Marine Geology 345:113–142.

McGinnis, S.M., and R.C. Stebbins. 2018. Field Guide to the Amphibians and Reptiles of California, 4th Edition. University of California Press, Berkeley, California, USA.

Measey, G.J., M. Vences, R.C. Drewes, Y. Chiari, M. Melo, and B. Bourles. 2006. Freshwater paths across the ocean: molecular phylogeny of the frog *Ptychadena newtoni* gives insights into amphibian colonization of oceanic islands. Journal of Biogeography 34:7–20.

Perry, F. 1984. East Brother: History of an Island Light Station. East Brother Light Station, Inc., Richmond, California, USA.

Reilly, S.B., A. Corl, and D.B. Wake. 2015. An integrative approach to phylogeography: investigating the effects of ancient seaways, climate, and historical geology on multi-locus phylogeographic boundaries of the Arboreal Salamander (*Aneides lugubris*). BMC Evolutionary Biology 15:241.

Rosenthal, G.M., Jr. 1957. The role of moisture and temperature in the local distribution of the plethodontid salamander *Aneides lugubris*. University of California Publications in Zoology 54:371–420.

Schoenherr, A.A. 2007. A Natural History of California, 2nd Edition. University of California Press, Berkeley, California, USA.

Slevin J.R. 1928. Amphibians of western North America. Occasional papers of the California Academy of Sciences 16: 1–152.

Stebbins, R.C. 1951. Amphibians of Western North America. University of California Press, Berkeley, California, USA.

Storer, T.I. 1925. Synopsis of the amphibia of California. University of California Publications in Zoology 27:1–342.

Sweet, S.S. 2019. Book Review: Peterson Field Guide to Western Reptiles & Amphibians, 4th Edition. Herpetological Review 50:169–171.

Thiel, M., and P.A. Haye. 2006. The ecology of rafting in the marine environment. III Biogeographical and evolutionary consequences. Oceanography and Marine Biology: An Annual Review 44:323–429.

Tyler, M.J. 1991. Declining amphibian populations - A global phenomenon? An Australian perspective. Alytes 9:43–50.

VanDenburgh, J. 1905. The reptiles and amphibians of the islands of the coast of North America from the Farallons to Cape San Lucas and the Revilla Gigedos. Proceedings of the California Academy of Sciences 4:1–38.

VanDenburgh, J., and J.R. Slevin. 1914. Reptiles and amphibians of the islands of the West Coast of North America. Proceedings of the California Academy of Sciences 4:129–152.

Vences, M., D.R. Vieites, F. Glaw, H. Brinkmann, J. Kosuch, M. Veith, and A. Meyer. 2003. Multiple overseas dispersal in amphibians. Proceedings of the Royal Society of London Series B, Biological Sciences 270:2435–2442.

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BEHAVIOR PATTERNS OF DENNING PACIFIC MARTENS (*MARTES CAURINA*)

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Abstract.—**Reproductive success has substantial implications for mammal populations yet evaluating female behavior during critical reproductive periods can be particularly difficult for cryptic species. North American martens (American Marten, *Martes americana*; Pacific Marten, *M. caurina*) are small-bodied, solitary, and wide-ranging carnivores of conservation concern, whose reproductive behaviors have largely been observed in captive populations. Our primary objective was to assess duration of den use and den attendance patterns of wild female Pacific Martens relative to stages of marten kit development. We tracked five individual female Pacific Martens over seven denning periods in 2016–2017 in the Lassen National Forest, California, using a combination of radio-telemetry and remotely triggered cameras. Pacific Martens used natal dens for significantly longer periods of time than maternal dens (19.6 ± 15.2 [standard deviation] d vs. 5.5 ± 7.5 d; $t = -6.168$, $P < 0.001$) and spent significantly less time away from the den during lactation than after the onset of weaning (2.8 ± 1.7 h/d vs. 5.5 ± 3.0 h/d; $t = -3.544$, $P = 0.002$). Following first detection (i.e., removal from the natal den), kits were semi-mobile at 60.6 ± 5.3 d, were mobile at 86.9 ± 4.4 d, and were independent at 153.6 ± 26.3 d, although we estimated that four kits (31%) died prior to independence. Female Pacific Marten behavior was consistent with a central-place foraging strategy and appears to be closely tied to kit developmental stage. Our results indicate that the 2–3 mo following parturition are a critical and sensitive period for both female Pacific Martens and their kits.**

Key Words.—behavior; California; den; foraging strategy; Pacific Marten; remote camera; reproduction; telemetry.

INTRODUCTION

Rearing offspring from parturition to independence is a critical portion of the reproductive cycle for female mammals and reproductive success has substantial implications for population dynamics (Heppell et al. 2000). Observing and describing behavior of wild animals during reproduction can be inherently difficult, however, especially for secretive or cryptic species. For example, North American martens (American Marten, *Martes americana*; Pacific Marten, *M. caurina*) are solitary carnivores that have large home ranges relative to their small body size (Buskirk and MacDonald 1989), may exhibit arrhythmic diel activity patterns (Zielinski et al. 1983; Foresman and Pearson 1999), and commonly rear their kits in concealed locations such as tree cavities (Bull and Heater 2000). Marten behavior during kit-rearing has largely been observed in captive animals, which may not be subject to the same stressors as wild animals, such as the energetic costs of acquiring food or variability in environmental conditions (e.g., temperature or precipitation; Cuthill 1991; McPhee and Carlstead 2010). Discerning patterns of behavior in wild female martens may inform whether or how behavior influences reproductive success.

In general, reproduction incurs substantial energetic requirements for female mammalian carnivores (Harvey 1986; Gittleman and Thompson 1988). For instance, female energetic expenditures by the closely related Fisher (*Pekania pennanti*) while rearing kits may be more than 2–3 times greater than expenditures during non-reproductive periods (Powell and Leonard 1983). While the long, thin body profile of a marten confers advantages when hunting prey such as small mammals (Andruskiw et al. 2008), there are also energetic consequences, including a high metabolic rate and a limited ability to store substantial body fat reserves (Buskirk and Harlow 1989). In non-reproductive periods, female martens must consume >700 kJ/d or roughly 1/5 of their body mass in prey to balance energetic expenditures (Gilbert et al. 2009; Martin et al. 2020), equivalent to two chipmunks (*Tamias* spp.) or eight Deer Mice (*Peromyscus maniculatus*; Martin et al. 2020). During kit-rearing, female martens must meet their own energetic requirements as well as those of their growing offspring, which likely obligates them to increase food acquisition, decrease energetic expenditures, or both.

Some have postulated that a central-place foraging strategy is exhibited by female martens during critical reproductive periods such as lactation (Slauson and Zielinski 2019). In theory, central-place foraging should allow female martens to optimize their energetic budgets by maximizing foraging effort while minimizing energy expended (e.g., Orians and Pearson 1979). A variety of behaviors could be indicative of such a strategy, including reproductive female martens selectively capturing prey whose body size most closely approximates their daily energetic needs (Slauson and Zielinski 2019), positioning dens proximal to abundant prey resources (Pearson and Ruggiero 2001), or synchronizing activity periods with activity of their primary prey (Nichols 2016). Alterations to behavior patterns during reproduction that incur increased energetic expenditures may have fitness consequences (French et al. 2011; Leblond et al. 2013). For martens, traveling increased distances to forage, relocating kits to new dens, or modifying activity periods could influence fitness outcomes such as female survival.

Despite the potential ramifications for marten fitness, information is lacking on many behavioral aspects of wild martens during denning periods. Therefore, our primary objective was to describe fine-scale patterns of denning behavior by female Pacific Martens, including duration of den use, den attendance, stages of kit development, and kit survival. Characterizing behavior patterns may reveal critical portions of the denning period when female martens and their kits are most vulnerable, the identification of which can direct future research and guide management actions intended to support successful marten reproduction.

Methods

Study area.—Our study area was in the Lassen National Forest in northeastern California, encompassing an area of approximately 100 km^2, at elevations ranging from 1,800–2,100 m (Fig. 1). Annual mean temperatures ranged from 5–16° C, annual mean precipitation ranged from 50–200 cm, and mean snow depth in April was 114 cm (http://cdec.water.ca.gov/snow/). The study area was montane and largely forested but intermixed with shrub fields, perennial meadows, and riparian corridors. Forests were conifer-dominated, primarily Red Fir (*Abies magnifica*) and White Fir (*A. concolor*), but also including Incense Cedar (*Calocedrus decurrens*), Jeffrey Pine (*Pinus jeffreyi*), Lodgepole Pine (*P. contorta*), Ponderosa Pine (*P. ponderosa*), Sugar Pine (*P. lambertiana*), and Western White Pine (*P. monticola*). Common shrub species included Bush Chinquapin (*Chrysolepis sempervirens*), manzanita (*Arctostaphylos* spp.), and Tobacco Brush (*Ceanothus velutinus*). Hardwood trees (e.g., Aspen, *Populus tremuloides*) were uncommon and restricted to riparian and stream corridors.

Data collection.—We captured Pacific Martens from September 2015 to March 2017 using live traps (model 106, Tomahawk Live Traps, Tomahawk, Wisconsin) and anesthetized martens using a combination of ketamine and midazolam (Mortensen and Moriarty 2015). We determined sex and age, weighed Pacific Martens, and removed a vestigial upper premolar tooth to confirm age via cementum annuli analysis (Poole et al. 1994; Matson's Laboratory LLC, Manhattan, Montana). We classified individuals as young-of-the-year (< 1 y old), yearling (1–2 y old), or adult (≥ 2 y old; Jonkel and Weckwerth 1963) and fitted yearlings and adults with a VHF radio-collar (28 g; M-1800, Advanced Telemetry Systems, Isanti, Michigan). Capture techniques adhered to guidelines for research with wild mammals established by the American Society of Mammalogists (Sikes et al. 2016).

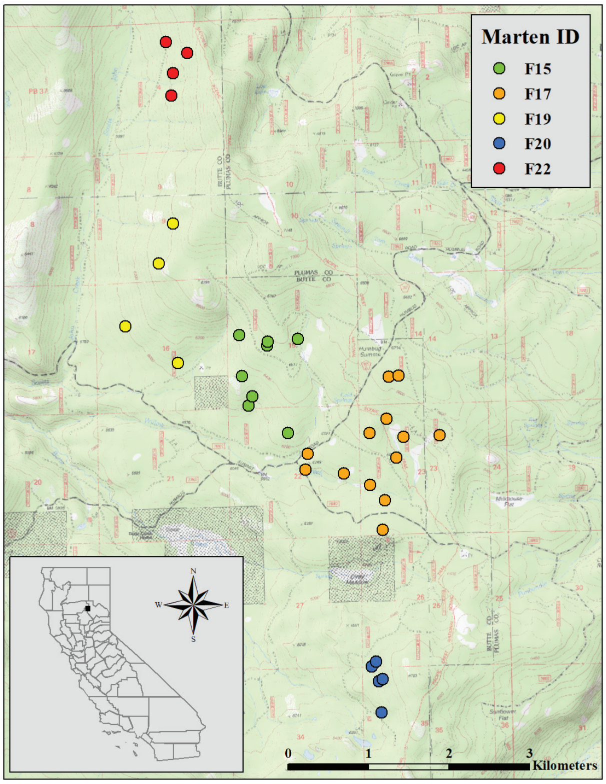

Figure 1. Study area in the Lassen National Forest, California. Points indicate the 34 dens monitored for use by female Pacific Martens (*Martes caurina*) and their kits in 2016–2017.

We tracked radio-collared female Pacific Martens during denning periods (i.e., expected parturition to beginning of kit dispersal; Johnson et al. 2009; Delheimer et al. 2021) from approximately mid-April to late-September. We assessed behavior consistent with parturition (e.g., localization of movement or inactivity for > 24 h; Kleef and Tydeman 2009) and when indicated, we used homing techniques to identify the natal den (e.g., the location of parturition; Ruggiero et al. 1998) and assumed that parturition occurred within 24 h (Kleef and Tydeman 2009). We considered any location used after the natal den but prior to kit dispersal to be a maternal den (Ruggiero et al. 1998; Robitaille et al. 2020) and confirmed each as a den by presence of kits. At all dens identified, we installed two or more remotely triggered cameras (Aggressor Trophy, Bushnell, Overland Park, Kansas or Hyperfire, Reconyx Inc., Holmen, Wisconsin). We checked cameras on an approximately two week interval, when the female marten was absent to reduce disturbance, and we left cameras in place for the duration of the denning period, similar to other den monitoring methods (Green et al. 2017; Smith et al. 2020).

We processed photographs from den monitoring using Picasa software (version 3.9.141; Google LLC, Mountain View, California). Data had a non-normal distribution with unequal variances and we log-transformed (den use duration) and square root-transformed (den attendance) data prior to analysis, which met assumptions of parametric tests. We compared duration of den use (days) by female Pacific Martens between natal and maternal dens, using a Two-tailed *t*-test and a significance level of $P \leq 0.05$. For den attendance, we determined Away Events (Henry et al. 1997) by pairing instances of females leaving their dens with subsequent instances of females returning to their dens. We calculated the sum of the duration (minutes) of away events by a female during each daily or 24-h period (0000–2359) and then binned daily events by each week following parturition (e.g., days 1–7 = week 1, days 8–14 = week 2). We considered weeks 1–6 to be the Lactation Period and weeks 7–8 to be the Early Weaning period, as weaning begins when kits are approximately 42 d old (Brassard and Bernard 1939). We used a Two-tailed *t*-test and a significance level of $P \leq 0.05$ to compare duration of daily away events between lactation and early weaning and calculated average duration of away events by week. We did not estimate den attendance after eight weeks, as females began to move dens frequently, kits became increasingly active, and we were unable to determine if kits remained at the den during away events or were traveling with their mother.

We described stages of Pacific Marten kit development by estimating dates for advancements that likely corresponded with decreasing levels of dependence and increasing levels of coordination (e.g., ability to travel without assistance, hunt or forage, or escape predators). Developmental advancements included: (1) first detection; removal of kits from the natal den by the female; (2) semi-mobility; evidence of kits active outside of the den in the presence of the female; (3) mobility; evidence of kits active outside of the den, in the absence of the female; and (4) independence; evidence that kits were no longer with the female (e.g., detections of the female with no kits present, and no kits subsequently detected). Marten kits may disperse as early as 4 mo of age (Johnson et al. 2009) and we assumed that kits < 4 mo old that we could no longer account for had died and that 4 mo old was the minimum age for kit independence.

We estimated monthly kit survival in the first 4 mo following parturition (May, June, July, and August) and calculated kit survival as the number of kits observed at the end of each month divided by the total number of kits produced. While it is possible that kits were abandoned at the natal den, Fisher studies have indicated this as an infrequent occurrence and unverifiable without climbing the natal den to perform kit counts (Matthews et al. 2013; Green et al. 2018; Matthews et al. 2019). We assumed that no kits died prior to first detection when initially estimating number of kits produced (see Delheimer et al. 2021) and subsequently estimating survival. Similar to our estimates of kit independence, to estimate survival we assumed that kits < 4 mo old that we could no longer account for had died. Given that we did not radio-collar kits and could not assess their ultimate fates, survival estimates represent minimum numbers of presumed kit deaths.

RESULTS

Den use and attendance.—We tracked five female Pacific Martens over seven denning periods in 2016–2017. We assessed use of 34 individual den structures (Figs. 1, 2); some structures were used more than once as

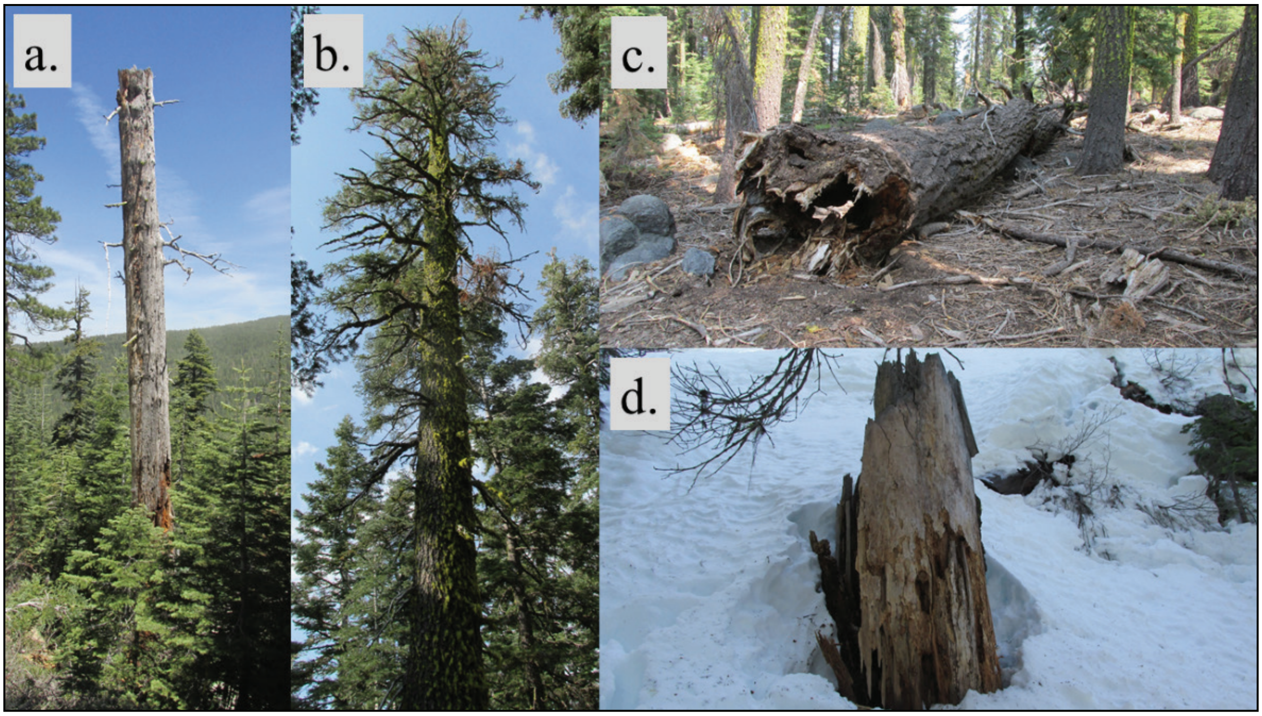

FIGURE 2. Examples of the most commonly used den types by female Pacific Martens (*Martes caurina*) in the Lassen National Forest, California, in 2016–2017: (a) snags, (b) live trees, (c) logs, and (d) stumps. (Photographed by Matthew Delheimer).

