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Brackish Tidal Marsh Management and the Ecology of a Declining Freshwater Turtle

Mickey Agha [1,2] · Charles B. Yackulic [3] · Melissa K. Riley [1,4] · Blair Peterson [1] · Brian D. Todd [1]

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Abstract
Water management practices in tidal marshes of the San Francisco Bay Estuary, California are often aimed at increasing suitable habitat for threatened fish species and sport fishes. However, little is known about how best to manage habitat for other sensitive status species like the semiaquatic freshwater Western Pond Turtle (*Actinemys marmorata*) that is declining throughout much of its range. Here, we examined the basking activity, abundance, survival, and growth of Western Pond Turtles at two brackish water study sites in Suisun Marsh, California that differed in how they were managed, with one having passive management (i.e., no active water regulation) and another having active management (i.e., water regulated for seasonal hunting). Our results revealed that basking activity was greatest when salinity, water stage, and air temperatures were low, shortwave radiation was high, and wind levels were intermediate. These preferred habitat characteristics often reflected conditions that were naturally maintained at the passively managed, muted tidal site. We also found that turtles were more abundant and had higher survival rates in the passively managed habitat compared to the actively managed habitat (201–323 turtles/km^2 and 96% survival versus 11–135 turtles/km^2 and 77% survival, respectively). Finally, characteristic growth constants from von Bertalanffy models showed that turtles grew more quickly in passively managed habitat compared to the actively managed habitat. Our results suggest that management strategies for this sensitive status species may be more effective if they protect passively managed muted tidal systems that limit or delay extreme cycles of salinity and water levels and conserve elevated terrestrial buffer zones adjacent to muted and full tidal systems.

Keywords Freshwater turtles · Western Pond Turtle · *Actinemys marmorata* · Habitat suitability · Tidal marsh wetland

Introduction

Tidal marshes often form in river mouths and estuaries along coastlines, supporting high species diversity, and productive plant communities. They also function to filter sediments and sequester carbon (Bridgham et al. 2006). Despite their ecological value and relative importance to humans, more than half of salt marshes have been lost or degraded due to land conversion, water diversion, and demands for irrigation water (Byrd et al. 2015; Jeppesen et al. 2015; Naiman and Turner 2000; Wright et al. 2013). To offset these impacts, many tidal marshes are managed or restored to improve ecological function (i.e., productivity, energy storage, food networks, and critical wildlife habitat), and economic, social, historical, and recreational roles (Propato et al. 2018). However, tidal marsh management strategies are often difficult to create and prioritize as they can require information on species' population ecology and dynamics, estimates for marsh response time, and distinct,

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✉ Mickey Agha
mickey.agha@dfw.wa.gov

1 Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA

2 Washington Department of Fish and Wildlife, 1111 Washington St. SE, Olympia, WA 98501, USA

3 US Geological Survey, Southwest Biological Science Center, MS-9394, Flagstaff, Arizona 86001, USA

4 California Department of Fish and Wildlife, Bay-Delta Region 3, 2825 Cordelia Rd #100, Fairfield, CA 94534, USA

economically feasible objectives (Propato et al. 2018). Consequently, as managers seek efficient and effective strategies to restore or manage tidal marsh systems, conservation planning for data-deficient species and their critical habitats can sometimes be undervalued, misguided, or given low priority.

Suisun Marsh rests at the upper reaches of the San Francisco Bay Estuary (SFBE) and is the largest contiguous brackish water tidal marsh in the western United States (Moyle et al. 2014). Its surrounding uplands encompass many terrestrial and aquatic habitats that support both migratory and resident species (Moyle et al. 2014). These species benefit from continued management of the region's wetland ecosystem and via the commitment of joint state-federal planning groups, waterfowl hunting club owners, and research biologists (Moyle et al. 2010, 2014). Nevertheless, water management in Suisun Marsh creates a unique predicament for fish and wildlife as it influences the balance of fresh and saline waters, water temperature, and the relative availability of terrestrial and aquatic habitat (Meng et al. 1994). Although much of the Suisun Marsh wetland system is actively managed for endangered aquatic and terrestrial species or migratory waterfowl, the effects of water transport control (i.e., salinity, temperature, and depth variation) on habitat suitability for semiaquatic species that spend time in both the water and adjacent upland habitats are poorly understood.

