# CALIFORNIA FISH AND GAME

## "Conservation of Wildlife Through Education"

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# California Fish and Game

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California Fish and Game 104(4):162-163; 2018

# Change in Editorship

With this issue, Dr. Ange Baker, Senior Environmental Scientist (Specialist) with the Department of Fish and Wildlife's Habitat Conservation Planning Branch Cannabis Environmental Compliance Program assumes the duties of editor-in-chief of California Fish and Game.

Under her guidance, the journal will continue its policy of presenting to the public the results of scientific investigations as they relate to management programs and the conservation of California fish and wildlife resources. Dr. Baker will strive to maintain and enhance the excellent reputation the journal has earned over the past 104 years.

To Armand Gonzalez, editor-in-chief over the past three years, we wish to express our appreciation for a job well done.

Charlton H. Bonham, *Director, California Department of Fish and Wildlife*

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# Notes from the Editor

I am privileged and excited to begin as editor-in-chief of the *California Fish and Game* journal, as I take over from Armand Gonzales, who held the position for nearly three years until his recent retirement from the Department. The journal, which is California's longest-running, continuously published scientific journal, has an excellent reputation, which I plan to continue. Although I am relatively new to the Department, my experience with California's fish and wildlife resources goes back many years. I received my Master's degree from the Wildlife Department of Humboldt State University, and, after finishing my PhD, I returned to teach there for several semesters. I hope to one day see some of my former students publishing their work in this journal!

The journal is under the banner of the Department's Science Institute, whose mission is to "…ensure quality, visibility, and integrity of the science that is conducted and used within the California Department of Fish and Wildlife." Given this mission, the journal may experience some exciting changes in the coming months as we strive to increase its visibility and readership. The relatively new leader of the Science Institute, Dr. Christina Sloop, and I will be collaborating on ways to further better the journal and increase its reputation among wildlife scientists in our state.

This fall issue, the final of the 104th volume, while coming late due to the change in editorship, includes several excellent articles. The first article is a scientific note on a unique ecological event for one of California's most charismatic predators, the great horned owl. The authors describe an incidence of ground-nesting behavior, a rare occurrence for the species. The second article in this issue is also a note that sheds light on the life history of neonate leopard sharks in San Francisco Bay, specifically their diet. This information offers important insight into the estuarine ecology of the San Francisco Bay with implication for conservation. The final article is a full research article that provides insight into a temperature-sensitive mammal that faces extreme challenges as our climate changes. The authors discovered that aboveground air and surface temperatures, and not within-talus temperatures, are likely what limits pika persistence in the Sierra Nevada Mountains.

With this issue, there is one change to the editorial board. James Harrington, who has served as Associate Editor for numerous years is retiring. James started working for CDFG in November 1987 as a water quality biologist. He retired at the end of 2018 as a Senior Environmental Scientist, but he still considers himself a Water Quality Biologist since that is what he did for 30 years. First, he monitored rice pesticides in the Sacramento River and our Department's rotenone treatments throughout the State. Then in 1991, he went to the Water Pollution Control Laboratory (WPCL) as the State-wide Water Quality Biologist helping the regions with complicated monitoring projects and in spill response covered under Fish and Game Code 5650. He testified as expert witness and worked with Regional Water Quality Control Boards on several cases. While monitoring the discharge of one of our hatcheries, he established a protocol for biological monitoring using benthic macroinvertebrates or bioassessment. Over the years, he was able to hustle up dozens of contracts to hire additional staff and apply our protocols in streams and rivers throughout the State. He stayed in the same position until the end and now leave the Aquatic Bioassessment Laboratory, which is part of OSPR, in the hands of many devoted scientists he considers friends. However, he will stay involved as a volunteer on a few projects and continue teaching his bioassessment workshops since there are not enough of the Department's staff that understand what bugs tell you about healthy streams.

I am excited to be a part of this journal for the next few years. Please send all future manuscript submissions to me at angela.baker@wildlife.ca.gov.

Ange Darnell Baker, PhD
Editor-in-Chief
*California Fish and Game*

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# Ground-nesting great horned owl in Suisun Marsh, California

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Key words: *Bubo virginianus*, great horned owl, ground-nest, nesting behavior, Suisun Marsh

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Great horned owls (*Bubo virginianus*) are widespread throughout North, Central, and parts of South America (Artuso et al. 2013). Across this range, great horned owls are generalists, occupying a diverse range of habitats including deciduous and coniferous forests, wetlands, and agricultural landscapes. Within these habitats, great horned owls are generally found near upland or short-vegetation habitat suitable for locating prey (Artuso et al. 2013). In Suisun Marsh, California, great horned owls primarily occupy stands of non-native eucalyptus (*Eucalyptus* spp.), as well as man-made structures like waterfowl-nesting platforms (Figure 1) and on dock pilings over water (Figure 2), and they forage in nearby upland fields and seasonally flooded, diked wetlands managed primarily for waterfowl (USGS unpublished data).

Similar to other owl species, great horned owls do not construct their own nests; instead, they utilize unoccupied nests constructed by other birds, usually raptors or corvids, or arboreal squirrels (e.g., Baumgartner 1938, Errington1932, Franks and Warnock 1969). However, their nest sites are described as “extraordinarily variable” and have been found in the crooks of large tree limbs, inside tree cavities, on cliffs, on and in man-made structures, and occasionally on the ground (e.g., Artuso et al. 2013, Bendire1982, Bent 1938, Bohm 1977, Bohm 1980, Dixon 1914, Errington 1932, Fitch 1940, Fitch 1947, Kirkwood 1925, Murie 1922, Seidensticker and Reynolds 1971, Van Damme 2013). Though their nest sites are known to be diverse, little documentation exists to support some of these observations, especially the use of ground nests. For example, Artuso et al. (2013) mention two observations of ground-nesting, one nest in a log on the ground, and one nest in a waterfowl nest on the ground (Bendire 1892). Indeed, a literature search of ground-nesting specifically

**Figure 1.**—Great horned owl nesting in an elevated waterfowl-nesting platform on Grizzly Island Wildlife Area, California in 2016. Photo credit: Michael Casazza/USGS.

yielded no results aside from cliff nesting, where nests are elevated above ground level (see references above). In California, variability in nest sites occurs within pairs of owls across seasons (Dixon 1914) and among pairs and seasons (Fitch 1947), with nests occurring in stick nests in trees, on tree limbs, and on cliffs and ledges of steep slopes. Here, we document the first recorded evidence for ground-nesting in a great horned owl pair during three consecutive breeding seasons (2016-2018) on the Grizzly Island Wildlife Area, Suisun Marsh, California (38°08' N, 121°59' W). Grizzly Island Wildlife Area consists of ~5,200 ha of tidal and diked marshes, and upland habitat managed primarily for waterfowl, and is located within Suisun Marsh, which is a large (~46,900 ha) brackish water estuary in the San Francisco Bay Delta Watershed. The dominant vegetation across the wildlife area includes bulrushes (*Schoenoplectus* spp.), cattails (*Typha* spp.), rushes (*Juncus spp.*), pickleweed (*Salicornia virginica*), and various forbs (e.g., *Atriplex patula, Lotus corniculatus*) and grasses (e.g., *Distichlis spicata, Frankenia salina, Bromus* spp.*, Elymus* spp.*, Hordeum* spp.).

During waterfowl nest searches in 2016, U.S. Geological Survey (USGS) researchers discovered an active great horned owl ground-nest with 2-3 eggs (exact number not documented) in a small eucalyptus stand (~50 trees). The nest was located at the base

**Figure 2.**—Great horned owl nestling in a nest on a dock piling over water near Wheeler Island in Suisun Marsh, California in 2016. Photo credit: Sarah Peterson/USGS.

of a eucalyptus tree with Grizzly Island Road along the southern edge, and a dry, diked marsh along the northern edge. This nest was found on 4 April 2016, but was observed as completely depredated due to the presence of crushed eggshells during the next visit on 25 April 2016. At this time, at least one adult owl was still present in nearby trees after the nest was depredated. Because this nest was found incidentally to the primary research goals of 2016, no nest characteristics were recorded and no further monitoring occurred.