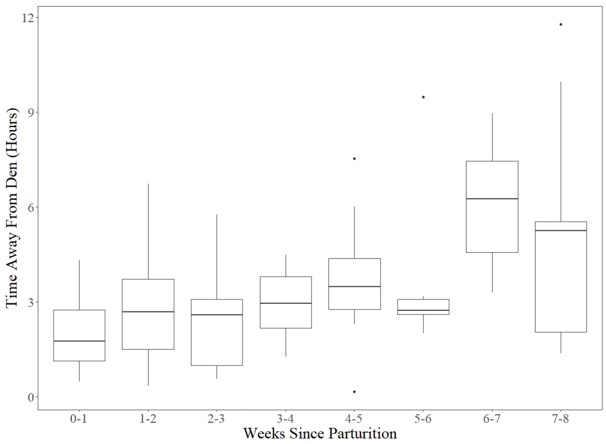

Figure 3. Weekly medians (horizontal lines) of daily time spent away from the den by female Pacific Martens (*Martes caurina*) in the Lassen National Forest, California, in 2016–2017. Boxes bound 25% and 75% quartiles, and black dots represent extreme values.

a den within a denning period and we determined duration of use for a total of seven natal dens and 66 maternal dens, respectively. Pacific Martens used natal dens for significantly longer amounts of time than maternal dens (t = -6.168, df = 12, $P < 0.001$). Natal dens were used for 19.6 ± 15.2 d (mean ± standard deviation; range, 7–50 d), including live trees (14.9 ± 8.7 d; n = 5) and snags (31.1 ± 26.5 d; n = 2). Maternal dens were used for 5.5 ± 7.5 d (range, 1–35 d), including snags (8.6 ± 9.7 d; n = 28), logs (2.3 ± 3.3 d; n = 13), live trees (4.6 ± 6.1 d; n = 12), stumps (2.3 ± 2.1 d; n = 9), and rock piles (3.6 ± 2.7 d; n = 4).

We documented 110 away events by female Pacific Martens during lactation (n = 75 events; kit age = 0–42 d) and early weaning (n = 35 events; kit age = 43–56 d). Daily time spent away from the den was significantly lower during lactation than early weaning (t = -3.544, df = 19, P = 0.002) with Pacific Martens spending 2.8 ± 1.7 h and 5.5 ± 3.0 h away during lactation and early weaning, respectively. Pacific Martens spent the least time away from the den in the first week after parturition (2.0 ± 1.2 h/day; Fig. 3) and left for as little as 0.5 h per day. Time spent away from the den generally increased from 2.7 ± 1.7 h/day in the second week after parturition to 3.8 ± 2.8 h per day in the sixth week after parturition (Fig. 3). Time spent away from the den increased substantially beginning in the seventh week after parturition (i.e., at the onset of weaning) to 6.1 ± 2.1 h/day.

Stages of kit development and survival.— Pacific Marten kits were typically small and immobile upon first detection at 19.6 ± 15.2 d (median date = 19 May). Kits were moved from the natal den to the first maternal den by being scruffed (moved by the neck) by the female, regardless of age (Fig. 4). Kits were moved one-at-a-time and in litters > 1, kits were moved an average of 19.7 ± 15.2 min apart (range, 6–36 min). Kits were semi-mobile at 60.6 ± 5.3 d (range, 54–68 days; median date = 1 July), mobile at 86.9 ± 4.4 d (range, 82–95 d; median date = 27 July), and appeared to be independent

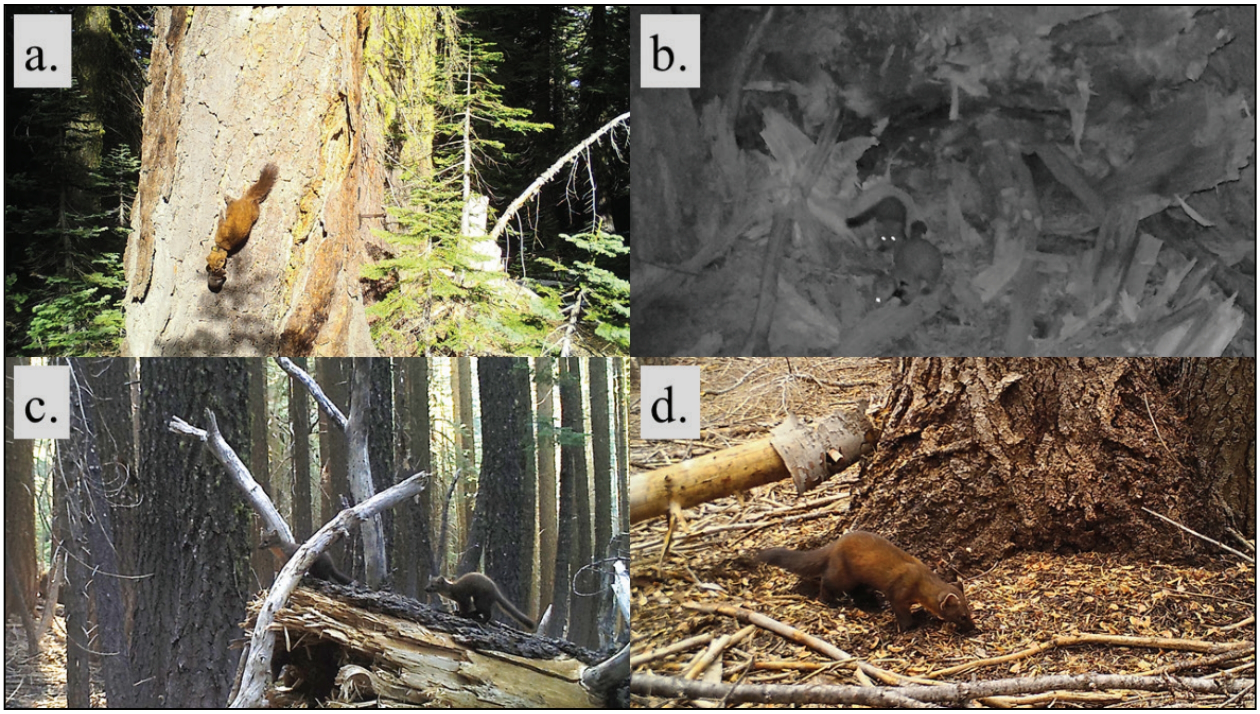

Figure 4. Stages of kit development of Pacific Martens (*Martes caurina*) in the Lassen National Forest, California, in 2016–2017: (a) first detection (about 20 d old), kit is scruffed in mouth of mother; (b) semi-mobility (about 60 d old); (c) mobility (about 90 d old); and (d) independence (about 150 d old). (Photographed using remotely triggered cameras: Aggressor Trophy, Bushnell, Overland Park, Kansas or Hyperfire, Reconyx Inc., Holmen, Wisconsin).

at 153.6 ± 26.3 d (range, 131–195 d; median date = 29 September).

We documented the loss or presumed mortality of zero Pacific Marten kits in the months of April, May, and June, one kit in July, and three kits in August. Based on initial litter size determinations, we estimated that four of 13 kits (31%) died prior to presumed independence. While we were unable to assess most sources of presumed mortality, we suspected that two kits were killed by a Bobcat (*Lynx rufus*) outside of a maternal den in August, based on photographs and forensic evidence.

Discussion

Our results indicate that both duration of den use and daily time spent at the den by female Pacific Martens decreased with increased kit age, corroborating previous evidence that female martens exhibit behavior consistent with a central-place foraging strategy (e.g., Pearson and Ruggiero 2001; Slauson and Zielinski 2019). Female marten behavior during denning appears to be largely driven by the needs of their kits at different developmental stages, although other factors (e.g., changing caloric needs or continued territory maintenance) are likely to influence female behavior as well. Pacific Martens used natal dens on average for significantly longer periods of time than maternal dens (20 d versus 6 d), which was relatively short compared to previous reports of other North American marten populations (43 d; Henry and Ruggiero 1993) and European Pine Martens (*M. martes;* 56 d; Kleef and Tydeman 2009). Den relocation, particularly moving from the natal den to the first maternal den, likely requires a substantial energetic expenditure by female martens (e.g., physically moving kits from one den to another) while also exposing both the female and her kits to predation. It is reasonably intuitive then, that female martens should occupy natal dens for a relatively long duration. The benefits of den relocation, however, likely increase over time as kits increase in size, prey resources near the natal den are depleted, or feces, parasites, or prey remains begin to accumulate in the den (Henry and Ruggiero 1993; Nichols 2016). Although it is often unclear why den relocation occurs, including in our study, a suite of other factors have been suggested as influential to den relocation including presence of predators or male martens at dens, observer disturbance, kit death, or limited availability of other suitable den locations (Henry and Ruggiero 1993; Kleef and Tydeman 2009; Nichols 2016).

Female Pacific Martens spent significantly increased amounts of time away from the den during weaning compared to lactation, and although this finding has previously been reported for martens (Henry et al. 1997; Kleef and Tydeman 2009), our study is the first to present even finer-scale patterns. Similar to female Fishers in California (Cummins 2016), female Pacific Martens spent the least amount of time away from the den in the first week following parturition and spent generally increasing amounts of time away from the den in subsequent weeks during lactation. We acknowledge that our numbers of away events represent minimum estimates, as we were not always able to pair instances of females leaving the den with returning to the den, or vice-versa. Yet given that marten kits are born blind, sparsely-furred, and weighing only 28g (Ashbrook and Hansen 1927) and are completely dependent on their mothers (e.g., for food in the form of milk), our results are consistent with the premise that female martens are obligated to minimize time away from the den in the weeks immediately following parturition. As kits grow larger and require more food resources, females may have to spend more time or travel further distances to acquire sufficient prey, with the trade-off that their growing kits should require less provisioning of other resources (e.g., body heat). Because lactation is a particularly taxing phase of raising offspring (Gittleman and Thompson 1988), the onset of weaning and an increasing ability to deliver solid foods may relax energetic stress on female martens, despite the increasing energetic requirements of their kits.

Pacific Marten kit development following the onset of weaning appears to occur rapidly: for example, captive marten kits did not fully open their eyes until 37–39 d yet ventured forth from the den by 45–56 d (Ashbrook and Hansen 1927; Brassard and Bernard 1939). Indeed, in our study, weaning coincided with a marked decrease in den attendance by females, followed shortly by coordinated movement by kits outside of the den (accompanied by the female) by approximately eight weeks old. By 12 weeks old, kits in our study were active outside of the den while the female was away, corresponding with the time at which marten kits achieve full body length (Brassard and Bernard 1939) and develop the ability to climb trees (Henry and Ruggiero 1993). This important developmental advance was not without consequence, as 75% (3 of 4) of suspected kit mortalities occurred when kits were approximately three months old, two of which we attributed to Bobcat predation. Bobcats appear to be common predators of adult martens (Bull and Heater 2001; Woodford et al. 2013; Wilk and Raphael 2018) and may also be important predators of kits. Although we detected male Pacific Martens, which may kill other adult martens and unweaned kits (Bull and Heater 2001; Dubruiel et al. 2013), as well as several other potential predator species at dens (Coyote, *Canis latrans*; Fisher; Mountain Lion, *Puma concolor*; Fig. 5), there was no indication that species other than Bobcats were responsible for kit mortalities during our study.

The 3 mo following parturition appears to be the most critical portion of the denning period for martens. For the first 2 mo, marten kits are completely dependent on their mothers for food and such a degree of kit dependence may have fitness consequences for females. For example, survival of adult female Pacific Martens

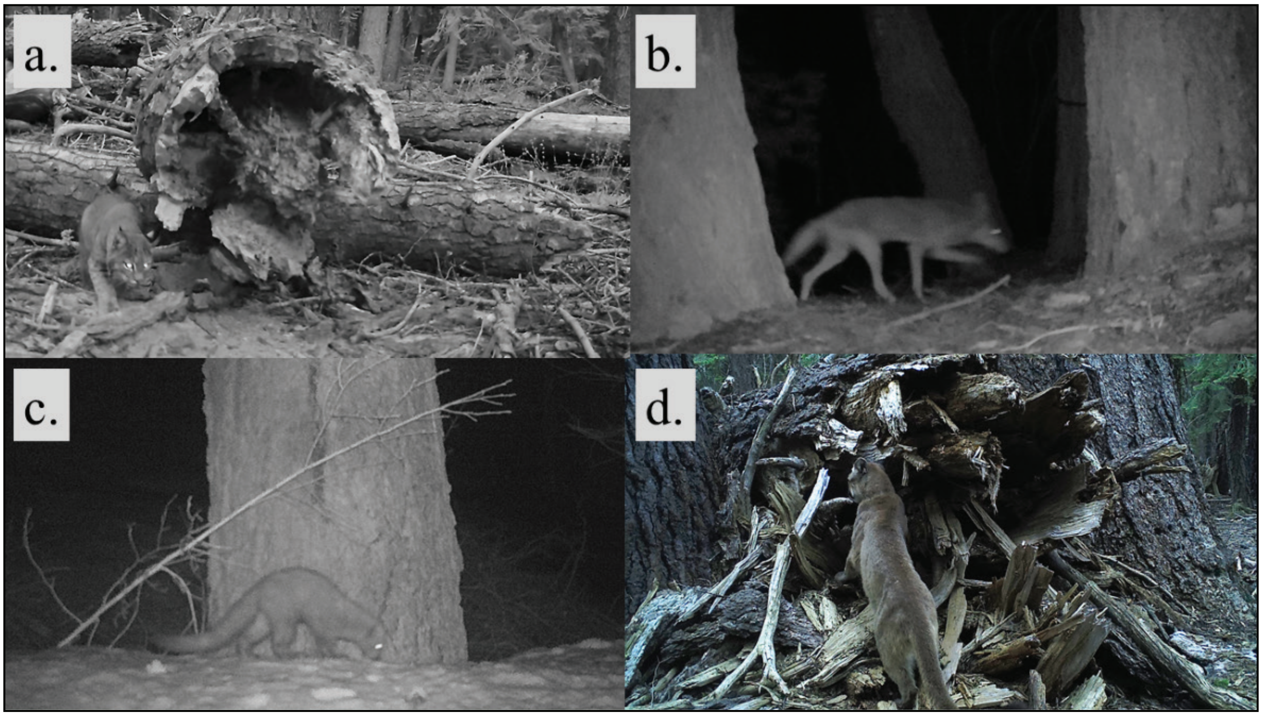

Figure 5. Examples of potential predators detected at Pacific Marten (*Martes caurina*) dens in the Lassen National Forest, California, in 2016–2017: (a) Bobcat (*Lynx rufus*), (b) Coyote (*Canis latrans*), (c) Fisher (*Pekania pennanti*), and (d) Mountain Lion (*Puma concolor*). We suspected that a Bobcat was responsible for the loss of a litter of two kits. (Photographed using remotely triggered cameras: Aggressor Trophy, Bushnell, Overland Park, Kansas or Hyperfire, Reconyx Inc., Holmen, Wisconsin).

was lowest from March to May in Oregon (Wilk and Raphael 2018), which would directly correlate to the timing of active pregnancy through lactation in our study area (Delheimer et al. 2021). In another population in Oregon, 50% of female Pacific Martens died before their kits were independent (Bull and Heater 2001). The death of a female marten at any time prior to kit independence could result in the death of her kits as well; if the female died within the first 2 mo, kit death would be an almost certain outcome, resulting in the simultaneous loss of multiple generations. Given that martens exhibit delayed sexual maturity and produce small numbers of offspring, despite their relatively short lifespans (Strickland and Douglas 1987), such losses could have important implications for marten population dynamics (Buskirk et al. 2012).

The third month following parturition may bring about more direct survival consequences for kits. Although now capable of traveling with their mothers, kits of this age have not reached adult body size, are likely still gaining coordination and agility, and may be most susceptible to predation. For instance, two of three Pacific Marten litters that did not survive to independence in Wyoming were lost in the third month (65 and 76 d post-parturition, respectively; Henry and Ruggiero 1993). We similarly documented the loss of a kit during the third month and an additional three kits in the following month, prior to presumed independence. Kit survival may not improve subsequent to independence: for instance, only 38% of kits (54 of 143) survived from dispersal initiation to adulthood in Canada (Johnson et al. 2009). Given this, developing management strategies that support female martens and their kits during their most vulnerable times may represent the best opportunity to influence marten reproductive success. Further investigations that better elucidate relationships between behavior patterns and survival outcomes may offer vital information to guide such strategies.

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Literature Cited

Andruskiw, M., J.M. Fryxell, I.D. Thompson, and J.A. Baker. 2008. Habitat-mediated variation in predation risk by the American Marten. Ecology 89:2273–2280.

Ashbrook, F.G., and K.B. Hanson. 1927. Breeding Martens in captivity. Journal of Heredity 18:499–50.

Brassard, J.S., and R. Bernard. 1939. Observations on breeding and development of Marten, *Martes americana*. Canadian Field Naturalist 53:15–21.

Bull, E.L., and T.W. Heater. 2000. Resting and denning sites of American Martens in northeastern Oregon. Northwest Science 74:179–185.

Bull, E.L., and T.W. Heater. 2001. Survival, causes of mortality, and reproduction in the American Marten in northeastern Oregon. Northwestern Naturalist 82:1–6.

Buskirk, S.W., and H.J. Harlow. 1989. Body-fat dynamics of the American Marten (*Martes americana*) in winter. Journal of Mammalogy 70:191–193.

Buskirk, S.W., and L.L. MacDonald. 1989. Analysis of variability in home-range size of the American Marten. Journal of Wildlife Management 53:997–1004.

Buskirk, S.W., J. Bowman, and J.H. Gilbert. 2012. Population biology and matrix demographic modeling of American Martens and Fishers. Pp. 77–92 *in* Biology and Conservation of Martens, Sables, and Fishers: A New Synthesis. Aubry, K.B., W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk (Eds.). Cornell University Press, Ithaca, New York.

Cummins, C. 2016. Environmental and anthropogenic influences on Fisher (*Pekania pennanti*) den attendance patterns in California. M.S. Thesis, Humboldt State University, Arcata, California. 104 p.

Cuthill, I. 1991. Field experiments in animal behaviour: methods and ethics. Animal Behaviour 42:1007–1014.

Delheimer, M.S., K.M. Moriarty, K.M. Slauson, A.M. Roddy, D.A. Early, and K.A. Hamm. 2021. Comparative reproductive ecology of two subspecies of Pacific Marten (*Martes caurina*) in California. Northwest Science 94:271–285.

Dubruiel, A., J.E. Woodford, and D.M. MacFarland. 2013. Documentation of infanticide in American Marten (*Martes americana*). Canadian Field Naturalist 127:178–179.

Foresman, K.R., and D.E. Pearson. 1999. Activity patterns of American Martens *Martes americana*, Snowshoe Hares *Lepus americanus*, and Red Squirrels *Tamiasciurus hudsonicus*, in west-central Montana. Canadian Field Naturalist 113:386–389.

French, S.S., M. Gonzalez-Suarez, J.K. Young, S. Durham, and L.R. Gerber. 2011. Human disturbance influences reproductive success and growth rate in California Sea Lions (*Zalophus californianus*). PLoS ONE 6:1–8. https://doi.org/10.1371/journal.pone.0017686.