Semiaquatic wildlife like freshwater turtles require varied, interconnected terrestrial, and aquatic habitats to support growth, survival, reproduction, and overall fitness (Ernst and Lovich 2009; Hamer et al. 2018). For these species, aquatic habitats are used for mating and foraging, whereas terrestrial buffer zones along the fringe of wetlands and adjacent to water sources provide critical basking, nesting, and overwintering habitats during all life stages of freshwater turtles (Gibbons 1970; Hamer et al. 2018; Steen et al. 2012; Ficetola et al. 2004). Basking habitat in particular is a critical resource for freshwater turtles because they are ectotherms and thus rely on suitable basking areas for thermoregulation to maintain physiological performance and fitness (Boyer 1965; Cadi and Joly 2003; Ficetola et al. 2004; Snover et al. 2015). In addition, basking can dramatically increase metabolic rate and digestion, which is associated with increased overall activity, reproduction, and foraging (Bulté and Blouin-Demers 2010; Janzen et al. 1992). As a consequence, observation of basking freshwater turtles can be an effective proxy for aquatic and terrestrial habitat suitability across an area, as well as occupancy and overall activity (Boyer 1965; Burke and Gibbons 1995; Ficetola et al. 2004; Holland and Goodman 1996; Lambert et al. 2013; Snover et al. 2015; Semeñiuk and Alcalde 2017).

To improve our understanding of responses of semiaquatic turtles to different tidal marsh management practices and their associated environmental effects, we evaluated basking activity, population dynamics, and growth of Western Pond Turtles (*Actinemys marmorata*) at two wildlife areas in Suisun Marsh that have differing water management strategies. One site was a muted tidal system with levee maintenance but no active water regulation (i.e., passive management), whereas the other was a drainage ditch system with water actively regulated for waterfowl and elk that relies on controlled, seasonal flooding (i.e., active management). We predicted that turtles inhabiting the muted tidal passively managed system would have greater basking activity compared to those in the drainage ditch system where controlled flooding can dramatically reduce basking habitat and increase variability and extremes in water quality parameters like salinity, a factor important to freshwater turtles. Secondly, because semiaquatic freshwater turtles require varied thermal habitats and are behaviorally and physiologically sensitive to changes in salinity in their aquatic environments (Agha et al. 2019), we predicted that water salinity would restrict overall basking activity and reduce survival and growth rates. Thus, our objectives were to (1) evaluate the effects of environmental variables such as water temperature, air temperature, visible sunlight shortwave radiation, water stage, water salinity, and wind speed on daily and seasonal basking activity patterns of Western Pond Turtles, (2) quantitatively assess daily basking activity of Western Pond Turtles in passive and actively managed brackish water habitats of Suisun Marsh, and (3) estimate abundance, temporary emigration, survivorship, and growth rates across years in both passive and actively managed habitat.

Because there is little information available on Western Pond Turtle ecology in brackish water environments, these data are particularly useful for identifying suitable habitat characteristics for maintaining healthy populations of this declining species (Spinks et al. 2003). In addition, it may assist habitat managers with finding a balance between passive and active water management that allows for stable semiaquatic turtle habitat in estuarine environments. Further, because the Western Pond Turtle is declining across parts of its range due to habitat loss and climate variability, these data may prove useful when designing effective species management and conservation strategies for the future.

Materials and Methods

Study Locations

Suisun Marsh is a highly managed brackish water marsh located in the upper reaches of the SFBE and it extends inland to the city of Fairfield in Solano County, CA, USA (Moyle et al. 2014). The Suisun Marsh system includes a

Fig. 1 Topographic image of Suisun Marsh in ArcGIS. Passive and actively managed study sites—Hill Slough Wildlife Area (Passive) and Grizzly Island Wildlife Area (Active)—located with stars, in Suisun Marsh, Solano County, California

combination of both tidal and diked marshlands composed of ecologically diverse sloughs and bays (Moyle et al. 2014). On average, annual salinities range from 0 to 15 ppt (~24,000 uS/m) at the southern extent and 0–10 ppt (~10,000 uS/m) at the northern extent of Suisun Marsh in tidal sloughs and bays (Data accessed: Bay Delta Live: https://www.baydeltalive.com), and are regulated by state-operated salinity control gates at the southern portion of the marsh.

