

Prepared in cooperation with the California Department of Water Resources

Literature Review of Giant Gartersnake (*Thamnophis gigas*) Biology and Conservation



Open-File Report 2015-1150

Cover: A giant gartersnake (*Thamnophis gigas*). Photograph by Matt Meshriy, U.S. Geological Survey, September 2010.

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By Brian J. Halstead, Glenn D. Wylie, and Michael L. Casazza

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Conversion Factors

Inch/Pound to International System of Units

Multiply	By	To obtain
Length		
inch (in.)	2.54	centimeter (cm)
inch (in.)	25.4	millimeter (mm)
foot (ft)	0.3048	meter (m)

International System of Units to Inch/Pound

Multiply	By	To obtain
Length		
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
Area		
hectare (ha)	2.471	acre
square hectometer (hm ²)	2.471	acre
Volume		
liter (L)	0.2642	gallon (gal)
Flow rate		
meter per day (m/d)	3.281	foot per day (ft/d)
Mass		
gram (g)	0.03527	ounce, avoirdupois (oz)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as °F = (1.8 × °C) + 32.

Literature Review of Giant Gartersnake (*Thamnophis gigas*) Biology and Conservation

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Identification and Physical Description

The following description is based primarily on Fitch (1940), Rossman and Stewart (1987), and Rossman and others (1996). *Thamnophis gigas* is the longest gartersnake, with a maximum total length of 1,626 mm (64 in.; Stebbins, 2003). Its large size has been attributed to conditions in the Central Valley of California, which include:

1. Warm water that provides a thermally stable environment for much of the year and allows for nocturnal activity during the hottest part of the active season,
2. An effective growing season of 8 months for adults and longer for juveniles,
3. A plentiful food supply, and
4. Selection for large size because of predation pressure (Fitch, 1940; Hansen, 1980).

Thamnophis gigas has variable coloration and pattern, ranging from distinct vertebral and lateral stripes to no stripes. Stripes appear most distinct in northern Sacramento Valley populations, and are less distinct to absent in southern (San Joaquin Valley) populations. When present, the lateral stripe is located on scale rows two and three. The dorsal ground color of *T. gigas* ranges between black and olive, and two alternating rows of dark spots usually are present. *Thamnophis gigas* has 21 or 23 scale rows at midbody. Males and females are dimorphic in the number of subcaudals, with males having 73–81 subcaudals and females having 65–73 subcaudals. Eight supralabial scales are present, with the sixth supralabial shorter and narrower than the seventh (fig. 1; Hansen, 1980). Other scale counts include a single preocular, three postoculars, and 10–11 infralabial scales. *Thamnophis gigas* is characterized by a long muzzle with a narrow tip, with a muzzle length-to-frontal length ratio of 0.847–0.850 in males and 0.954–0.959 in females, an internasal-rostral contact-to-nasal-rostral contact ratio of 0.756 in males and 0.651 in females. *Thamnophis gigas* also has very long parietals and 23–27 maxillary teeth.

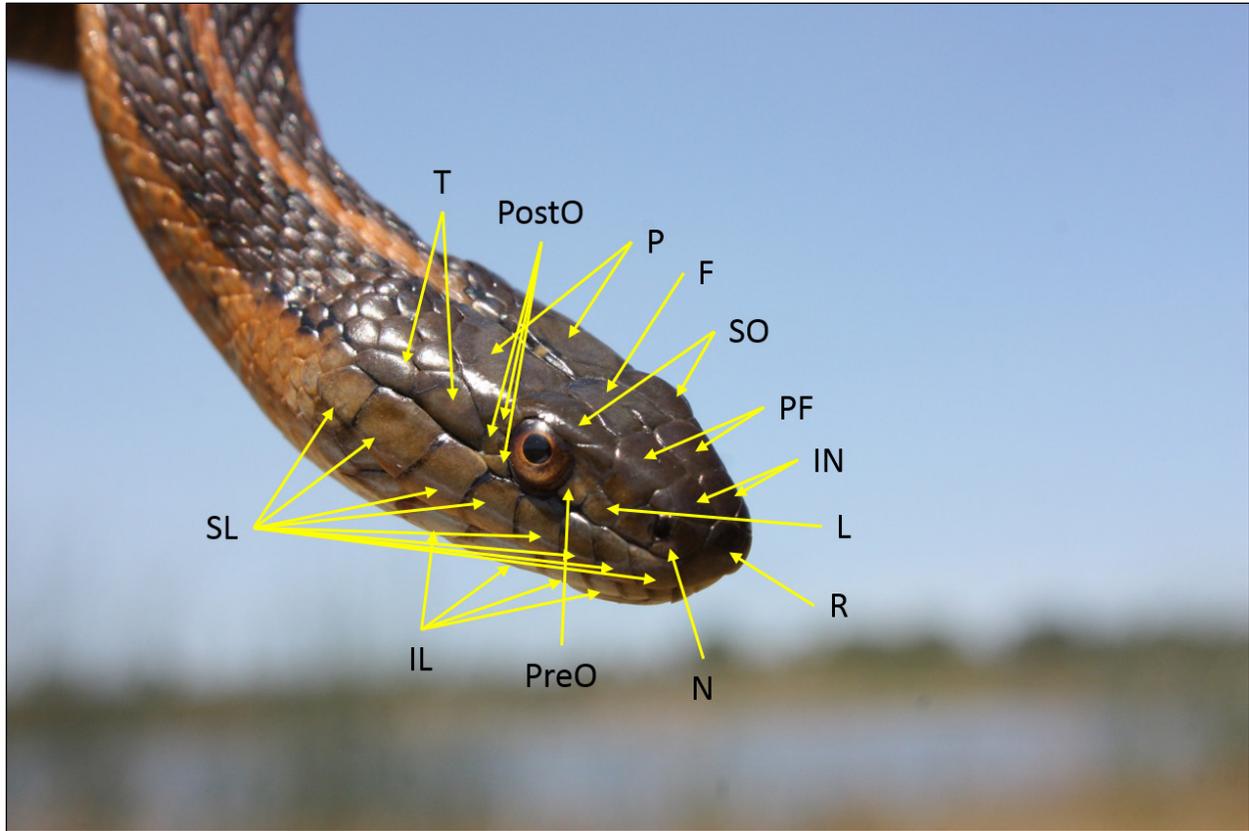


Figure 1. Photograph of a giant gartersnake (*Thamnophis gigas*) head, showing head scales. Key to head scales: T, temporals; PostO, postoculars; P, parietals; F, frontal; SO, supra-oculars; PF, prefrontals; IN, internasals; L, loreal; R, rostra; N, nasal; PreO, preoculars; IL, infralabials (only 4 of 10–11 labelled); SL, supralabials. Photograph taken by Matt Meshriy, U.S. Geological Survey.

Confusing Species

Only two species in the genus *Thamnophis* are sympatric with *T. gigas*. *Thamnophis sirtalis fitchi* (valley gartersnake) is a widespread subspecies of *T. sirtalis* whose range entirely encompasses that of *T. gigas*. Several characteristics help to distinguish *T. gigas* from *T. sirtalis fitchi*. The presence of red markings on the sides and seven supralabials usually confirms an individual as *T. sirtalis fitchi* (Rossman and others, 1996; Stebbins, 2003). Other distinguishing characteristics of *T. sirtalis fitchi* include 19 scale rows at midbody; a wider, shorter muzzle; and relatively large eyes (Stebbins, 2003).

Thamnophis elegans elegans (mountain gartersnake), which is a subspecies of the terrestrial gartersnake, is sympatric with *T. gigas* at only a few locations near the Sierra Nevada foothills and Sutter Buttes. *T. e. elegans* has a shorter, wider muzzle than *T. gigas*, with the internasals broader than long and not pointed in front (Stebbins, 2003), and in areas where *T. e. elegans* occurs with *T. gigas*, it has very distinct stripes on a dark dorsal ground color. The sixth supralabial of *T. e. elegans* often is much taller than the fifth supralabial, and at least as tall as the seventh supralabial.

Evolutionary History and Fossil Record

Evolutionary relationships of *T. gigas* with its congeners are broadly understood, although its relationships with its closest relatives remain relatively poorly resolved. *Thamnophis gigas* is placed within the “widespread clade” of gartersnakes, which contains all gartersnakes native to California except *T. sirtalis* (de Queiroz and others, 2002). Based on morphology, Rossman and Stewart (1987) elevated *T. gigas* to species status, and supported the hypothesis that *T. gigas* evolved from *T. atratus* (aquatic gartersnake) that colonized the Central Valley following the closure and draining of the San Joaquin Embayment and re-emergence of marsh habitat (Hansen, 1980; Rossman and Stewart, 1987). More recent studies on the basis of biochemical analyses supported two alternative relationships. Using allozymes and one mitochondrial gene, de Queiroz and Lawson (1994) provided support for the hypothesis that *T. gigas* and *T. atratus* were sister taxa (de Queiroz and others, 2002). However, additional research based on four mitochondrial genes placed *T. gigas* into a clade containing *T. couchii* (sierra gartersnake) and a well-supported group containing *T. atratus* and *T. elegans* (de Queiroz and others, 2002), but whether *T. gigas* was sister to *T. couchii* or the *T. atratus* and *T. elegans* sister group was unclear (de Queiroz and others, 2002). Thus, the clade containing *T. gigas*, *T. couchii*, *T. atratus*, and *T. elegans* appears well-supported, but whether *T. gigas* is more closely related to *T. couchii* or to the sister clade containing *T. atratus* and *T. elegans* remains unresolved (de Queiroz and others, 2002). No fossil *T. gigas* have been found to date.

Distribution

Historically, *T. gigas* ranged throughout the Sacramento and San Joaquin Valleys from Butte to Kern Counties (Rossman and others, 1996). This distribution corresponds to the distribution of river floodplains, which consisted largely of freshwater marshes (Hansen, 1980; U.S. Fish and Wildlife Service, 1993), and is located between 0 and 122 m in elevation (Rossman and others 1996).

Thamnophis gigas was extirpated from much of the San Joaquin Valley by the late 1980s (Hansen, 1988), and no longer occurs south of northern Fresno County (Hansen and Brode, 1980):

“Land development, particularly the reclamation of wetlands for agriculture, has eliminated much of the original habitat. South of Fresno County virtually no suitable freshwater habitats remain” (Hansen and Brode, 1980, p. 3).

Indeed, several large basins that provided expansive marshes (including Tulare Lake, the largest [by surface area] freshwater lake west of the Great Lakes) have been completely drained and converted to agriculture and other uses (Garone, 2007). Between the mid-1970s and mid-1980s, flooding and deterioration of giant gartersnake habitat further threatened giant gartersnake populations in the San Joaquin Valley (Hansen and Brode, 1980; Hansen, 1988). Small populations of *T. gigas* still occur at Volta Wildlife Area, Mendota Wildlife Area, and the southern Grasslands Ecological Area (Sloan, 2004; Dickert, 2005); however, *T. gigas* remains at risk of extirpation in the southern 75 percent of its range (U.S. Fish and Wildlife Service, 2006).