Gilbert, J.H., P.A. Zollner, A.K. Green, J.L. Wright, and W.H. Karasov. 2009. Seasonal field metabolic rates of American Martens in Wisconsin. American Midland Naturalist 162:327–334.

Gittleman, J.L., and S.D. Thompson. 1988. Energy allocation in mammalian reproduction. American Zoologist 28:863–875.

Green, R.E., M.J. Joyce, S.M. Matthews, K.L. Purcell, J.M. Higley, and A. Zalewski. 2017. Guidelines and techniques for studying reproductive ecology of wild Fishers (*Pekania pennanti*), American Martens (*Martes americana*), and other members of the *Martes* complex. Pp. 313–358 *in* The *Martes* Complex in the 21st Century: Ecology and Conservation. Zalewski, A., I. Wierzbowska, K.B. Aubry, J.D.S. Birks, D. O'Mahony, and G. Proulx (Eds.). Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland.

Green, R.E., K.L. Purcell, C.M. Thompson, D.A. Kelt, and H.U. Wittmer. 2018. Reproductive parameters of the Fisher (*Pekania pennanti*) in the southern Sierra Nevada, California. Journal of Mammalogy 99:537–553.

Harvey, P.H. 1986. Energetic costs of reproduction. Nature 321:648–649.

Henry, S.E., and L.F. Ruggiero. 1993. Den use and kit development of Marten in Wyoming. Proceedings of the XXI International Congress of Game Biologists 21:233–237.

Henry, S.E., E.C. O'Doherty, L.F. Ruggiero, and W.D. van Sickle. 1997. Maternal den attendance patterns of female American Martens. Pp. 78–85 *in Martes*: Taxonomy, Ecology, Techniques and Management. Proulx, G., H.N. Bryant, and P.M. Woodard (Eds.). Provincial Museum of Alberta, Edmonton, Alberta, Canada.

Heppell, S.S., H. Caswell, and L.B. Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Johnson, C.A., J.M. Fryxell, I.D. Thompson, and J.A. Baker. 2009. Mortality risk increases with natal dispersal distance in American Martens. Proceedings of the Royal Society B: Biological Sciences 276:3361–3367.

Jonkel, C.J., and R.P. Weckwerth. 1963. Sexual maturity and implantation of blastocysts in the wild Pine Marten. Journal of Wildlife Management 27:93–98.

Kleef, H.L., and P. Tydeman. 2009. Natal den activity patterns of female Pine Martens (*Martes martes*) in the Netherlands. Lutra 52:3–14.

Leblond, M., C. Dussault, and J.P. Ouellet. 2013. Impacts of human disturbance on large prey species: do behavioral reactions translate to fitness consequences? PLoS ONE 8:1–9. https://doi.org/10.1371/journal.pone.0073695.

Martin, M.E., K.M. Moriarty, and J.N. Pauli. 2020. Forest structure and snow depth alter the movement patterns and subsequent expenditures of a forest carnivore, the

Pacific Marten. Oikos 129:356–366.

Matthews, S.M., J.M. Higley, K.M. Rennie, R.E. Green, C.A. Goddard, G.M. Wengert, M.W. Gabriel, and T.K. Fuller. 2013. Reproduction, recruitment, and dispersal of Fishers (*Martes pennanti*) in a managed Douglas-fir forest in California. Journal of Mammalogy 94:100–108.

Matthews, S.M., D.S. Green, J.M. Higley, K.M. Rennie, C.M. Kelsey, and R.E. Green. 2019. Reproductive den selection and its consequences for Fisher neonates, a cavity-obligate mustelid. Journal of Mammalogy 100:1305–1316.

McPhee, M.E., and K. Carlstead. 2010. The importance of maintaining natural behaviors in captive mammals. Pp. 303–313 *in* Wild Mammals in Captivity: Principles and Techniques for Zoo Management. Kleiman, D.G., M. Allen, and K. Thompson (Eds.). University of Chicago Press, Chicago, Illinois.

Mortenson, J.A., and K.M. Moriarty. 2015. Ketamine and midazolam anesthesia in Pacific Martens (*Martes caurina*). Journal of Wildlife Disease 51:250–254.

Nichols, M.J. 2016. American Marten denning behavior in Michigan. M.S. Thesis, Grand Valley State University, Allendale, Michigan. 81 p.

Orians, G.H., and N.E. Pearson. 1979. On the theory of central place foraging. Pp. 155–177 *in* Analysis of Ecological Systems. Horn, D.J., R.D. Mitchell, and G.R. Stairs (Eds.). Ohio State Press, Columbus, Ohio.

Pearson, D.E., and L.F. Ruggiero. 2001. Test of the prey-base hypothesis to explain use of Red Squirrel midden sites by American Martens. Canadian Journal of Zoology 79:1372–1379.

Poole, K.G., G.M. Matson, M.A. Strickland, A.J. Magoun, R.P. Graf, and L.M. Dix. 1994. Age and sex determination for American Martens and Fishers. Pp. 204–223 *in* Martens, Sables, and Fishers: Biology and Conservation. Buskirk, S.W., A.S. Harestad, M.G. Raphael, and R.A. Powell (Eds.). Cornell University Press, Ithaca, New York.

Powell, R.A., and R.D. Leonard. 1983. Sexual dimorphism and energy expenditure for reproduction in female Fisher *Martes pennanti*. Oikos 40:166–174.

Robitaille, J.F., G. Proulx, and E.D.L. San. 2020. On the use of den and resting site terminology for species in the *Martes* complex. Canadian Wildlife Biology and Management 9:137–151.

Ruggiero, L.F., E. Pearson, and S.E. Henry. 1998. Characteristics of American Marten den sites in Wyoming. Journal of Wildlife Management 62:663–673.

Sikes, R.S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Slauson, K.M., and W.J. Zielinski. 2019. Diets of denning female Pacific Martens vary with the developmental stage of their kits. Ecology and Evolution 9:5963–5974.

Smith, K., A. Facka, and R. Powell. 2020. Using reintroduction to elucidate breeding system, breeding phenology, and infanticide for a solitary carnivore (Fisher, *Pekania pennanti*). Canadian Journal of Zoology 98:433–447.

Strickland, M.A., and R.J. Douglas. 1987. Marten. Pp. 530–547 *in* Wild Furbearer Management and Conservation in North America. Novak, M., J.A. Baker, M.E. Obbard, and B. Malloch (Eds.). Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Wilk, R.J., and M.G. Raphael. 2018. Survival and predators of Pacific Marten in a salvage-logged pine forest, south-central Oregon. Northwestern Naturalist 99:115–123.

Woodford, J.E., D.M. MacFarland, and M. Worland. 2013. Movement, survival, and home range size of translocated American Martens (*Martes americana*) in Wisconsin. Wildlife Society Bulletin 37:616–622.

Zielinski, W.J., W.D. Spencer, and R.H. Barrett. 1983. Relationship between food habits and activity patterns of Pine Martens. Journal of Mammalogy 64:387–396.

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NOTES

NEW PREY ITEM OF THE BANDED ROCK RATTLESNAKE (*CROTALUS LEPIDUS KLAUBERI*) FROM SOUTHWESTERN COAHUILA DE ZARAGOZA, MEXICO

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***Abstract*.—We report for the first time the consumption of the Texas Banded Gecko (*Coleonyx brevis*) by the Banded Rock Rattlesnake (*Crotalus lepidus klauberi*) in southwestern Coahuila de Zaragoza, Mexico. We consider that this event might be more widespread given the broad sympatry of both species, albeit rarely documented.**

Key Words.—feeding; natural history; northwestern Mexico; Texas Banded Gecko

***Resumen*.—Reportamos por primera vez el consumo del Gecko Bandeado de Texas (*Coleonyx brevis*) por la Cascabel Bandeada de Roca (*Crotalus lepidus klauberi*) en el suroeste de Coahuila de Zaragoza, México. Consideramos que este evento puede ser más común dada la amplia simpatría de ambas especies, pero rara vez documentado.**

Palabras Clave.—alimentación; Gecko Bandeado de Texas; historia natural; noroeste de México

Diet is one of the most important aspects of organisms, as it may vary within species, populations, and even ontogenetically, and determines survival and life-history traits (Greene 1983, 1989; Beaupre 1995; Wiseman et al. 2019). In snakes it has been identified as one of the factors that promotes evolution of the group (e.g., Greene 1983; Sherratt et al. 2018), but due to the difficulty of observing snakes feeding in the wild, many records on their dietary habits come from anecdotical and opportunistic events, and/or the review of museum specimens (e.g., Holycross et al. 2002; Wiseman et al. 2019). The Banded Rock Rattlesnake (*Crotalus lepidus klauberi*) is a medium-sized snake distributed from the southeastern U.S. southward to Jalisco and Zacatecas, México, encompassing the states of Arizona, New Mexico, Sonora, Chihuahua, Durango, Coahuila, Zacatecas, Nayarit, Jalisco, and San Luis Potosí (Campbell and Lamar 2004; Heimes 2016). Its diet has been studied in many populations and throughout its range, either as detailed follow-up observations in particular populations (Beaupre 1995) or as anecdotical and opportunistic field observations reporting novel prey items. Holycross et al. (2002) made an exhaustive compilation of the diet items of *C. l. klauberi* from throughout its range based on data collected in the field, museum specimens, and literature records, and found that the most consumed type of prey were lizards, centipedes, and mammals. Here we report on a novel prey item of *C. l. klauberi*.

On 17 September 2020, at 2136, we found an adult male *C. l. klauberi* (Fig. 1) near the road between Ejido Vicente Guerrero and Tacubaya (25.61451°N, -103.07316°W; 1,110 m elevation), Coahuila de Zaragoza, México. The snake measured 412 mm snout-vent length and 39 mm in tail length. It was active when we found it and the left hemipenis was protruding from the cloaca. We captured the snake for gathering morphometric data and to allow it time to retract the hemipenis to prevent its dehydration, but the specimen died the next morning after regurgitating its prey. Upon close examination, the regurgitated prey consisted of an adult Texas Banded Gecko (*Coleonyx brevis*), some mammal hair, and scales that can be assigned to the tail of a whiptail lizard of the genus *Aspidoscelis* (Fig. 1).

This is the first reported record of consumption of a lizard in the genus *Coleonyx* by *C. l. klauberi* or for any subspecies of *C. lepidus* (Holycross et al. 2002). Most of the works detailing the prey items of *C. lepidus* recognize lizards as the most frequently consumed type of prey of this rattlesnake (Beaupre 1995; Holycross et al. 2002) and even consider this snake as a specialist predator on lizards (Carbajal-Márquez and Quintero-Díaz 2015). All the previously reported lizards consumed by *C. lepidus* were of diurnal genera such as whiptails (*Aspidoscelis*), Mexican alligator lizards (*Barisia*), greater earless lizards (*Cophosaurus*), horned lizards (*Phrynosoma*), toothy skinks (*Plestiodon*), spiny

Figure 1. (Bottom) A Banded Rock Rattlesnake (*Crotalus lepidus klauberi*). Prey items we found in an individual near the road between Ejido Vicente Guerrero and Tacubaya, Coahuila de Zaragoza, México, were (A) a partially digested Texas Banded Gecko (*Coleonyx brevis*) and (B) the tail scales of a whiptail lizard (*Aspidoscelis* sp.). (Photographed by Ricardo Palacios-Aguilar).

lizards (*Sceloporus*), and brush lizards (*Urosaurus*; Beaupre 1995; Holycross et al. 2002; Lazcano et al. 2004; Carbajal-Márquez et al. 2012; Banda-Leal et al. 2015; Carbajal-Márquez and Quintero-Díaz 2015). Armstrong and Murphy (1979) suggested that *Sceloporus* lizards likely represent the most important component of the diet of these rattlesnakes, and Beaupre (1995) noted that while the lizards consumed were mainly diurnal species, mammalian species in their diet were mostly nocturnal or crepuscular species. The consumption of other squamate prey such as snakes, however, includes conspecifics and genera with crepuscular or nocturnal habits such as hook-nosed snakes (*Gyalopion*; Milstead et al. 1950) and kingsnakes (*Lampropeltis*; Carbajal-Márquez et al. 2012). An adult male *C. lepidus* was reported to have consumed a San Luis Potosí Nightsnake (*Hypsiglena jani*) at night (Mata-Silva et al. 2010). Thus, the opportunistic consumption of a nocturnal lizard like *Coleonyx brevis* may not be rare. The distribution range of *C. brevis* widely overlaps with the northern portion of that of *C. lepidus* spp. (Dixon 1970), suggesting that its consumption might be widespread, although infrequently observed.

Literature Cited

Armstrong, B.L., and J.B. Murphy. 1979. The natural history of Mexican rattlesnakes. University of Kansas, Museum of Natural History Special Publications 5:1–88.

Banda-Leal, J., D. Lazcano, M. Nevárez-De Los Reyes, and A. Huereca-Delgado. 2015. *Crotalus lepidus* (Rock Rattlesnake). Diet. Herpetological Review 46:102.

Beaupre, S.J. 1995. Comparative ecology of the Mottled Rock Rattlesnake, *Crotalus lepidus*, in Big Bend National Park. Herpetologica 51:45–56.

Campbell, J.A., and W.W. Lamar. 2004. The Venomous Reptiles of the Western Hemisphere. Volume II. Cornell University Press, Ithaca, New York, USA.

Carbajal-Márquez, R.A., and G.E. Quintero-Díaz. 2015. Diet of *Crotalus lepidus* (Serpentes: Viperidae) in Mesa Montoro, Aguascalientes, Mexico. Revista Mexicana de Herpetología 1:18–21.

Carbajal-Márquez, R.A., G.E. Quintero-Díaz, Z.Y. González-Saucedo, and J.J. Sigala-Rodríguez. 2012. *Crotalus lepidus* (Rock Rattlesnake). Diet. Herpetological Review 43:658.

Dixon, J.R. 1970. *Coleonyx brevis* Stejneger. Catalogue of American Amphibians and Reptiles 88:88.1–88.2.

Greene, H.W. 1983. Dietary correlates on the origin and radiation of snakes. American Zoologist 23:431–441.

Greene, H.W. 1989. Ecological, evolutionary, and conservation implications of feeding biology in Old World cat snakes, genus *Boiga* (Colubridae). Proceedings of the California Academy of Sciences 46:193–207.

Holycross, A.T., C.W. Painter, D.B. Prival, D.E. Swann, M.J. Schroff, T. Edwards, and C.R. Schwalbe. 2002. Diet of *Crotalus lepidus klauberi* (Banded Rock Rattlesnake). Journal of Herpetology 36:589–597.

Lazcano, D., J. Banda-Leal, and R.W. Bryson, Jr. 2004. *Crotalus lepidus* (Rock Rattlesnake). Diet. Herpetological Review 35:62–63.

Mata-Silva, V., S. Dilks, and J.D. Johnson. 2010. *Crotalus lepidus* (Rock Rattlesnake). Diet. Herpetological Review 41: 235–236.

Milstead, W.W., J.S. Mecham, and H. McClintock. 1950. The amphibians and reptiles of the Stockton Plateau in northern Terrel County, Texas. Texas Journal of Science 2:543–562.

Sherratt, E., A.R. Rasmussen, and K.L. Sanders. 2018. Trophic specialization drives morphological evolution in sea snakes. Royal Society Open Science 5:172141. https://doi.org/10.1098/rsos.172141.

Wiseman, K.D., H.W. Greene, M.S. Koo, and D.J. Long. 2019. Feeding ecology of a generalist predator, the California Kingsnake (*Lampropeltis californiae*): why rare prey matter. Herpetological Conservation and Biology 14:1–30.

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BAT FORAGING RESPONSE TO INTRODUCED FISH IN THE SIERRA NEVADA

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***Abstract*.—Stocking of trout into naturally fishless water bodies in the mountains of western North America has reduced populations of many native species in those systems, with benthic aquatic invertebrates being particularly impacted. Although many bats consume emergent aquatic insects, no published studies have focused on how they could be affected by changes to prey populations at lakes subsequent to trout stocking. The aim of this study was to determine whether fishless lakes or lakes stocked with trout provide higher quality foraging habitat for bats. We recorded and analyzed bat echolocation calls to assess overall bat activity, foraging activity, and foraging rates at nine feature-matched pairs of stocked and unstocked high elevation lakes in the central Sierra Nevada of California. Bat species with echolocation calls classified as around 25 kHz and 50 kHz showed little to no behavioral change between stocked lakes and fishless lakes. In contrast, bats that echolocate around 40 kHz showed higher levels of overall activity, foraging activity, and foraging rates at stocked lakes. These higher activity levels could indicate the presence of higher quality foraging habitat. Alternatively, these bats could be foraging on suboptimal prey, pursuing small insects such as mosquitoes, and this could represent a cost to these bats due to the lower energetic return of small prey. Because of the recent arrival in California of the potentially deadly fungus *Pseudogymnoascus destructans*, which causes White-nose Syndrome (WNS), introduced trout may constitute an additional challenge to populations of bats that are already threatened by WNS.**

Key Words.—bats; introduced trout; conservation; emergent aquatic insects; echolocation; foraging habitat; restoration

INTRODUCTION

Introduction of trout into naturally fishless water bodies in the mountains of western North America has been shown to have profound negative impacts on native species diversity and trophic exchange in these systems (Bahls 1992; Knapp 1996; Finlay and Vredenburg 2007). Many organisms with aquatic life stages, such as amphibians and emergent aquatic insects, have experienced population declines as a result of trout predation (Knapp and Matthews 2000; Pilliod and Peterson 2001; Tyler et al. 1998; Pope et al. 2009). Terrestrial predators that rely on prey from aquatic ecosystems have likewise been affected, including spiders (Benjamin et al. 2011), garter snakes (Matthews et al. 2002; Lawler and Pope 2006), and the Gray-crowned Rosy-finch (*Leucosticte tephrocotis dawsoni*), which nests at high elevations (Epanchin et al. 2010).

The presence of trout particularly impacts the abundance, diversity, and biomass of benthic aquatic invertebrates (Knapp et al. 2001; Finlay and Vredenburg 2007; Pope et al. 2009). In the Sierra Nevada of California, Knapp et al. (2001) found significantly lower numbers of most orders of invertebrates at lakes with fish compared to those without, including emergent aquatic insects such as mayflies (Ephemeroptera) and caddisflies (Trichoptera). Pope et al. (2009) showed that removing trout from lakes in the Trinity Alps Wilderness of California increased the abundances of emerging Ephemeroptera and Trichoptera, as well as overall insect biomass. In these studies, the only prevalent insects that were found in high abundance at stocked lakes were small dipterans, particularly midges (Chironomidae) and mosquitos in the genus *Culex*; the aquatic larvae of these insects avoid being eaten by trout due to their small size, and they also experience lowered predation pressure as fish reduce populations of large predatory insects.