From July to August 2016, we conducted visual surveys by driving levee roads across Suisun Marsh to detect Western Pond Turtle presence/absence, and to determine whether sites could feasibly be trapped based on water depth. To accommodate traps, the water depth had to be >0.75 m across tidal cycles (Fig. S1). We identified two main, brackish water marshland areas that were suitable for continuous trapping—Hill Slough Wildlife Area and Grizzly Island Wildlife Area (Fig. 1). Our primary sampling area in Suisun Marsh—Hill Slough Wildlife Area—is a state-managed 688-hectare brackish water system that includes both muted tidal and diked marshlands. The Hill Slough Wildlife Area is a passively managed system, where ponds inside the leveed areas are intermittently influenced by flooding from tidal flow regimes in adjacent tidal sloughs (i.e., muted tidal system). Our secondary sampling area in Suisun Marsh—Grizzly Island Wildlife Area—is a state-managed 36,000-hectare brackish water system where drainage ditches are actively managed to support elk and waterfowl hunting seasons. Turtle trapping areas in GIWA primarily included drainage ditches that are regulated by the California Department of Fish and Wildlife and local waterfowl clubs. From February to April 2018, waterfowl clubs conducted leach cycles adjacent to Grizzly Island Wildlife Area, where water was drained from hunting areas and outflow moved through the drainage ditches, flooding them for intermittent periods of time, which increased salinity.

Basking Activity Observation

Following the methods of Bluett and Cosentino (2013) and Bluett and Schauber (2014), we built artificial basking platforms for both study sites. Basking platforms were made with water-resistant plywood (122 × 61 cm) and two cedar boards (122 × 30 cm) attached to the long-edge on each side at a 45° angle (Fig. S2). To float the platforms just above the surface of the water, we glued 3.8-cm-thick insulation foam boards to the bottom. We fixed a flexible black plastic mesh screen over the entire platform so turtles could easily climb out of the water. Finally, to ensure that the platform would be stationary and move smoothly up and down with the tide, we drilled two holes through each platform and secured them in place with 1.3 × 205-cm rebar encased in 1.9-cm PVC pipes (Fig. S2).

During the summer of 2018, we placed a single basking platform ~2 m from the shore at both of our main study sites (Fig. 1). We monitored basking turtles by placing wildlife cameras (Browning Strike Force Pro Trail Camera, Model #BTW-5HDP) attached to 2.4-m T-posts facing each basking platform. Wildlife cameras were configured to take photos at 1-h time-lapse intervals and were deployed at each study site from April to September 2018. Data from each camera trap were retrieved monthly.

Environmental Data Collection

Using HOBO data loggers placed under each basking platform, we obtained hourly records for water temperature (°C) and water salinity (uS/cm) for each sampling site from April to September 2018. Using local water/weather NOAA monitoring stations <1 km from each sampling site (Data accessed: Bay Delta Live: https://www.baydeltalive.com), we obtained hourly records for air temperature (°C), wind speed (mph), and river stage (m). Using a Mosaic land–surface model from the North American Land Data Assimilation System, we obtained hourly measurements of shortwave radiation for each site (W/m^2; Xia et al. 2012).

Basking Activity Analysis

We modeled counts of basking Western Pond Turtles in Suisun Marsh using a Poisson regression and a log-link with modifications to account for potential residual auto-correlation among counts in successive hours of the day and across successive calendar days of the year. Models were fit using Stan (Version 2.18.2; Carpenter et al. 2017), a Bayesian program that uses Hamiltonian MCMC to draw posterior samples and can be accessed through R with the rstan package. Specifically, we modeled predicted counts ($y_{t,d}$) in hour, t, and day, d, according to:

$$\log\left(y_{t,d}\right) = \beta_{\mathrm{int,d}} + \rho \cdot \log\left(y_{t-1,d}\right) + \beta \cdot X_{t,d} + \varepsilon_{t,d}, \quad (1)$$

$$\beta_{int,d} = \varphi \cdot \beta_{int,d-1} + \eta_d, \quad (2)$$

where $\beta_{\mathrm{int},d}$ are intercepts that are autocorrelated among successive days, ρ and φ are parameters describing correlation in the predicted log counts among successive hours in a day and successive days respectively, $\boldsymbol{X}$ is a three-dimensional array of environmental covariates with dimensions given by the number of covariates, the number of hours in a day, and the number of days with measurements, $\boldsymbol{\beta}$ is a vector of estimated coefficients, and $\varepsilon_{t,d}$ and η_d are independent and identically distributed deviates.

We used the above model framework to fit various models based on six environmental covariates: river stage, water temperature, salinity, shortwave radiation, wind speed, and air temperature representing conditions in the water and in the terrestrial habitat used for basking. These environmental parameters were selected for analysis as they are known to affect activity and heat transfer for aquatic turtles (Boyer 1965; Crawford et al. 1983). For each covariate, we considered a linear effect alongside a quadratic term as data exploration revealed nonlinear relationships between counts and environmental parameters. We chose our model for inferences based on running all possible combinations of environmental covariates (always allowing for both a linear and a quadratic term) and using out-of-sample prediction to score each possible model (Hooten and Hobbs 2015). We chose the actively managed site for fitting and the passively managed site data for out-of-sample because the former site generally had more variation in the environmental covariates. Having determined the environmental covariates that maximized out-of-sample prediction, we then fit a model to all the data from both sites to estimate parameter values for inference.