The prevalence of rice agriculture in the Sacramento Valley has allowed persistence of *T. gigas* after conversion of wetlands to agriculture (Halstead and others, 2010). Rice agriculture and its supporting infrastructure of canals provide marsh-like habitat through much of the

T. gigas active season (Halstead and others, 2010). The distribution of rice agriculture in the late 20th and early 21st centuries and the distribution of historical wetlands is not entirely congruent. The distribution of *T. gigas* in the Sacramento Valley is nonetheless affected by the proximity of suitable habitat to historical tule (*Schoenoplectus acutus*) marshes (Halstead and others, 2014), despite apparently suitable habitat elsewhere in the valley. Thus, the distribution of *T. gigas* is limited by both habitat suitability and relatively poor dispersal and colonization abilities.

Delimiting the distribution of *T. gigas* is hampered by low detection probabilities. Visual surveys for *T. gigas* are most effective during March–June, when individuals are most active (Hansen, 1986). Visual surveys are greatly affected by heterogeneity among observers in both detecting and capturing snakes, and trapping with floating funnel traps (Casazza and others, 2000) generally is preferred for conducting standardized surveys. Even with floating funnel traps, detection probabilities are low (Halstead and others, 2011a). Trap surveys for giant gartersnakes are most effective early in the active season, in warmer water, and when a large number of traps are deployed (Halstead and others, 2011a). Even after accounting for these variables, much heterogeneity in detection probabilities exists among sites, likely because of variation among sites in *T. gigas* abundance or other characteristics (such as variation among individuals in their skill at setting traps, or the configuration of shoreline or vegetation edge) that affect trappability of snakes (Halstead and others, 2011a). Detection probabilities can be enhanced by modifications to commercially available traps. In particular, extending the large opening of the funnel to increase sampled area and to promote better contact with habitat edges, and installing cable ties to act as a one-way valve in the small funnel opening led to capture rates 5.55 times greater (95% credible interval = 2.45–10.51) than those of unmodified traps (Halstead and others, 2013a). Indeed, the use of modified traps increased mean daily detection probabilities from 0.116 (0.092–0.145) to 0.457 (0.167–0.705) (Halstead and others, 2014). Incorporating these modified traps in future studies should improve estimation of occupancy, abundance, and other demographic parameters in studies of *T. gigas* ecology (Halstead and others, 2014), and should result in a better understanding of the distribution of *T. gigas* and the variables that affect its probability of occurrence.

Because of their low detection probabilities, reports of negative results of surveys for *T. gigas* must be interpreted with caution. Several surveys, including those of Partners for Fish and Wildlife project sites (Wylie and Martin, 2004a), various locations in Solano County (Wylie and Martin, 2004b, 2005), and the Bacon and Webb tracts in the Sacramento-San Joaquin Delta (Patterson, 2004), resulted in no detections of giant gartersnakes. Survey effort, sampling conditions (date, temperature, etc.), and trap type must be taken into consideration when interpreting the results of non-detection surveys. Although absence can never be proven, methods to calculate the probability that a site is occupied, given the sampling conditions and that the species was not detected (Kéry, 2002; Halstead and others, 2011a), can be used to quantify evidence against occurrence and aid in the interpretation of non-detection surveys. To accomplish this, the variables that affect the probability of detection are recorded at each survey, and this information is used to estimate probability that *T. gigas* occurs at the site, but was missed (Halstead and others, 2011a). Such an approach was used in the interpretation of non-detection surveys for *T. gigas* for the Yolo County Resource Conservation District (Yolo County Resource Conservation District, 2012).

Systematics and Geographic Variation

Thamnophis gigas was first described by Fitch (1940) as a subspecies of *T. ordinoides* (northwestern gartersnake). Since its initial description in the literature, *T. gigas* has gone through several taxonomic re-evaluations. Johnson (1947) and Fox (1951) considered *T. gigas* to be a subspecies of *T. elegans*. Later, Fox and Dessauer (1965) and Lawson and Dessauer (1979) described *T. gigas* as a subspecies of *T. couchii*. In 1987, *T. gigas* was afforded status as a full species by Rossman and Stewart (1987) because of its distinct morphology and geographic and ecological isolation from closely related *Thamnophis* spp.

No subspecies of *T. gigas* are recognized (Rossman and others, 1996), but the species indicates some genetic structuring (Paquin and others, 2006; Engstrom, 2009). The mitochondrial ND4 gene has high F_{ST} values, which indicates that a large proportion of the total genetic variance is contained in subpopulations (Paquin and others, 2006; Engstrom, 2009). Population structuring was further indicated by a high frequency of unique collections of alleles (Paquin and others, 2006), with Sacramento-San Joaquin Delta populations containing haplotypes not observed elsewhere (Engstrom, 2009).

A recent study based on 15 microsatellite loci developed specifically for *T. gigas* identified five genetic clusters that were largely consistent with regional drainage basins, although three basins in the Sacramento Valley east of the Sacramento River clustered together (Wood and others, 2015). The genetic clusters identified included the Colusa Basin, the Sacramento Valley east of the Sacramento River (Butte, Sutter, and American Basins), the Yolo Basin, Badger Creek, and the Volta Wildlife Area. Higher genetic connectivity existed among populations in the northern (Sacramento Valley) drainage basins than among the Sacramento-San Joaquin Delta and San Joaquin Valley populations (Wood and others, 2015). The Delta and San Joaquin Valley populations, which are more geographically isolated, also were more genetically differentiated (Wood and others, 2015). Basins also differed in genetic diversity, with southern basin populations containing less genetic diversity than northern basin populations (Wood and others, 2015). About one-half of the populations exhibited inbreeding and evidence of population bottlenecks (Wood and others, 2015). Effective population size varied greatly among locations, but remained well below recommended thresholds to avoid deleterious effects of inbreeding (Wood and others, 2015).

Habitat

The habitat of *T. gigas* has been described by many researchers and organizations, but quantitative analysis of its habitat relationships is incomplete. *Thamnophis gigas* is one of the most aquatic gartersnakes, and occupies a niche similar to that of watersnakes (extremely aquatic, rarely found away from water, and forages for aquatic prey; Rossman and others, 1996). It occurs in aquatic habitats with a mud bottom (Fitch, 1940; Hansen, 1986, 1988), especially marshes and sloughs (Hansen and Brode, 1980; Hansen, 1986) where emergent vegetation such as tules and cattails (*Typha* spp.) serve as cover, with broken tules also serving as important basking sites that allow ready escape into the water below (Van Denburgh and Slevin, 1918; Hansen, 1986). Tules, especially dense stands of perennial growth, are chosen over cattails as basking sites where both plants occur (Hansen, 1986). *T. gigas* is only occasionally found in slow-moving creeks (Hansen and Brode, 1980; Hansen, 1986). *T. gigas* habitat typically is treeless (Hansen, 1980, 1986), and occurs at low elevations (10–40 ft [3.0–10.2 m] above sea level in the Sacramento area; Hansen, 1986). It is notably absent from large rivers or bodies of

water with little vegetation (Hansen, 1986). In the contemporary agricultural landscape of the Central Valley, *T. gigas* also can be found in canals and drains associated with rice fields (Hansen, 1988). Regardless of habitat type, *T. gigas* generally is found close to the water's edge, except in late autumn or early spring, when individuals can travel as much as 600 ft (183 m) from water to reach the high water line to avoid flooding during brumation (Hansen, 1986; Wylie, 1998). Cover, in the form of vegetation, debris, or burrows, is a necessary component of *T. gigas* habitat (Hansen, 1986; Wylie, 1998). During the inactive season (November to mid-March), *T. gigas* brumates in muskrat, crayfish, or ground squirrel burrows (Hansen, 1980), or riprap (Wylie and others, 2003a). Access to upland retreats that provide refuge from flooding is important, but brumation sites near active-season marsh habitat is preferred (Hansen, 1986, 1988). Sunny aspects along south- or west-facing slopes often are chosen for brumation (U.S. Fish and Wildlife Service, 1993). Based largely on these observations, the listing decision for *T. gigas* indicated that its habitat requirements were (1) adequate water during the active season, (2) emergent herbaceous wetland vegetation, (3) grassy banks and openings in waterside vegetation, and (4) higher elevation uplands for cover and refuge from floodwaters during winter (U.S. Fish and Wildlife Service, 1993).

Habitat suitability analysis at the scale of the Sacramento Valley has reinforced many of the observed habitat relationships. The niche of *T. gigas* at the landscape scale consists of areas close to rice agriculture and wetlands, with a high density of canals and a low density of streams (Halstead and others, 2010). Further examination of variables affecting the probability of occurrence of *T. gigas* in the Sacramento Valley indicated that *T. gigas* is more likely to occur near historical tule marsh than areas far from historical tule marsh (Halstead and others, 2014), indicating that although contemporary habitats might be suitable for *T. gigas*, they might not be occupied because of dispersal limitations or past extirpations of *T. gigas* from these locations.

Radio telemetry has indicated habitat relationships of *T. gigas* at a much finer resolution than habitat suitability or occupancy analysis. Active-season home ranges (95-percent fixed kernel utilization distributions) of *T. gigas* at Gilsizer Slough in 2008 and 2009 were composed of 5–13 percent (interannual range) water, 32–49 percent terrestrial vegetation, and 38–50 percent emergent vegetation (Valcarcel, 2011). The importance of cover for *T. gigas* is reinforced by radio telemetry studies as well. Forty percent of locations of *T. gigas* in late summer and early autumn at the Colusa Drain were underground in burrows (Wylie and Martin, 2004a). Radio telemetry at seven sites throughout the Sacramento Valley indicated that use of the terrestrial environment by individual *T. gigas* was more than 50 percent during the summer, and nearly 100 percent during brumation (Halstead and others, in press). While in the terrestrial environment, *T. gigas* were underground more than one-half of the time during the early afternoon in summer; the probability of being underground increased to nearly 100 percent at all hours during brumation (Halstead and others, in press). Extreme heat or cold increased the probability that *T. gigas* would be found underground (Halstead and others, in press). Under most conditions, except during brumation and for individuals found underground, *T. gigas* were within 10 m of water during 95 percent of the observations (Halstead and others, in press). Although these patterns are evident for the average *T. gigas* individual, there was much individual variation in the use of the terrestrial environment; therefore, making predictions about the behavior of individuals was highly uncertain (Halstead and others, in press). If an area burns, *T. gigas* typically do not use it until the vegetation grows back (Wylie and Amarello, 2006). Terrestrial vegetation at the wetland edge is a particularly important habitat component (Wylie and others, 2004a).

