RESEARCH NOTE

Observations on the phenology of the threatened Alameda whipsnake

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The Alameda whipsnake (Masticophis lateralis euryxanthus) is a federally and State threatened subspecies of the California whipsnake (M. lateralis) and is restricted to a specific geographic range (Jennings 1983, USFWS 1997, USFWS 2002, Stebbins and McGinnis 2012). Until recently, the subspecies was believed to occur in Alameda and Contra Costa Counties, and in small portions of northwest San Joaquin County and northern Santa Clara County. Recent work suggests that the range of the subspecies may include eastern Santa Clara County and northern San Benito County, making the subspecies active in a wider area than previously believed (Richmond et al. 2016). Within its accepted range, the Alameda whipsnake has been the subject of study for nearly four decades, yet there remains a paucity of published work on this subspecies. After its initial description (Riemer 1954), Hammerson (1978, 1979) was the first to study the subspecies, and described its thermal ecology and reproduction; Larsen et al. (1991) and Shafer and Hein (2005) reported on the snake's feeding ecology with little detail about its general natural history; and Swaim and McGinnis (1992), Swaim (1994), Alvarez et al. (2005), Alvarez (2006), and Alvarez et al. (in press) looked at the subspecies' use of habitat, with conflicting conclusions. These conflicts included a disagreement on the types of habitats, and slope aspects used. Currently, the natural history of the Alameda whipsnake remains mostly conjecture and assumption, with inferences made from work by Swaim (1994) or stemming largely from grey literature (i.e., unpublished technical reports). The draft recovery plan for the Alameda whipsnake, which summarizes the natural history, also uses limited published literature related to the Alameda whipsnake's biology. Here we examine and analyze a large data set on Alameda whipsnake activity and add to the published literature by reporting on its annual activity period.

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We reviewed and compiled 610 records in Alameda and Contra Costa Counties, and small portions of San Joaquin and Santa Clara Counties, *a posteriori*. In previous compilations we looked at habitat use; here we recompiled and updated our data to look at phenology of the subspecies (Alvarez et al. 2005, Alvarez 2006). Our analysis included both pure Alameda whipsnakes and any intercross specimens (between *M. l. euryxanthus* and *M. l. lateralis*) delineated within the "zone of intergradation" by Jennings (1983). Due to the ambiguity of the phenotypic and genetic boundary, we elected to limit our analyses to specimens throughout the zone of intergradation, as far south as extreme northern Santa Clara County. Our methodology closely incorporates the guidelines proposed by the USFWS (1996), which suggest that any listed species, subspecies, and possible intercross specimens be managed as if all were listed species or subspecies. Here we will refer to both Alameda whipsnakes and the intercross specimens as Alameda whipsnakes.

We analyzed the following aggregate data: our own observations; all known published accounts; reports from the California Natural Diversity Data Base (CNDDB 2020); records and specimens from museums and universities; publicly accessible consulting reports from survey efforts; and anecdotal observations (i.e., personal communications) from demonstrably knowledgeable individuals. Data collected, analyzed, and used in this study included the reported date and location of each observation. If the date or location was ambiguous in any manner, the record was discarded.

Twenty-one percent of the observations used here were also used in Alvarez et al. (2005). As in that study, we acknowledge the shortcomings of using this aggregate data in our analysis, including the potential for misidentification of snakes by the various observers. Verifications of observations followed that of Alvarez et al. (2005) whenever possible. Questionable observational reports were discarded. We also acknowledge the inherent sampling biases of randomly reported sightings, including, but not limited to: the highly variable expertise of biologists working seasonally in the field; omissions in reporting when the species was observed and identified; our inclusion of focused field efforts to detect the snake (i.e., trapping surveys); and the inaccessibility of some habitats (i.e., closed/muddy roads) during specific times of year (see: Oliver 1947). Despite the shortcomings of this data set, we believe the methodology reasonably supports the conclusions drawn.

We also attempted to collect high and mean temperatures for dates where snakes were active between November and February (subjectively categorized as winter months due to increased rain potential and the mean temperature dropping below the reported emergence temperature for the subspecies). Historic weather data were collected from the nearest weather station (\leq 4.0 km [2.5 miles] in all cases) to a snake observation. The subset of data points from which we were able to collect location and temperature data reflect a significantly narrower window (1953–2006) than the total range of our reported observations (i.e., 1940–2020). We therefore only analyzed temperature data for those observations that occurred between November and February 1953–2006.

The 610 reported observations we reviewed included data collected or reported from 10 November 1940 to 1 August 2020, in all months of the year. Our data set indicated an obvious peak in observations (31.5%) in the month of May for all observations combined, followed by a minor, secondary peak (6.4%) in September (Fig. 1). More than 72% (n = 440) of all observations were reported April–June, with only 2.5% (n = 15) of the observations reported during the coldest months of the year (i.e., November–February; Table 1).

We found that the Alameda whipsnake appears to follow the typical seasonal pattern of many snake species in North America—a reduced period of activity during the winter

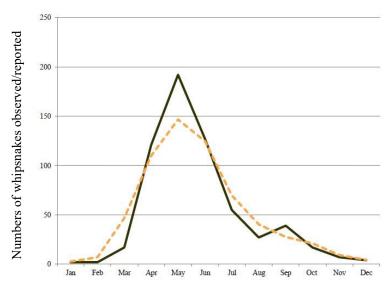


Figure 1. The frequency of reported observations of Alameda whipsnakes (solid line) over the course of 12-month year, collected from observations between 1940 and 2020 in Alameda, Contra Costa, and portions of San Joaquin and Santa Clara Counties. Dashed line is a 3-point moving average, which was used as a smoothing function.