Capture-Mark-Recapture

We used nondestructive live sampling with hoop nets to conduct monthly capture-mark-recapture (7–10 consecutive days/month) in our passively managed study area from August to September 2016, March to September 2017, March to September 2018, and March to September 2019. We used the same trapping technique for our actively managed study area from June to July 2017, April to July 2018, and April to July 2019. Sampling timing differed between sites due to seasonal hunting that occurred in our actively managed study area. Hoop nets were ~1.8-m long, 63.5-cm hoop diameter with 3.8-cm squared mesh, made with knotted nylon netting tied to three galvanized steel hoops (Memphis Net and Twine, Memphis, TN; Fig. S1). The funnel hoop net design creates a large opening for entry and a small opening to exit, making it difficult for animals to escape. Each net was fitted with horizontal PVC piping with flotation tubes to maintain the top of the trap above water so that turtles could surface to breathe. Hoop net traps were secured to stakes on land and were baited with free-floating sardine cans packed with oil. Punctures were made in the sardine cans, which released oils and attracted turtles while preventing consumption of the bait. At the passively managed site, traps were set ~15–20 m apart at minimum, as well as placed haphazardly across a 1 km^2 survey area. At the actively managed site, traps were set ~5–20 m apart and placed across a single ditch line <0.5 km^2.

During our monthly deployments, six hoop net traps were set at each study site (i.e., passive and active) and checked daily (42–60 trap nights site/month). Upon capture by hoop net trap, we marked, measured, and photographed the carapace (top) and plastron (bottom) of each Western Pond Turtle for future identification. We recorded the sex using secondary sexual characteristics and measured straight mid-line carapace length (MCL), plastron length, carapace width, and shell depth (height) in cm. We uniquely marked the marginal scutes of each turtle's carapace using a triangular metal file (Ernst et al. 1974; Honegger 1979). Using the photograph of the plastron we measured age by counting the growth rings on the femoral or anal scutes of each individual turtle (Wilson et al. 2003). Growth rings were only discernable to the age of 13 across both the passive and actively managed study areas.

Capture-Mark-Recapture Analysis

We used a robust design framework to assess survival rate, temporary emigration rate, abundance, and capture probability of Western Pond Turtles in Suisun Marsh. The robust design model is based on primary and secondary sampling occasions, where the population is assumed closed during secondary occasions and open between primary occasions (Lebreton et al. 1992; Pollock 1982). We used years (2016, 2017, 2018, and 2019) as primary occasions, and months (March–September) during the active season as secondary occasions. Population closure assumptions were based off daily tracking data from 20 turtles (10 M, 10 F) with GPS/GSM tags in our passive and actively managed study areas where we documented individuals staying within our 1 km^2 trapping areas during our study season within years (*unpublished data*, M. Agha). Using robust design models, we estimated apparent survival, temporary emigration rates, and population abundance (Lebreton et al. 1992; Pollock 1982; Kendall et al. 1995, 1997).

A set of models composed of parameters for abundance, apparent survival, temporary emigration, and capture probability were fit to the data with program R (*package RMark*; Laake 2013). We tested two possible temporary emigration patterns: (1) no temporary emigration, and (2) random temporary emigration, where the availability of the animal for capture did not depend on its status in the previous trapping session. For each of these temporary emigration patterns, we tested all possible combinations of models where apparent survival was either constant or varying between primary occasions, and capture probability was either constant, varying between primary occasions, varying between both primary and secondary occasions, or driven by a trap response within primary occasions. We used Akaike's Information Criterion with a correction for small sample sizes (AICc) to rank our candidate models, and we model averaged all models within Δ7 AICc of our top model (Burnham and Anderson 2004).

Growth Models

We fit von Bertalanffy growth models to body size (MCL) and interval data (age) to evaluate growth rate and body size differences between turtles at the active and passively managed study areas (Kimura 2008). von Bertalanffy models have previously been used for long-lived reptiles such as turtles and often provide a better fit than logistic models (Tuberville et al. 2014). We parametrized von Bertalanffy models with common and site-based (active vs. passive) growth coefficient constants (K), asymptotic body sizes (A), and growth intercept or time-zero coefficients (T_0). For example, candidate models were fit with different combinations of a site-specific or common K parameter, a site-specific or common A parameter, and site-specific or common T_0 parameter. All von Bertalanffy models were run using packages 'FSA' and 'nlstools' in Program R and function 'vbStarts' to generate reasonable starting values for parameters in specific parameterizations, and we used AICc to compare all candidate von Bertalanffy models. Model assumptions and normality were validated using residual plots from the most generalized model in our candidate set.