Although Kalcounis-Ruppell et al. (2007) reported the effects of a wastewater treatment plant on bat foraging on aquatic emergent insects, there are no published studies that focus on how bats are affected by changes in insect abundance, diversity, and biomass at mountain lakes subsequent to trout stocking. High-elevation ecosystems are resource limited, and seasonal pulses of emergent aquatic insects make up a large part of their overall ecosystem productivity (Finlay and Vredenburg, 2007; Epanchin et al. 2010). Subsequently, trout stocking in naturally fishless lakes could cause a loss of high-quality foraging habitat for some species of local bats such as has been reported for other vertebrates (Lawler and Pope 2006; Pope et al. 2009; Joseph et al. 2011).

For bats that breed in the high Sierra Nevada, where the maternity season is short (Elizabeth Pierson et al., unpubl. report), a loss of foraging habitat near a maternity roost could reduce reproductive success. Although bats can fly far in search of prey, during lactation bats decrease their average foraging range size so that they can return to a roost several times a night to nurse non-volant young (Henry et al. 2002). If abundance or biomass of nearby available prey is reduced, bats would suffer energetic costs by foraging for longer time periods or flying further distances to find suitable prey, which could result in poor body condition for mothers or offspring (Kurta et al. 1989).

Bats have been shown to respond to anthropogenic modifications of aquatic habitats, especially when modifications result in changes to insect emergence, but responses vary among species, and most likely depend on the prey base of a bat (Vaughan et al. 1996; Fukui et al. 2006; Kalcounis-Rueppel 2007; Abbott et al. 2009; Akasaka et al. 2009; Scott et al. 2010). For example, Abbott et al. (2009) found that the Common Pipistrelle (*Pipistrellus pipistrellus*) is more active downstream of sewage outflows, whereas the Daubenton's Bat *(Myotis daubentonii*) is more active upstream. In this case, *P. pipistrellus* may be foraging for small Chironomidae, which are abundant in eutrophic conditions; while *M. daubentonii* are likely concentrating on Trichoptera that do not occur in eutrophic conditions.

We hypothesize that foraging behavior of bats at lakes without trout would be different than their foraging behavior at lakes with introduced trout. We predict that bats that emit echolocation calls at 40 kHz and 50 kHz and which forage on aquatic emergent prey would forage more at lakes without introduced trout than at lakes with introduced trout. Both Yuma Myotis (*Myotis yumanensis*), a 50 kHz bat, and the Little Brown Bat (*M. lucifugus*), a 40 kHz bat, forage over still water (Herd and Fenton 1983; Buchler 1976). We also predict that bats that emit echolocation calls in the 25 kHz range would not exhibit a response to changes in the aquatic environment as these bats are open aerial foragers and prey on terrestrial insects (Barclay 1991; William Rainey et al., unpubl. report). To determine the differences in foraging behavior, we assessed the amount and timing of overall bat activity, foraging activity, and foraging effort at lakes with and without stocked trout using echolocation detectors. Assessing foraging effort might be a way to establish whether trout stocking is changing insect availability and causing bats to hunt for atypical prey. We also measured the timing of bat activity throughout the night to look for increases in foraging effort that may indicate energetic stress (Duverge et al. 2000).

Methods

Study design.—In July of 2012 and 2013, we recorded bat echolocation calls at 18 lakes (nine feature-matched pairs) in the central Sierra Nevada of California (i.e., we recorded at two lakes for each of nine non-consecutive nights totaling 18 survey nights). We paired lakes based on elevation, location (within 2 km of each other), area, and depth. We surveyed partner lakes simultaneously to reduce the impact of temporal variability.

Study area.—Our sites comprised naturally fishless lakes in the central Sierra Nevada. In the first season (July 2012), we used study lakes in the northwest corner of Yosemite National Park. In the second season (July 2013), we used sites in the southwest corner of the Emigrant Wilderness in Stanislaus National Forest. Study lakes were small (0.2–1.8 ha) and located in granite basins surrounded by conifers, meadows, and rock features. The average distance between lake pairs was 499 m and sites were between 1,800 and 2,700 m above sea level (MASL), which places them between the lower montane and upper montane forest zones (Storer et al. 2004). We chose lake pairs based on accessibility and the availability of site information. Lake locations, fish status data, and some variables we assessed for covariance (lake depth, lake area, and lake perimeter) were provided by the Division of Resources Management and Science of Yosemite National Park, the North Central Region of the California Department of Fish and Wildlife, and the Mi-Wok Ranger District of Stanislaus National Forest. We computed other potential covariates (the distance from the lake to the nearest river, the distance from the lake to the nearest lake, and the distance from the lake to the nearest water feature) with images from Google Earth (Google Inc., Mountain View, California)

Field methods.—During each of nine survey nights, we recorded bat echolocation calls at both lakes in a given pair (one with fish, one without) using Anabat II™ detectors and Zero-crossings Analysis Interface Modules (Z-CAIM)™ recorders (Titley Electronics, Ballina, New South Wales, Australia). To maximize coverage, we placed four bat detectors, one at each of the four cardinal directions, with microphones on 3-m-tall poles and facing the interior of the lake from the edge of the lake. The detectors recorded bat activity for roughly 8 h, from the evening of placement (usually an hour before sunset, but occasionally later) to an hour after sunrise, when we collected the units. We discarded data collected on nights with low temperatures, high wind speeds, and/or heavy precipitation and the area we resurveyed as recommended by Hayes (1997) and Erickson and West (2002).

Anabat data analysis.—After we collected bat detectors, we extracted the data, identified echolocation call sequences, and sorted calls into groups for statistical analysis. Echolocation call sequences are defined as a series of two or more consecutive echolocation clicks produced by a bat as it flies within range of the detector (Fenton 1977; Hayes 1997; Johnston, D.S. 2002. Data collection protocol: Yuma bat (*Myotis yumanensis*). Wetlands Regional Monitoring Program Plan, Part 2: Data Collection Protocols:1–6. https://calisphere.org/item/ark:/86086/n2fj2fq2/). We extracted call data with CF Read 4.4s™ and processed it using AnalookW 4.1b™ (Titley Electronics, https://www.titley-scientific.com/us/downloads/firmware-software), which creates a file showing an acoustic frequency (kHz) by time display

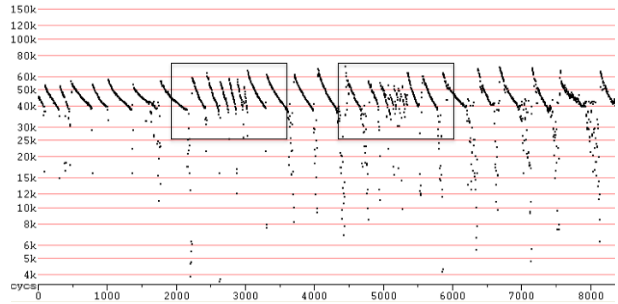

Figure 1. A bat call sequence with two feeding buzzes (shown in boxes), which indicate foraging attempts.

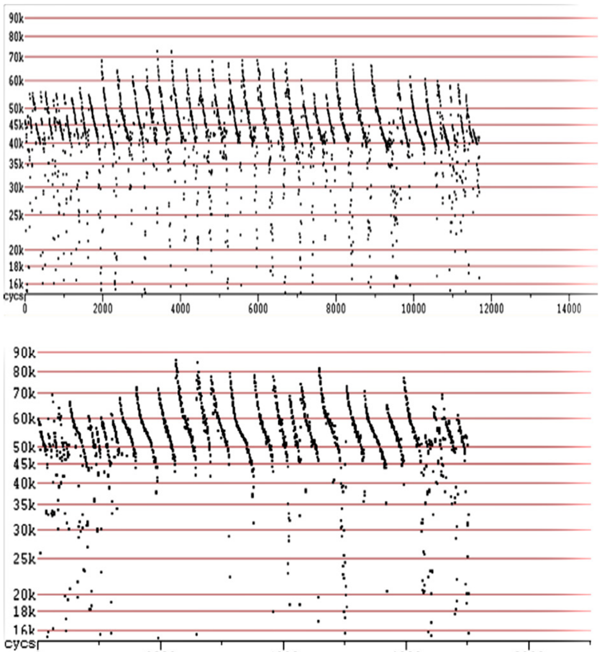

Figure 2. An example of call sequences included in the 50 and 40 kHz echolocation categories. Bats in the 50 kHz category that echolocate at characteristic frequencies of 45-50 kHz include California Myotis (*Myotis californicus*) and Yuma Myotis (*Myotis yumanensis*). Bats in the 40 kHz category that echolocate at characteristic frequencies of 35–40 kHz include the Little Brown Bat (*Myotis lucifugus*), Long-legged Myotis (*Myotis Volans*), and Western Small-footed Myotis (*Myotis ciliolabrum*).

(O'Farrell et al. 1999). After visual assessment of each file, we labeled call sequences according to their phonic grouping and extracted those labels into a text file using the Anabat utility Dataget (after Miller 2001; from Titley Scientific, Brendale, Queensland 4500, Australia).

We quantified foraging activity by identifying foraging attempts known as feeding buzzes (Fig. 1), which are sequences in which echolocation clicks move closer together as a hunting bat closes in on its prey (Griffin et al., 1960, Johnston 2002, *op. cit*.). We determined foraging effort by computing the ratio of foraging activity to overall activity (feeding buzzes per unit of activity). We chose zero-crossing technology for ease of use in remote locations. We classified echolocation call sequences of bats to phonic group, which is ecologically related to size of prey (Barclay and Brigham 1991), to reduce the number of calls that would need to be discarded when calls could not be classified to a specific species. Therefore, we organized all recorded call sequences into four phonic groups based on the characteristic call frequency (Keinath 2004; Joeseph Szewczak et al., unpubl. report; Elizabeth Pierson et al., unpubl. report; Figs. 2 and 3). Each of these four groups contains calls from one or more of the 11 species of bats that are commonly found in the Sierra Nevada above 2,000 MASL (Elizabeth Pierson et al., unpubl. report). Bats in the 50 kHz emitting group (*M. californicus* and *M. yumanensis*) and the 40 kHz group (*M. lucifugus*, Long-legged Myotis, *M. volans*, and Western Small-footed Myotis, *M. ciliolabrum*) are relatively small and have diets restricted to smaller prey. Of these, *M. lucifugus* (40 kHz) and *M. yumanensis* (50 kHz) are most reliant on emergent aquatic insects. Bats in the 25 kHz (Big Brown Bat, *Eptesicus fuscus*, Hoary Bat, *Lasiurus cinereus*, Silver-haired Bat, *Lasionycteris noctivagans,* Brazilian Free-tailed Bat, *Tadarida brasiliensis*, and Long-eared Myotis, *Myotis evotis*) emitting group and the 10 kHz (Western Mastiff Bat, *Eumops perotis*, and Spotted Bat, *Euderma maculatum*) emitting group tend to be larger and can take a wider variety of prey items, including large prey such as moths (Waters et al. 1995).

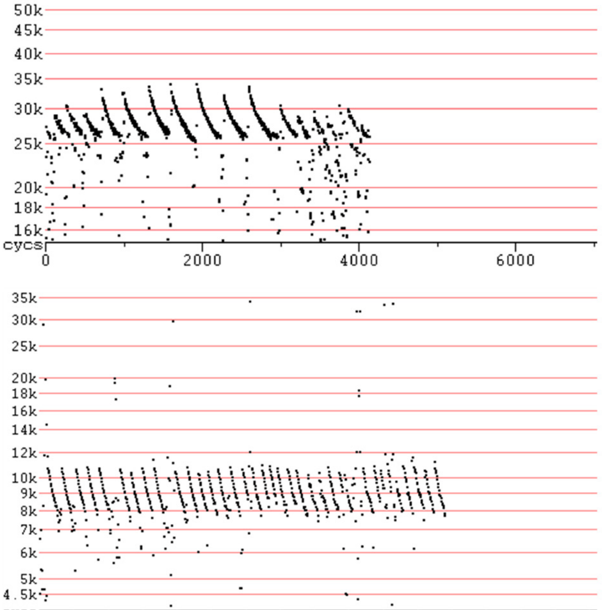

Figure 3. An example of call sequences included in the 25 and 10 kHz echolocation categories. Bats in the 25 kHz category that echolocate at characteristic frequencies of 20–30 kHz include the Big Brown Bat (*Eptesicus fuscus*), Hoary Bat (*Lasiurus cinereus*), Silver-haired Bat (*Lasionycteris noctivagans*), Brazilian Free-tailed Bat (*Tadarida brasilienses*), and Long-eared Myotis (*Myotis evotis*). Bats in the 10 kHz category that echolocate at characteristic frequencies of 8–15 kHz include the Western Mastiff Bat (*Eumops perotis*) and Spotted Bat (*Euderma maculatum*).

We completed further categorization to improve analysis. To reduce the chance of over- or underestimating the activity of a given species, we used the acoustic activity index described in Miller (2001). In this index, a survey period is separated into 1-min blocks and then bat activity is defined as the number of minutes in a survey period that contain at least one echolocation call sequence. Also, to compare activity levels of each of the phonic groups at different times, we divided data from a night of recording into three time periods of bat activity: Early (1900–2300), Mid (2300–0300), and Late (0300–0600).

Statistical analysis.—One complication in assessing differences in bat activity is that variables unrelated to prey abundance, such as weather, proximity to roosting habitat, and nearby vegetation and landscape features, can influence bat behavior in an area (Furlonger et al. 1987; Hayes 1997; Erickson and West 2002; Downs and Racey 2006; Hagen and Sabo 2011). To control for these variables, we used a block design with feature-matched (elevation, location, area, and lake depth) pairs of lakes (one with trout, one without) as blocks (Hayes 1997; Seidman and Zabel 2001) in the analyses. For each of the three dependent variables: overall bat activity, foraging activity, and foraging effort (each measured in minutes of echolocation call sequences), we used a separate Three-way Analysis of Covariance (ANCOVA; Zar 1999) to determine the effect of whether or not the lake was stocked, phonic group (25 kHz, 40 kHz, and 50 kHz), and time period of bat activity (Early: 1900–2300, Mid: 2300–0200, Late: 0200–0500) on the dependent variable. Lake pair was used as a block. We included lake depth, area, perimeter, and the distance of the lake to the nearest river as covariates in the analyses to filter out their effects on an analysis. If all of the covariates did not significantly impact an analysis, we reanalyzed the data with a Three-way Analysis of Variance (ANOVA; Zar 1999) to maximize the power of the analysis. We used planned (*a priori*) comparisons to test for differences among means in lieu of post-hoc tests because the power and assumptions of the planned comparisons were the same as the ANOVA and ANCOVA. To determine if the assumption of homogeneity of variance was met, we initially conducted Levene's tests for each ANOVA or ANCOVA; for all tests the P-value was > 0.05 indicating that the dependent variables did not need to be transformed. We analyzed data with IBM SPSS (Statistical Package for the Social Sciences) statistical software (IBM Corporation, New York, New York).

Invertebrate sampling.—We also sampled emergent insect populations to evaluate the potential prey base for bats and to see whether invertebrate populations at our study lakes are consistent with past research. We placed insect traps at the lakes at the same times and roughly the same locations as the bat detectors and we collected traps in the morning when we collected detectors. In 2012, we used floating emergence traps (Epanchin et al. 2010; William Rainey et al., unpubl. report), and in 2013 we switched to sticky traps (Collier and Smith 1994). Emergence traps were round, floating 0.25 m^2 traps constructed of wire, bicycle tubes, and 0.3 mm white mesh. We constructed sticky traps using one 21.6 × 28 cm (8.5 × 11 in) transparency sheet bent into a cylindrical shape and covered with liquid Tangle Trap (Tanglefoot, Grand Rapids, Michigan). We collected the invertebrates in these traps, identified them to order (Bland and Jaques 1978), and preserved them in 70% ethanol.

To determine if the relative abundances of insect orders at the stocked and unstocked lakes reflected trends found in other studies, we assessed the differences in the ratio of small (< 3 mm) to large (> 3 mm) insects using an ANCOVA as done in Ober and Hayes 2008). The independent variable was trout stocking (Yes/No). We included lake depth, lake area, lake perimeter, the distance from the lake to the nearest river, the distance from the lake to the nearest lake, and the distance from the lake to the nearest water feature (whether a river or lake) as covariates.

Conditions associated with location (elevation, location, area, and depth) differed sufficiently such that significant differences might be obscured with a simple random design. We initially assessed the importance of lake depth, area, perimeter, and the distance of the lake to the nearest river as sources of variation that might obscure results using those parameters as covariates in a Three-way ANCOVA. Because none were significant ($P > 0.050$), we used the results of the Three-way ANOVA instead to obtain more power.

RESULTS

For 18 survey nights (nine non-consecutive nights, two lakes per night), we recorded 7,889 min of total activity, which included 4,249 min of foraging activity, from bats in the 25 kHz, 40 kHz, and 50 kHz phonic groups. Only about 3.5% (276) of the calls recorded were from bats in the 10 kHz group. Because of the small numbers, we did not use the 10 kHz group in our analysis. We recorded calls in small numbers from this group at nearly every lake, however, and routinely heard audible echolocation calls (most likely from *Euderma maculatum*) over study areas.

Overall activity.—The significant Stocked × Phonic Group interaction in the analysis (Table 1) shows that differences in overall bat activity with respect to stocked and unstocked lakes differed among Phonic Groups (Fig. 4). Bats in the 40 kHz phonic category exhibited much greater activity (approximately four times) at stocked lakes than unstocked lakes, the 50 kHz phonic group also showed greater activity (approximately one and a third times) at stocked lakes than unstocked lakes, whereas the

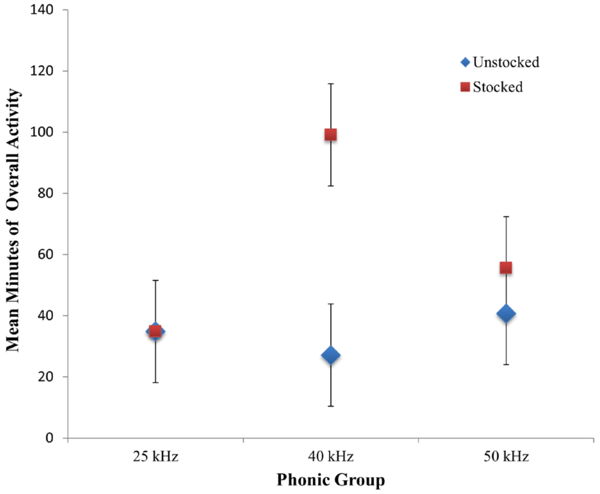

Figure 4. The number of minutes of activity (minutes with echolocation call sequences recorded) by stocked lake (yes or no) and phonic group (25 kHz, 40 kHz, and 50 kHz). The dependent variable of Lake pair was used as a block. Confidence bars are 95%.