After the initial discovery of a ground-nest in 2016, we made a concerted effort to document ground-nesting behavior for this pair of owls in 2017 and 2018. On 30 March 2017, while conducting a survey for raptor nests along Grizzly Island Road, we discovered a female great horned owl incubating one egg (Figures 3 and 4) on the ground at the southeast base of a large eucalyptus tree (~ 23 m tall and 0.71 m DBH) in the same stand of trees where the ground-nest was previously found in 2016 by flushing the female from the nest after approaching on foot. The nest substrate consisted of loose eucalyptus sticks, bark and leaf litter. After briefly inspecting the nest and taking pictures, we immediately left so as not to cause prolonged disturbance or nest abandonment. The pair of adult owls was observed in a nearby (15-20 m away) tree while we inspected the nest.

**Figure 3.**—Initial great horned owl ground nest with one intact egg at the base of a eucalyptus tree on Grizzly Island Wildlife Area, California on 30 March 2017. Photo credit: Shannon Skalos/USGS.

A few hours after discovering the nest, we returned with a camera to document the female at the nest (Figure 5). We remained in our vehicle on Grizzly Island Road approximately 20 m away from the nest. The female incubated while we took pictures, she did not appear to show signs of stress, and she remained at the nest as we drove away.

During the second nest visit on 5 April 2017, the female was not on the nest so we approached on foot and the egg was cold, indicating that the female had likely abandoned the nest. During this visit, both adults were still present in a nearby tree, therefore we then searched the surrounding trees and ground for a possible second nesting attempt. After careful searching, we discovered two additional nest locations that appeared to be earlier nesting attempts from the 2017 season. A second nest was located on the ground at the southeast base of another eucalyptus tree (~18 m tall and 0.27 m DBH) with eggshell fragments and several adult great horned owl feathers present (Figure 6). A third nest with eggshell fragments was located in the crook of two limbs of a large eu-

**Figure 4.**—Placement and size of initial great horned owl ground nest with one intact egg at the base of a eucalyptus tree on Grizzly Island Wildlife Area, California on 30 March 2017. Photo credit: Shannon Skalos/USGS.

calyptus tree (~29 m tall and 1.67 m DBH) a few meters away from the second nest and approximately 2.5 m above the ground (Figure 7). The substrate of both nests consisted of loose eucalyptus sticks, bark and leaf litter. The two additional nests were approximately 50 m from the first discovered ground-nest in the same stand of eucalyptus trees.

We checked this stand of eucalyptus trees weekly, noting if the adults were present and if any additional nesting activity occurred. One or both adults were observed on subsequent visits in nearby trees, but we never discovered an additional nest or observed any nesting behavior. The egg was present in the initial nest through at least 5 May 2017, after which on 12 May 2017 the egg was gone without any signs of eggshells, suggesting a predator may have removed the whole egg. We stopped weekly nest checks after 19 May 2017.

In 2018, on 4 April we observed a female great horned owl incubating two eggs on the ground at the southeast base of a large eucalyptus tree (~16 m tall and 0.44 m DBH) in the same stand of trees as the ground-nests from the previous two years (Figure 8). We discovered the

**Figure 5.**—Female great horned owl incubating one egg within a ground nest on Grizzly Island Wildlife Area, California on 30 March 2017. Photo credit: Andrea Mott/USGS.

**Figure 6.**—Second great horned owl ground nest discovered with eggshell fragments and several adult owl feathers at the base of a eucalyptus tree on Grizzly Island Wildlife Area, California on 5 April 2017. Photo credit: Shannon Skalos/USGS.

**Figure 7.**—Third great horned owl nests discovered in the crook of two limbs of a eucalyptus tree approximately 2.5 meters off of the ground on Grizzly Island Wildlife Area, California on 5 April 2017. Photo credit: Shannon Skalos/USGS.

nest by flushing the female from the ground while searching on foot for evidence of ground-nesting. A second ground-nest was discovered and believed to be a nest attempt from earlier in 2018 because it was in the same location as the second ground-nest from 2017 and contained fresh eggshell fragments. Similar to 2017, the substrate of both nests was loose eucalyptus sticks, bark and leaf litter. The female returned to the ground-nest to resume incubation from a nearby tree as we were walking away. After initial discovery, we monitored the nest from a vehicle on Grizzly Island Road on a weekly basis. On 25 April 2018 the female was no longer seen incubating eggs so the nest was approached on foot and there were no eggs or eggshells present. We did not see any owls or nesting behavior in this tree stand after 25 April 2018.

Of 14 raptor or raven stick nests found in trees in 2017, and 11 nests found in trees in 2018 on Grizzly Island Wildlife Area, only two were unoccupied in 2017 and none were unoccupied in 2018. Because all or nearly every stick nest was occupied, this may suggest a potential saturation of nesting locations for great horned owls. A stick nest was present in 2015 within the same tree stand where the ground-nests were found, potentially indicating that the absence of an alternate nesting substrate led this pair of great horned owls to

**Figure 8.**— Female great horned owl incubating two eggs within a ground nest on Grizzly Island Wildlife Area, California on 4 April 2018. Photo credit: William Thein/USGS.

establish nests on the ground in 2016-2018. Indeed, the next closest eucalyptus trees are >1 km away (straight-line distance) and were occupied by other great horned owls during the 2017 and 2018 nesting seasons (USGS unpublished data). Additionally, strong nest site fidelity and territoriality despite nest failure has been documented in great horned owls (Bendire 1892, Baumgartner 1939), and may also explain why this pair remained in this territory and nested on the ground instead of relocating to a territory with a more suitable nest location. Regardless of the mechanisms for ground-nesting in this pair, this observation is the first documented case in California. Additional research to establish the range-wide rate of ground nesting in great horned owls and the underlying mechanisms resulting in this behavior could elucidate how this life history trait affects nest success and fitness.

## ACKNOWLEDGMENTS

We thank the California Department of Fish and Wildlife, Grizzly Island Wildlife Area for access and logistical support of the Suisun Marsh Waterfowl and Waterbird Research Program. It is our hope that this note, as well as other research conducted in Suisun Marsh associated with this note, will contribute to the continued management and conservation of this ecologically, culturally, and economically important ecosystem. We also thank the Suisun Marsh Program at the California Department of Water Resources for funding this research. All work was conducted in accordance with the California Department of Fish and Wildlife Scientific Collecting Permit SCP-8090 and the University of California, Davis Animal Care and Use Protocol 19781.

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# Prey of neonate leopard sharks in San Francisco Bay, California

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Key words: bay shrimp, elasmobranchs, jointworms, lugworms, marine pill bug, neonate, polychaete

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The leopard shark (*Triakis semifasciata*) is one of the most recognizable inshore elasmobranchs along the Pacific Coast from Oregon to the Gulf of Mexico. While several studies have focused on the diet of leopard sharks (Ackerman 1971, Russo 1975, Talent 1976, Webber and Cech Jr. 1998, Kao 2000, Webber 2003), most have examined juvenile to adult stage animals. Although fish eggs have been found in the stomachs of neonates from Humboldt Bay (Ebert and Ebert 2005), detailed information on the specific diet of neonate leopard sharks has been fragmentary at best, and not previously reported for San Francisco Bay.