The composition of microhabitats at locations of radio-tracked individuals indicates that they use a variety of microhabitats and vegetation types. At the Elverta Site in the Natomas Basin in 1998, 54 percent of *T. gigas* locations were in canals, and 45 percent were in rice (Wylie, 1998). At Fisherman's Lake in the Natomas Basin the same year, 92 percent of locations were in the slough, and 6 percent were in rice (Wylie, 1998). When these sites were combined, 36 percent of locations were in irrigation canals, 32 percent in rice, and 31 percent in the slough (Wylie, 1998). At Colusa National Wildlife Refuge (NWR) in 2000, radio-marked *T. gigas* locations were composed, on average, of 50 percent aquatic vegetation, 28 percent aquatic and upland vegetation, and 16 percent upland vegetation (Wylie and others, 2000). In 2001, radio-marked *T. gigas* locations at Colusa NWR were composed of 49 percent aquatic vegetation, 37 percent upland vegetation, 8 percent aquatic and upland vegetation, and 4 percent riprap/rocks (Wylie and others, 2002). In 2003 at Colusa NWR, a greater proportion of upland habitats (46 percent) was used, but aquatic vegetation (31 percent) and aquatic and upland vegetation (15 percent) also were used extensively (Wylie and others, 2002). In permanent created marsh habitats at Colusa NWR in 2004, terrestrial locations comprised 50–75 percent of *T. gigas* locations, with emergent vegetation comprising 5–25 percent of locations (Wylie and others, 2004a). Vegetation at *T. gigas* locations was composed of forbs (25–50 percent), grasses (5–25 percent), and cattails (5–25 percent; Wylie and others, 2004a). Emergent vegetation comprised 75–95 percent of *T. gigas* locations in the Glenn-Colusa Irrigation District (GCID) canal at Colusa NWR in 2004, with water primrose (*Ludwigia* spp.) comprising 50–75 percent of the vegetation at snake locations (Wylie and others, 2004a). Habitat and vegetation types were more equitably distributed at the J-Drain (a major drainage canal running north-south through the refuge) in the same year, with *T. gigas* locations composed of 25–50 percent emergent vegetation, 25–50 percent litter, 5–25 percent terrestrial vegetation, and 5–25 percent bare ground (Wylie and others, 2004a). Dominant vegetation at *T. gigas* locations was composed of grasses (25–50 percent), tules (5–25 percent), forbs (5–25 percent), and water primrose (5–25 percent; Wylie and others, 2004a).

Although these studies provide much information about the habitat where adult (usually female) *T. gigas* were located, conclusions drawn from them are difficult to generalize because they do not account for the influence of habitat availability on habitat use. Studies of habitat selection compare habitat use to availability (Manly and others, 2002), and are more directly comparable among sites. Edges of patches of emergent vegetation were selected more than patch interiors relative to their availability (Valcarcel, 2011). Additional studies of *T. gigas* habitat selection are needed to provide information about which habitats and habitat components are most important for these snakes.

For ectothermic animals like snakes, thermal aspects of habitat often are important. At Gilsizer Slough, the daytime operative environmental temperature in terrestrial habitats was consistently greater than the field-preferred body temperature of *T. gigas*, and the operative environmental temperature in open water was consistently less than field-preferred body temperature (Valcarcel, 2011). The operative environmental temperature of emergent vegetation was within or less than the limits of field-preferred body temperature (Valcarcel, 2011). All habitats were of similar thermal quality in the early morning and late evening (Valcarcel, 2011).

Many aspects of the habitat relationships of *T. gigas* remain elusive. In particular, characteristics of selected overwintering sites and subterranean shelters relative to similar sites that are not selected remain unknown. Similarly, the effects of water-depth profiles on *T. gigas*, independent of their effects on vegetation, also are unknown. Perhaps the greatest research needs regarding the relationships of *T. gigas* with habitat are its response to habitat construction/restoration features and water management regimes. Knowledge of these relationships would improve habitat construction and management for *T. gigas*.

Behavior

Some aspects of the behavior of *T. gigas* have been well-studied, but much remains to be learned. Behavior related to reproduction, foraging, avoiding predation, and habitat relationships are treated elsewhere in this review; here, we consider patterns of activity, thermoregulation, and movement.

The annual cycle of *T. gigas* varies somewhat with climatic conditions. On average, individuals emerge from brumation in mid-to-late March and remain active until October (Rossman and others, 1996; Wylie and others, 2009a). In the spring, individuals can be observed basking on tules in open water or at the edge of steep canal banks in agricultural settings (Hansen, 1986). Greater proportions of females captured during visual searches than trap surveys (U.S. Fish and Wildlife Service, 1999) could be a function of their propensity to bask while gravid, their larger size (making them easier to visually observe or excluding them from traps), or both.

Daily patterns of activity of *T. gigas* also are variable. *T. gigas* can be diurnal, nocturnal, or crepuscular, depending on environmental conditions, with nocturnal activity favored during periods of extreme heat (Hansen, 1980). One individual *T. gigas* was observed foraging 1.5 hours after dark in Kern County (Cunningham, 1959).

Temperature-sensitive radio telemetry has indicated much about the thermal biology of *T. gigas* (Wylie and others, 2009a). The field-preferred body temperature of *T. gigas* is 29.8 °C (27.6 °C–31.7 °C; Wylie and others, 2009a). Males and females differ in their thermal ecology. Females elevate their body temperatures relative to the environment (and males) during July and August, which coincides with the latter part of gestation (Wylie and others, 2009a). In contrast, males elevate their body temperatures relative to the environment (and females) during late winter and early spring, just before the mating season (Wylie and others, 2009a). Body temperatures of both sexes are depressed relative to environmental temperatures during late autumn and winter, perhaps as a mechanism to conserve energy during brumation (Wylie and others, 2009a). Daily patterns in body temperatures also vary between the sexes. Females have elevated body temperatures relative to the environment in the morning, especially during spring and early summer, and they tend to maintain a more stable thermal profile than males (Wylie and others, 2009a). Whether these patterns are caused by the greater mass and thermal inertia of females, or because they actively select warmer overnight refuges, remains unknown.

In addition to thermal biology, radio telemetry has indicated much about the movement behavior and spatial ecology of *T. gigas*. Reported home range sizes vary greatly, both within and among studies. In rice agricultural habitat in the Natomas Basin in 1997, *T. gigas* had a median home range area of 35 ha (range of 10–87 ha; method not given; Wylie, 1998). At Colusa National Wildlife Refuge in 2000, mean home range area, based on the adaptive kernel method, was 18 ha (range of 1.0–35 ha; Wylie and others, 2000); in 2002, mean home range at the same site was 29.3 ha (range of 7–95 ha; Wylie and others, 2002). Along a regional drain

through rice agriculture (the Colusa Drain) in 2004, median home range area was 25.9 ha (range of 0.4–3,744 ha; method not given; Wylie and Martin, 2004c). At the Colusa Drain in 2006, mean minimum convex polygon home range area was 37.5 ha (range of 3–239 ha; Wylie and Amarello, 2006). Mean home range area was greater in created marsh than rice agricultural habitats in and adjacent to Gilsizer Slough, with home ranges also varying by year (in 2008, mean 95-percent fixed kernel in agricultural habitats=13.3 ha [range of 1.4–32.3 ha], created marshes=77.3 ha [range of 22.5–203.5 ha], 95-percent confidence interval [CI] of difference 0–127 ha; in 2009, agricultural habitats=7.2 ha [range of 5.4–8.2 ha], created marshes=30.9 ha [range of 10.2–61.2 ha], 95-percent CI of difference=2–46 ha; Valcarcel, 2011). In agricultural areas, the utilization distribution overlap index was 0.46 (95-percent CI=0.16–0.77) in 2008 and 0.42 (95-percent CI=0.21–0.63) in 2009. Individuals occupying created marsh had less home range overlap, with utilization distribution overlap indices of 0.26 (range of 0.14–0.37) in 2008 and 0.17 (range of 0.05–0.30) in 2009.

Less information is available about core areas than home ranges. At and near Gilsizer Slough, relationships of core areas (defined as the 50 percent isopleth of the fixed kernel utilization distribution) were similar to patterns observed for home range size in 2008 and 2009 (Valcarcel, 2011). Mean core area in agricultural habitats in 2008 was 3 ha (range of 0.3–7.0 ha), and that of created wetlands in the same year was 20 ha (range of 5.5–53.1 ha); the 95-percent CI of the difference was 0–33 ha. In 2009, mean core area in agricultural habitats was 1 ha (range of 1.0–1.7 ha), and that in created marshes was 7 ha (range of 1.2–15.1 ha), with a 0–11 ha 95-percent CI of the difference in core area between these habitats.

Like home ranges, movement statistics of *T. gigas* vary greatly. Hansen (1986) reported that individuals move less than 100 ft (30.5 m) during the spring in favored habitat. At the Colusa Drain, distances between captures of individuals ranged from 0.7 to 3.3 km (Wylie, 2003). Using radio telemetry at the same location in 2006, individual mean movement distance was 104 m (range of 12–287 m), with a corresponding individual movement rate of 63 m/d (range of 3–173 m/d; Wylie and Amarello, 2006). Mean maximum individual movement distance was 862 m (range of 34–2,791 m), and total movement over the time radio-tracked averaged 4,761 m (range of 107–16,995 m; Wylie and Amarello, 2006). Active-season minimum total distance moved at the same site in 2004 ranged from 0.7 to 215 km (Wylie and Martin, 2004c). Although *T. gigas* apparently are capable of long-distance movements, less movement is observed when water is maintained on-site through the summer (Wylie and others, 2002). Movements across busy highways, such as California Highway 99 in the Natomas Basin, likely occur through culverts (Halstead and others, 2013b), but the extent to which such movements occur is unknown.

Reproduction

Mating and reproduction of *T. gigas* is similar to that of other *Thamnophis* species. Most mating occurs in the spring (March–May), with males searching for mates immediately upon emergence from brumation (U.S. Fish and Wildlife Service, 1993). Some mating also might occur in the autumn (U.S. Fish and Wildlife Service, 1999).

Like most natricine snakes, *T. gigas* gives birth to live young. Females give birth to 10–46 young (Cunningham, 1959; Hansen, 1990; Halstead and others, 2011b) between mid-June and early October (Hansen and Hansen, 1990; Halstead and others, 2011b), with a mean date of parturition of August 13 in the Sacramento Valley (Halstead and others, 2011b). In Fresno and Sacramento Counties, neonates average 206.4 mm snout-vent length (SVL; Hansen and Hansen,

1990) and 3–5 g mass (U.S. Fish and Wildlife Service, 1993). At a collection of sites in the Sacramento Valley, mean neonate size was similar (208.8 mm [95-percent CI=196.5–221.1 mm] SVL; 4.87 g [95-percent CI=4.07–5.67 g] mass; Halstead and others, 2011b). The latter study found that SVL was correlated within litters, but unaffected by maternal SVL (Halstead and others, 2011b). Sex ratios at birth typically are near 1:1, with deviations from an even sex ratio non-significant (Halstead and others, 2011b). Larger females appear to invest energy in producing more, rather than larger, offspring, a pattern consistent with other natricine snakes (Halstead and others, 2011b). Because much of what is known about *T. gigas* reproduction is based on studies with small sample sizes, additional research on the reproductive ecology of *T. gigas* is needed, particularly in relation to spatial and temporal variation and the extent to which prey resources contribute to this variation.