25 kHz group showed virtually no difference (Fig. 4). Total bat activity varied between time periods (Table 1). The planned comparisons between Early, Mid, and Late periods showed that the combined mean of bat activity from all three phonic groups during the Early and Late periods was significantly greater than the mean activity in the Mid period and the mean activity level during the Early period was significantly higher than during the Late period (Fig. 5). Controlling for elevation, location, area, and lake depth with a paired lake design (block) was essential for determining the effects of the independent variables on overall bat activity (Table 1). This was indicated by the highly significant Lake Pair (block) effect.

Foraging activity.—The significant Stocked × Phonic Group interaction shows that differences in overall bat activity with respect to stocked and unstocked lakes differed among Phonic Groups (Table 2). Bats in the 40 kHz phonic category exhibited much greater activity (approximately four times) at stocked lakes than unstocked lakes, the 50 kHz phonic group also showed greater activity (approximately one and a third times) at stocked lakes than unstocked lakes, whereas the 25 kHz group showed virtually no difference (Fig. 6). There was a slight effect of lake area and distance to the nearest river on foraging activity (Table 2). The Lake Area covariate was significant and indicated a slight, positive correlation ($r = 0.201$, $t = 0.54$, df = 7, $P = 0.011$) between lake area and the amount of foraging activity and greater area would tend to inflate the estimate of activity. The significant Distance to Nearest River covariate indicated a slightly negative correlation ($r = -0.083$, $t = 0.22$, df = 7, $P < 0.010$) between foraging activity at a lake and the distance of that lake from the nearest river.

Foraging effort.—Differences in foraging effort (feeding buzzes per unit of activity) varied significantly with respect to whether or not the lakes were stocked among the three phonic groups (Stocked × Phonic Group interaction; Table 3). Bats in the 40 kHz phonic group had about one and a third times more foraging effort at lakes with stocked trout; 25 kHz bats showed about one and a quarter times more foraging effort at lakes that did not have stocked trout; and 50 kHz bats show almost no difference (Fig. 6). Overall, foraging effort did not vary significantly between time periods, and the power for this test is relatively low (Table 3).

The responses of the three phonic groups to stocking did not vary significantly among the three time periods, based on the Stocked × Phonic Group × Time Period

Table 1. Results of a Three-Way ANOVA for the total activity of bats at surveyed lakes. The dependent variable is the number of minutes of activity (minutes with echolocation call sequences recorded). The independent variables are stocked (yes or no), phonic group (25 kHz, 40 kHz, and 50 kHz), and time period of bat activity (Early: 1900–2300, Mid: 2300–0200, Late: 0200–0500). The two planned comparisons for Time Period are included: Early and Late versus Mid, and Early versus Late. Lake pair was used as a block. Lake depth, area, perimeter, and the distance of the lake to the nearest river were initially included as covariates but were not significant and were not included in final analysis. The abbreviation df = degrees of freedom.

Source	df	Mean Square	*F*	*P*-value	Observed Power
Stocked	1	34002.5	17.66	N/A	0.987
Phonic Group	2	10807.3	5.612	N/A	0.852
Time Period	2	18072.0	9.385	< 0.001	0.977
Early and Late vs. Mid	1	12970.7	6.736	0.010	0.731
Early vs. Late	1	23173.4	12.03	0.001	0.931
Lake Pair	8	11370.2	5.905	< 0.001	1.000
Stocked×Phonic Group	2	19487.1	10.12	< 0.001	0.984
Phonic Group×Time Period	4	3153.2	1.637	0.168	0.493
Stocked×Time Period	2	649.4	0.337	0.714	0.103
Stocked×Phonic Group×Time Period	4	2148.5	1.116	0.352	0.344
Error	136	1925.6			

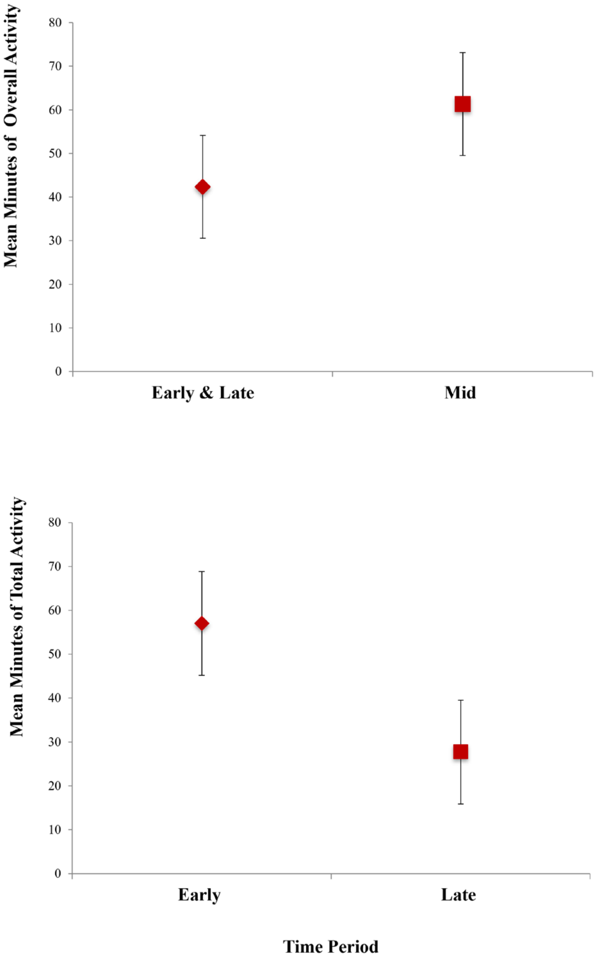

Figure 5. The number of minutes of total activity (minutes with echolocation call sequences recorded) by time period of bat activity (Early: 1900–2300, Mid: 2300–0200, Late: 0200–0500). (Top) Comparison of activity for Early and Late activity versus Mid activity and (Bottom) Early versus Late. Lake pair was used as a block. Confidence bars are 95%.

interaction (Table 3). Based on the Stocked × Phonic Group interaction, stocked trout did not affect the level of foraging effort for bats as a whole over the course of the night (Table 3). The Phonic Group × Time Period interaction suggests the three phonic categories do not change their foraging effort during the three time periods (Table 3). Lake pair was found to have a block effect, indicating that the blocking parameters (elevation, location, area, and depth) could have significantly impacted results if they were not taken into account. Lake depth, area, perimeter, and the distance of the lake to the nearest river were assessed as covariates, but none was a significant correlate at the 0.05 level.

Invertebrate sampling.—Frequencies of insect captures at both emergence traps and sticky traps were very low and variable (stocked lakes: mean = 40.2, standard deviation [SD] = 21.0 from insects; unstocked lakes: mean = 32.0, SD = 19.1). Total emergent aquatic insect sampling comprised three orders: Diptera that were all < 3 mm (92 % of total; 220 from stocked lakes and 178 from unstocked lakes), Ephemeroptera (0.6% of total; one from stocked lakes and two from unstocked lakes, and Trichoptera (7.3% of total; 20 from stocked lakes and 12 from unstocked lakes). Stocking did not change the abundance of insect orders at the study lakes ($F_{1,4} = 2.111, P = 0.220$). The extremely low power of this analysis (power = 0.203) suggests that a larger sample size and higher capture rates are needed to address this question.

Discussion

Response from different bat species.—The results of our study are consistent with previous studies showing that bats that forage over aquatic ecosystems change

Table 2. Results of a Three-Way ANCOVA for the foraging activity time (min) of bats at surveyed lakes. The dependent variable is the number of minutes of foraging activity (minutes with feeding buzzes recorded). The independent variables are stocked (yes or no), phonic group (25 kHz, 40 kHz, and 50 kHz), and time period (Early: 1900 – 2300, Mid: 2300 – 0200, Late: 0200 – 0500). Lake pair was used as a block. Lake area and the distance of the lake to the nearest river were significant covariates. The abbreviation df = degrees of freedom.

Source	df	Mean Square	*F*	*P*-value	Observed Power
Stocked	1	55.8	17.66	N/A	0.987
Phonic Group	2	16451.7	5.612	N/A	0.852
Time Period	2	4808.0	9.385	< 0.001	0.977
Early and Late vs. Mid	8	4726.1	6.736	0.010	0.731
Early vs. Late	1	5492.5	12.03	0.001	0.931
Lake Pair	1	3259.7	5.905	< 0.001	1.000
Stocked×Phonic Group	2	10251.5	10.12	< 0.001	0.984
Phonic Group×Time Period	4	2379.2	1.637	0.168	0.493
Stocked×Time Period	2	888.7	0.337	0.714	0.103
Stocked×Phonic Group×Time Period	4	791.1	1.116	0.352	0.344
Error	136	818.8			

their behavior when modifications to these systems affect their prey base (Vaughan et al. 1996; Kalcounis-Rueppel 2007; Abbott et al. 2009; Scott et al. 2010). We found that the 40 kHz group (*M. lucifugus, Myotis volans,* and *M. ciliolabrum*) displayed greater overall activity, foraging activity, and foraging effort at lakes with stocked trout, suggesting that bats in this phonic group might be spending more time searching for insects at lakes with trout. Given the paucity of aquatic emergent insects caught in the emergent traps, the greater overall activity, foraging activity, and foraging effort of these bats at lakes with stocked trout are not likely because of higher quality foraging habitat. As predicted, we did not find a difference in activity levels from bats in the 25 kHz (*Eptesicus fuscus*, *Lasiurus cinereus*, *Lasionycteris noctivagans, Tadarida brasilienses*, and *Myotis evotis*). Although we also predicted that the 50 kHz bats (*M. californicus* and *M. yumanensis*) would forage more at lakes without introduced trout, this phonic group exhibited no difference between the overall activity, foraging activity, and foraging effort between lakes with and without introduced trout.

We believe that the majority of calls recorded in the 40 kHz category can be attributed to *M. lucifugus*, indicating that this species shows a strong response to the presence of stocked trout. *Myotis lucifugus* is very active over aquatic habitats, forages on aquatic insects, and is common above 2,000 feet in the Sierra Nevada (Ober and Hayes 2008; Clare et al. 2011; Elizabeth Pierson et al., unpubl. report). The other potentially occurring 40 kHz bats, *M. ciliolabrum* and *M. volans,* are not associated with aquatic habitats and are not common at the elevations of our study area (Elizabeth Pierson et al., unpubl. report). There are few diet records for *M. ciliolabrum*, but it is known to forage over rocky bluffs and cliffs, and the closely related Eastern Small-footed Myotis (*M. leibii*) consumes moths, beetles, and flies (Rodriguez and Ammerman 2004; Moosman et al. 2007; Johnson et al. 2012). *Myotis volans* forages mainly on moths (Johnson et al. 2007) primarily under the canopy of trees (Bell and Fenton 2011).

We expected to see a response from the 50 kHz group because this group included *M. yumanensis*, which is known to concentrate on emergent aquatic prey (Ober and Hayes 2008; Clare et al. 2011). Because we used zero-crossing technology, we were unable to reliably separate *M. yumanensis* calls from those of *M. californicus*, which does not typically forage over aquatic areas, and may have shown no response to the presence or absence of

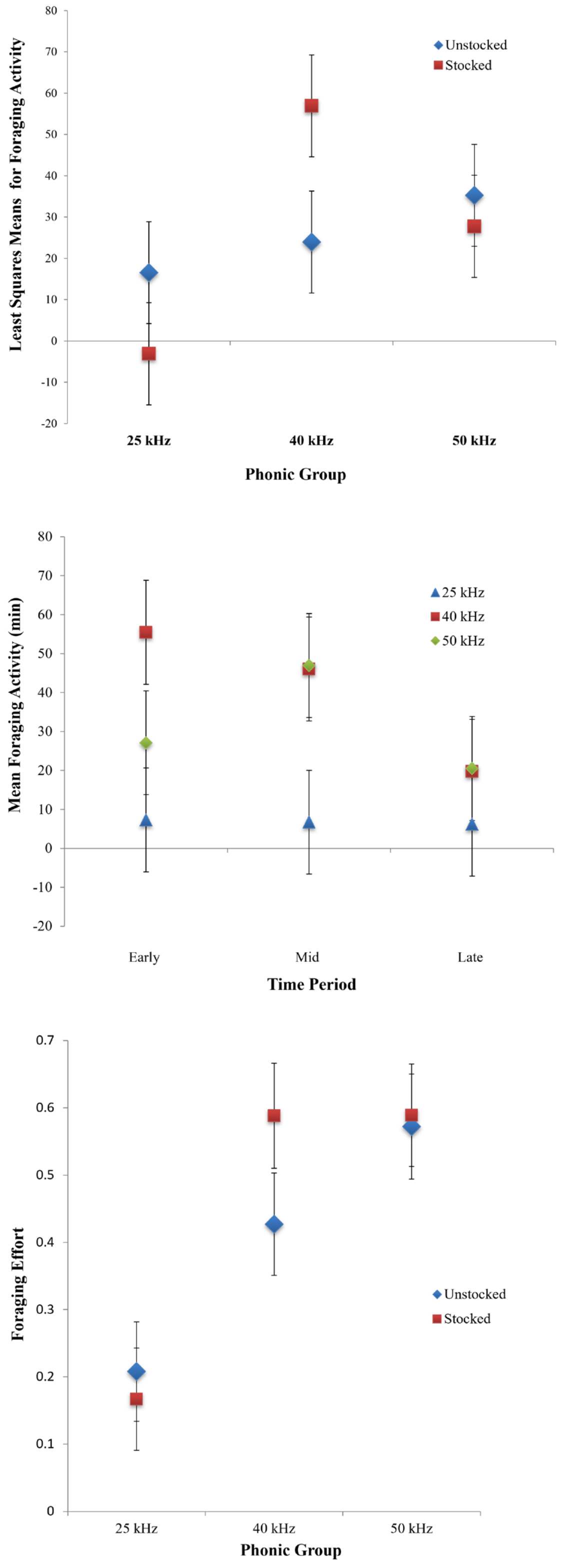

Figure 6. (Top) The number of minutes of foraging activity (minutes with feeding buzzes recorded) for the interaction of stocked (yes or no) lakes and phonic group (25 kHz, 40 kHz, and 50 kHz) based on ANCOVA adjusted for area of the lake and distance of the lake from the nearest river. (Middle) The number of minutes of foraging activity (minutes with feeding buzzes recorded) for the interaction of phonic group (25 kHz, 40 kHz, and 50 kHz) and time period (Early: 1900–2300, Mid: 2300–0200, and Late: 0200–0500) based on ANCOVA adjusted for area of the lake and distance of the lake from the nearest river. (Bottom) The number of minutes of foraging effort (feeding buzzes per unit of activity) for the interaction of stocked (yes or no) and phonic group (25 kHz, 40 kHz, and 50 kHz) based on ANCOVA adjusted for area of the lake and distance of the lake from the nearest river. For all, lake pair was used as a block and confidence bars are 95%.

Table 3. Results of a Three-Way ANOVA for the foraging effort of bats at surveyed lakes. The dependent variable is the ratio of the number of minutes of activity to the number of minutes of foraging activity. The independent variables are stocked (yes or no), phonic group (25 kHz, 40 kHz, and 50 kHz), and time period (Early: 1900 – 2300, Mid: 2300 – 0200, Late: 0200 – 0500). Lake pair was used as a block. Lake depth, area, perimeter, and the distance of the lake to the nearest river were initially included as covariates but were not significant and were not included. The abbreviation df = degrees of freedom.

Source	df	Mean Square	*F*	*P*-value	Observed Power
Stocked	1	0.08	2.078	N/A	0.299
Phonic Group	2	2.28	59.42	N/A	1.000
Time Period	2	0.05	1.249	< 0.001	0.268
Lake Pair	8	0.17	4.531	< 0.001	0.996
Stocked×Phonic Group	2	0.14	3.653	< 0.001	0.664
Phonic Group×Time Period	4	0.04	0.931	0.168	0.289
Stocked×Time Period	2	0.03	0.757	0.714	0.176
Stocked×Phonic Group×Time Period	4	0.03	0.831	0.352	0.260
Error	129	0.04			

trout (Ober and Hayes 2008; Harvey et al. 2011). Using a full-spectrum analysis to separate these species from one another might yield more definitive results for these species.

The species in the 25 kHz group do not specialize on aquatic insects, so as predicted, we did not observe a response to changes in the aquatic environment. *Eptesicus. fuscus*, *L. cinereus*, *L. noctivagans,* and *M. evotis* prefer prey of terrestrial origin such as lepidopterans and non-aquatic coleopterans (Barclay 1991; Agosta 2002; Ober and Hayes 2008). *Tadarida brasiliensis, E. fuscus*, *L. cinereus*, and *L. noctivagans* are open aerial foragers in the 25 kHz group that typically forage in wide open spaces, usually well above the landscape (Johnson et al. 2007). *Tadarida brasiliensis* is a generalist with a broad diet; although this bat will take advantage of large swarms of aquatic insects, it also appears to prefer large, terrestrial prey (Whitaker et al. 1996; McWilliams 2005). Relatively low levels of foraging activity coupled with consistent foraging effort indicated that bats in this group were probably pursuing prey that are occasionally present at lakes regardless of fish status. A diet analysis would confirm that trout stocking does not impact the prey base of these bats.

Timing of activity.—The timing of bat activity changed throughout the night in unexpected ways, but the stocked status of the lakes did not influence the temporal pattern. Bats that depend on crepuscular swarms of insects generally follow a bimodal activity pattern, with a peak at dusk and a second peak at dawn (Rydell et al. 1996; Hayes 1997); however, in our study, foraging activity for 40 kHz and 50 kHz bats stayed relatively high from sunset to 0200 and then dropped off in the early morning. These results were expected because all surveys took place at the height of maternity season when lactating females forage for longer periods of time and return to the roosts several times a night to nurse young (Henry et al. 2002). Activity levels for bats in the 25 kHz category remained constant, and relatively low, throughout the night; bats that feed on insects that do not swarm at dusk or dawn do not tend to follow a bimodal pattern, and any peaks in activity may not have been recorded in this group because most of their foraging takes place away from the lakes (Jones and Rydell 1994).

Foraging effort and the response to trout stocking.—The high levels of foraging effort (minutes with feeding buzzes per minutes of overall activity) from 40 kHz bats (likely *M. lucifugus*) at lakes with trout, coupled with invertebrate data based on the literature, suggest that bats were foraging at these lakes for small, abundant insects. Previous studies in these systems found increased abundance of < 3 mm dipterans (mostly mosquitoes and midges), but substantially reduced populations of larger-bodied Ephemeroptera and Trichoptera (Finlay and Vredenburg 2007; Knapp et al. 2007; Pope et al. 2009; Epanchin et al. 2010). Because a higher number of small prey compared to large prey are needed to satisfy energy requirements, a bat hunting relatively small insects will exhibit greater foraging effort than one eating higher-calorie insects (Gonsalves 2013).