A study designed to collect general biological data from elasmobranchs in San Francisco Bay, California was conducted from 1970 to 2001 on a monthly basis between the San Francisco Bay Bridge (37° 48' N, 122° 22' W) and the entrance to Alviso Slough in the south end of San Francisco Bay (37° 27' N, 122° 01' W). Methods included long-line (1.5 h sets), otter trawl (7-15 min runs), and rod and reel (3-5 h) at over 130 locations with many stations repeated. While each catch event had a data collection purpose, priorities changed over time as data gaps developed. In advance of gastric evacuation techniques (Webber and Cech Jr. 1998), data collection on dietary habits and reproductive condition involved internal examination of specimens. Although "catch and release" was the dominant paradigm, early stomach contents analysis of adults and juveniles (Russo 1975) reduced the need for further euthanization for that purpose in this study.

Otter trawl and rod and reel were used to capture 378 neonates and 318 young-of-the-year (YOY) for the primary purposes of identifying sex, size, location and condition. Trawl runs were restricted to shallow, near-shore eelgrass beds along the East Bay shoreline and the entrances to marsh channels such as Newark and Mowry Sloughs or inside major sloughs like Guadalupe and Alviso. Despite efforts to minimize impacts with short run times and avoidance of sensitive habitats, the volume of oyster shell or other materials in the trawl net was thought to have been responsible for neonate mortality of a cluster of specimens during two such trawls in May of 1982 (Arrowhead Marsh, San Leandro) and 1985 (Guadalupe Slough, Alviso), presenting an opportunity for a combined diet analysis of 19 neonates (Figure 1). This diet anaylsis was simply a snapshot in time and represented only that month. Identification of prey items was determined by using the keys in Light's Manual (Smith and Carlton 1975). The Index of Relative Importance (IRI) (Pinkas et al. 1971) along with the percentage IRI (%IRI) (Cortés 1997) could not be calculated due to the absence of weight measurements. Specimens were measured in centimeters total length (cm TL) with a mean total length (cm MTL) calculated along with the standard deviation (± SD). Prey items were calculated between male and female neonates as percentage frequency of occurrence (%FO) followed by the percentage frequency total (%FT) for both sexes.

The stomach contents of deceased neonates, ranging in size from 17.7 - 24.5 cm (20.1 cm MTL ±1.8 SD), were examined in the laboratory. Two neonates (10.5%) had empty stomachs. Seventeen neonates (89.5%) had been feeding on three species of crustaceans and three species of polychaete worms with 88.2% (*n*=15) of the stomachs examined containing identifiable prey items (Table 1). Two or more prey species occurred in five neonate stomachs (29.4%). Ten neonates (58.8%) contained single prey species.

**Figure 1.**— Map of overall study area of San Francisco Bay with circles marking the trawl areas related to this study including Arrowhead Marsh and Guadalupe Slough at the southern end of the Bay. Map courtesy of the East Bay Regional Park District.

**Table 1.**— The analysis of 19 leopard shark neonates with regard to the sex, type of prey or condition of the stomach, and number of prey items removed, using common names for table simplicity.

| Neonate # | Neonate Sex | Prey Item(s)(whole or pieces) | Number |
|---|---|---|---|
| | | Trawl 1 Arrowhead Marsh 21 May 1982 | |
| 1 | M | Unidentified | – |
| 2 | F | shrimp/crab | 6/2 |
| 3 | M | polychaete pieces | 5 |
| 4 | M | Unidentified | – |
| 5 | M | shrimp | 7 |
| 6 | M | jointworm | 3 |
| 7 | F | jointworm/lugworm | 2/3 |
| 8 | M | shrimp/jointworm | 3/3 |
| 9 | F | shrimp | 9 |
| 10 | F | pileworm | 4 |
| 11 | M | pill bug | 3 |
| 12 | M | crab/pileworm | 1/4 |
| | | Trawl 2 Guadalupe Slough 15 May 1985 | |
| 13 | F | shrimp | 8 |
| 14 | F | shrimp | 9 |
| 15 | F | shrimp | 7 |
| 16 | F | empty | – |
| 17 | F | empty | – |
| 18 | F | shrimp | 7 |
| 19 | M | shrimp/pileworm | 6/2 |

Eleven (64.7%) of the neonates contained crustaceans. Bay shrimp, *Crangon franciscorum*, especially small, young specimens 1.5 - 2 cm long, appeared to be the single most significant prey species found in 52.9%FT (*n*=9) (Table 2.) of the stomachs with 35.3% (*n*=6) of the neonates containing bay shrimp only. Of the seven neonates collected from the Guadalupe Slough, five (71.4%) of the neonates were full of bay shrimp, while the remaining two (28.5%) had empty stomachs. In comparison, of the 12 neonates from Arrowhead Marsh (San Leandro), only four neonates (33.3%) contained shrimp and of those only two were full to apparent capacity. This suggests that bay shrimp are more readily available in the southern end of the Bay, which likely correlates with the extensiveness of leopard shark nurseries in the area (Russo 2015). Other crustaceans, including small shore crabs, *Hemigrapsus oregonensis*, 11.8%FT (*n*=2) and marine pill bugs, *Gnorimosphaeroma luteum*, 5.9%FT (*n*=1), both of which tend to be found under rock and gravel or among eelgrass roots and therefore less exposed (Ricketts et al. 1985), were found in three of the stomachs examined. In the case of the ten neonates (58.8%) mentioned earlier with single prey species, the stomachs were packed to near capacity with >7 specimens of small shrimp (*n*=6) or polychaete worms (*n*=4) suggesting "gorge" feeding, which has been observed in aquarium-raised neonates (R. Russo, East Bay Regional Park District, unpublished data).

**Table 2.**— The analysis of prey items from 17 neonate leopard sharks including nine males and eight females measured by the number of shark stomachs with a prey item (N), the frequency of occurrence (%FO), and the combined frequency of occurrence for males and females per prey item (%FT).

| Neonate Stomach Contents (*n*=17) | | | | | | |
|---|---|---|---|---|---|---|
| | Males (*n*=9) | | Females (*n*=8) | | Combined | |
| Food Items | N | %FO | N | %FO | NT | %FT |
| Crustaceans | | | | | | |
| *Crangon franciscorum* | 3 | 33.3 | 6 | 75.0 | 9 | 52.9 |
| *Hemigrapsus oregonensis* | 1 | 11.1 | 1 | 12.5 | 2 | 11.8 |
| *Gnorimosphaeroma luteum* | 1 | 11.1 | – | – | 1 | 5.9 |
| Worms | | | | | | |
| *Axiothella rubrocincta* | 2 | 22.2 | 1 | 12.5 | 3 | 17.6 |
| *Neanthes cf. brandti* | 2 | 22.2 | 1 | 12.5 | 3 | 17.6 |
| *Arenicola brasiliensis* | – | – | 1 | 12.5 | 1 | 5.9 |
| Unidentifiable polychaete pieces | 1 | 11.1 | – | – | 1 | 5.9 |
| Unidentified material | 1 | 11.1 | 1 | 12.5 | 2 | 11.8 |

The second most important prey were various species of polychaete worms (whole or identifiable pieces) in neonates (*n*=7, 41.2%) with 35.3% (*n*=6) of these neonates (Table 1) containing one or more of the following: the pile worm, *Neanthes cf. brandti*, jointworms, *Axiothella rubrocincta*, and lugworms, *Arenicola brasiliensis*. *N. cf. brandti* worms appeared in four (17.6%FT) of the neonates with a fourth neonate containing pieces likely *Neanthes* but too damaged to be precisely determined. *A. rubrocincta* occurred in three (17.6%FT) of the neonates. *A. brasiliensis* was found only once (5.9%FT). Additionally, 23.6% (*n*=4) of the stomachs contained polychaete worms only, while 11.8% (*n*=2) contained unidentified material. Finally, 10.5% (*n*=2) of the stomachs were empty.

