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Arboreality in the California Whipsnake (*Masticophis lateralis*): Implications for Survey Techniques

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Historically, new species were defined by mensural characters and descriptive analyses of external features (i.e., coloration, patterning, behavior) that attempted to delineate new species from those previously described. Ecological associations (e.g., habitat, microhabitat, geographic extent or location, etc.) further defined the differences between one species and those closely related (Van Denburgh 1897). Over time, the species' niche becomes better defined as various researchers use different foci or perspectives to investigate natural history traits (Storer 1925). Occasionally, natural history traits that were once considered putative, particularly in older references, are lost to the cognizance of modern researchers and become rarely referenced.

The California whipsnake [*Masticophis* (=*Coluber*) *lateralis*], first described by Hallowell in 1853, provides an example of this phenomenon. This species is a relatively long, narrow-bodied snake that is found throughout the foothills or low- to mid-elevations of portions of the Coast, Cascade, Sierra Nevada, Transverse and Peninsular Ranges in California, as well as northwestern Baja California (Stebbins 1954; Brown 1997; Grismer 2002; Flaxington 2021). Early investigators described the California whipsnake as arboreal (Grinnell and Grinnell 1907; Grinnell and Storer 1924; Ortenburger 1928; Pickwell 1947; Stebbins 1954; Appendix I), but when an extended gap in published work on snake habitat occurred, awareness of the snake's arboreal traits did not span that gap. Here, we draw upon our own recent investigations to describe arboreal traits of the California whipsnake and use those observations to suggest that it be considered semi-arboreal, and that survey and management techniques should reflect this snake's behavior. Further, we describe survey techniques designed to examine habitat features that best support the arboreal nature of this snake. Following Stebbins (1954) general natural history account, nearly 40 yrs elapsed before new information on California whipsnake habitat and microhabitat was published. Subsequent to subspeciation of *M. lateralis*, with one subspecies becoming listed as threatened in the San Francisco Bay region by state and federal wildlife agencies, a new focus on the natural history of the species was initiated (Reimer 1954; CDFW 1987; USFWS 1997, 2002). Interest in the listed Alameda whipsnake subspecies (*M. l. euryxanthus*) sparked a flurry of new observations and research beginning with Swaim and McGinnis (1992) who reported habitat associations for the Alameda whipsnake, including preferred habitat features. However, they made no mention of the arboreal behavior in the species or subspecies, nor the potential effects of this behavior on their methodology for study. Lind (1992) picked up the thread carried by early researchers when she reported that a California whipsnake was "found 2 m above ground in a canyon live oak (*Quercus chrysolepis*)..." supporting the arboreal nature of the species described in historical accounts. In 1994, Swaim prepared a detailed report on the ecology of *M. l. euryxanthus,* but arboreality and climbing ability, and its potential impact on the ground-level trapping surveys used to

Fig. 1. California whipsnake basking and potentially foraging in a manzanita (*Arctostphylus* sp.) shrub in Napa County, California. Photo by J.A. Alvarez.

determine presence, were not discussed. Subsequent work by Alvarez et al. (2005), Alvarez (2006), and Miller and Alvarez (2016) also focused on habitat use, but few (<2%) observations used in those analyses included specimens that were of arboreal or climbing animals. Shafer and Hein (2005) reported a detailed account of an *M. l. euryxanthus* that was feeding on an adult Lesser Goldfinch (*Carduelis pasaltria*) in a coast live oak (*Quercus agrifolia*) and included additional detail on the climbing behavior (Appendix I).

Recently, our work with *M. l. euryxanthus* has included numerous (~35) observations of arboreality (Alvarez et al. 2021). Our observations also include the species engaged in early morning basking at the top of chamise shrubs (*Adenostoma fasciculatum*), as well as closed-canopy coyote bush (*Baccharis pilularis*) stands in Contra Costa County, CA. We also noted 2 separate adult *M. lateralis* gliding (i.e., moving steadily), approximately 2 m above the ground in manzanita (*Arctostaphylos* sp.) shrubs in Napa County, CA (Fig. 1). This gliding behavior has also been reported by Pickwell (1947). During our trapping investigations we released *M. lateralis* on the ground and closely observed their movement into surrounding vegetation. Frequently these snakes sought cover as escape refuge, and immediately climbed adjacent vegetation, often 2-3 m above the ground, and then froze in a manner that made them immediately cryptic. This was in contrast to sympatric species that never attempted to climb (e.g., Pacific gopher snake [*Pituophis catenifer*], California kingsnake [*Lampropeltis californiae*], and ring-necked snake [*Diodophis punctatus*], and others) when released.