To help implement meaningful conservation strategies for bats in the Sierra Nevada, we suggest more studies to determine what bats and introduced trout are eating. A dietary study of both groups should reveal any overlap in diets and might explain why the 40 kHz group of bats has higher activity levels at lakes with trout. It is unknown whether abundant small dipterans represent a high-quality prey base for *M. lucifugus*, or if the scarcity of larger, preferred prey is driving compensatory feeding on smaller prey (Cruz-Rivera and Hay 2000). Optimal foraging theory predicts that marginally profitable prey items will be included in the diet of a predator only as more profitable prey becomes unavailable (Davies 1977), but some studies have found that the inclusion of small prey items is positively correlated with their abundance (Turner 1982). While the relative availability of small dipterans will decrease the amount of energy bats spend pursuing them, this may not offset their small size.

Turner et al. (1982) showed that the inclusion of many small items in the diet of foraging swallows resulted in a decrease in their energy gain rate.

The energetic costs associated with compensatory feeding would particularly impact bats during maternity season. While *M. lucifugus* does consume midges and mosquitoes, females have been shown to selectively forage on larger bodied insects such as ephemeropterans and trichopterans as those prey become available during the summer maternity season (Anthony and Kunz 1977; Ober and Hayes 2008; Clare et al. 2011). In fact, the increased energetic demands of lactation may cause bats to prey switch. Clare et al. (2011) found that small dipterans comprised 63% of the diet of pregnant *M. lucifugus*, but ephemeropterans made up 66% of their diet during lactation. If stocking of trout in lakes causes preferred high-calorie prey to be absent from the foraging habitat, local breeding populations of *M. lucifugus* could suffer reduced survivorship, growth, and fecundity (Cruz-Rivera and Hay 2000).

Removing introduced trout from lakes may be one straightforward way to restore foraging habitat for bats and add to their resilience in the face of other environmental threats. Populations of *M. lucifugus* and other bat species at winter hibernacula have plummeted by 75–99% because of White-nose Syndrome (Harvey et al. 2011). Now that White-nose Syndrome has arrived in northeastern California, the Sierra Nevada bat populations are facing additional challenges and the implementation of conservation strategies are becoming more important. A long-term comparison of bat foraging behavior, diets, and population dynamics before and after trout removal from a lake would clarify how bats are being impacted.

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LITERATURE CITED

Abbott, I.M., D.P. Sleeman, and S. Harrison. 2009. Bat activity affected by sewage effluent in Irish rivers. Biological Conservation 142:2904–2914.

Agosta, S.J. 2002. Habitat use, diet and roost selection by the Big Brown Bat (*Eptesicus fuscus*) in North America: a case for conserving an abundant species. Mammal Review 32:179–198.

Akasaka, T., D. Nakano, and F. Nakamura. 2009. Influence of prey variables, food supply, and river restoration on the foraging activity of Daubenton's bat (*Myotis daubentonii*) in the Shibetsu River, a large lowland river in Japan. Biological Conservation 142:1302–1310.

Anthony, E.L.P., and T.H. Kunz. 1977. Feeding strategies of the Little Brown Bat, *Myotis lucifugus*, in southern New Hampshire. Ecology 54:775–786.

Bahls, P. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Science 66:183–193.

Barclay, R.M.R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. Journal of Animal Ecology 60:165–178.

Barclay, R.M.R., and R.M. Brigham. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? American Naturalist 137:693–703.

Bell, G., and M.B. Fenton. 2011. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). Canadian Journal of Zoology 57:1271–1277.

Benjamin, J.R., K.D. Fausch, and C.V. Baxter. 2011. Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. Oecologia 167:503–512.

Bland, R.G., and H.E. Jaques. 1978. How to Know the Insects. 3rd Edition. WCB/McGraw-Hill, New York, New York.

Buchler, E.R. 1976. Prey selection in *Myotis lucifugus* (Chiroptera: Vespertilionidae). American Naturalist 110:619–628.

Collier, K., and B. Smith. 1995. Sticky trapping of adult mayflies, stoneflies and caddisflies alongside three contrasting streams near Hamilton, New Zealand. New Zealand Natural Sciences 22:1–9.

Clare, E.L., B.R. Barber, B.W. Sweeney, P.D.N. Hebert, and M.B. Fenton. 2011. Eating local: influences of habitat on the diet of Little Brown Bats (*Myotis lucifugus*). Molecular Ecology 20:1772–1780.

Cruz-Rivera, E., and M.E. Hay. 2000. Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. Ecology 81:201–219.

Davies, N.B. 1977. Prey selection and the search strategy of the Spotted Flycatcher (*Muscicapa striata*): a field study on optimal foraging. Animal Behaviour 25:1016–1033.

Duvergé, P.L., G. Jones, J. Rydell, and RD. Ransome. 2000. Functional significance of emergence timing in bats. Ecography 23:32–40.

Downs, N.C., and P.A. Racey. 2006. The use by bats of habitat features in mixed farmland in Scotland. Acta Chiropterologica 8:169–185.

Epanchin, P.N., R.A. Knapp, and S.P. Lawler. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. Ecology 91:2406–2415.

Erickson, J.L., and S.D. West. 2002. The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. Acta Chiropterologica 4:17–24.

Fenton, M.B., N.G.H. Boyle, T.M. Harrison, and D.J. Oxley. 1977. Activity patterns, habitat use, and prey selection by some African insectivorous bats. Biotropica 9:73–85.

Finlay, J.C., and V.T. Vredenburg. 2007. Introduced trout sever trophic connections in watersheds: consequences for a declining amphibian. Ecology 88:2187–2198.

Fukui D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75:1252–1258.

Furlonger, C.L., H.J. Dewar, and M.B. Fenton. 1987. Habitat use by foraging insectivorous bats. Canadian Journal of Zoology 65:284–288.

Griffin, D.R., F.A. Webster, and C.R. Michael. 1960. The echolocation of flying insects by bats. Animal Behaviour 8:141–154.

Gonsalves, L., B. Law, C. Webb, and V. Monamy. 2013. Foraging ranges of insectivorous bats shift relative to changes in mosquito abundance. PLoS ONE 8(5):1-11. https://doi.org/10.1371/journal.pone.0064081.

Hagen, E.M., and J.L. Sabo. 2011. A landscape perspective on bat foraging ecology along rivers: does channel confinement and insect availability influence the response of bats to aquatic resources in riverine landscapes? Oecologia 166:751–60.

Harvey, M.J., J.S. Altenbach, and T.L. Best. 2011. Bats of the United States and Canada. Johns Hopkins University Press, Baltimore, Maryland.

Hayes, J.P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. Journal of Mammalogy 78:514–524.

Henry, M., D.W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating Little Brown Bats (*Myotis lucifugus*). Journal of Mammalogy 83:767–774.

Herd, R.M., and M.B. Fenton. 1983. An electrophoretic, morphological and ecological investigation of a putative hybrid zone between *Myotis lucifugus* and *Myotis yumanensis* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 61:2029–2050.

Johnson, J.S., L.E. Dodd, J.D. Kiser, T.S. Peterson, and K.S. Watrous. 2012. Food habits of *Myotis leibii* along a forested ridgetop in West Virginia. Northeastern Naturalist 19:665–672.

Johnson, J.S., M.J. Lacki, and M.D. Baker. 2007. Foraging ecology of Long-legged Myotis (*Myotis volans*) in north-central Idaho. Journal of Mammalogy 88:1261–1270.

Jones, G., and J. Rydell. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 346:445–455.

Joseph, M.B., J. Piovia-Scott, S.P. Lawler, and K.L. Pope. 2011. Indirect effects of introduced trout on Cascades Frogs (*Rana cascadae*) via shared aquatic prey. Freshwater Biology 56:828–838.

Kalcounis-Rueppell, M.C., V.H. Payne, S.R. Huff, and A.L. Boyko. 2007. Effects of wastewater treatment plant effluent on bat foraging ecology in an urban stream system. Biological Conservation 138:120–130.

Keinath, D.A. 2004. Anabat call key for the Greater Yellowstone Ecosystem. Wyoming Natural Diversity Database, University of Wyoming, Laramie, Wyoming.

Knapp, R.A. 1996. Non-native trout in natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. Pp. 363–407 *in* Sierra Nevada Ecosystem Project: Final Report to Congress. Volume III. Assessments and Scientific Basis for Management Options. Centers for Water and Wildland Resources, University of California, Davis.

Knapp, R.A., and K.R. Matthews. 2000. Non-native fish introductions and the decline of the Mountain Yellow-legged Frog from within protected areas. Conservation Biology 14:428–438.

Knapp, R.A., K.R. Matthews, and O. Sarnell. 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecological Monographs 71:401–421.

Kurta A., G.P. Bell, K.A. Nagy, T.H. Kunz. 1989. Energetics of pregnancy and lactation in free-ranging Little Brown Bats (*Myotis lucifugus*). Physiological Zoology 62: 804–818.

Lawler, S.P., and K.L. Pope, 2006. Non-native fish in mountain lakes: effects on a declining amphibian and ecosystem subsidy. Technical Completion Report 987, University of California Water Resources Center, Berkeley, California. 22 p.

Matthews, K.R., and R.A. Knapp. 2002. Garter snake distributions in high-elevation aquatic ecosystems: is there a link with declining amphibian populations and nonnative trout introductions? Journal of Herpetology 36:16–22.

McWilliams, L.A. 2005. Variation in diet of the Mexican Free-tailed Bat (*Tadarida brasiliensis mexicana*). Journal of Mammalogy 86:599–605.

Miller, B. 2001. A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. Acta Chiropterologica 3:93–105.

Moosman, P.R., Jr., H.H. Thomas, and J.P. Veilleux. 2007. Food habits of Eastern Small-footed Bats (*Myotis leibii*) in New Hampshire. American Midland

Naturalist 158:354–360.

Ober, H.K., and J.P. Hayes, 2008. Prey selection by bats in forests of western Oregon. Journal of Mammalogy 89:1191–1200.

O'Farrell, M.J., B.W. Miller, and W.L. Gannon. 1999. Qualitative identification of free-flying bats using the Anabat detector. Journal of Mammalogy 80:11–23.

Pilliod, D.S., and C.R. Peterson. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems 4:322–333.

Pope, K.L., J. Piovia-Scott, and S.P. Lawler. 2009. Changes in aquatic insect emergence in response to whole-lake experimental manipulations of introduced trout. Freshwater Biology 54:982–993.

Rodriguez, R.M., and L.K. Ammerman. 2004. Mitochondrial DNA divergence does not reflect morphological difference between *Myotis californicus* and *Myotis ciliolabrum*. Journal of Mammalogy 85:842–851.

Rydell, J., A. Entwistle, and P. Racey. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76:243–252.

Scott, S.J., G. McLaren, G. Jones, and S. Harris. 2010. The impact of riparian habitat quality on the foraging and activity of Pipistrelle bats (*Pipistrellus* spp.). Journal of Zoology 280:371–378.

Seidman, V.M., and C.J. Zabel. 2001. Bat activity along intermittent streams in northwestern California. Journal of Mammalogy 82:738–747.

Storer, T.I., R.L. Usinger, and D. Lukas. 2004. Sierra Nevada Natural History. University of California Press, Berkeley, California.

Turner, A.K. 1982. Optimal foraging by the swallow (*Hirundo rustica*): prey size selection. Animal Behaviour 30:862–872.

Tyler, T., W.J. Liss, L.M. Ganio, G.L. Larson, R. Hoffman, E. Deimling, and G. Lomnicky. 1998. Interaction between introduced trout and larval salamanders (*Ambystoma macrodactylum*) in high-elevation lakes. Conservation Biology 12:94–105.

Waters, D.A., J. Rydell, and G. Jones. 1995. Echolocation call design and limits on prey size: a case study using the aerial-hawking bat *Nyctalus leisleri*. Behavioral Ecology and Sociobiology 37:321–328.

Whitaker, J.O., C. Neefus, and T.H. Kunz. 1996. Dietary variation in the Mexican Free-tailed Bat (*Tadarida brasiliensis mexicana*). Journal of Mammalogy 77:716–724.

Vaughan, N., G. Jones, and S. Harris. 1996. Effects of sewage effluent on the activity of bats (Chiroptera: Vespertilionidae) foraging along rivers. Biological Conservation 78:337–343.

Zar, J.H. 1999. Biostatistical Analysis. Pearson Education, Upper Saddle River, New Jersey.

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VARIATION AND PHENOLOGY OF *AMBYSTOMA MAVORTIUM* (WESTERN TIGER SALAMANDER) EGGS IN COLORADO

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***Abstract*.—Western Tiger Salamanders (*Ambystoma mavortium*) occur throughout Colorado, occupying an elevational range in the state from about 1,045 m to 3,660 m. These salamanders exhibit great variation in the onset of egg deposition. For breeding localities at elevations below about 2,000 m with permanent water, egg deposition takes place as early as March. At temporary pools at low elevation, rainfall, which may occur as late in the activity season as August, initiates breeding and egg deposition. At sites about 2,000 m and above, eggs appear later in the season with increasing elevation. Eggs of *A. m. mavortium* at low elevation sites have comparatively reduced jelly layers, but the diameter of the jelly layers surrounding the ovum increases with elevation for *A. m. nebulosum*, *A. m. melanostictum*, and *A. m. mavortium* × *nebulosum* intergrades.**

Key Words.—Colorado; egg characteristics; embryo; mole salamanders; phenology

INTRODUCTION

Western Tiger Salamanders (*Ambystoma mavortium*) occur throughout Colorado and occupy an elevational range of about 1,045 m to 3,660 m (Hammerson 1999; Stephen Mackessy, unpubl. report). Studies of mitochondrial DNA in the tiger salamander complex distinguished an eastern lineage (*Ambystoma tigrinum*) from the western lineages, including *A. mavortium* and its subspecies (Shaffer and McKnight 1996). Reese (1969) mapped the distribution of three subspecies present in Colorado. *Ambystoma m. mavortium* primarily inhabits the low elevations of the eastern plains, whereas *A. m. nebulosum* occurs in mountainous areas in the western half of the state; some intergradation between *A. m. mavortium* and *A. m. nebulosum* occurs where the two subspecies meet. *Ambystoma m. melanostictum* occurs in north-central and northwestern Colorado with limited intergradation with *A. m. nebulosum* (Fig. 1).

The larval and adult life-history stages of *A. mavortium* span months to years. Although larvae at many breeding sites metamorphose by the end of summer, at other sites larval or paedomorphic individuals (salamanders retaining the larval form but sexually mature) are resident throughout the year (Hammerson 1999). The presence of eggs and embryos at a breeding site is comparatively transitory. In Colorado, Reese (1969) stated that eggs generally hatch in 12–14 d or longer at high elevations. Laboratory observations for *A. m. nebulosum* in Utah indicate that development to hatching lasts from 6.5 d to 2–3 weeks depending on temperature (Tanner et al. 1971). In addition, the eggs and embryos can be as small as 4.2 mm total diameter and easily overlooked (pers. obs.). Consequently, fewer observations of eggs and embryos make it into the scientific literature, reports, or citizen science projects. Here I use the terminology recommended by Altig and McDiarmid (2007, 2015), who considered eggs to includes both the gamete (ovum) and jelly layers produced in the oviduct. The egg diameter is the distance across the outer jelly layer for a particular egg. Hatching, the stage at which the larva emerges from the egg (Voss 1993), occurs at approximately Harrison stage 40 (pers. obs.). In this paper I summarize the variability in the appearance of *A. mavortium* eggs, their modes of deposition, and observed phenology in Colorado.

METHODS

Generally incidental to other work, I observed eggs and embryos at *A. mavortium* breeding sites on 34 occasions between 1976 and 2020. When possible, I photographed representative eggs and made notes on the manner of deposition and other features. I noted where the eggs were deposited: on the substrate (pond or pool bottom); on submerged branches; or on vegetation. At 14 sites I measured an average of 10 (range one to 38) egg diameters (ovum/embryo plus jelly layers). At some sites I directly measured egg diameters with calipers, while at other sites I estimated egg diameters from photographs containing images of eggs and a ruler. I searched pertinent literature, reports, and obtained personal communications to compile additional information on egg phenology or characteristics (Hamilton 1949; Reese 1969; Sexton and Bizer 1978; Kiesecker 1991; Lambert 2001). Sources were excluded if they lacked the date of observation or enough information to determine elevation. I mapped localities using TOPO! 4.5.0 (National Geographic Holdings, San Francisco, California) to obtain estimates of breeding site elevations. Seasonal temperature and hydrologic regimes differ considerably between lowland sites versus sites in the mountains (considered here to be localities above 2,000 m elevation), so these were analyzed separately in terms of date of egg deposition.

Jelly layers of amphibian eggs rapidly absorb water after oviposition (Stebbins 1949; Thurow 1997), and I observed all eggs after this initial water absorption. Because I encountered eggs and embryos at different

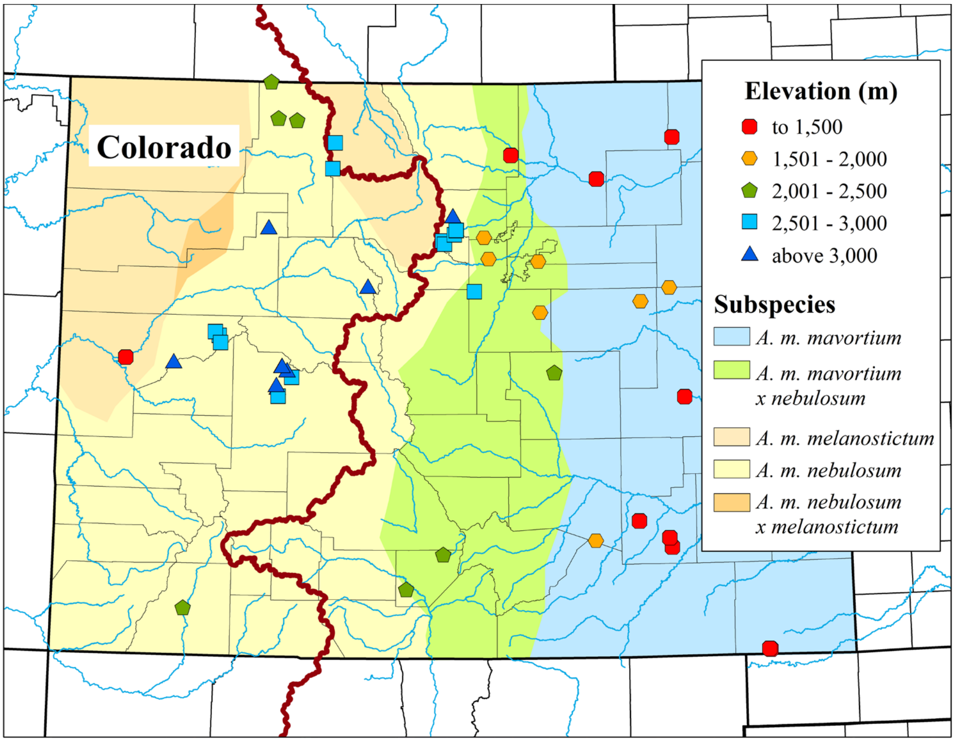

Figure 1. Distribution of subspecies of the Western Tiger Salamander (*Ambystoma mavortium*) in Colorado, including areas of intergradation, based on Figure 1 in Reese (1969). Blue background: *A. m. mavortium*; Green background: *A. m. mavortium* × *nebulosum*; Yellow background: *A. m. nebulosum*; Light tan background: *A. m. melanostictum*; Medium tan background: *A. m. nebulosum* × *melanostictum*. Symbols are sites where *A. mavortium* eggs were observed or described; they are coded by elevation (e.g., red octagons = lowest, blue triangles = highest). The red line depicts the Continental Divide and blue lines represent significant rivers and creeks.

developmental stages, comparisons of ovum diameters were not feasible; consequently, I do not include information about ovum diameter. In cases where I encountered eggs while the developing gamete was still roughly spherical, I sometimes was able to judge egg color. I used Pearson's Product Moment Correlation ($\alpha = 0.05$) to determine correlations between elevation and Julian date and between elevation and egg diameter.