In mixed prey stomachs (29.4%, *n*=5) crustaceans and various polychaetes were found together without any indication of a preference of one species over another. Instead, the mixture of prey contents, either crustaceans and polychaetes or mixed species of polychaetes, seemed random and suggested that the neonates in this sample simply consumed what was available at the moment of feeding encounter. Based on shrimp trawl observations (Russo 2015), the southern end of the South San Francisco Bay south of the Dumbarton Bridge has historically been a shrimp nursery area where the likelihood of a neonate predator encountering large masses of shrimp is common as reflected in the contents of five of the seven neonate's stomachs from the Guadalupe Slough area.

Missing from these prey samples were other mudflat worms including specimens of peanut worms, *Siphonosoma ingens*, burrowing polychaetes, *Glycera robusta*, and gallery worms, *Capitella capitata*, identified as abundant members of the intertidal mudflat community in shorebird prey surveys conducted in 1980 (R. Russo, East Bay Regional Park District, unpublished data). Although neonates are expected to feed on these worms as well as others, their absence in this analysis may be explained by the small sample size of the sharks examined.

Furthermore, no fish eggs were found in stomachs of these specimens at this time even though herring, *Clupea pallasii*, and smelt, *Atherinopsis californiensis*, eggs are an important seasonal component for leopard sharks, which are known to also gorge themselves when this food is available (Russo 1975, Ebert and Ebert 2005). The absence of fish eggs in the specimens examined in contrast to Ebert and Ebert (2005) is most likely an issue of timing and availability in the area of capture given the sheer seasonal abundance of herring and smelt eggs in several areas of the South Bay.

Leopard sharks are opportunistic feeders, taking anything that is available at the point of contact (Ackerman 1971, Russo 1975, Talent 1976). The frequency of bay shrimps and polychaete worms in individual stomachs in this sample can be explained by suspected behavior of neonates simply taking all they could at the point of encounter as mentioned earlier.

The diversity of benthic prey, including many other species of worms and invertebrates not mentioned here, but known to occur in the mudflat, eelgrass, and marsh slough environments (MacGinitie and MacGinitie 1968, Morris et al. 1980, Ricketts et al. 1985) provides for ample feeding opportunities. Bay shrimp tend to live either partially buried or on the surface of sandy or muddy bottom and are therefore exposed. The polychaete worms mentioned here are periodically active at the surface of their exposed tubes or burrows making them vulnerable to the quick-acting, suction and burrowing habits of leopard sharks (Ackerman 1971, Russo 1975, Talent 1976). This behavior has been observed in aquarium feeding studies where pieces of clam necks, squid, and polychaete worms were buried into the sediments. Tank neonates responded quickly by locating the potential prey and thrusting their faces deep into the sediments to reach the food. As observed, leopard shark neonate's feeding schedule consists of short periods of hunting and consumption followed by long periods of resting on the bottom with intermittent slow cruising during digestion (R. Russo, East Bay Regional Park District, unpublished data).

In South San Francisco Bay, many of the larger sloughs and channels (Mowry, Newark, Guadalupe, and Alviso) retain water during low tide, which allows neonate leopard sharks to stay in place but exposes them to greater danger from avian predators (Russo 2015). In some cases and theoretically in response to tidal or temperature conditions, neonate leopard sharks are suspected to move out of the smaller channels to feed in nearby eelgrass beds where they have been captured along with neonate brown smoothhound sharks, *Mustelus henlei*, and neonate sevengill sharks, *Notorynchus cepedianus* (Russo 2015). Since neonate brown smoothhounds were not captured south of the Dumbarton Bridge or inside marsh sloughs and channels, it appears that neonate leopard sharks have nearly exclusive access as elasmobranchs to an abundant food supply in an area that has long been known as a bay shrimp nursery habitat (Russo 2015).

While a larger sampling of neonates' stomach contents during other months would expand our understanding of the diversity of invertebrate prey items, this study indicates the importance of small, easily accessible and generally ignored prey during the earliest growth phases of leopard sharks. These prey species, and others yet to be determined, apparently serve as "starter foods" that help facilitate rapid growth of 20 cm or more during the first year of life (R. Russo, East Bay Regional Park District, unpublished data).

Inshore, shallow water areas have been studied as nursery feeding grounds for various elasmobranchs (Medved and Marshall 1981, Cortés and Gruber 1990, Wetherbee et al. 1990, Heupel and Hueter 2002, Rechisky and Wetherbee 2003, McCandless et al. 2007, Carlisle and Starr 2010). While there is a growing body of data on the variety of prey items consumed in some species' nursery areas, data on the dietary needs of smaller, coastal elasmobranch neonates remain incomplete. Such in-depth studies must be conducted in order to develop effective management decisions and conserve essential early-stage neonate habitat.

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# Within-talus temperatures are not limiting for pikas in the northern Sierra Nevada, California, USA

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The American pika (*Ochotona princeps*) is a temperature-sensitive lagomorph reported to be in decline in warmer sites in California, Nevada and portions of Utah. Talus is used for denning and retreat habitat by the species. Climate envelope modeling and climate projections suggest the species' distribution will retract in coming decades—but other studies suggest pikas may be resilient in the face of warming by taking advantage of talus as a thermal refuge from warming air temperatures. We investigated the thermal environment of mid to low elevation talus habitats in the northern Sierra Nevada between 2010 and 2012 using automated temperature loggers placed generally 0.5 to 1 m below the talus surface. We found temperatures within talus are rarely challenging to pikas—even in taluses well below the inhabited elevational range of pikas. Occurrence of temperature extremes within talus was only weakly correlated with elevation, and exhibited substantial variation between talus patches. Temperatures deeper in talus than we were able to probe but that pikas can likely reach are certain to be even more stable and less physiologically challenging. Despite buffered temperatures in the subsurface talus environment, we observed multiple instances of pika-accessible, previously-inhabited talus patches that did not support pikas in our surveys. Summer daily maximum air temperatures at these taluses averaged more than 2°C warmer than occupied taluses, and taluses that pikas occupied in some years but not in others were intermediate in temperature. Sites with no evidence of past pika occupancy averaged warmest of all. We suggest aboveground air and surface temperatures, rather than temperatures within talus, pose a greater challenge to pika persistence, through effects on foraging and dispersal. Our results indicate that the thermal refuge provided by talus is likely to be necessary and beneficial to American pikas, but sufficient only to partially offset the ongoing impacts of warming ambient temperatures on waning pika distribution.

Key words: American pika, climate warming, distribution, extirpation, microclimate, talus, temperature logger

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Conserving biodiversity in the face of climate change requires that we know how species will respond over the coming decades and centuries. Accurate predictions inform smart conservation planning, such as identifying species and populations vulnerable and not vulnerable, emphasizing the conservation of corridors important for climate-mediated range shifts, and protecting refugial habitat areas projected to remain suitable for taxa of concern as climate change proceeds.

The American pika (*Ochotona princeps*) has emerged as a model organism for investigating the impact of climate change on animal population viability and distribution (Galbreath et al. 2009, Beever et al. 2010, 2011, Guralnick et al. 2011, Stewart et al. 2015, Wilkening et al. 2015a, Castillo et al. 2016, Mathewson et al. 2017). Pikas are small lagomorphs of the family Ochotonidae, with a single living genus. Two species occur in North America, with only the American pika within the continental USA (see https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=2359&inline=1, Smith and Weston 1990 for species accounts). Montane habitat use and cold adaptation are widespread in the genus (Leach et al. 2015, Yang et al. 2008). In response to a state listing petition, which presented climate change as a primary threat (Wolf et al. 2007), the California Department of Fish and Wildlife in 2007 and in 2013 reviewed the status of pikas in California and recommended against listing, but indicated monitoring and more information were needed (CDFW 2013). The pika is currently included by the State as a Species of Greatest Conservation Need.