Growth and Longevity

Thamnophis gigas, like most natricine snakes, is sexually dimorphic for size, with females the larger sex (Wylie and others, 2010). In a comparison of four sites, Wylie and others (2010) found that the sexual dimorphism index at each site was greater than 1. Females were both longer (log-normal mean female SVL=692 mm [95-percent CI=377–1168 mm]; log-normal mean male SVL=581 mm [95-percent CI=387–839 mm]) and heavier (log-normal mean female mass=250 g [95-percent CI=24–1030g]; log-normal mean male mass=101 g [95-percent CI=26–274g]) than males (Wylie and others, 2010). For their length, females also were heavier than males, with greater body condition than males (Wylie and others, 2010). This was especially pronounced in large individuals, with neonates of both sexes beginning life at a similar size (Wylie and others, 2010). Size at sexual maturity is unknown in *T. gigas*, but age at sexual maturity has been reported to be 3 years for males and 5 years for females (U.S. Fish and Wildlife Service, 1993). The maximum lifespan of *T. gigas* is unknown, but is thought to be greater than 10 years.

Body condition of *T. gigas* varies seasonally, with the pattern of variation differing between the sexes (Coates and others, 2009). The difference between male and female body condition is greatest in the spring, although the sexes enter brumation in similar condition in the autumn (Coates and others, 2009). Several mechanisms contribute to this pattern, including anorexia of males during the spring mating season, females gaining mass early in the active season to invest in reproduction later in the year, and a potential relationship between the elevated body temperature of males relative to females during the winter months (Coates and others, 2009).

To attain their large size, *T. gigas* grows quickly. Young typically grow very rapidly, more than doubling in size within a year (U.S. Fish and Wildlife Service, 1993). Growth slows with age, with the largest individuals growing very slowly (Coates and others, 2009). In association with their mating season anorexia and low body condition, adult male *T. gigas* do not grow during spring, likely foregoing feeding and growth for mating opportunities (Coates and others, 2009). Whether and how this contributes to the observed sexual size dimorphism of adult *T. gigas* are unknown.

Physiology

Perhaps one of the least-known aspects of the biology of *T. gigas* is its physiology. Ecdysis of adult males and females occurs every 4–6 weeks (Wylie and others, 2004a); younger snakes likely shed more frequently. Wack and others (2012) compared blood cell counts and plasma biochemistry of *T. gigas* with *T. sirtalis fitchi* at four sites in the Central Valley (one in the Sacramento Valley, one at the eastern edge of the Sacramento-San Joaquin Delta, and two in the San Joaquin Valley) in 2008, and found several notable differences. *Thamnophis gigas* had leukocyte values nearly twice those of *T. sirtalis fitchi*; significant differences between the species included total white blood cells (*T. gigas* mean=11,500/ μ L), heterophils (990/ μ L), lymphocytes (7,900/ μ L), and azurophils (1,750/ μ L; Wack and others, 2012). Elevated values for these types of blood cells could indicate chronic infection or immunological challenge (Wack and others, 2012). The plasma biochemistry of *T. gigas* also differed from that of *T. sirtalis fitchi*. In particular, aspartate aminotransferase and potassium concentrations were higher in *T. gigas* at 22 International Units per liter (IU/L) and 5.2 milliequivalents per liter (meq/L), respectively, and globulin concentrations were lower in *T. gigas* (3.6 grams per liter [g/L]). No statistical differences between the sexes were found in blood cell counts or plasma biochemistry, but several blood cell counts (heterophils, basophils, and azurophils), mineral concentrations (calcium, phosphorus, potassium, and sodium), and protein concentrations (albumin and globulin) varied among sites (Wack and others, 2012). Much remains to be learned about the physiology of *T. gigas*, and how different aspects of its physiology affect individual fitness and population growth rate.

Food and Feeding

Thamnophis gigas feeds primarily on aquatic prey. Historically, *T. gigas* likely preyed on native fish, such as the Sacramento blackfish (*Orthodon microlepidotus*) and the thicketail chub (*Gila crassicauda*; Cunningham, 1959; Hansen, 1980), and amphibians. The contemporary diet of *T. gigas* consists largely of introduced species, including common carp (*Cyprinus carpio*; Fitch, 1940; Hansen, 1980, 1986), western mosquitofish (*Gambusia affinis*; Hansen, 1980, 1986), and all life stages of American bullfrogs (*Lithobates catesbeianus*; Fitch, 1940; Hansen, 1980, 1988). Because of the often turbid water in which it occurs, and the likelihood of nocturnal foraging, it is likely that *T. gigas* locates small fish tactilely (Hansen, 1980). Prey abundance is not likely to be a limiting factor for most populations (Hansen, 1980; Wylie and others, 2010).

Many questions remain regarding the innate prey preferences and prey selection of *T. gigas*, particularly given the highly altered prey communities on which they now depend.

Predators and Defense

Many potential predators of *T. gigas* occur in the Central Valley; indeed, predation pressure has been hypothesized as a potential mechanism both for the large size of *T. gigas* (Hansen, 1980) and for its extreme wariness (Fitch, 1940; Wright and Wright, 1957). Nearly all large individuals in the American Basin had scars or recent injuries (Hansen, 1986). Potential native predators include raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), gray foxes (*Urocyon cinereoargenteus*), great blue herons (*Ardea herodias*), great egrets (*Ardea alba*), and American bitterns (*Botaurus lentiginosus*; U.S. Fish and Wildlife Service, 1999). Introduced predators likely take a large toll on *T. gigas*, especially young individuals. American bullfrogs

prey on neonate *T. gigas*, and are estimated to take 22 percent of annual *T. gigas* production (Wylie and others, 2003b). Large introduced predatory fishes likely also prey on neonates (Hansen, 1986). Other potential introduced predators include Virginia opossums (*Didelphis virginiana*) and red foxes (*Vulpes vulpes*; U.S. Fish and Wildlife Service, 1999).

Animals can subvert the predation process at several different stages, and *T. gigas* has several defense tactics in its repertoire to avoid succumbing to predation. The first line of defense *T. gigas* uses is to avoid detection by potential predators. It does this through both crypsis and taking refuge in burrows and decaying piles of vegetation (Rossman and others, 1996).

Thamnophis gigas also is very wary, and readily drops into water on approach to within 15 m (Fitch, 1940; Rossman and others, 1996). Once grabbed by a perceived predator, *T. gigas* may thrash; excrete musk, feces, and uric acid; and occasionally may bite its attacker (Hansen, 1980; Rossman and others, 1996).

Population Ecology

Much attention has been given to estimating the abundance and density of *T. gigas*. Density, as measured by both fixed and telemetry-based buffers, varied among sites in the Sacramento Valley (Wylie and others, 2010). Regardless of the method used, density was greatest in a natural marsh (Badger Creek; 8.0 individuals/ha [95-percent CI=7.6–9.0 individuals/ha]), was lowest in moist-soil wetlands managed for food for overwintering waterfowl (Colusa NWR; 0.83 individuals/ha [95-percent CI=0.63–1.5 individuals/ha]), and was intermediate at a site containing a remnant natural marsh and rice agriculture (Gilsizer Slough; 3.1 individuals/ha [95-percent CI=2.2–4.9 individuals/ha]) and a site consisting entirely of rice agriculture (Natomas Basin; 1.7 individuals/ha [95-percent CI=1.5–2.1 individuals/ha]). The mechanism underlying these differences in density was not determined, but habitat quality and prey abundance were considered likely candidates (Wylie and others, 2010). Notably, body condition followed similar patterns, so prey limitation was unlikely a factor at even the site with the greatest density of *T. gigas* (Wylie and others, 2010).

Linear density estimates are available for many locations in the Sacramento Valley. In the Colusa Drain, linear density was estimated at 27 individuals/km (95-percent CI=21–35 individuals/km) in 2003 (Wylie, 2003), 16 individuals/km (95-percent CI=12–23 individuals/km) in 2004 (Wylie and Amarello, 2006), and 20 individuals/km (95-percent CI=16–31 individuals/km) in 2006 (Wylie and Amarello, 2006). Monitoring at the Sacramento NWR complex in 2005 resulted in three density estimates for Colusa NWR and one for Sacramento NWR. In Logan Creek at Sacramento NWR, density was estimated at 31 individuals/km (95-percent CI=21–57 individuals/km). At Colusa NWR, density in the GCID canal was estimated at 97 individuals/km (95-percent CI=64–163 individuals/km), and density in the J-Drain (a major drainage canal running north-south through the refuge) was estimated at 103 individuals/km (95-percent CI=65–181 individuals/km). Tract 24.11, which was restored to marsh habitat, had a density of 126 individuals/km (95-percent CI=89–185 individuals/km; Wylie and others, 2005).

Previous work at Colusa NWR provided density estimates at these and other sites. In 2004, density in the GCID canal was 19 individuals/km (95-percent CI=16–33 individuals/km), and that in the J-Drain was 78 individuals/km (95-percent CI=54–128 individuals/km; Wylie and others, 2004a). The restored wetland sites—Tracts 24.2, 24.6, and 24.11—had densities of 34 individuals/km (95-percent CI=25–105 individuals/km), 69 individuals/km (95-percent CI=43–122 individuals/km), and 59 individuals/km (95-percent CI=46–83 individuals/km), respectively (Wylie and others, 2004a). In 2000, locations north of the restoration had a density of 104 individuals/km, and locations west of the restoration had a density of 53 individuals/km (Wylie and others, 2000). Abundance often is observed to vary annually, likely because of migration of individuals (Wylie and Martin, 2004c).

Long-term monitoring of *T. gigas* in the Natomas Basin has provided abundance and density estimates at many sites within the basin (table 1). Different survey locations and study designs among years makes direct comparison of these estimates difficult. In 2011, a new study design was proposed to enable statistical estimation of trends in abundance at five demographic monitoring sites (ICF International, 2012).