We noted that while climbing, *M. lateralis* regularly "reached out" with the head and up to 2/3 of the body and was able to span a distance of approximately 1 m with the body held straight vertically, horizontally, or in other postures. These observations were supported by work from Shafer and Hein (2005), who reported a *M. l. euryxanthus* extending its body straight up to move between branches. Grinnell and Storer (1924) remarked of this species, "The long slender form of the body seems to be correlative of climbing ability, as 'tree' snakes in all parts of the world are of this general form." We noted that observations of this snake's climbing behavior mimicked unrelated species we have observed in tropical habitats, like the green parrot snake (*Leptphis ahaetulla*), brown vine snake (*Oxybelis aeneus*), and brown tree snake (*Boiga irregularis*), all of which are considered fully arboreal (Rodda 1992; Savage 2002; Guyer and Donnelly 2005). California whipsnakes have similar morphological characteristics to other snakes that are considered arboreal: slender body, long length, relatively long tail (Hollowell 1853; Van Denburgh 1897, 1922; Ortenburger 1928; Grismer 2002; Stebbins 2003). Guimarães et al. (2014) suggested that body slenderness is an adaptation common among many species of arboreal snake. Pizzatto et al. (2007) also stated that body slenderness and tail length are attributes of arboreal snakes. Ortenburger (1928) reported that all members of the genus *Masticophis* have long tails (mean 27.5% of the total length), while Sheehy et al. (2016) correlated the relative length of tail with arboreality in snakes, such that snakes that are arboreal have long relative tail lengths. Guyer and Donnelly (1990) determined that arboreal snakes have a high length to mass ratio. Although we did not make any attempt to measure this in snakes we handled, we feel that the results would be self-evident, that the California whipsnake is adapted for climbing. This is not meant to imply we categorize *M. lateralis* as arboreal, but it appears clear that it is has some adaptation to arboreality and is likely a semi-arboreal snake.

Shafer and Hein (2005) reported that *M. l. euryxanthus* used the lower third of its body to grasp branches for support while climbing. Our own observations corroborate this in that we noted on several occasions that *M. lateralis* would use it's prehensile tail and posterior portion of the body to anchor itself, not only when climbing, but while grasping and swallowing prey items. The tail is, in fact, prehensile. We also noted the snake commonly moves through the habitat with its head up and away from the ground, a behavior reported by many researchers (Brown 1997; Stebbins and McGinnis 2012; Flaxington 2021). Our direct observations included two additional behaviors that indicate this species should be considered semi-arboreal. First, the head is the initial surface with which the snake perches on a branch, rocks, cliffs, or other object on to which it will eventually climb. This snake, like other well-known climbing Colubrid snakes, tilts its head at a steep angle downward at contact with the next surface above, anchoring the anterior portion of the body as it moves upward. Finally, within a tree or shrub *M. lateralis* remains relatively level while moving extremely quickly through the disjunct surfaces (Pickwell 1947).

Our experiences with this species, and those reported by numerous previous researchers, suggest that this species fills a niche that is not commonly seen in most other California snake species; a niche where known prey items, such as birds, bird eggs, and lizards, are readily available (Grinnell and Storer 1924; Grismer 2002; Flaxington 2021; Alvarez and Murphy *in Press*). Although this species can often be found foraging and basking on the ground (Hollowell 1853; Swaim and McGinnis 1992; Alvarez et al. 2005; Miller and Alvarez 2016), we feel that classifying *M. lateralis* as a semi-arboreal snake may aid in its management, particularly for the threatened subspecies. In particular, *M. l. euryxanthus* is subject to focused survey efforts that frequently declare the snake absent from areas that may be scheduled to be disturbed or developed. We suggest that habitat

occupancy by *M. l. euryxanthus* may often be underestimated or missed because traps are set at ground level and never in shrub or tree canopies (Swaim and McGinnis 1992; Swaim 1994, Alvarez et al. 2021). This may be due, in part, to current investigators being relatively ignorant of the habitat use (Appendix I), and/or because the species is difficult to observe in the canopy and therefore is assumed to not occur when it is actually present (Stephens 1921).

We contend that historical observations, and our own direct observations of California whipsnakes have shown that they are adapted to arboreal habitats and should be considered potentially present both on the ground and in emergent micro-habitat such as shrubs and trees. Within the range of *M. l. euryxanthus*, preconstruction surveys (i.e., visual encounter surveys) are conducted to look for snakes that may be in harm's way. This may be ineffective if that habitat is dominated by vegetation that exceeds 2 m in height (Stephens 1921). Visual encounter surveys could be improved by employing a two-step approach: cut and remove vegetation under the supervision and direction of a qualified biological monitor weeks in advance of ground disturbing activity, then conduct additional preconstruction surveys one or two days prior to ground disturbance. Alvarez et al. (2021) also suggested investigating vegetative structure, as opposed to a simple vegetation type (i.e., chaparral/scrub), when assessing potentially occupied habitat for California whipsnakes.