Table 1. High and mean daily temperatures associated with the dates of Alameda whipsnake observations during the months of November through February 1952–2015^a. Weather station location was the nearest recording station to the observed location (measured in km to the nearest 0.5 km). Data source for weather from: Weather Underground (http://www.wunderground.com). Three data points discarded due to imprecise location (e.g., location = "Contra Costa County").

Season	Date	Daily High	Daily Mean	Weather Station Location
Fall	2 Nov 1990	20.5° C (69° F)	15.5° C (60° F)	Berkeley (3.5 km)
	18 Nov 1990	16.1° C (61° F)	13.3° C (56° F)	Berkeley (3.5 km)
	12 Nov 1952	18.8° C (66° F)	12.8° C (55° F)	Berkeley (1.5 km)
	12 Nov 2013	21.6° C (71° F)	16.1° C (61° F)	Walnut Creek (4.0 km)
	22 Nov 1989	16.7° C (62° F)	10.6° C (51° F)	Livermore (2.5 km)
	2 Dec 2006	16.1° C (61° F)	10.6° C (51° F)	Mt Diablo (4.0 km)
	12 Dec 2015	13.9° C (57° F)	10.0° C (50° F)	Pittsburg (3.0 km)
Winter	26 Jan 1953	13.9° C (57° F)	10.0° C (50° F)	Oakland (1.5 km)
	25 Feb 1991	17.7° C (64° F)	11.7° C (53° F)	Oakland (4.0 km)
	28 Feb 1992	18.8° C (66° F)	15.5° C (60° F)	Berkeley (3.0 km)

^a The subset of data points from which we were able to collect precise location and temperature data reflect a significantly narrower window (1952–2015) than the total range of our reported observations (i.e., 1940–2020).

months (Conant 1938; Cowles 1941; Oliver 1947; Seigel et al. 1987). Work conducted by Swaim (1994) showed a similar pattern of activity to that provided here, but our robust sample size eliminates the site-specific and time-limited potential biases that may result from a short-term project. Both studies suggest that the activity pattern of the Alameda whipsnake is annually bimodal, however in our work, a peak in fall observations was significantly less well defined (Fig. 1) than that reported by Swaim (1994), whose data were comprised primarily of hatchling and juvenile specimens during the fall. Larsen et al. (1991) reported a relative abundance of juvenile Alameda whipsnakes peaking in mid-October and declining through November and December (estimated from their Fig. 5, absent specific reported data)—representing a decline at least one month later than that found in our data set. This may suggest inter-annual variability in the peak timing of activity in this species. Nevertheless, the bimodal activity pattern we found in Alameda whipsnakes follows very closely with that reported for the ring-necked snake (*Diadophis punctatus*), common kingsnake (*Lampropeltis getula*), and other North American species (Conant 1938; Oliver 1947; Gibbons and Semlitsch 1982; see also: Seigel et al. 1987).

Heliothermic animals, including many snake species, require solar exposure in order to attain an activity level sufficient for foraging (Brattstrom 1965) and reproduction (Hammerson 1978, 1979). During tests in semi-natural outdoor enclosures from May through July, Hammerson (1979) found that Alameda whipsnakes emerged from refugia to bask and later to forage when soil surface temperatures were as low as 19° C (66° F; inferred from his Fig. 1.). Our data show that the vast majority (72.1%) of the 610 reported observations we analyzed occurred within the mating, gravid, and egg-laying period, which is generally April—late June (Hammerson 1978; personal observation). This three-month period also coincided with typical average daily air temperatures ranging above the lowest temperature for emergence reported by Hammerson (1979).

The acceptance of whipsnakes as endogenously inactive during the winter months has been treated as putative, particularly in the grey literature (i.e., technical reports; pers. obs.). Although Swaim (1994) reported that this subspecies is in brumation during this period, we note that Alameda whipsnakes were reported active on the surface on 10 days when daily high temperatures were as low as 13.9° C (Table 1). The USFWS (2002) suggested that "short, above-ground movements may occur in the winter" with no reference to the origin of their contention. The data analyzed here show that these above-ground movements occur at temperatures that are lower than previously reported and may occur more frequently than indicated by the data set we analyzed.

Siegel et al. (1987) reported that, "...evidence suggests that movement by snakes is highly deterministic and the potential exists to predict the conditions under which individuals will be active." We contend that predicting the phenology of Alameda whipsnake activity will require substantially more research. When compared to Larsen et al. (1991), our data indicate the possibility of inter-annual variability in peak activity timing. We strongly suggest that land managers and regulators consider management conditions that are climate-focused, rather than focused on the months of the year. In this way, adjustments for climate change would be automatically incorporated into regulatory compliance and land-management policy. Because the Alameda whipsnake can be at the surface and potentially active at any time of year, albeit differentially, habitat-altering activities (i.e., ground disturbing and vegetation clearing) within areas suspected to be occupied by Alameda whipsnake should carefully consider this species and, more specifically, assume that active snakes may be pres-

ent above ground when daily high temperatures are as low as 13.9° C. More specifically, we recommend conducting vegetation clearing activities in winter months, when snakes are less active. Care should be taken within this subspecies' range if vegetation is stacked to be burned, as the use of brush piles by Alameda whipsnakes remains undetermined. Ground disturbing activity (grading, trenching excavating, etc.) may pose a very significant risk to snakes that are inactive and underground during winter months (Cowles 1941). We would recommend that ground disturbing activity take place after the majority of snakes have emerged from winter hibernacula (i.e., March), so that active snakes may be able to move out of harms-way as opposed to being unearthed when they are inactive. We would further add that a biological monitor should be in place during any ground disturbing activity in order to prevent loss of snakes, and also to record behaviors that then should be reported.

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