Relatively little is known about demographic rates of *T. gigas*. The best estimates of survival for *T. gigas* are for radio-tracked adult females. Mean annual survival of adult females in the Sacramento Valley was 0.61 (95-percent CRI=0.41–0.79), with variation among study populations and years (Halstead and others, 2012). The risk of mortality of adult females while in terrestrial habitats was 0.38 (95-percent CRI= 0.09–0.89) times that of adult females while in aquatic habitats (Halstead and others, 2012), likely because individuals in terrestrial habitats usually are in burrows or other refuges, and those in aquatic habitats often are foraging and exposed to predators. Much variation existed in the effects of linear habitat on risk of mortality. At some locations, notably where both marshes and canals were available, the risk of mortality was greatest in linear habitats (canals; Halstead and others, 2012). In contrast, where wetland habitats consisted entirely of canals and rice agriculture, the risk of mortality was less in linear habitats (such as canals) than in areal habitats, which lack water, cover, or both for much of the active season (Halstead and others, 2012). Little is known about the survival of male and subadult *T. gigas* that are too small for radio telemetry, although appropriately designed long-term capture-mark-recapture (CMR) studies could yield such data. Although estimates of litter size are available, recruitment rates are poorly known because survival rates of neonate snakes are unknown.

The sex ratio of *T. gigas* populations usually is near 1:1. Although sex ratios of individual litters are variable, overall (pooled across litters) sex ratios at birth generally do not differ from 1:1 (Halstead and others, 2011b). Studies of adult populations of *T. gigas* also indicate sex ratios very near 1:1 (Wylie and others, 1997, 2010).

Table 1. Abundance (number of individuals) and density (individuals per kilometer) estimates at study sites, by year, in the Natomas Basin, Sacramento Valley, California, 2000–2012.

[**Years:** 2000, 2001, 2002, years in which density was estimated and expressed as maximum likelihood estimate \pm 1 standard error; 2003, 2004, 2005, years in which density was estimated and expressed as maximum likelihood estimate (95-percent confidence interval); 2006, 2007, 2008, years in which abundance was estimated and expressed as maximum likelihood estimate (95-percent confidence interval); 2011, 2012, years in which abundance was estimated and expressed as model-averaged (temporal heterogeneity, ephemeral behavioral response, water temperature, sex, and length effects on daily capture probability) posterior mean (95-percent credible interval). References include Wylie and Casazza (2000, 2001), Wylie and others, (2003c, 2004b), Jones & Stokes (2005, 2006, 2007), ICF Jones & Stokes (2008, 2009), and ICF International (2011, 2012, 2013)]

Site	Location	Year					
		2000	2001	2002	2003	2004	2005
Airstrin canal		69 \pm 6.09					
Atkinson						10 (4–8) [<i>sic</i>]	
Bennett North							
Bennett South	Q drain Wetland	39 \pm 10.09		45 \pm 9.98	50 (35–87)		
Bianchi West							
BKS	Silva west ditch Kismat SW wetland Silva SW wetland Western edge				48 (30–98)	11 (5–25)	19 (7–29)
Elsie							
Fisherman’s Lake							
Frazer North							16 (5–28)
Frazer South							
Huffman East							
Huffman West							16 (8–65)
Lone Tree canal		16 \pm 6.09			4 (3–13)		
Lucich North	T-drain SW wetland Southern edge		22 \pm 7.17	32 \pm 5.79	40 (27–68)	60 (42–58) [<i>sic</i>]	42 (12–126) 118 (34–262)
Lucich South	North drainage canal North wetland Eastern edge	63 \pm 22.81		55 \pm 12.5	39 (28–73)	59 (14–170)	55 (8–27) [<i>sic</i>]
Metro Air Park							
Nestor							
Sills	Lateral 3C Drain 13				19 (12–41)		
Snake Alley		19.5 \pm 6.90		20 \pm 4.01		17 (8–15) [<i>sic</i>]	26 (10–32)
Tufts							30 (11–43)
Vestal							

Site	Location	Year				
		2006	2007	2008	2011	2012
Airstrip canal				7 (6–21)		
Atkinson						
Bennett North						
Bennett South	Q drain	47 (22–154)	10 (7–31)	43 (16–200)		
	Wetland		7 (7–16)			
Bianchi West			10 (7–30)	13 (9–42)		
BKS	Silva west ditch	16 (8–69)	8 (7–20)			
	Kismat SW wetland			42 (20–139)		
	Silva SW wetland			6 (5–25)		
	Western edge				175 (101–318)	205 (125–348)
Elsie				10 (7–29)		
Fisherman's Lake		4 (4–14)			3 (1–24)	48 (1–388)
Frazer North						
Frazer South			23 (17–46)			
Huffman East		15 (8–65)				
Huffman West		107 (50–297)	18 (14–35)	11 (undefined)		
Lone Tree canal						
Lucich North	T-drain	10 (6–44)	14 (8–60)	13 (9–33)		
	SW wetland					
	Southern edge				264 (68–673)	100 (58–183)
Lucich South	North drainage canal	61 (21–291)	11 (9–23)	19 (14–41)		
	North wetland			8 (8–17)		
	Eastern edge				309 (70–854)	390 (88–945)
Metro Air Park		11 (6–47)				
Nestor			10 (6–44)			
Sills					44 (28–75) ¹	27 (18–42)
	Lateral 3C		4 (4–4)			
	Drain 13		13 (12–23)	31 (24–52)		
Snake Alley		31 (16–101)		35 (14–161)		
Tufts		4 (4–14)		29 (19–69)		
Vestal		17 (14–31)		16 (10–51)		

¹Linear density at Sills in 2011 as calculated with spatial capture-mark-recapture models was 43 (28–68) individuals per kilometer.

Community Ecology

Relatively little is known about the community relationships of *T. gigas*. *T. gigas* commonly occurs with *T. sirtalis fitchi*; indeed, all sites at which *T. gigas* was observed also were occupied by *T. sirtalis fitchi* in the southern Sacramento Valley (Hansen, 1986). The highly aquatic nature of *T. gigas* and its propensity for feeding on aquatic prey such as tadpoles and fishes likely reduces competition with *T. sirtalis fitchi*. Another congener, *T. elegans*, only rarely occurs with *T. gigas* and also likely feeds on more terrestrial prey than *T. gigas*. Other potential competitors of *T. gigas* include American bullfrogs, wading birds, and fishes. These species also can be predators and (or) prey of *T. gigas* (see sections, “Food and Feeding” and “Predators and Defense”), forming complex community interactions characterized by high levels of intraguild predation.

Conservation Biology

Thamnophis gigas was listed as Threatened by the State of California in 1971 (California Department of Fish and Game Commission, 1971) and by the U.S. Fish and Wildlife Service in 1993 (U.S. Fish and Wildlife Service, 1993), largely because of extensive habitat loss resulting from damming of rivers and streams, diversion of water, and conversion of habitat to agriculture and other uses. Indeed, the diversion of water and conversion of marsh habitats extirpated *T. gigas* from south of Fresno (Hansen, 1988), and nearly extirpated the species from the entire San Joaquin Valley (U.S. Fish and Wildlife Service, 1993). Despite its protected status, numerous threats to *T. gigas* still exist. Perhaps the greatest threat to *T. gigas* is continuing habitat loss (U.S. Fish and Wildlife Service, 1993, 2006). Although more than 93 percent of its historical marsh habitat was already lost by the mid-1980s (Frayer and others, 1989; Garone, 2007; Huber and others, 2010), the threat of habitat loss and fragmentation remains. Urbanization throughout the Central Valley has resulted and likely will continue to result in the loss of *T. gigas* habitat (Hansen, 1986; Wylie and Casazza, 2001; U.S. Fish and Wildlife Service, 2006). Agricultural development, including cultivation, heavy grazing, and pest control practices, also can reduce the quality and extent of *T. gigas* habitat (Hansen, 1986). The loss of rice acreage has the potential to threaten the giant gartersnake as well (U.S. Fish and Wildlife Service, 2006). Perhaps the greatest threat of habitat loss for *T. gigas* is water management practices; without a reliable supply of freshwater to marshes, canals with vegetated banks, and rice fields, persistence of *T. gigas* is unlikely (U.S. Fish and Wildlife Service, 1993; Halstead and others, 2010).

The importance of water to *T. gigas* ecology is exemplified by additional threats related to flooding. Flood control was largely responsible for the conversion of historical marshes to other uses, and flood control practices remain a threat to *T. gigas* insofar as they affect the formation and maintenance of marshes (Hansen, 1986). Construction and maintenance of flood control structures also can result in the direct loss of *T. gigas* habitat or mortality of individuals in areas inhabited by *T. gigas* (U.S. Fish and Wildlife Service, 2006). Conversely, flooding also has the potential to kill individual *T. gigas*, and possibly even result in the extirpation of populations. Severe flooding results in the loss of upland habitat appropriate for overwintering (Hansen, 1988), and repeated deep, high flow rate flooding is apparently incompatible with *T. gigas* occurrence (Wylie and others, 2005; U.S. Fish and Wildlife Service, 2006).

Pest control also can pose a threat to *T. gigas* (Hansen, 1988). Dredging waterways to remove sediment and vegetation can result in direct mortality and in some cases habitat loss or reduction (U.S. Fish and Wildlife Service, 1993). Mowing can likewise result in direct mortality and reduce cover from predators and extreme environmental temperatures. Disking and other mechanical disturbances are even more detrimental than mowing because they have the potential to directly kill snakes and disrupt burrows and cracks in the soil, which are an important component of *T. gigas* habitat (U.S. Fish and Wildlife Service, 2006). Pesticides have unknown effects on *T. gigas*, but some likely have negative consequences for snake health (U.S. Fish and Wildlife Service, 1993). Similar aquatic snakes inhabiting rice fields in Spain, however, have shown marked resilience to high levels of organochlorines (Santos and others, 1999). Whether this resilience also occurs in *T. gigas* remains to be evaluated. Regardless of the direct effects of pesticides on *T. gigas*, these chemicals have documented negative effects on prey communities that could indirectly result in *T. gigas* declines (U.S. Fish and Wildlife Service, 2006).

Chemicals unrelated to pest control also can threaten *T. gigas* (Hansen, 1988). In particular, many areas of the Central Valley have naturally or artificially elevated levels of heavy metals, particularly selenium and mercury. Despite high levels of mercury and selenium in wetlands in much of its range, *T. gigas* had relatively low levels of these metals in their tissues compared to other snake species (Wylie and others, 2009b). In contrast, *T. gigas* had among the highest levels of arsenic and chromium recorded in snakes, with the exception of *Nerodia fasciata* (southern watersnake) in a coal ash settling basin (Hopkins and others, 1999). Little is known about the effects of heavy metals on snakes. Chronic exposure to arsenic, selenium, cadmium, strontium, and vanadium resulted in no mortality and little measurable physiological response in *Nerodia fasciata*, despite some of the highest blood concentrations of these contaminants recorded in any vertebrate (Hopkins and others, 2002). Obviously, much remains to be learned about the effects of chemicals on snakes in general and *T. gigas* in particular; non-destructive tissue sampling for contaminant studies could aid in this effort (Wylie and others, 2009b).