Results

Over the course of our study we collected and analyzed over 4600 camera trap photos over 170 days, across two different sites. Basking activity in Western Pond Turtles increased throughout the year and peaked in June and July (Fig. 2). These overall patterns differed by study site, and turtles were less active earlier in the year at the actively managed site (Figs 2 and S3). Basking turtle counts ranged from 0 to 18 turtles, and averaged ~5 turtles per hourly count. On average, basking activity increased through the morning, peaking near mid-day, and then tapered off around sunset (Fig. 3). These daily trends were consistent across different months of the year but differed by study site as turtles in the passively managed study site were more active during the early part of the year, whereas turtles in the actively managed study site were more active during the latter part of the year (Figs 3 and S4). We fit a total of 64 models based on all combinations of the environmental covariates and scored models based on out-of-sample predictive ability. Parameter ρ was estimated near zero at 0.08 (SE: 0.04), suggesting that there was minimal residual temporal autocorrelation in counts within days; however, φ was estimated at 0.99 (SE: 0.01),

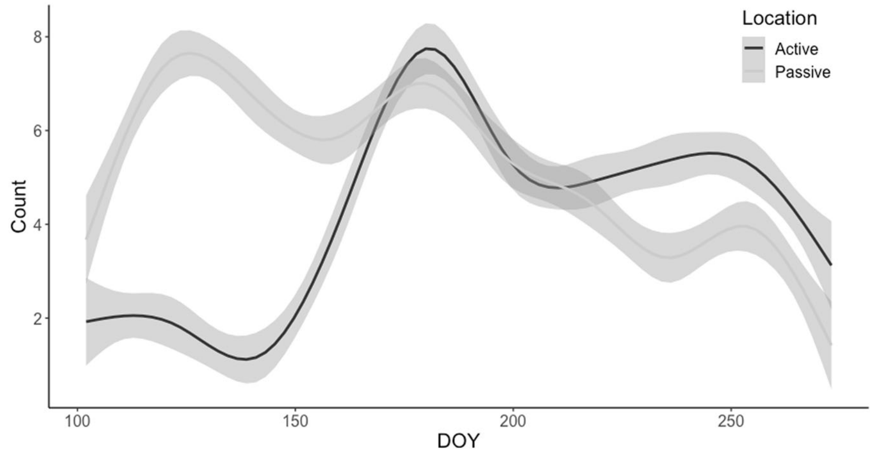

Fig. 2 Average Western Pond Turtle basking counts by calendar day of year (DOY) from April to early September in a passively managed study area (passive) and actively managed study area (active) in Suisun Marsh, Solano County, California. Shaded areas around each line represent standard error

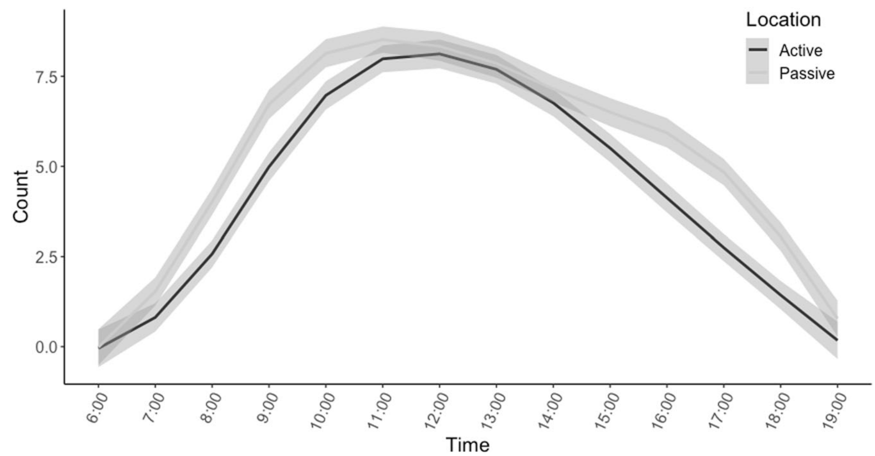

Fig. 3 Average Western Pond Turtle basking counts by hour of day (Time) from April to early September in a passively managed study area (passive) and actively managed study area (active) in Suisun Marsh, Solano County, California. Shaded areas around each line represent standard error

suggesting a high degree of autocorrelation among calendar days. A model without water temperature, but maintaining all other environmental covariates had the best out-of-sample predictive score (lowest negative log-likelihood). Models without river stage or without wind speed (in addition to removing water temperature) performed slightly worse, suggesting weaker support for these covariates. Fitting of the model to all data using the best model structure identified by out-of-sample prediction suggested a positive relationship between shortwave radiation and counts of basking turtles, negative relationships between salinity and air temperature and basking counts, and hump-shaped relationships with river stage and wind speed (Fig. 4 and Table S1).