We note that focused academics and dedicated (i.e., permitted) researchers may in fact understand this snake's full range of behavior. However, in the last 40 years in California, the industry of biological and ecological consulting supports a much greater number of biologists than does the field of academia. The fast-paced field of consulting does not always allow for in-depth understanding of a focal species. Extensive literature reviews and field investigations are not always feasible. Our historical review of the species behavior is in support of adding methods to surveys that may allow the snake, even when uncommon in a specific location, to be detected or assumed present.

To improve detection success, surveys conducted for the threatened subspecies should consider a variety of habitat types, and testing of new survey techniques to determine ideal areas and methods for encountering snakes. This may include conducting time constrained, but lengthy visual encounter surveys of vegetation tops for basking snakes during the morning warming period (Rodda et al. 2007; timing to be tested); searching tree canopy for snakes that may have sought cover from approaching biologists, and/or testing the effectiveness of new tools such as vegetation mounted photographic devices (Siers et al. 2019). Efforts should be made to investigate the pathways by which this species crosses between large openings in and between patches of complex vegetative structure, such as habitat openings. Simultaneously, additional ground-based traplines, vegetation-based and ground-based camera traps, and visual encounter surveys should be conducted within and outside of patches of complex vegetative structure, along with inserting ground-based trap lines perpendicular to the edge of vegetative complexes. Methods should be tested that facilitate collecting snakes from within the canopy. This may include modifications to trap systems developed by Rodda et al. (1999), where traps are placed within vegetation canopies and connected by a length of rope upon which lizards or mice would have been kept for several days. The rope would replace a drift fence in ground trapping, but instead would act as a scent trail, directing snakes into traps. These and other methods should be tested to better understand how *M. lateralis* could be targeted with the intent of better understanding habitat use and developing science-based best management practices.

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Appendix I. Quotations from historic sources regarding the climbing ability of the California whipsnake.

Author	Year	Statement (quotation)	Citation
Van Denburgh	1897	Nothing is known of the habits of this snake, except that, like other members of the genus, it is very active and a skillful climber.	Van Denburgh, J. 1897. The reptiles of the Pacific coast and Great Basin. Occas. P. Calif. Acad. Sci. 5:1-236
Grinnell and Grinnell	1907	The striped racer is a good climber and we have often seen it many feet above the ground in scrub oaks and wild lilac bushes. A curious habitat is that of lying in a rigid coil on top of a leafy branch.	Grinnell, J. and H.W. Grinnell. 1907. Reptiles of Los Angeles County, California. Throop Institute Bulletin 25:1-64.
Grinnell and Storer	1924	All the racers are rapacious snakes, and live more or less upon vertebrates; the present species, at the appropriate season, takes toll of nestling birds. The long slender form of the body seems to be correlative of climbing ability, as 'tree' snakes in all parts of the world are of this general form.	Grinnell, J., and T.I. Storer. 1924. Animal life in the Yosemite: an account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. University of California Press, xviii+752 pp.
Ortenburger	1928	They appear to leave the ground more frequently than red racers.	Ortenburger, A.I. 1928. Whipsnakes and racers. Plimpton Press, Norwood, xviii+247 pp.
Pickwell	1947	This racer is especially adept at climbing through the trees of the chaparral, where it may be seen gliding along at great speed three or four feet above the ground, seeming only to brush gently over the twigs and branches as it glides rapidly to the ground some fifty to sixty feet away.	Pickwell, G. 1947. Amphibians and Reptiles of the Pacific States. Stanford University Press, xiv+236 pp.
Stebbins	1954	This snake is a good climber and has been observed foraging and sunning in bushes and trees. When alarmed it may seek escape by climbing into vegetation.	Stebbins, R.C. 1954. Amphibians and reptiles of western North America, McGraw Hill Book Company, xxii+536 pp.
Shafer and Hein	2005	The snake was first observed about 5 meters above the ground in a coast live oak (*Quercus agrifolia*) with an adult lesser goldfinch (*Carduelis pasaltria*) in its mouth. After several minutes, the snake released the goldfinch onto a clump of oak leaves, repositioned itself, and began to consume the bird again. While gripping the branch with the lower third of its body, and with the bird in its mouth, the snake extended about two thirds of its body straight up to a higher branch with a grip on the lower branch as it's only support. After reaching the upper branch, it continued to climb while simultaneously swallowing the bird. The snake finished swallowing the goldfinch after 20 minutes, and was last seen on a branch about 6 meters high near the trunk of the tree.	Shafer, C., and S. Hein. 2005 *Masticophis lateralis euryxanthus* (Alameda striped racer). Diet. Herpetological Review 36:195.