Results

The 134 eggs that I measured ranged in diameter from 3.9–16.7 mm, with the largest egg diameters observed at high elevations (Table 1). I used records of *Ambystoma mavortium* eggs from 46 unique sites (27 personal records, 20 records from other sources, with one site having information from both personal observations and literature sources), throughout Colorado at elevations ranging between 1,322–3,281 m. Reports of eggs were found at breeding site elevations up to 3,410 m (Sexton and Bizer 1978). The localities represent each of the three subspecies present (*A. m. mavortium*, *A. m. nebulosum*, and *A. m. melanostictum*) in Colorado as well as the zone of intergradation between *A. m. mavortium* and *A. m. nebulosum.*

There were distinctly different patterns of egg presence related to elevation (Fig. 2). At elevations below about 2,000 m (the approximate elevation at which the foothills begin along the Front Range), eggs have been observed from 1 March to 21 August. There was no significant correlation between elevation and Julian date for sites at elevations below 2,000 m ($r = -0.276$, $t = -1.200$, df = 19, $P > 0.050$). At sites above 2,000 m, the earliest reports

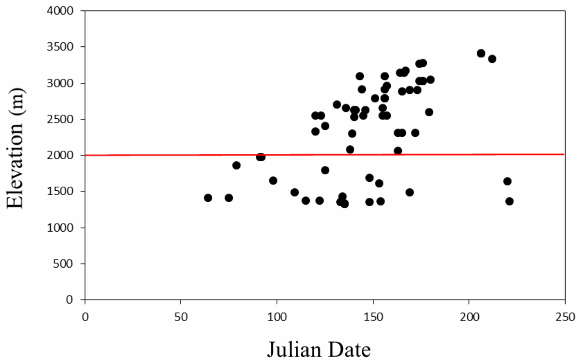

Figure 2. Relationship between elevation and Julian date at which the presence of eggs of Western Tiger Salamanders (*Ambystoma mavortium*) was noted at 67 breeding sites (pers. obs.; Steve Warren, pers. comm.) and literature sources (Hamilton 1949; Reese 1969; Sexton and Bizer 1978; Kiesecker and Clarke 1991; Lambert 2001). The red line at 2,000 m represents the approximate boundary between low elevation and montane sites. Where eggs were observed on different dates, the same site may be represented multiple times.

Table 1. Egg diameters of salamanders in Colorado by county. Subspecies codes are m = *A. m. mavortium*, m × n = *A. m. mavortium* × *nebulosum,* and n = *A. m. nebulosum.* Sites represented by images in Figure 3 are indicated in the Image column. The abbreviation SE = standard error.

County	Elevation (m)	Subspecies	Range (mm)	Mean and SE (mm)	n	Image
Otero	1,355	m	5.0–9.0	7.6 ± 0.40	10	
Otero	1,361	m	5.0–6.9	6.2 ± 0.42	4	3B
Otero	1,432	m	5.0–9.0	7.2 ± 0.51	10	
Lincoln	1,490	m	5.0–5.4	5.2 ± 0.09	4	3E
Lincoln	1,617	m	3.9–5.4	4.5 ± 1.77	8	
Boulder	1,793	m × n	8.4–8.7	8.5 ± 0.06	4	3G
Jefferson	1,975	m × n	4.2–5.4	4.5 ± 0.18	6	3H
Alamosa	2,334	m × n	6.8–7.1	6.9 ± 0.15	2	3J
Boulder	2,553	m × n	10.3–12.8	11.0 ± 0.38	6	
Mesa	2,632	n	6.4–10.4	8.4 ± 0.19	30	
Mesa	2,632	n	6.3–11.8	9.0 ± 0.23	38	
Gilpin	2,790	m × n		12.0	1	
Gilpin	2,960	m × n	9.3–16.9	12.4 ± 1.35	6	
Gilpin	2,960	m × n	13.1–16.2	14.6 ± 0.55	5	3O

of eggs were 30 April in both 1947 and 2006 (Hamilton 1949; pers. obs.) and the latest 31 July 1975 (Sexton and Bizer 1978). For breeding areas above 2,000 m, elevation and Julian date were significantly correlated ($r = 0.657$, $t = 4.339$, df = 44, $P < 0.010$).

I observed striking variations in the deposition mode and appearance of eggs across region and elevation (Fig. 3). Of 34 sites, five sites had eggs on both the substrate and submerged vegetation, seven sites had eggs on the substrate only, and 19 sites had eggs on submerged vegetation. For example, the only eggs I found at a breeding site were in a cluster of four that had been deposited in shallow water directly on the substrate (Fig. 3G). Detectability of eggs located on substrate likely was hindered with increasing water depth or turbidity. Most eggs are attached to a long stick raised slightly above the substrate, but several eggs are scattered directly on the substrate (Fig. 3D). When attached to branches or plant stems, eggs could be deposited singly or in short linear rows. Eggs sometimes are spaced along stems well above the substrate. One pond in western Boulder County had an especially distinctive example of egg deposition in which the eggs with large jelly layers were crowded along a stem several cm above the substrate (Fig. 3L).

Although I encountered eggs at different developmental stages, my impression was that ova from at least some low elevation sites seemed to be much lighter in color than ova encountered at high elevation sites, which were generally black. These light ova from low elevations were not dead and appeared to be developing normally. The amount of jelly surrounding the ovum or embryo was distinctly variable, with high elevation eggs having a much larger diameter (ovum or embryo and jelly layers) than eggs from low elevations (Fig. 4). There was a significant correlation between elevation and egg diameter for eggs measured from 14 breeding sites ($r = 0.611$, $t = 14.805$, df = 132, $P < 0.010$).

DISCUSSION

At elevations below 2,000 m in eastern Colorado, most populations are *A. m. mavortium* or intergrades with *A. m. nebulosum* (Reese 1969). The earliest instances of egg deposition occur when ponds already contain water and ambient temperatures are high enough to clear ice from the surface of the pond as well as allow overland movement to the pond by salamanders from their overwintering sites. In contrast, more temporary sites often require rainfall to fill pools with sufficient water for breeding and egg deposition. Two instances of late season egg deposition occurred in August at temporary, low elevation sites after the first sufficient rainfalls of the year (Reese 1969; pers. obs.). This pattern is consistent with the timing of reproduction observed in *A. m. mavortium* in New Mexico (Webb and Roueche 1971; Jones and Collins 1992). The occasional presence of larvae of different size classes in a pond suggests egg deposition, presumably by different females, can occur asyncronously during the activity season (Hammerson 1999; pers. obs.).

The mountains of Colorado are occupied by both *A. m. nebulosum* and *A. m. melanostictum*, the intergrade populations of *A. m. nebulosum* × *mavortium*, as well as the limited area of intergradation of *A. m. nebulosum* × *melanostictum* (Reese 1969). Breeding of *A. m. nebulosum* in the mountains of Arizona and New Mexico takes place in the spring but apparently not later in the season (Jones and Collins 1992). In the mountains of

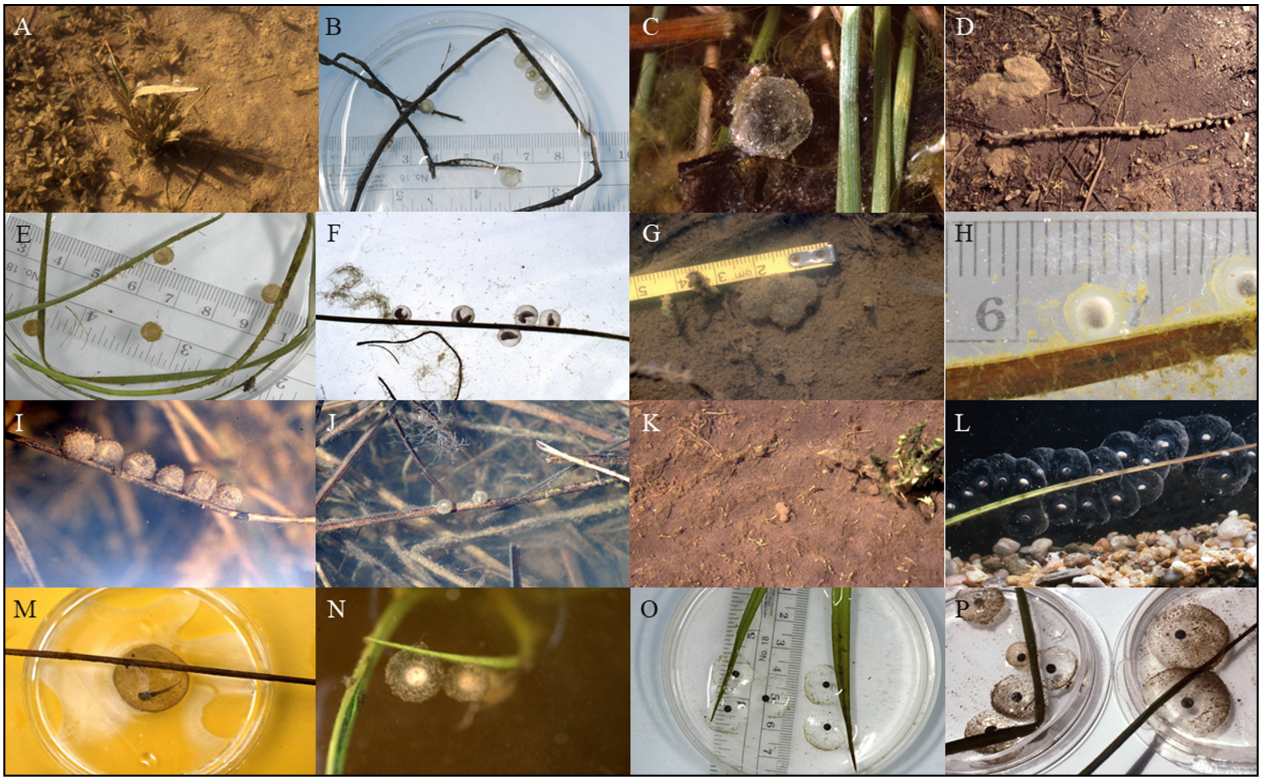

Figure 3. Representative eggs of Western Tiger Salamander (*Ambystoma mavortium*). (A) Otero County, 1,355 m elevation. (B) Otero County, 1,361 m elevation. (C) Weld County, 1,370 m elevation. (D) Otero County, 1,432 m elevation. (E) Lincoln County, 1,490 m elevation. (F) Lincoln County, 1,617 m elevation. (G) Boulder County, 1,793 m elevation. (H) Jefferson County, 1,975 m elevation. (I) La Plata County, 2,084 m elevation. (J) Alamosa County, 2,334 m elevation. (K) Mesa County, 2,528 m elevation. (L) Boulder County, 2,553 m elevation. (M) Jefferson County, 2,598 m elevation. (N) Boulder County, 2,656 m elevation. (O) Jackson County, 2,701 m elevation. (P) Gilpin County, 2,960 m elevation. Fig. 3A, 3C, 3D, 3G, 3I, 3J, 3K, and 3N photographed *in situ*. (Photographed by Lauren J. Livo).

Colorado, *A. mavortium* breeding sites generally begin the season with sufficient water as a result of snowmelt even if the sites dry up later, but elevation and other factors, including the source of water, water volume, and amount of solar radiation on the water body (Sexton and Bizer 1978), affect the thermal regime. Elevation and date are strongly correlated for montane sites, with earlier deposition at sites closer to 2,000 m elevation and with egg deposition later in the season at higher elevation sites.

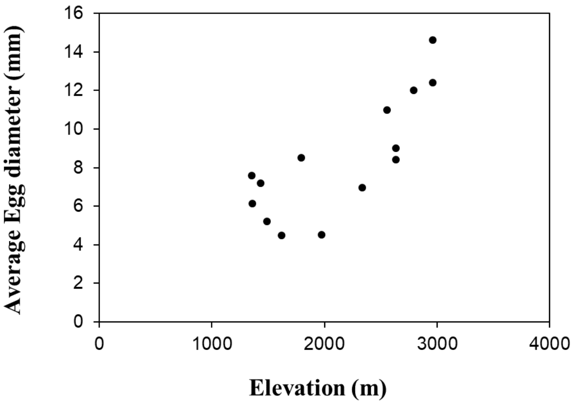

Figure 4. Relationship between average egg diameter (ovum or embryo and jelly layers) of Western Tiger Salamanders (*Ambystoma mavortium*) and elevation for 14 localities.

The most comprehensive review of *A. mavortium* in Colorado, including information about eggs, was provided by Reese (1969). He described eggs as having three jelly layers, generally being deposited singly or in a row, and having an average total diameter (ovum and surrounding jelly layers) of 5.5 mm, but he did not describe variation across the state (Reese 1969). Altig and McDiarmid (2015) state that *A. mavortium* has egg diameters ranging from 5.0–12.0 mm. Egg diameters observed by Hamilton (1949) from the mountains of Boulder County varied from 5 to 18 mm.

The eggs I measured varied substantially, with the lowest egg diameters being smaller than previously reported and the largest approaching the largest reported. Although Reese (1969) considered the diameter of 18 mm stated by Hamilton (1949) to be a *lapsus*, I measured egg diameters that approached 18 mm so I consider the measurement by Hamilton to be valid. Eggs from areas inhabited by *A. m. mavortium* had the smallest diameters, and *A. m. mavortium* × *nebulosum* and *A. m. nebulosum* the largest diameters.

Eggs sometimes are deposited on the bottom of the pond, but when available, most eggs are observed on sticks, plant stems, or other structures. Shallow, clear water likely increased the opportunity to detect eggs on substrate, while deep, stained, or turbid water reduced detection of eggs on the substrate. This agrees with observations by others (Hamilton 1949; Reese 1969; Wissinger and Whiteman 1992) including egg deposition in populations in Utah (Tanner et al. 1971), New Mexico (Collins et al. 1980), and southeastern Idaho (Jones et al. 2005). With respect to the mode of egg deposition, the eggs deposited by *Ambystoma mavortium* in the mountains of Boulder County are of particular interest. Hamilton (1949) collected eggs from two ponds in this area as part of his study of polydactyly at one of the ponds. He provided descriptions and photographs of a more typical linear arrangement of eggs along stems as well as what he described as a cluster of eggs, likely from Mud Lake, which he described as enclosed in a large mass of gelatinous material. Nearly half a century later, I observed eggs at Mud Lake with large jelly layers crowded along stems in a manner that could be described as an egg cluster. This is the only site at which I have observed eggs deposited in this manner. I observed the more typical deposition mode of eggs singly or in linear rows along stems at three breeding sites in the mountains within 3.8–14 km of Mud Lake.

In *A. mavortium* eggs that I observed, the amount of jelly surrounding the ovum or embryo increased with increasing elevation of the breeding site. This increase in egg jelly with elevation may be the result of several potential selective factors because amphibian egg jelly is thought to be protective in several possible ways, including: permitting or blocking fertilization (Elinson 1974); protecting or delaying desiccation when water levels drop (Marco and Blaustein 1998); protecting against water molds (Gomez-Mestre et al. 2006); protecting against ultraviolet radiation (Calfee et al. 2006); and making predation by both vertebrates and invertebrates more difficult (Werschkul and Christensen 1977; Ward and Sexton 1981; Pearl 2003). Although at least some light colored ova were observed at low elevation breeding sites, at most high elevation sites the ova I observed were heavily pigmented. The melanin in dark ova can be protective against ultraviolet radiation (Licht 2003).

Deposition of eggs on stems, leaves, and other structures may also be protective, especially against predation. Because I often found relatively few eggs compared to the expected clutch size of up to 666 eggs (Moore and Whiteman 2016), eggs may have been deposited in a variety of ways that I did not observe. Although I occasionally observed egg deposition on the substrate, especially in temporary pools at low elevations that at least initially would lack most egg predators, I did not observe egg deposition on the substrate at high elevation sites. High elevation breeding sites often had permanent water, potentially resulting in a greater existing load of egg predators such as leeches, beetle larvae, and even paedomorphic *A. mavortium*, which at least in the laboratory are known to cannibalize conspecific eggs (Hamilton 1948).

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LITERATURE CITED

Altig, R., and R.W. McDiarmid. 2007. Morphological diversity and evolution of egg and clutch structure in amphibians. Herpetological Monographs 21:1–32.

Altig, R., and R.W. McDiarmid. 2015. Handbook of Larval Amphibians of the United States and Canada. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, USA.

Calfee, R.D., C.M. Bridges, and E.E. Little. 2006. Sensitivity of two salamander (*Ambystoma*) species to ultraviolet radiation. Journal of Herpetology 40:35–42.

Collins, J.P., J.B. Mitton, and B.A. Pierce. 1980. *Ambystoma tigrinum*: a multispecies conglomerate? Copeia 1980:938–941.

Elinson, R.P. 1974. A block to cross-fertilization located in the egg jelly of the frog *Rana clamitans*. Embryology and Experimental Morphology 32:325–335.

Gomez-Mestre, I., J.C. Touchon, and K.M. Warkentin. 2006. Amphibian embryo and parental defenses and a larval predator reduce egg mortality from water mold. Ecology 87:2570–2581.

Hamilton, R. 1948. The egg-laying process in the Tiger Salamander. Copeia 1948:212–213.

Hamilton, R.S. 1949. Natural history of the Rocky Mountain Tiger Salamander *Ambystoma tigrinum* and the occurrence of polydactylism in a local population. M.A. Thesis. University of Colorado, Boulder, Colorado, USA. 72 p.