Using the upper quartile of basking turtle counts (10–18 turtles), we plotted density of counts across parameter space for each of our most informative environmental parameters (Figs S5 and S6). These plots revealed that over the course of the year and day, turtles were most active at water salinities ranging from ~2000 to 5000 uS/cm (~0–3 ppt), water temperatures ranging from ~20 to 21 °C, river stages at ~0.5 m, air temperatures ranging from ~13 to 14 °C, and shortwave radiation ~1000 (Figs S5 and S6).

From August 2016 to September 2019 we captured 393 Western Pond Turtles overall, including 139 recaptures (35.4% collective recapture rate). At the passively managed site, we captured and marked 178 individuals and had 107 recaptures (37.5% recapture rate) and at the actively managed site we captured and marked 76 individuals and had 32 recaptures (29.6% recapture rate). Our capture-mark-recapture analysis for our passive and actively managed sites supported constant survival, monthly and yearly variation in capture probability, and no emigration (Tables S2 and S3). Averaged parameter estimates showed that turtles in passively managed habitats had a constant annual survival rate of 96% and a capture probability rate ranging from 1 to 14%, with April of each year having the highest capture estimates (Table S4). In the actively managed habitat, turtles had a constant annual survival rate of 77% and a capture probability rate ranging from 1 to 15%, with June and July having the highest capture estimates (Table S4). In addition, the models estimated that turtles had an annual abundance ranging from 201 to 323 per km^2 in passively managed sites and 11–135 per km^2 in actively managed sites (Table S4).

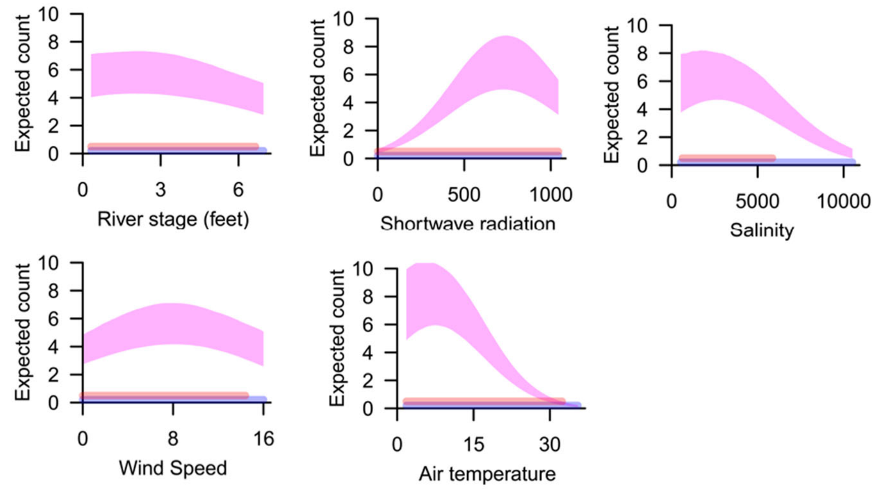

Fig. 4 Expected count of basking turtles as a function of river stage, shortwave radiation, salinity, wind speed, and air temperature. Pink curves represent the 95% credible intervals of the marginal response (i.e., with random effects set to zero and other covariates set to their mean) of the number of basking turtles to variation in five environmental factors. Blue and red lines represent the range of variability in the environmental condition at active and passively managed study sites, respectively