Other direct anthropogenic threats to *T. gigas* also exist. Natural gas exploration might pose a threat to *T. gigas* (U.S. Fish and Wildlife Service, 2006). Roads have a negative effect on many wildlife, especially herpetofauna (Roe and others, 2004, 2006). The propensity for *T. gigas* to stay within a few meters of marsh habitats for most of the year might help to reduce this risk (Roe and others, 2004, 2006; Attum and others, 2007, 2008), but not eliminate it altogether. Erosion control and other netting can result in the direct mortality of snakes, and when placed near marshes or canals, these materials could threaten *T. gigas* (U.S. Fish and Wildlife Service, 2006). Human activities, including angling and crayfish trapping, can result in disturbance to *T. gigas* (U.S. Fish and Wildlife Service, 2006).

Introduced species comprise a substantial part of the biotic communities in which *T. gigas* is present, and these species potentially can have negative effects on *T. gigas*. Introduced predators are perhaps the most obvious example of how introduced species can affect *T. gigas* (U.S. Fish and Wildlife Service, 1993). Introduced predatory fishes likely prey on *T. gigas*, and their effects could be exacerbated by the typical behavioral response of *T. gigas* to flee into water upon disturbance (Hansen, 1986; Rossman and others, 1996). American bullfrogs are documented predators of *T. gigas* (U.S. Fish and Wildlife Service, 1993; Carpenter and others, 2002), taking as much as 22 percent of annual *T. gigas* reproductive effort (Wylie and others, 2003b). Other potential introduced predators include domestic cats (*Felis catus*) and raccoons (*Procyon lotor*; Hansen, 1986; U.S. Fish and Wildlife Service, 2006). Native predators, such as

North American river otters (*Lontra canadensis*) and striped skunks (*Mephitis mephitis*), that are subsidized by humans or introduced prey also can increase in abundance and, therefore, have a stronger negative effect on *T. gigas* than would otherwise occur (U.S. Fish and Wildlife Service, 2006).

Introduced competitors also might pose a threat to *T. gigas*. Introduced populations of *Nerodia sipedon* (northern watersnake) and *Nerodia fasciata* near Sacramento pose a potential incipient threat if these populations spread to the Central Valley (U.S. Fish and Wildlife Service, 2006; Rose and others, 2013; Rose and Todd 2014). Habitat conversion could favor other *Thamnophis* species and bring them into contact with *T. gigas*, promoting competition where it previously did not exist (Hansen, 1986). Some introduced fish species also likely compete with *T. gigas* for prey (Hansen, 1986).

Introduced plants also can affect *T. gigas*, often in complex ways. Water primrose (*Ludwigia* spp.) and cattails (*Typha* spp.) are used by *T. gigas*, but use is generally restricted to edges between these plants and open water (Hansen and others, 2010; Valcarcel, 2011). If left unchecked, the growth of these plant species can be detrimental to *T. gigas* by eliminating open water habitat or restricting movements and increasing susceptibility to predators (U.S. Fish and Wildlife Service, 2006; Hansen and others, 2010). Mechanical control is an effective way to remove water primrose and form open water/vegetation edges important to *T. gigas*, but adequate depth and water availability or repeated treatments are necessary to maintain habitat in a suitable condition (Hansen and others, 2010). Introduced and native floating vegetation can be detrimental to *T. gigas* because of altered water chemistry, shading, and prey communities in the presence of these species, and also because of control measures (pulling, herbicides, etc.) used for these species (U.S. Fish and Wildlife Service, 2006).

Disease also might threaten *T. gigas* populations (U.S. Fish and Wildlife Service, 1993). Multiple parasites have been observed to infest *T. gigas*, with mortality ensuing from particularly high parasite loads (U.S. Fish and Wildlife Service, 1999). An emerging infectious fungus, snake fungal disease, has recently been observed in several snake species in the Eastern United States (Sleeman, 2013). Whether this disease occurs in the West in general or *T. gigas* in particular is unknown.

Several strategies would help to conserve *T. gigas*. Perhaps the most important of these is the protection and enhancement of habitat near known *T. gigas* populations (U.S. Fish and Wildlife Service, 2006). Ensuring a reliable water supply is an essential component of habitat management for *T. gigas* (U.S. Fish and Wildlife Service, 2006). Corridors (including passages under roads) to promote connectivity of populations also might benefit *T. gigas* (U.S. Fish and Wildlife Service, 2006).

Translocation generally is considered a last resort for conservation of species in the wild. Factors that resulted in the extirpation of the species must be known and mitigated before attempting translocation (Burke, 1991; Dodd and Seigel, 1991; Reinert 1991; Germano and Bishop, 2009). The health of donor populations must be assured, so that they are not threatened by the loss of individuals for translocation (Burke, 1991; Dodd and Seigel, 1991; Reinert, 1991; Germano and Bishop, 2009). Genetic considerations also must be taken into account, both for preserving locally-adapted genotypes and genetic diversity, and to rescue populations from inbreeding depression, genetic drift, and other detrimental conditions arising from low effective population sizes (Madsen and others, 1996, 2004; Madsen and Shine, 2000). Nonetheless, translocation following habitat restoration will be necessary if *T. gigas* is to inhabit its entire former range.

Research Methods

Research methods directly applicable to *T. gigas* conservation primarily include occupancy studies that examine species distributions and the variables affecting distribution, CMR studies to estimate demographic parameters, and radio telemetry studies of behavior. Additional study designs that might be useful for *T. gigas* conservation include methods that rely on replicated counts of individuals, such as binomial mixture models and their extensions, and other methods of tracking individuals, such as passive integrated transponder (PIT) tagging combined with detector arrays. These general methods are most useful when incorporated into well-designed studies addressing specific research questions.

Occupancy studies (MacKenzie and others, 2002, 2005, 2006; Tyre and others, 2003; Thompson and others, 2004) focus on whether a species is present in a given sample unit, and can be extended to look at multiple states (Royle, 2004; Nichols and others, 2007; Miller and others, 2012) and how sites are colonized or extirpated over time (Royle and Kéry, 2007; Miller and others, 2012). Repeated observations of sample units provide information on detection probabilities, and estimates of the proportion of area occupied (and the variables that affect whether sample units are occupied) are essentially corrected for imperfect detection. This is particularly important when detectability and probability of occurrence are confounded (Royle and others, 2005). An example of this situation is an animal that prefers dense cover, but is more difficult to detect in dense cover than in other habitats. In occupancy studies, a relatively large sample of sites might be required to detect relationships between occurrence and variables of interest. The number of repeat surveys at each sample unit depends on survey-specific detection probabilities; the goal here is to minimize uncertainty about the occurrence status of sites where the species is not detected. Thus, trade-offs between number of sites monitored and survey effort per site often are involved in occupancy study design (MacKenzie and Royle, 2005; Bailey and others, 2007).

CMR studies are used to estimate abundance (Dorazio and Royle, 2003; Chao and Huggins, 2005a; Wylie and others, 2010; Halstead and others, 2011c; Couturier and others, 2013); density (Efford, 2004; Royle and Young, 2008; Royle and others, 2009; Kéry and others, 2011); survival (Williams and others, 2002; Stanford and King, 2004; Lind and others, 2005; Royle and Dorazio, 2008; Halstead and others, 2011c; Kéry and Schaub, 2011); recruitment (Gimenez and others, 2007; Dupuis and Schwarz, 2007; Halstead and others, 2011c); population growth rate (Kéry and Royle, 2009; Schaub and Abadi, 2011; Halstead and others, 2011c; Couturier and others, 2013); and individual growth rate, age, and asymptotic size (Eaton and Link, 2011; Fellers and others, 2013). The purpose of CMR methods is to obtain unbiased estimates of demographic parameters that account for the imperfect detection of individuals in the population (Williams and others, 2002; Amstrup and others, 2005; Royle and Dorazio, 2008; King and others, 2009; Kéry and Schaub, 2011) and the variables that affect the probability that an individual is detected or captured (for example, weather, effort, date, etc.). In general, lower capture probabilities result in less precise estimates of demographic parameters, and snakes have notoriously low capture (and detection) probabilities (Wylie and others, 2010; Halstead and others, 2011a, 2013a; Durso and others, 2011). Trap modifications show some promise for increasing the probability of capture for *T. gigas* (Halstead and others, 2013a). Capture probabilities likely are limited by *T. gigas* behavior, however, because more than 50 percent of the *T. gigas* time budget is spent in terrestrial refuges adjacent to aquatic habitats, with most of this time spent underground (Halstead and others, in press). Sampling in the spring, when males are searching for females and females are foraging heavily after a winter fast, likely will increase

the availability of *T. gigas* for capture. Other methods of capture, including other evaluated trap designs and visually searching for and capturing individual snakes, have proven less efficient and less repeatable than the modified floating funnel traps used in most studies of *T. gigas* biology.

Analysis of CMR data can take numerous forms, depending on the parameters of interest and assumptions of the model. Estimating within-year abundance generally is done with closed-population models that assume no additions or losses to the population (Williams and others, 2002; Amstrup and others, 2005; Chao and Huggins, 2005a). To meet these assumptions, the sampling period should be as short as possible and preferably not occur when additions to or removals from the population are most likely (for example, during bouts of reproduction). A short sampling frame must be balanced with the capture probability of the organism of interest; if capture probabilities are low, more samples are necessary to obtain precise estimates of abundance.

Historically, closed-population models could only account for variation in capture probability caused by a behavioral response to being captured and (or) handled, temporal variation, or individual heterogeneity (Chao and Huggins, 2005b), although models accounting for individual heterogeneity are not uniquely identifiable (that is, a different model form [logit-normal, compared to beta-binomial mixtures compared to finite mixtures, etc.] will result in very different inference about abundance, and there is no way to ascertain which model performs better; Link, 2003). Modern closed-population models allow for heterogeneity in individual capture probabilities caused by individual characteristics using the Horvitz-Thompson estimator (Chao and Huggins, 2005a). Bayesian methods allow another extension to closed-population models by using data augmentation to account for individual variation in detection probabilities (Royle 2009); these models further allow the estimation of latent sex ratios and size distributions (Tenan and others, 2013). Bayesian analysis of closed-population models also provides a cohesive framework for accounting for missing covariates and incorporating prior information on the detection process (Link and Barker, 2010). Spatial capture-recapture models, which explicitly estimate density based on the locations of capture of individuals, are a particularly useful extension of closed-population models that can be fitted by either maximum likelihood or Bayesian methods (Efford, 2004; Royle and Young, 2008; Royle and others, 2009; Kéry and others, 2011).