Much of American pikas' sensitivity to global warming appears to be due to direct thermal-physiological limitations. Thermal metabolic experiments and thermal models have indicated that the species' susceptibility to mortality is due to a poor ability to shed excess body heat (MacArthur and Wang 1973, 1974, Moyer-Horner et al. 2015). Death at temperatures 25.5 – 30° C has been observed in small studies (Smith 1974, *n*=2 pikas; MacArthur and Wang 1973, *n*=2 pikas). Field observations have shown pika hours of activity are restricted by warmer ambient temperatures commonly experienced by the animal, particularly at lower elevation sites or during the peak of summer (MacArthur and Wang 1974, Smith 1974, Henry et al. 2012, Otto et al. 2015, Moyer-Horner et al. 2015). Stafl and O'Connor (2015), studying American pikas in southeastern British Columbia, Canada, found foraging activity decreased by 3% for each 1°C increase in aboveground air temperature, declining to near inactivity at 20°C. Wilkening et al. (2015b) found summertime stress metabolite concentrations were greater in fresh pika scat from an area that experienced both higher within-talus temperatures in summer and more extreme within-talus cold conditions during the preceding winter. Increasing temperatures or declining snowpack due to local effects of global warming have widely been implicated in shrinking pika distribution in the North American Great Basin and California (Beever et al. 2013, 2016, Nichols et al. 2017, Stewart and Wright 2012, Stewart et al. 2015, 2017, Wilkening et al. 2011).

We investigated the ability of subsurface talus temperatures to predict pika occupancy and persistence patterns in mid to low elevation talus patches in the northern Sierra Nevada. Millar and others (Millar and Westfall 2010, Millar et al. 2014b, Smith et al. 2016) have suggested pikas may be resilient to local climate warming because they have a thermal refuge in cool taluses, allowing them to thermoregulate behaviorally. Stable thermal refuge in talus also was suggested as the reason for pika persistence in seemingly anomalous, low-elevation lava habitats (Rodhouse et al. 2017). Millar et al. (2014a) offered an interesting counterpoint, suggesting Great Basin taluses are less likely to be strong thermal refugia and expecting continuing pika range contraction there. Mathewson et al. (2017) built a mechanistic model of pika response to their various thermal microenvironments and estimated the thermal refuge provided by talus would protect against pika population loss at 8 to 19% of sites where extirpation would otherwise be expected—conversely, talus would not protect against pika loss at 81 to 92% of sites.

## MATERIALS AND METHODS

We sampled in 46 talus habitats across the northern Sierra Nevada extending from Yosemite National Park to central Sierra County (37.7 – 39.6° latitude) and ranging in elevation from 1208 to 2933 m (Figure 1). Fifteen were sites we visited in studies of historical and other pika locations (Stewart and Wright 2012, Stewart et al. 2015, Stewart et al. 2017), 31 others we selected for accessibility, apparent suitability for pikas in terms of rock size, depth and amount of talus, and for adequate representation of taluses at a variety of elevations (Figure 2). In order to focus on the "hot zone" of potentially tenuous pika viability near the lower edge of its elevation range, we worked relatively low in the elevational range of the pika (which extends to well above 4000 m in the Sierra Nevada: Millar et al. 2010, Stewart et al. 2015). We included sites across a range of elevations in areas like the Yosemite Valley/Merced River drainage, Mariposa County, and the Lovers Leap/Horsetail Falls area, El Dorado County, that have abundant talus throughout both low and higher elevations. Unlike many authors, because we wanted to determine whether within-talus temperatures at low elevation sites were limiting the distribution of pikas, we included sites lower in elevation and warmer than the occupied range.

Temperature loggers (Lascar "EasyLog USB"), programmed to record hourly and housed in waterproof aluminum cases, were wired to a surface rock and lowered into the talus—typically a depth of 0.5—1 m. Often talus is deeper than this, but it was rarely feasible to reach lower depths. We took care that loggers would not be exposed to direct sunlight from any angle. We recorded logger locations on a handheld Global Positioning System (GPS) unit and thoroughly photographed each site of placement to enable relocation of the site for retrieval. Each talus patch received one logger, placed where fecal pellets were abundant relative to other areas sampled within the talus—or, at sites without pika evidence, at locations that resembled pika-preferred microhabitat in our experience, based on rock size, talus depth, and rock niche geometry. Temperatures have been shown to vary within talus patches in other studies (Millar et al. 2014b, Rodhouse et al. 2017, Wilkening et al. 2011); however examining multiple locations per site was beyond the scope of this study. Instead we used consistent, unbiased sampling at many sites to maximize power in detecting trends across locations. Each logger remained in place and recording for approximately one year, depending on site revisit schedule. At many locations loggers were replaced upon retrieval with another logger and recording continued for another year.

We surveyed for pika following the methods of Stewart and Wright (2012, also Stewart et al. 2015) upon each occasion of logger placement or retrieval. We searched for both current sign and relict sign (old pika fecal pellets can remain for decades on rocks or in soil or duff collecting in pockets in the talus: Nichols 2010, Stewart et al. 2017). For analysis, each site was categorized as having current pika sign (pikas present), old pika sign only (buried pellets, old surface pellets), no pika sign, or as "marginal". We defined marginal sites as those that had current pika sign in at least one year of survey but only old sign in at least one other year. Current pika sign included visual confirmation, auditory confirmation,