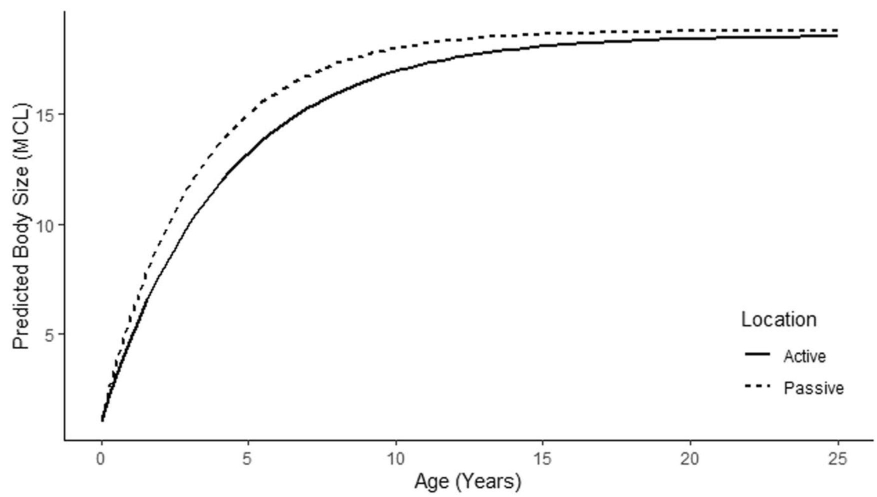

Fig. 5 Estimated growth rate curves generated from von Bertalanffy growth models for Western Pond Turtles at active and passively managed study areas in Suisun Marsh, Solano, County, California. Mid-line carapace length was measured in cm and estimated age was counted via rings on plastron scutes from each individual turtle

The top performing von Bertalanffy model based on AICc (>2 AICc from all competing models) was parameterized with a single, common asymptotic body size coefficient—18.78 (95% CI: 18.55–19.02), site-specific growth constants, and site-specific time-zero coefficients (i.e., size at hatching). Estimated growth rate constants differed between passive—0.39 (95% CI: 0.33–0.45)—and actively managed—0.17 (95% CI: 0.13–0.21)—study areas (Fig. 5). Although the top model supported site-specific time-zero coefficients, the size at hatching was not significantly different between the two sites (Fig. 5).

Discussion

Environmental conditions in the SFBE vary across time and space and influence habitat availability and suitability for native fauna (Moyle et al. 2010). Because present conditions are often poorly suited for many native species (e.g., salmonids and Delta Smelt), hydrodynamic regimes, and water quality are actively managed in a variety of ways: salinty control gates manage inflow and outflow to manipulate temperature and salinity and ongoing passive and active habitat management is used to restore aquatic habitats. In addition, sport fishing, waterfowl, elk hunting, and endangered aquatic and terrestrial species are primary targets for active management in different parts of the SFBE; thus, hydrological regimes are often highly regulated (i.e., leach cycles, flooding, and draining) during the year for species such as Delta Smelt (*Hypomesus transpacificus*), Salt marsh harvest mouse (*Reithrodontomys raviventris*), and a range of waterfowl species. While these management activities may support many native and non-native species, they have often left semiaquatic species, such as Western Pond Turtles, with little to no guidelines for their management. Our present examination of the native Western Pond Turtle addresses that issue by summarizing basking activity patterns and population dynamics (i.e., proxies for habitat suitability) and their interaction with different environmental attributes that vary in time and space, some of which are directly tied to area-specific water management strategies (i.e., passive and active) and habitat restoration (i.e., water salinity and stage).

We found that basking activity patterns of Western Pond Turtles were highly correlated with salinity, water levels, air temperature, wind speed, and solar radiation in both passive and actively managed habitats of Suisun Marsh. These results agree with previous studies that have suggested that terrestrial basking in freshwater turtles is often driven or constrained by temperature and sunlight (Gatten 1974; Ernst 1972; Crawford et al. 1983). For instance, our data show that Western Pond Turtles at both sampling sites in Suisun Marsh increased basking activity with increasing visible sunlight, decreasing air temperatures, and intermediate wind speeds. Our data also show that optimal periods for basking include mid-day and the summer months June and July. Previous studies have noted that temperature, as well as sunlight availability, are critical factors for freshwater turtles as they rely on external heat to achieve optimal metabolic function and immunological protection (Cadi and Joly 2003; Crawford et al. 1983; Nebeker and Bury 2000). In addition, energy gained from basking and optimal water and air temperatures provide turtles with the ability to mature at faster rates, search for mates, move longer distances, and forage for longer periods of time, thus increasing overall fitness (Nebeker and Bury 2000; Snover et al. 2015).