Open-population models, which allow additions to (births, immigration) and (or) removals from (deaths, emigration) populations between sampling periods, allow the estimation of many demographic parameters. Open-population models assume that the sampling period is short (so that the population is closed) relative to the amount of time between samples, for which the population can be assumed open (Williams and others, 2002). Cormack-Jolly-Seber (CJS) models condition on the first capture of individuals and are used to estimate survival (Williams and others, 2002; Nichols, 2005; Gimenez and others, 2007; Royle 2008). A key assumption of CJS models is that marked individuals are a random subset, and, therefore, are representative of the population (Williams and others, 2002; Nichols, 2005). Modeling group, site, or temporal effects in CJS models is relatively straightforward, but individual covariates that vary over time (such as mass, size, condition, etc.) can be problematic because these values are missing whenever individuals are not captured. These missing values can be easily handled in a Bayesian analysis by providing a prior distribution or model for the missing covariates (Royle, 2008; King and others, 2009). Jolly-Seber (JS) models, in contrast to CJS models, do not condition on first capture and explicitly model recruitment and abundance in addition to survival (Williams and others, 2002; Nichols, 2005; Halstead and others, 2011c). Several different parameterizations of

the JS model exist (Williams and others, 2002; Nichols 2005), and it can be implemented in a Bayesian analysis in many different ways (King and others, 2009; Kéry and Schaub, 2011). Both the CJS and JS models can incorporate the robust design, which uses information from both open and closed sampling occasions to improve inference about abundance and survival (Pollock, 1982) and account for temporary emigration (Kendall and others, 1997).

Radio telemetry is another important tool for studying animal behavior. Although other types of transmitters, such as Global Positioning System transmitters and Platform Terminal Transmitters, exist, these are inappropriate for use in snakes because of the need to surgically implant transmitters in the body cavity (coelom) of snakes. Even with radio transmitters, limitations of transmitter size and battery life make radio telemetry practical only for large adult giant gartersnakes. Most individuals of this size are adult females (Wylie and others, 2010). Despite the limitation of radio telemetry to studies of adult, mostly female, snakes, this tool can provide much information about the behavior and ecology of *T. gigas*. For example, radio telemetry has been used to examine the thermal ecology (Wylie and others, 2009a), terrestrial ecology (Halstead and others, in press), and patterns of space use (Valcarcel, 2011) of *T. gigas*. In addition to this behavioral information, radio telemetry also can provide demographic information, such as survival rates (Halstead and others, 2012). Although more expensive to collect and intrusive to individual snakes, radio telemetry data offers remarkably rich, detailed information on snake behavior that cannot be obtained in any other way.

Radio telemetry data are analyzed in several different ways, depending on the objectives of the study. Home ranges generally are estimated as minimum convex polygons, kernel density estimates of utilization distributions (Worton, 1989; Row and Blouin-Demers, 2006), and local convex hulls (LoCoH; Getz and Wilmers, 2004; Getz and others, 2007). Local convex hulls seem particularly promising for analysis of *T. gigas* home ranges because they allow holes and sharp edges in the utilization distribution (Getz and Wilmers, 2004; Getz and others, 2007) that likely are typical of animals inhabiting linear features, such as canals. Movements can be modeled using various types of random walk (Turchin, 1998; Halstead and others, 2007; Holdo and Roach, 2013) or state-space (Jonsen and others, 2005; Patterson and others, 2008) models. Thermal ecology is studied using temperature-sensitive radio transmitters, and with the use of operative temperature models (Huey and others, 1989; Huey 1991), can quantify the degree of thermoregulation and breadth of the thermal niche of species. Perhaps the greatest utility of radio telemetry for conservation is study of the habitat relationships of organisms. In particular, analyses of habitat selection, which compare use of resources to their availability, are informative about how individuals and populations relate to their environment (Manly and others, 2002). Habitat selection occurs at multiple spatial scales (Johnson, 1980), and can be analyzed by a great variety of methods (Boyce and others, 2002; Manly and others, 2002; Gillies and others, 2006; Johnson and others, 2006; Millspaugh and others, 2006; Rittenhouse and others, 2008; Baasch and others, 2010; Duchesne and others, 2010; Rota and others, 2013).

The exact method used to examine habitat selection will depend on the scale of inference and the data available. Regardless of the exact method used, the most important consideration in studies of an organism's relationship with habitat is accounting for habitat availability when describing habitat use. Estimation of survival from radio telemetry usually involves modeling survival as a conditional continuous process observed at discrete intervals, although other models also are available (Pollock and others, 1989; Banerjee and others, 2003; Murray, 2006; Halstead and others, 2012). Because it is relatively expensive, the greatest limitation of radio telemetry for use in studies of animals is the number of animals tracked. In general, increasing the number of individuals followed is the best way to increase statistical power to detect differences among treatments or groups (Börger and others, 2006).

Conceptual Model of Giant Gartersnake Ecology at the Population Level

A conceptual model of *T. gigas* population ecology and the variables that hypothetically affect it are shown in figure 2. The conceptual model depicts a simple female-based life cycle diagram, in which life stages are indicated by photographs of *T. gigas*, and transitions between life stages (the vital rates of birth, growth, survival, etc.) are represented by solid black arrows (fig. 2). The effects of habitat conditions, climatic conditions, prey communities, predator communities, and human actions appear within the life cycle diagram as photographs or cartoon drawings (fig. 2). Relationships among these variables and relationships between these variables and vital rates are shown by arrows of different sizes, line types, and colors (fig. 2). Arrow thickness represents the importance of the relationship, with thicker lines representing parent nodes that are hypothesized to be more influential in determining the status of the child nodes. The color of the arrow represents our understanding of the relationship between nodes, with red indicating a low level of understanding, blue indicating a moderate level of understanding, and green indicating a high level of understanding. Finally, the line type used for the arrow indicates the predictability of the relationship between nodes. In this case, solid lines have high predictability (that is, the relationship between variables is largely deterministic), dashed lines have moderate predictability, and dotted lines have low predictability (that is, the relationship between variables is largely stochastic). Signs associated with each arrow indicate whether the parent node has a positive correlation with the child node (+); a negative correlation with the child node (-); or an unknown, variable, or nonlinear relationship with the child node (~).

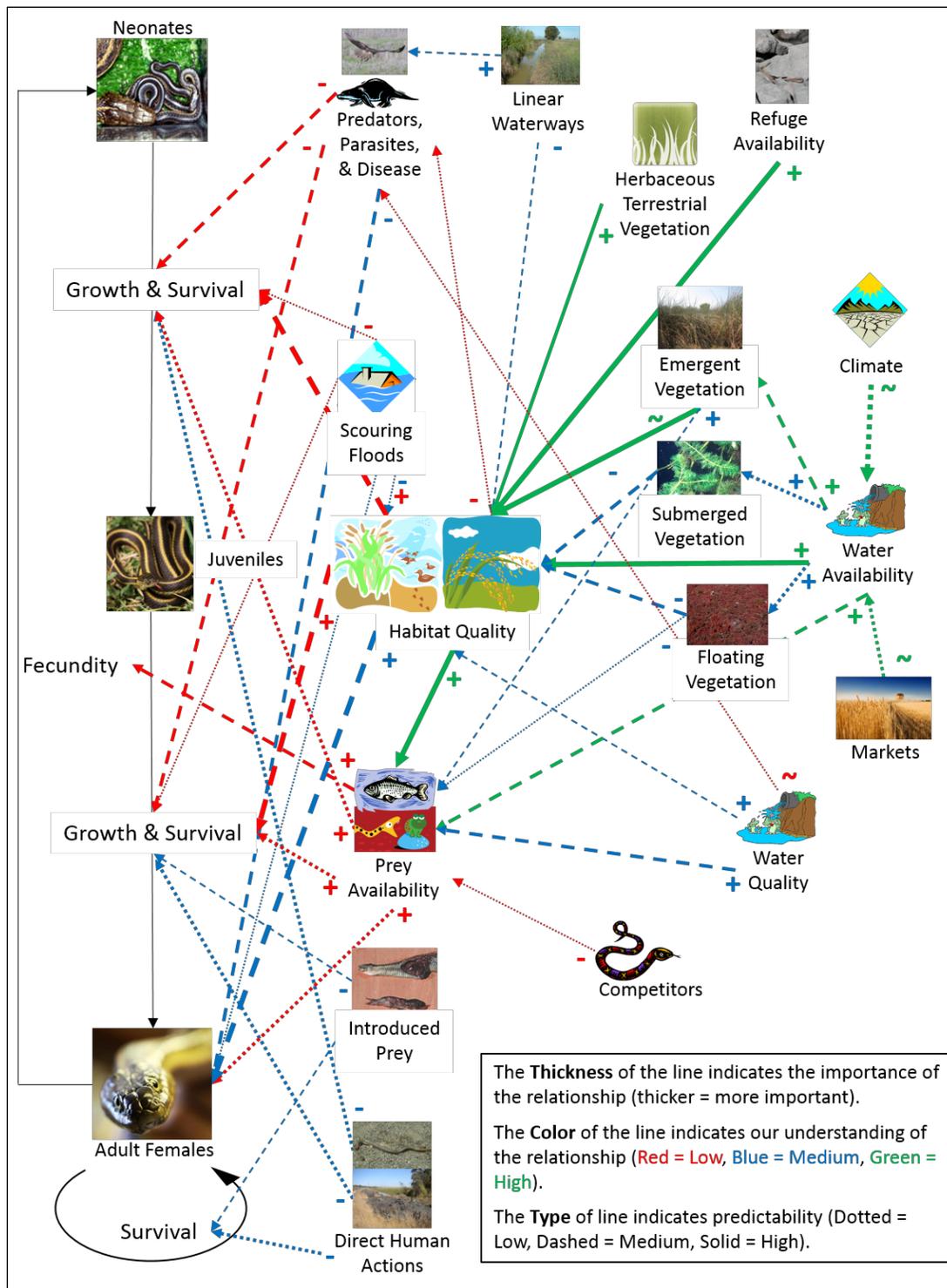


Figure 2. Conceptual model for giant gartersnake population ecology in the Sacramento Valley, California. Black arrows indicate stage transitions in the giant gartersnake (*Thamnophis gigas*) life cycle. Weights of colored arrows indicate the strength of relationships (thicker lines = stronger relationships), line color indicates existing knowledge about the relationship (green = most knowledge, red = least knowledge), and line type indicates the predictability of the relationship (solid = most predictable, dotted = least predictable).

Several patterns are apparent in the conceptual model. Habitat quality plays a central role in the population ecology of *T. gigas*. In particular, habitat quality has a strong, positive, and direct influence on growth and survival of *T. gigas*, but this relationship is thought to be only moderately predictable. Understanding of this relationship is poor for subadult life stages, but moderate for adult females. Habitat quality also affects growth, survival, and fecundity indirectly through its influence on prey availability.

Habitat quality is itself strongly and directly affected by other variables. Water and refuge availability had strong, positive, well-understood, and direct relationships with habitat quality; the relationship of emergent vegetation with habitat quality was similar, but assumed to be nonlinear because emergent vegetation can degrade *T. gigas* habitat at high densities. Herbaceous terrestrial vegetation had a weaker positive influence on habitat quality; this weaker relationship was posited primarily because *T. gigas* historically occurred in expansive marshes and likely did not require terrestrial vegetation because refuges were likely available within these expansive marshes, rather than restricted to their edges. In today's environment, however, herbaceous terrestrial vegetation likely is more important than it was prior to development of the Central Valley and could assume greater influence than depicted in the conceptual model. Floating vegetation, submerged vegetation, linear waterways, and scouring floods all had relatively weak negative effects on habitat quality.