Hammerson, G.A. 1999. Amphibians and Reptiles in Colorado. 2nd Edition. University Press of Colorado, Niwot, Colorado, USA.

Jones, L.L.C., W.P. Leonard, and D.H.Olson (Eds.). 2005. Amphibians of the Pacific Northwest. Seattle Audubon Society, Seattle, Washington, USA.

Jones, T.R., and J.P. Collins. 1992. Analysis of a hybrid zone between subspecies of the Tiger Salamander (*Ambystoma tigrinum*) in central New Mexico, USA. Journal of Evolutionary Biology 5:375–402.

Kiesecker, J.M. 1991. Acidification and its effects on amphibians breeding in temporary ponds in montane Colorado. M.A. Thesis. University of Northern

Colorado, Greeley, Colorado, USA. 78 p.

Kiesecker, J.M., and J. Clarke. 1991. Effects of pH levels on a montane population of the Tiger Salamander in Colorado. Journal of the Colorado-Wyoming Academy of Science 23:9 [Abstract].

Lambert, B. 2001. Colorado Natural Heritage Program Boreal Toad Survey and Monitoring Project 2001. Colorado Natural Heritage Program, Fort Collins, Colorado, USA.

Licht, L.E. 2003. Shedding light on ultraviolet radiation and amphibian embryos. BioScience 53:551–561.

Marco, A., and A.R. Blaustein. 1998. Egg gelatinous matrix protects *Ambystoma gracile* embryos from prolonged exposure to air. Herpetological Journal 8:207–211.

Moore, M.P., and H.H. Whiteman. 2016. Natal philopatry varies with larval condition in salamanders. Behavioral Ecology and Sociobiology 70:1247–1255.

Pearl, C.A. 2003. *Ambystoma gracile* (Northwestern Salamander). Egg predation. Herpetological Review 34:352–353.

Reese, R.W. 1969. The taxonomy and ecology of the Tiger Salamander (*Ambystoma tigrinum*) of Colorado. Ph.D. Thesis. University of Colorado, Boulder, Colorado, USA. 154 p.

Sexton, O.J., and J.R. Bizer. 1978. Life history patterns of *Ambystoma tigrinum* in montane Colorado. American Midland Naturalist 99:101–118.

Shaffer, H.B., and M.L. McKnight. 1996. The polytypic species revisited: genetic differentiation and molecular phylogenetics of the Tiger Salamander *Ambystoma tigrinum* (Amphibia: Caudata) complex. Evolution 50:417–433.

Stebbins, R.C. 1949. Observations on laying, development, and hatching of the eggs of *Batrachoseps wrighti.* Copeia 1949:161–168.

Tanner, W.W., D.L. Fisher, and T.J. Willis. 1971. Notes on the life history of *Ambystoma tigrinum nebulosum* Hallowell in Utah. Great Basin Naturalist 31:213–222.

Thurow, G. 1997. *Rana sylvatica* (Wood Frog). Egg mass features and larval behavior. Herpetological Review 28:148.

Voss, S. R. 1993. Effect of temperature on body size, developmental stage, and timing of hatching in *Ambystoma maculatum*. Journal of Herpetology 27:329–333.

Ward, D., and O.J. Sexton. 1981. Anti-predator role of salamander egg membranes. Copeia 1981:724–726.

Webb, R.G., and W.L. Roueche. 1971. Life history aspects of the Tiger Salamander (*Ambystoma tigrinum mavortium*) in the Chihuahuan Desert. Great Basin Naturalist 31:193–212.

Werschkul, D.F., and M.T. Christensen. 1977. Differential predation by *Lepomis macrochirus* on the eggs and tadpoles of *Rana*. Herpetologica 33:237–241.

Wissinger, S.A., and H.H. Whiteman. 1992. Fluctuation in a Rocky Mountain population of salamanders: anthropogenic acidification or natural variation? Journal of Herpetology 26:377–391.

Lauren J. Livo for several years conducted research on the Boreal Toad (*Anaxyrus boreas*) in collaboration with the Colorado Division of Wildlife. After receiving a Ph.D. from the University of Colorado, Boulder, USA, she continued her work on the Boreal Toad as a Post-Doctoral Fellow at the University of Colorado. Subsequent to retiring, she has been documenting the geographic distribution and phenology of amphibian and reptile species in Colorado, especially that of various introduced species including Pond Slider (*Trachemys scripta*)*,* Colorado Checkered Whiptail (*Aspidoscelis neotesselatus*)*,* and Chihuahuan Spotted Whiptail (*A. exsanguis*). (Photograph by Steve Wilcox).

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NOTES

PREVIOUSLY UNDOCUMENTED HABITAT USE BY THE CALIFORNIA TIGER SALAMANDER (*AMBYSTOMA CALIFORNIENSE*)

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***Abstract*.—Populations of the endangered California Tiger Salamander (*Ambystoma californiense*) have experienced declines throughout the species range. Although the species is relatively easy to detect in its aquatic breeding habitat, little remains known about the details of the non-breeding upland habitat by this species. We found seven adult California Tiger Salamanders beneath thatch of emergent vegetation at the bottom of a constructed pond that was known to be dry for 15 mo. This represents new information on the adult phase of the use of habitat by this species, and we suggest this behavior might be more widespread, yet undetected.**

Key Words.—dry pond; excavation; habitat; restoration

The California Tiger Salamander (*Ambystoma californiense*) is a bi-phasic amphibian species, which is endemic to California and in decline throughout its range (U.S. Fish and Wildlife Service [USFWS] 2000, 2002, 2004). Habitat loss and associated population declines supported listing of the species as threatened or endangered at both the federal and state levels (Stebbins and Cohen 1995; USFWS 2002, 2004; Fitzpatrick and Shaffer 2004). This species generally breeds in perennial and ephemeral ponds, vernal pools, slow sections of creeks, and other still waters (Storer 1925; Loredo and Van Vuren 1996; Alvarez 2004; Alvarez et al. 2021). The California Tiger Salamander spends the majority of its adult life stage underground, typically in rodent burrows (Storer 1925; Loredo and Van Vuren 1996; Stebbins and McGinnis 2012). Adults migrate to aquatic breeding habitat during fall and winter rains but are otherwise believed to remain underground (Storer 1925; Twitty 1941; Stebbins and McGinnis 2012). Recently, Alvarez et al. (2021) reported habitat use where California Tiger Salamanders were found breeding in sites not previously considered suitable. Herein, we report on previously unreported habitat use by the species.

We worked in a pond located in the upper Marsh Creek watershed, which is in eastern Contra Costa County, California (Fig. 1), and is comprised primarily of annual non-native grasses, Oak Savannah, Blue Oak (*Quercus douglasii*) and Valley Oak (*Q. lobata*) woodland, and mixed Chaparral habitats covering low rolling hills. This portion of the watershed is owned and managed by the Contra Costa Water District, which oversees special-status species and their habitat through a Programmatic Biological Opinion. As part of annual efforts to enhance habitat for California Tiger Salamanders and California Red-legged Frogs (*Rana draytonii*), we planned to remove silt and excess vegetation from a mitigation pond (Pond 3W) within the headwaters of a tributary to Marsh Creek. Pond 3W was a constructed wetland site (hereafter: pond) that functioned as a breeding site for California Tiger Salamanders, California Red-legged Frogs, and other native amphibians (unpubl. data; Fig. 2). The pond was approximately 4,400 m in area and 1.6 m maximum depth when inundated. During the construction of the pond in 1998, hundreds of vegetative plugs of Spikerush (*Eleocharis palustris*) were planted to establish a vegetated wetland feature with a mixed vegetation (upland and aquatic) component.

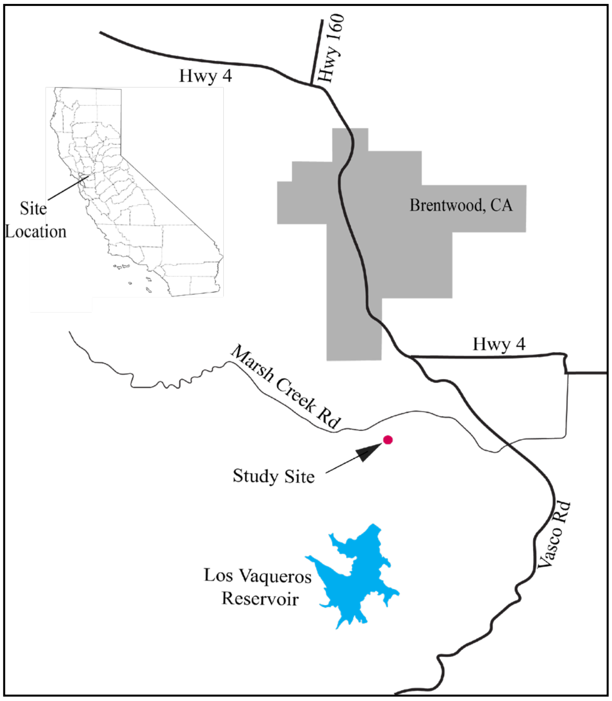

FIGURE 1. Vicinity and specific location of pond B3W (Study Site) in the upper Marsh Creek Watershed, north of the Los Vaqueros Reservoir, Contra Costa County, California.

Figure 2. Constructed wetland (i.e., pond) prior to removal of silt and vegetation (darker area), and the subsequent discovery of seven California Tiger Salamanders (*Ambystoma californiense*) under the dense thatch layer, Contra Costa County, California. (Photographed by Jeff A. Alvarez).

At the time of the restoration effort (September 2014), the pond had ≥ 90% vegetative cover comprised of cattail (*Typha* sp.) and Hard-stem Bulrush (*Schoenoplectus acutus*), with no open water component. Due to the conditions at the time, it was determined that silt (approximately 1 m in depth) and 70% of the emergent vegetation would be removed, and the bottom contour of the pond would be returned to the original design. An excavator was used to slowly remove vegetation first from the outer edges, progressing toward the center of the pond. The excavator operator was monitored by biologists who instructed the operator to remove layers of soil between 15 and 30 cm deep during each pass.

Biological monitors recovered animals that were found moving within the active construction zone or that were found within loose soil. As the excavator operator worked to the presumed center of the pond, biologists discovered a single adult California Tiger Salamander in the loose soil that was left after peeling the layer of emergent vegetation from the pond bottom. On the second pass through the vegetation, we discovered five additional adult California Tiger Salamanders (Fig. 3). At this time the monitoring biologists instructed the operator to work more slowly and to remove layers that were < 15 cm each. In doing so biologists found an additional single adult California Tiger Salamander nested in the loose soil at the pond bottom. Thereafter we observed no other California Tiger Salamanders within the work area or in the spoils deposition site upslope of the pond. In addition to the seven California Tiger Salamanders, biologists found 19 Pacific Treefrogs (*Hyliola regilla*), 13 Western Toads (*Anaxyrus boreas*), five Western Skinks (*Plestiodon skiltonianus*), four Western Fence Lizards (*Sceloporus occidentalis*), two Gopher Snakes (*Pituophis catenifer*), one Northern Pacific Rattlesnake (*Crotalus oreganus*), five California Voles (*Microtus californicus*), two Deer Mice (*Peromyscus* sp.), and two Botta's Pocket Gophers (*Thomomys bottae*).

This pond site, which had an artificial source for hydration (i.e., water pumped from a well) was monitored six times annually for its vegetation components and hydrology for 16 y, beginning in 1998. Water levels were typically maintained through an electrically powered well that was manually operated. Unpublished records from the Contra Costa Water District showed that the pond was determined to be dry (i.e., no standing water based on visual surveys and staff gauge readings) for 15 consecutive months prior to our restoration. We surmised that adult California Tiger Salamanders may have migrated to the pond site during their fall migration in the previous year, but the pond remained dry. These animals sought refuge in the pond, under a very dense (approximately 1 m thick) layer of cattail and bulrush thatch that lay flat over the center portion of the pond. This thick layer of thatch may have provided adequate refuge for these adult salamanders for many months. The dry vegetation and thatch layer may have also maintained high humidity levels at the soil surface and provided cover from many predators.

Although biologists were mandated to monitor the site by the Programmatic Biological Opinion, the presence, or even potential presence, of adult salamanders at the bottom of a pond that was dry for 15 mo was not anticipated. We considered this observation novel and surprising because most adult salamanders are found within rodent burrows in September (Storer 1925; Loredo and Van Vuren 1996; Stebbins and McGinnis 2012), the time of our work. Storer (1925) was the first to state that adult California Tiger Salamanders may be found under cover objects on the surface, and our own work corroborates this assertion, but this may only be true during the migratory period (unpubl. data).

Our findings reported here indicate a continued need to assess and investigate the natural history of this species. We have found that habitats such as a dry pond are often considered *a priori* unoccupied by salamanders. The only reason salamanders were found in the dry pond was because of the decision to conduct silt and vegetation removal without any expectation of finding California Tiger Salamanders. We contend that reports of novel observations of behaviors previously unreported may fill a gap in knowledge about species natural history that can be vital to the management and persistence of that species on a site. Bury (2006) pointed out the connection between natural history, field ecology, conservation biology, and wildlife management, fields that are critical to managing species at risk. We agree and suggest that our observation can be connected to many other singular observations that facilitate understanding the natural history of this species. This species has a cryptic natural history, particularly in upland portions of occupied habitats, where it can be difficult to detect (Searcy and Shaffer 2008; Wang et al. 2009). In our case, a pond that is typically a breeding site for the California Tiger Salamander served as upland habitat because it was dry for over a year.

Figure 2. Fresh excavation at the bottom of a pond that was dry for 15 mo, with adult California Tiger Salamanders (*Ambystoma californiense*) found among the loose soil and shallow cracks after the thick thatch layer of emergent vegetation was removed, Contra Costa County, California. (Photographed by Jeff A. Alvarez).

We suggest thorough pre-construction surveys of sites prior to land management actions that alter habitat components. Yet, even when the results of these types of surveys include no species observations, biological monitoring should still be required. The role of a biological monitor should include preconstruction surveys and on-site monitoring of ground disturbing projects, which can yield novel observations of protected species.

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LITERATURE CITED

Alvarez, J.A. 2004. Overwintering California Tiger Salamander (*Ambystoma californiense*). Larvae. Herpetological Review 35:344.

Alvarez, J.A., M.A. Shea, S.M. Foster, and J.T. Wilcox. 2021. Use of atypical aquatic breeding habitat by the California Tiger Salamander. California Fish and Wildlife Special CESA Issue: 235–240.

Bury, B.R. 2006. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. Herpetological Conservation and Biology 1:56–61.

Fitzpatrick, B.M., and H.B. Shaffer. 2004. Environment-dependent admixture dynamics in a tiger salamander hybrid zone. Evolution 58:1282–1293.

Loredo, I., and D.H. Van Vuren. 1996. Reproductive ecology of a population of the California Tiger Salamander. Copeia 1996:895–901.

Searcy, C.A., and H.B. Shaffer. Calculating biologically accurate mitigation credits: insights from the California Tiger Salamander. Conservation Biology 22:997–1005.

Stebbins, R.C., and N.W. Cohen. 1995. A Natural History of Amphibians. Princeton University Press, Princeton, New Jersey, USA.

Stebbins, R.C., and S.M. McGinnis. 2012. Field Guide to the Amphibians and Reptiles of California. University of California Press, Berkeley, California, USA.

Storer, T. I. 1925. A synopsis of the amphibia of California. University of California Publications in Zoology 27:1–342.

Twitty, V.C. 1941. Data on the life history of *Ambystoma tigrinum californiense* Gray. Copeia 1941:1–4.

U.S. Fish and Wildlife Service (USFWS). 2000. Endangered and threatened wildlife and plants; final rule to list the Santa Barbara County distinct population of the California Tiger Salamander as endangered. Federal Register 65:57242–57264.

U.S. Fish and Wildlife Service (USFWS). 2002. Endangered and threatened wildlife and plants; listing the Sonoma County distinct population segment of the California Tiger Salamander. Federal Register 67:47726–47740.

U.S. Fish and Wildlife Service (USFWS). 2004. Endangered and threatened wildlife and plants; determination of threatened status for the California Tiger Salamander; and special rule exemption for existing ranching activities. Federal Register 69:47212–47248.

Wang, I.J., W.K. Savage, and H.B. Shaffer. 2009. Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California Tiger Salamander (*Ambystoma californiense*). Molecular Ecology 18:1365–1374.

2021 ANNUAL MEETING REVIEW

68th Annual Meeting, Virtual

Program Chair: **Dan Airola,** Conservation Research and Planning

Attendance: 578 participants including 119 students and 41 Early Career Professionals.

Plenary Theme: *Conservation in Challenging Times*

Plenary Speakers: **Michael Lynes,** Audubon California; **Valerie Termini**, California Department of Fish and Wildlife; **Rachel Zwillinger,** Defenders of Wildlife; **Hugh Safford,** USDA-Forest Service's Pacific Southwest Region**;** **Rodney Siegel,** Institute for Bird Populations; **Zack Steel,** UC Berkeley.

Keynote Address: ***Merav Ben-David,*** *Professor Zoology and Physiology, University of Wyoming*

Awards Bestowed:

- In Memoriam: **Jim Brownell**, 1936-2020, and **Dr. Stanley "Doc" Harris**, 1929-2020.
- The Raymond F. Dasmann Award for the Professional of the Year went to **Dr. Geoffrey Geupel.**
- The Conservationist of the Year Award went to **Biologists without Borders.**
- The Chapter of the Year Award went to the **Southern California Chapter.**
- The James D. Yoakum for Outstanding Service and Commitment to The Western Section of The Wildlife Society went to **Kent Smith.**
- The Barrett A. Garrison Mentor of the Year Award went to **Jeff Lincer.**
- The TWS Fellows Award went to **Cynthia Perrine.**

Student Presentation Awards:

Oral Presentations

1st Place—Ellie Bolas, The Evolutionary History of Island Spotted Skunks on the California Channel Islands

and **1st Place—Kristin Brunk,** Management Reduces Density of a Highly Subsidized Generalist Predator in a Protected Area

2nd Place—Vanessa ZoBell, Playing in Traffic: Investigating Impacts of Commercial Shipping on Baleen Whales and Identifying Effective Solutions

2nd Place—Phoebe Parker-Shames, Consequences of Cannabis: Examining the Spatial Overlap of Cannabis with Aquatic and Terrestrial Habitats

and **2nd Place—Christine Wilkinson**, Quantifying Wildlife Responses to Conservation Fencing in East Africa

Poster Presentations

1st Place—Madison Dunlap, Adding Scent: Exploring Improvements to Pan Trapping to Monitor Pollinators

2nd Place—Scarlett Stromer, Comparison of Endoparasite Abundance and Species Richness in Relation to the Body Condition of two Roosevelt Elk Herds in Northern California

3rd Place—Ryan Vosbigain, Drivers of Movement and Density of San Joaquin Antelope Squirrels in the Carrizo Plain

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