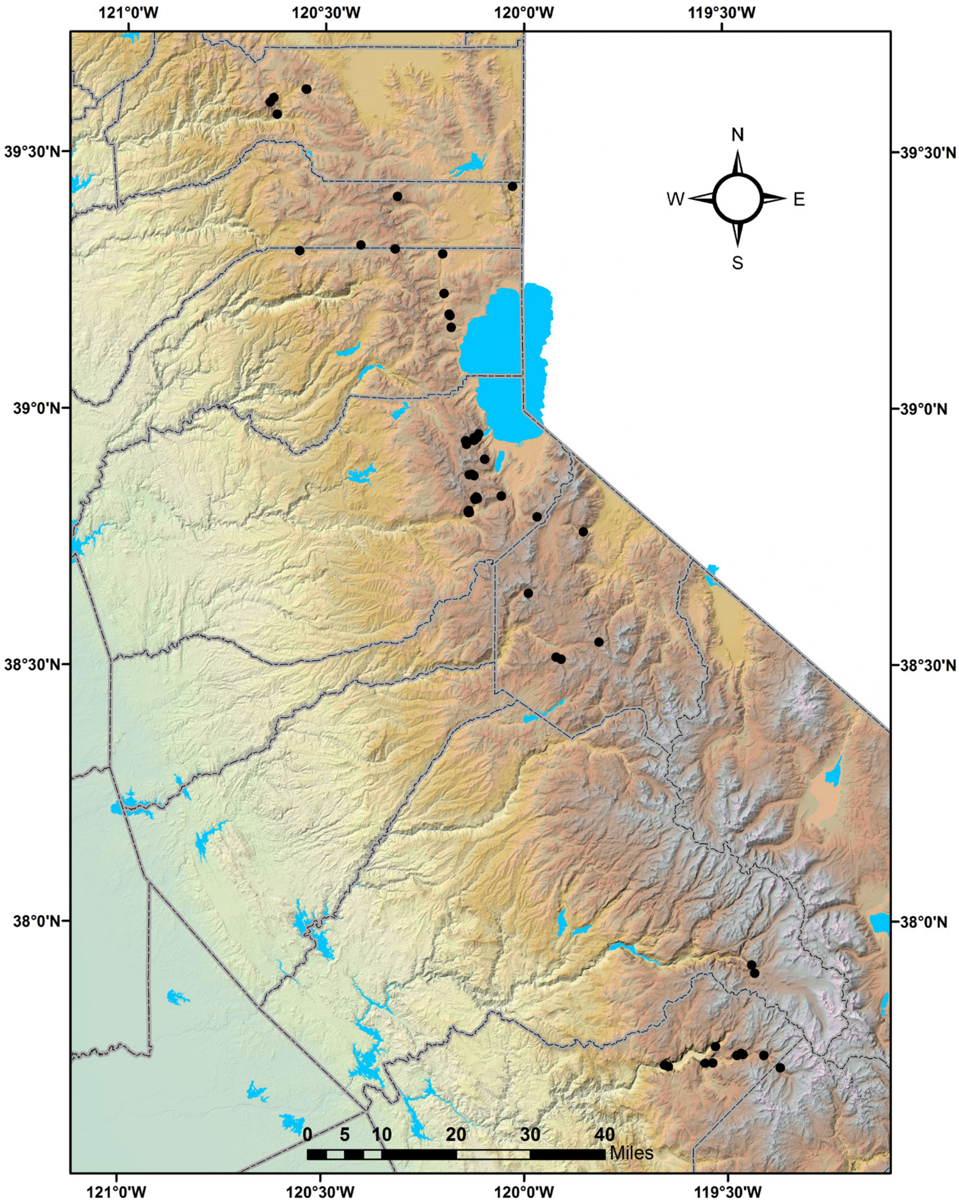

**Figure 1.**—Map showing locations of 46 sites (black dots) in northern California where temperature loggers were placed within talus that appeared appropriate for pika. Lake Tahoe is at north center of the figure; California county boundaries are also shown.

green haypiles, or fresh scat (pikas give distinctive calls, stockpile harvested vegetation in piles for winter consumption, and have distinctive scat: Smith and Weston 1990, Elbroch 2003). We commonly detected more than one type of current sign when pikas were present. Pikas have widely been reported to be highly detectable (Beever et al. 2008, 2011, Rodhouse et al. 2010, Hall et al. 2016).

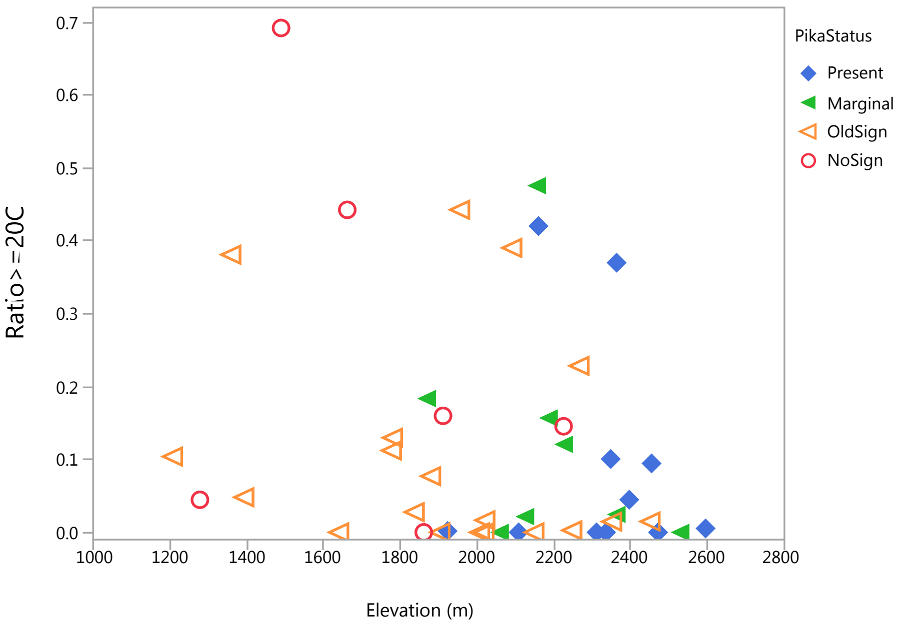

**Figure 2.**—Warm temperature exceedances (ratio of within-talus hours ≥ 20°C to all hours June 1 through September 30 in the record [R20+]), versus elevation, in meters. Symbol color and shape shows pika population status. R20+ was not strongly related to elevation (Spearman ρ = -0.22, n = 44, P = 0.15). Sites with few or no temperatures reaching 20°C occurred at all elevations. Pika-occupied (blue diamonds), marginal (intermittently occupied: green triangles) and absent (open triangles and circles) sites overlapped greatly, with many unoccupied and formerly occupied sites similar to occupied sites in within-talus 20°C temperature exceedances.

Logger data were downloaded using Lascar software and analyzed using JMP 9.0.2 statistical software (SAS Institute, Inc.). Because dates of placement and retrieval varied between sites and years, logger records covered differing durations of the summer months. For this reason, we report exceedances of warm and cold temperature thresholds as a ratio: the number of hourly records equal to or exceeding a given threshold, divided by the total number of hours recorded during the warm or cold season. We defined the warm season as June, July, August and September ("JJAS"); and the cold season as December, January, February and March ("DJFM"). We denote these ratios as R20+, R24+, R(-2.5)-, and R(-5)- (≥ 20°C, ≥ 24°C, ≤ -2.5°C, and ≤ -5°C, respectively). We chose exceedance thresholds based on values investigated previously in the literature as potentially significant to pika (Beever et al. 2010, Moyer-Horner et al. 2015, Yandow et al. 2015, Wilkening et al 2011). Ratio values were Box-Cox transformed before analysis if needed to correct non-normal distribution, adding 0.0001 to all values to prevent errors due to transforming zero values.

To check whether warm exceedances were biased by time of placement or retrieval of loggers, we assessed the correlation of Julian day of placement (start of record) and retrieval (end) with elevation, latitude, and with the most sensitive talus warm exceedance response variable: R20+. Elevation, for example, might reasonably be expected to interfere with timing of logger placement in a non-random way through delay of fieldwork by lingering snowpack at high elevations. If any factor related to temperatures was biasing logger timing we would expect a relationship between timing and R20+.

We used the Basin Characterization Model (BCM: Flint et al. 2013) data to estimate aboveground climatic conditions at sites. The BCM dataset is an interpolated, spatially continuous, downscaled climate dataset for the watersheds of California (270-m resolution). In addition to minimum and maximum temperature and precipitation, BCM has a variety of useful variables such as estimated water balance and snowpack, and provides past, recent, and future estimates of all climate variables for each 270-m cell.

In multi-variable analyses, we excluded moderately to highly correlated variables (nonparametric Spearman $|\rho| > 0.5$) from occurring together in the same model. We followed Vittinghoff and McCulloch (2007) in limiting the complexity of our statistical models to prevent overfitting. Model comparisons were performed using $AIC_C$ , and we used $\Delta AICc \leq 2$ as an indication of a well-fitting model (Anderson et al. 2000, Burnham and Anderson 2002).

## RESULTS

Within-talus temperature records were obtained from 46 sites (Figure 1, Appendix I). Full cold-season records were obtained at all sites, but we excluded two sites from analyses of warm temperature exceedences because battery failure curtailed their warm season records to fewer than 70 days.

Day of the year of logger placement correlated differently in different years with elevation, the correlation being negative in 2010 (Spearman rank test, $P = 0.02$, $n = 14$), non-significant in 2011 ($P = 0.16$, $n = 45$), and positive in 2012 ($P = 0.02$, $n = 13$). Day of logger retrieval was negatively correlated with elevation in 2012 ($P = 0.03$, $n = 45$) and non-significant in other years (2011, $P = 0.35$, $n = 14$; 2013, $P = 0.08$, $n = 13$).