Prey availability had moderate positive, although poorly understood and uncertain, effects on all vital rates. Water availability and emergent vegetation were posited to have positive, although relatively weak, effects on prey availability, and competitors were posited to have weak negative effects on prey availability although this relationship is poorly understood and uncertain. Introduced prey species were posited to have a weak negative influence on growth and survival, primarily because of the injurious nature of some introduced prey.

Predators, parasites, and disease were hypothesized to have negative effects on *T. gigas* survival. These relationships are relatively poorly understood, primarily because of a lack of quantitative data on predator communities and uncertainty associated with quantifying *T. gigas* survival. Direct human actions also were posited to have weak negative effects on *T. gigas* survival. Under certain conditions (for example, earthwork near wetlands during brumation), such effects could be strong.

Scouring floods are likely to have negative effects on *T. gigas* survival. This hypothesis is primarily based on anecdotal reports and few observations of *T. gigas* within floodwater bypasses.

The conceptual model presented here is properly viewed as a living document that should be periodically reviewed and updated as new information and ideas are developed about the relationships of *T. gigas* with various aspects of the biotic and abiotic environments in which they occur.

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Glossary

Abundance: The number of individual organisms in a population.

Adaptive kernel: A form of density estimation in which the size of the linear filters (also called kernels) used varies with location.

Albumin: A class of simple, sulfur-containing, water-soluble proteins that coagulate when heated.

Allele: Any of several forms of a gene.

Allozyme: Any of a number of different structural forms of the same enzyme coded for by a different allele.

Anorexia: Loss of appetite and inability to eat.

Areal: Of or related to an extent of space or surface.

Aspartate aminotransferase: An important enzyme in amino acid metabolism commonly measured as an indicator of liver health.

Azurophil: A white blood cell with cytoplasmic granules that stain with an azure dye.

Basophil: A white blood cell having a two-lobed nucleus and cytoplasmic granules that stain with a basic ($\text{pH} > 7$) dye.

Binomial mixture model: A model that uses spatially and temporally replicated counts to separately estimate abundance and detection probability for closed populations.

Body condition: Any of a number of indices that relate body mass to structural body size.

Bottleneck: An abrupt and severe reduction in the number of individuals during the history of a species, resulting in the loss of diversity from the gene pool.

Brumation: The dormant, hibernation-like state that ectothermic animals use during cold weather.

Capture-mark-recapture: A method commonly used in ecology to estimate abundance and other demographic parameters of imperfectly observed populations.

Child node: A node at the end of an edge (arrow) in a conceptual model.

Clade: A taxonomic group of organisms classified together on the basis of homologous features traced to a common ancestor.

Cladogram: A branching diagram depicting the successive points of species divergence from common ancestral lines without regard to the degree of deviation.

Closed population: A group of individuals of the same species that is closed to additions or removals.

Colonization: The process of establishment of organisms of a species in a new location.

Confidence interval: A statistical interval estimate of a parameter such that, if constructed across many replicated experiments, the proportion of such intervals that contain the true fixed value of the parameter equals the given confidence level. In other words, the stated confidence level is the probability that, when the interval is calculated from similar data or experiments, the interval will contain the true value of the parameter.

Congener: An organism belonging to the same genus as another.

Credible interval: An interval in the domain of the posterior probability distribution that represents the limits at the given credible level for the probability of the random value of the parameter. In other words, the stated credible level is the probability that the value of the parameter falls within the interval.

Crepuscular: Appearing or active at twilight or just before dawn.

Crypsis: The ability of an organism to avoid observation or detection by other organisms.

Data augmentation: Methods for constructing iterative optimization or sampling algorithms via the introduction of unobserved data or latent variables.

Demography: The study of populations, particularly changes over time in populations.

Density: The quantity of a substance per unit space. In ecology, the number of individuals in a population per unit area.

Detection probability: The probability that one or more individuals of a species is detected in a survey, given that the species is present at the location surveyed.

Deterministic: Of or relating to a process in which no randomness or uncertainty is involved in the predicting the state of one variable, given knowledge of the state of another.

Dimorphic: Having two forms.

Dispersal: The spread of organisms to new areas.

Diurnal: Active by day.

Dorsal: Situated on or toward the upper side of the body.

Ecdysis: The shedding or casting off of an outer coat or integument.

Ectotherm: An organism that regulates its body temperature by exchanging heat with its surroundings.

Effective population size: The number of individuals in a population that contribute offspring to the next generation.

Emergent vegetation: An aquatic plant having its stem, leaves, etc. extending above the surface of the water.

Extirpate: To cause a species (or other taxon) to cease to exist in a geographic area, though it still exists elsewhere.

F_{ST}: A measure of population differentiation caused by genetic structure; fixation index.

Field-preferred body temperature: The preferred body temperature of ectothermic animals as measured in natural environments.

Fixed kernel: A form of density estimation in which the size of the linear filters (also called kernels) used is the same for all locations.

Frontal: Of, relating to, or situated near the forehead or frontal bone.

Genetic drift: Random changes in the frequency of alleles in a gene pool, usually of small populations.

Genotype: The genetic makeup of an organism or group of organisms with reference to a single trait, set of traits, or an entire complex of traits.

Gestation: The process, state, or period of carrying developing young during pregnancy.

Globulin: Any of a group of proteins insoluble in pure water but soluble in dilute salt solutions and coagulable by heat.

Gravid: Pregnant.

Ground color: The background color.

Herbaceous: Of, relating to, or characteristic of an herb; not woody.

Heterophil: A granular white blood cell having cytoplasmic granules of variable sizes and staining characteristics.

Home range: The area in which an animal normally lives.

Horvitz-Thompson estimator: A method for estimating the total and mean of a superpopulation in a stratified sample.

Imperfect detection: Characterized by having detection probabilities of less than one.

Inbreeding: The breeding or mating of related individuals within an isolated or closed group of organisms.

Inbreeding depression: The loss of vigor and general health that sometimes characterizes organisms that are the product of inbreeding.

Infralabial: Below the lower lip.

Innate: Existing from birth; inborn; instinctive.

Internasal: Between the nares (nostrils).

Intraguild predation: The killing and eating of potential competitors.

Introduced species: A species living outside its native distributional range that has arrived there by human activity.

Lateral: Of or relating to or situated at the side or sides.

Leukocyte: A white blood cell.

Local convex hull: A non-parametric method for estimating the size of the home range of an animal, including its utilization distribution.

Locus: The chromosomal position of a gene as determined by its linear order relative to the other genes on that chromosome.

Lymphocyte: A type of white blood cell having a large, spherical nucleus surrounded by a thin layer of nongranular cytoplasm; lymphocytes comprise B cells and T cells.

Maxillary: Of or relating to a jaw or jawbone, especially the upper one.

Microsatellite: A section of DNA consisting of very short nucleotide sequences repeated many times, with the number of repeats varying between members of a species; used as a marker in determining genetic diversity and population genetic studies.

Minimum convex polygon: A non-parametric method of home range estimation that consists of the smallest possible convex polygon that contains all of an animal's observed locations.

Mitochondria: Organelles in the cytoplasm of cells that convert food to usable energy.

Morphology: The form and structure of an organism considered as a whole.

Musk: A substance having a strong odor secreted by some animals.

Nasal: Of or relating to the nose.

Natricine: Any of a member of a subfamily of the Colubridae family of snakes that comprises 28 genera; includes gartersnakes and watersnakes.

Neonate: A newborn.

Nocturnal: Active at night.

Node: A variable in a conceptual model.

Occupancy: The act, state, or condition of a species living at a site.

Open population: A group of individuals of the same species that is open to additions (births, immigration) or removals (deaths, emigration).

Operative environmental temperature: The temperature of the environment to which an ectothermic organism would equilibrate in the absence of thermoregulation.

Parent node: A node at the beginning of an edge (arrow) in a conceptual model.

Parietal: Of, relating to, or situated near the side and top of the skull or the parietal bone.

Parturition: The process of bringing forth young.

Perennial: Lasting or continuing throughout the entire year.

Plasma: The liquid part of blood or lymph.

Postocular: Located posterior to (behind) the eye.

Prefrontal: Anterior to, situated in, or pertaining to the anterior part of a frontal structure.

Preocular: Located anterior to (in front of) the eye.

Radio telemetry: A communications process by which a device that transmits a radio signal is attached to an animal, allowing one to locate the animal using a receiver tuned to the transmitter's frequency.

Random walk: The path taken by an organism in which the moves are defined as steps drawn from stochastic distributions of directions and lengths.

Robust design: A capture-mark-recapture sampling design in which the population is sampled multiple times during a short period when the population can be assumed closed (secondary sampling period), after which the population is unsampled for a longer time during which the population is considered open (primary sampling period), with repeated alternation of primary and secondary sampling periods.

Rostral: Of or relating to a rostrum (a beak or beaklike part).

Sex ratio: The proportional distribution of the sexes in a population, typically given as the proportion of males to females.

Sexual dimorphism index: The ratio of the size of the larger sex to the size of the smaller sex.

Sister taxon: The closest relatives of a taxon or group in a cladogram or phylogenetic tree.

State-space model: A class of probabilistic graphical models that describe the probabilistic dependence between the latent state variable and the observed measurement.

Stochastic: Of or relating to a process involving randomness or uncertainty in observations, which are considered as a sample of one element from a probability distribution.

Subcaudal: Enlarged scales on the underside of a snake's tail.

Subspecies: A subdivision of a species, especially a geographical or ecological subdivision.

Supralabial: In reptiles, scales that border the mouth opening along the upper jaw, not including the median (rostral) scale.

Sympatric: Originating in or occupying the same geographical area.

Systematics: The study and classification of organisms with the goal of reconstructing their evolutionary histories and relationships.

Tactile: Of or pertaining to the sense of touch.

Taxonomy: The science dealing with the description, identification, naming, and classification of organisms.

Temporary emigration: The temporary unavailability of an organism for sampling, caused either by temporary movement away from the study area or behavior that prohibits detection of the individual.

Thermoregulation: The regulation of body temperature.

Turbid: Not clear or transparent because of stirred-up sediment or the like; clouded; opaque; obscured.

Uric acid: The principal nitrogenous component of the excrement of reptiles and birds.

Utilization distribution: A probability distribution constructed from data providing the location of an individual in space at different points in time.

Utilization distribution overlap index: The joint distribution of two individuals' utilization distributions under the assumption that they use space independently of each other.

Vertebral: Of or relating to the vertebrae.

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