Recent studies have suggested that salinity may limit the distribution and activity of freshwater turtles along coastlines (Agha et al. 2018; Bower et al. 2016). Our results suggest that Western Pond Turtles in Suisun Marsh may have regulated their activity based on salinity in their surrounding habitats, decreasing their activity with increasing salinities. For instance, while turtles were active across a range of salinities up to 7 ppt (~12,000 uS/m), basking activity strongly decreased when salinity exceeded ~3 ppt (~5000 uS/m). These results may reflect habitat avoidance by Western Pond Turtles in Suisun Marsh, especially in actively managed sites, such that turtles respond to elevated salinities by temporarily moving between saline and freshwater areas within their immediate area or reducing overall activity to limit salt uptake (Agha et al. 2018, 2019). In addition, Western Pond Turtles restrict eating to minimize body water loss when salinity increases (Agha et al. 2019), thus, it is unlikely that turtles would bask to avoid salinity, as basking increases metabolic and growth rates and is associated with increased activity and food consumption (Bulté and Blouin-Demers 2010). While Western Pond Turtles at Suisun Marsh have been shown to have some tolerance to elevated salinity over short periods (Agha et al. 2019), during our field study, turtles likely moved to habitats with lower salinity to avoid dehydration when exposed to prolonged seasonal or frequent daily inundations of saltwater (i.e., tidal fluxes or management related). Habitat avoidance was readily apparent in our actively managed site, where turtles displayed reduced basking activity during the early part of the year when environmental conditions—salinity, temperature, and wind—were highly variable and unsuitable.

Water levels varied from 0.1 to 2.1 m across the year at the study sites and were often manipulated or regulated in our study areas. Our results indicated that Western Pond Turtles preferred to bask when water levels were at a low tide, ~0.5 m, and disappeared from basking sites at high tides or when water levels were above average (i.e., >1 m). For instance, basking turtle counts in April and May were lower in actively managed habitats than in passive, as actively managed site water levels were above average for extended periods of time due to leach and flood cycles from adjacent hunting areas. During high water levels, critical basking areas such as mud banks dissapeared, thereby reducing habitat suitability for Western Pond Turtles. The extent to which basking habitat loss affects overall fitness of Western Pond Turtles in Suisun Marsh is unknown; however, body size and age data revealed that Western Pond Turtles in the passively managed site grew more quickly compared to those in the actively managed site, which could reflect a greater amount of basking habitat, optimal environmental conditions, and prey items available continuously throughout the year at passively managed sites compared to actively managed.

Relative abundance, annual survival rates, and capture probability were estimated for Western Pond Turtles in passive and actively managed sites. Mean turtle abundance estimates were greater at our passively managed study site compared to the actively managed study site. Similarly, overall survival was greater at our passively managed study compared to the actively managed study site. Relatively high abundance and survival rates in passively managed areas may be associated with habitat features like sufficient terrestrial basking areas with high solar exposure, freshwater ponded habitat with salinities ranging from 0 to 3 ppt, and sufficient food resources (Horn and Gervais 2018). We frequently observed predators (*Lontra canadensis*, *Canis latrans*, *Mephitis mephitis*, *Procyon lotor*) in our actively managed study site, which we speculate may have resulted in the low survival estimates compared to the passively managed study area. Previous studies of semiaquatic turtles have suggested basking activity is modulated or constrained by predators (Ibáñez et al. 2015), thus, lower survival, abundance, and incidence of basking at our actively managed site may be a result of higher levels of predation.

While capture probability rates in passive and actively managed areas were relatively low, movement data from GPS tracked individuals (*unpublished data*, M. Agha) suggested that Western Pond Turtles move throughout the habitat adjacent to our trapping areas and are unobservable and not available for capture during brief periods.

Low capture rates may be related to water temperature and salinity variation, unobserved behaviors like summer estivation and mate searching, or the placement of traps across the sampling area (Holland and Goodman 1996). Indeed, capture probabilities were lowest in August and September, when relative salinity increased across the marsh from 2.1 to 3.5 ppt on average.

Management Implications

Habitat management practices that influence hydrological regimes and water quality can have both positive and negative effects on native flora and fauna in tidal marsh ecosystems. For freshwater turtles in the SFBE, key environmental variables like water salinity, temperature, and depth can affect behavior, survival, and growth. Our results suggest that factors like availability of basking habitat and overall water quality/quantity directly affect habitat suitability—measured via survival and growth—for Western Pond Turtles, but our work also highlights the need for research on movement behavior of Western Pond Turtles in relation to environmental variability and habitat management of tidal marshes. Thus, habitat management strategies will be most effective if they aim to maintain water temperature, salinity, and depth within suitable ranges during the main activity season of March–September to support healthy Western Pond Turtle populations in the SFBE. In addition, maintaining terrestrial habitat like levees adjacent to water sources at heights that exceed high tide, flooding regimes, and storm surges, may provide important basking and nesting habitat for turtles throughout the year. Finally, because our study reveals that population dynamics and growth rates of the Western Pond Turtle in Suisun Marsh potentially vary based on water management regimes, preserving passively managed muted tidal systems with freshwater may be critical when designing tidal marsh management strategies for freshwater turtles in coastal regions.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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