To check whether these effects might bias our assessment of warm season temperature exceedances, we examined effects of start and end day of the record on the most sensitive temperature metric, R20+: the ratio of within-talus hourly temperature records ≥ 20ºC to total hourly records during the warm season (transformed to approximate normality). Because elevation and latitude affect temperatures, we also included these variables and year in an all-combinations model comparison to evaluate variable importance (Burnham and Anderson 2002). The best model included elevation and year, only, explaining about 18% of the variance in transformed R20+ (Table 1). Eleven models had $\Delta AICc \leq 2$ (Table 1); of these, none of the top 5 ($\Delta AICc < 1.4$) included start or end day. Variable importance among the 11 models with $\Delta AICc \leq 2$ highlighted year and elevation (relative importance 0.75 and 0.72, respectively) and latitude (0.45), followed by end day and start day (0.23 and 0.15, respectively). The best single-factor models were year of survey ($\Delta AICc = 0.81$), elevation ($\Delta AICc = 1.92$), and latitude ($\Delta AICc = 2.37$), followed distantly by start day ($\Delta AICc = 5.99$) and end day ($\Delta AICc = 7.87$, which trailed the no-variable model $\Delta AICc$ of 7.06). We concluded that start and end dates had effects on R20+, but these effects were small relative to effects due to elevation and year.

*Acute warm temperature extremes.*—Acute warm temperature extremes within talus were uncommon. Only two of 44 sites experienced within-talus temperatures equal to or above 28°C, and both had ≤12 hourly exceedences of this threshold in any sampled year. Old pika sign was detected at one of these sites, and the other was currently occupied. More than two-thirds of sites (32 of 44: 73%) experienced ≤3 hours of within-talus temperature ≥ 24°C in any year of sampling.

**Table 1.**—Best models ($\Delta$AICc $\leq 2$) explaining within-talus warm temperature exceedances ($\geq$20ºC: R20+, transformed to approximate normality). Dots indicate variables included in each model.

| Model Rank | Model: | | | | | $\Delta$AICc | Weight |
|---|---|---|---|---|---|---|---|
| | Year | Elevation | Latitude | Start Day | End Day | | |
| 1 | • | • | | | | 0.00 | 0.103 |
| 2 | | • | • | | | 0.73 | 0.072 |
| 3 | • | | | | | 0.81 | 0.069 |
| 4 | • | | • | | | 1.09 | 0.060 |
| 5 | • | • | • | | | 1.29 | 0.054 |
| 6 | • | • | • | | • | 1.41 | 0.051 |
| 7 | | • | • | | • | 1.43 | 0.050 |
| 8 | • | • | | • | | 1.47 | 0.049 |
| 9 | • | | | • | | 1.56 | 0.047 |
| 10 | • | • | | | • | 1.79 | 0.042 |
| 11 | | • | | | | 1.92 | 0.040 |

*Acute cold temperature extremes.*—Extremely cold temperatures were also uncommon within talus. Only two sites of 46 experienced temperatures at or below -10°C in any year, each for fewer than 10 hours in a year. Pikas were present at one of these sites, and we detected old pika sign at the other.

Temperatures between -5° and -10° C were more common, with 25 sites (54%) experiencing $\geq$10 hours in at least one year of recording. These sites ranged widely in elevation, from 1278 – 2933 m. Other studies have associated within-talus temperatures substantially below 0°C or having wide fluctuations below 0°C with lack of snow cover (Kreuzer and Huntly 2003, Millar et al. 2014b, Beever et al. 2010, 2011).

*Comparing a heavy and a light snow winter.*—California's water year 2010 – 2011 was generally wetter than average, while 2011 – 2012 was dry. Snowpack during March 2011 averaged about 3 times the snowpack during March 2012, as estimated by BCM for the 13 sites we sampled in both years (mean ± standard deviation across sites: 1180 ± 173 mm in 2011, 370 ± 75 mm in 2012). Within-talus temperature loggers during 2010 – 2011 showed fewer warm temperature extremes in the warm season, and longer periods of winter temperatures hovering around 0°C as is typical under an insulating snow layer. There were fewer cold exceedences under this heavy snowpack: 0.7% vs. 3.1% of cold season hours $\leq$ -5° C in 2010-2011 vs. 2011-2012 (Wilcoxon signed ranks test, $Z = 3.56$, $P = 0.0004$); and 2.6% vs. 23.4% of hours $\leq$ -2.5° C ($Z = 3.83$, $P$=0.0001).

*Patterns in 2011 – 2012 within-talus temperatures.*—Here we restricted across-sites analysis to summer 2011 through summer 2012 (n = 44 sites), to control for weather differences between years. Variation among sites in within-talus temperature exceedances was considerable, and exceedances did not explain pika status.

Warm temperature exceedances in the talus hourly records were only very weakly negatively correlated with elevation (R20+ vs. elevation, Spearman $\rho = -0.22$, $P = 0.15$;

R24+ vs. elevation, $\rho = -0.15$, $P = 0.33$; $n = 44$). Correlation of talus warm temperature exceedances with BCM estimates of summer daily maximum air temperatures at each site (Jun through Sep, 2001 – 2010 averages) were still rather weak (R20+ vs. $Tmax$, $\rho = 0.30$, $P = 0.05$; R24+ vs. $Tmax$, $\rho = 0.19$, $P = 0.22$, due to great variation in within-talus temperatures that was not strongly tied to ambient air temperature: the well-known buffering effect of talus. For example, thirteen sites ranging from 1641 to 2530 m elevation logged zero hours ≥20°C within talus. There was substantial variation across elevations in the ratio of hours ≥ 20°C (Figure 2). Pika-occupied and pika-absent sites overlapped extensively in ≥20°C exceedances within talus (Figure 2).

Low temperatures within talus during 2011 – 2012 were also resistant to simple categorization. There was a significant but high-variance positive correlation of cold exceedances with elevation (R(-5)- vs. elevation, $\rho = 0.55$, $n = 45$, $P = 0.0001$; Figure 3). Of 45 sites, 16 had zero hourly records ≤ -5°C, and these sites ranged broadly in elevation: 1208 – 2530 m. Two sites with many hours ≤ -5°C were at modest elevations (1792 and 2156 m), one of which seemed topographically likely to be subject to cold air drainage. Patterns in R(-2.5)- were similar (R(-2.5)- vs elevation, $\rho = 0.62$, $P < 0.0001$). Correlation of within-talus cold exceedances with BCM's 2001 – 2010 average winter $Tmin$ (average daily minimum temperature DJFM) gave correlations of -0.30 (for both R(-5)- and R(-2.5), $n = 45$, $P = 0.05$, ). We doubt -2.5°C is acutely challenging to pikas, which routinely live for months at approximately 0° C, during snow cover, but subzero temperatures within talus may increase long-term winter energy demand (cf. Otto et al. 2015 Figure 1, MacArthur and Wang 1973 Figure 3).

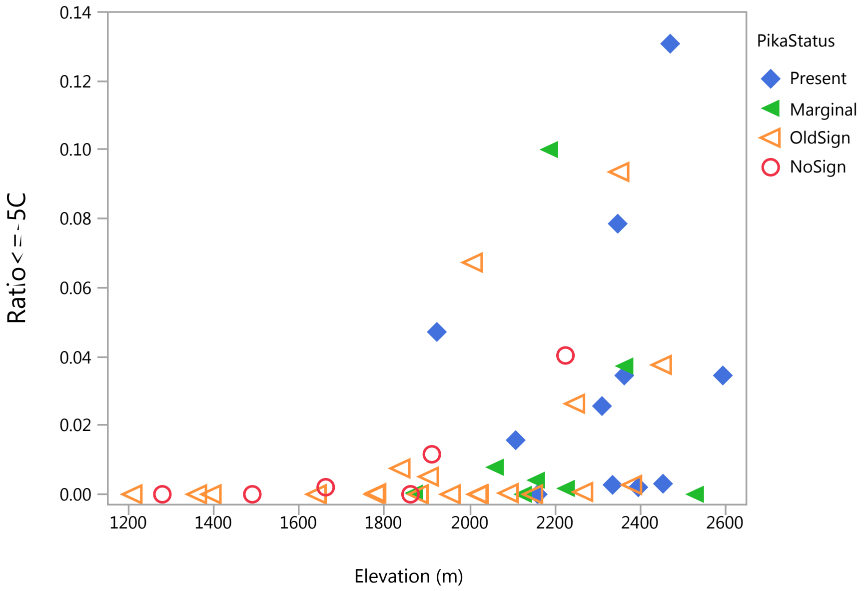

**Figure 3.**—Cold temperature exceedances (R(-5)-: the ratio of within-talus hours ≤ -5°C to all recorded hours December 1 through March 30, versus elevation. Symbol color and shape shows pika population status. R(-5)- was positively related to elevation (Spearman $\rho = 0.55$, $n = 45$, $P = 0.0001$). Sites with few or no temperatures ≤ -5°C occurred at all elevations. Pika-occupied (blue diamonds), marginal (intermittently occupied: green triangles) and absent (open triangles and circles) sites overlapped greatly, with many unoccupied and formerly occupied sites similar to occupied sites in within-talus -5°C temperature exceedances.

*Comparisons in relation to pika status at sites.*—Pika status was negatively associated with warm aboveground temperatures and positively with elevation. Sites where pika were present averaged higher elevation and cooler aboveground than marginal sites, sites with old sign, or sites lacking any sign, in that order (Figure 4). Model comparison of ordinal logistic regression on factors related to pika status, in which pika status was ranked no sign < old sign < marginal < present, showed aboveground average warm season daily maximum temperature (*Tmax*) to be the best single predictor examined (effect likelihood ratio chi-square 21.4, 1 *df*, $P < 0.0001$). Elevation and mean annual temperature also performed reasonably well ($\Delta AICc = 0.77$ and 2.10, respectively), although each was strongly correlated with *Tmax* ($r = -.96$ and .92, respectively). Along with aboveground average cold season daily minimum temperature (*Tmin*: $\Delta AICc = 8.8$), these four were the only factors related to pika status with $\Delta AICc < 10$.

Warm exceedances within talus did not effectively explain pika status (R20+, $\Delta AICc = 17.6$; R24+, $\Delta AICc = 18.9$). The direction of the effect of within-talus cold extremes (R(-2.5)-, $\Delta AICc = 11.3$) on pika status was not as expected from a hypothesis of cold stress—more cold extremes were positively associated with pika presence—but was consistent with its correlation with air temperatures, including *Tmax*. No quadratic effect was supported: pika presence was not maximized at intermediate values of cold exceedances within the limits of our study. The direction of the R(-5)- effect also was not consistent with a cold stress hypothesis within our data set, and a quadratic effect was not supported.

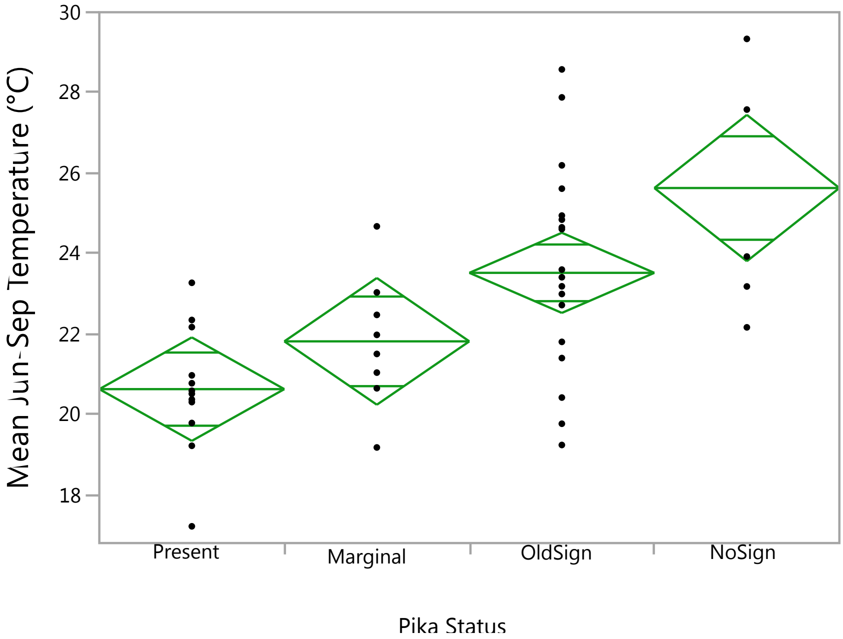

**Figure 4.**—Mean daily-maximum air temperature June-September during 2001-2010, from BCM (Flint et al. 2013) for each site, versus pika status at that site. Cooler daily maximum warm season temperatures were the best predictor of pika occurrence in our study (ordinal logistic regression, $\chi^2 = 21.4$, 1 *df*, $P < 0.0001$). Green diamonds center on the mean and extend vertically to the upper and lower 95% confidence limits of the mean; short internal horizontal lines show significant differences where not overlapping the internal lines of other diamonds. Dots show individual sites.

## Discussion

Soil acts to buffer deeper ground layers from variation in air temperature, and to an extent this has been proven true of talus as well (Millar et al. 2014b). The deeper one goes underground, the more variations in air temperature are buffered—first daily variations disappear, and ultimately annual variation is also smoothed to a constant value: the mean annual temperature of the site, barring geothermal effects (Hillel 1982). Pikas presumably are capable of exploring talus deposits to their very bottoms in many places, a freedom human researchers lack. Yet even at very modest depths within talus, typically less than 1 meter, we found substantial buffering of temperatures. We may presume pikas are capable of reaching depths within talus that are even more equable than we have documented. Remarkably, Smith et al. (2016) found pikas occurring at a site with summer within-talus temperatures (1 m depth) up to 30°C, albeit with some of the lowest feeding, haying, and other activity rates known for American pikas. The authors mention a possibility of sub-surface permafrost at the site, which in combination with pikas' presumed ability to move deep within talus or lava formations, might explain toleration of such warm temperatures at intermediate depths of their talus refuge.

Even at the modest depths where we were able to place recorders, temperatures did not appear particularly challenging to pikas. Otto et al. (2015) estimated 28°C as the lower limit of the thermal neutral zone for resting pikas from Colorado and Wyoming, while MacArthur and Wang (1973) observed a mortality at this temperature. Moyer-Horner et al. (2015) suggested American pika activity would likely be restricted at temperatures above 20°C, due to the extra heat production of activity above resting metabolism, solar insolation, and the limited capability of pikas to shed that heat. All but two of our sites never reached 28°C within talus even at only 0.5-1 m depth, and nearly one-third of 45 sites sampled during 2011-2012 never reached 20°C within talus. Further, many of our sites are at elevations lower than/experience air temperatures higher than sites where pikas currently occur, yet had within-talus temperatures that were suitable for pikas. We did not observe evidence these equable within-talus temperatures were related to the rock-ice features discussed by Millar et al. (2014b) as contributing to pika resiliency. We believe rock-ice features, which retain year-round ice beneath the talus surface, are rare or absent in the "hot zone" of the lower elevational limit of pika distribution within our study area. Instead, equable within-talus temperatures in or below the hot zone were likely the result of the buffering effects of depth.

Amount of talus in the vicinity may be a factor that affects pika status at sampled taluses (Stewart and Wright 2012, Stewart et al. 2015), but seems unlikely to be the whole story. We elected to survey in and around Yosemite Valley and Lovers Leap/Horsetail Falls because there are large areas of talus present, more than is typically found at elevations below 2000 m. The abundance of talus there did not support pikas, even though temperatures within many of those taluses sampled were suitable; the lowest current pika occupancy we found in Yosemite was at 2352 m, and near Horsetail Falls was at 2029 m (marginal). We also know from old sign that, in the past, pika have reached and probably lived at many taluses we sampled. These taluses overwhelmingly still have moderate within-talus temperatures, yet are not currently occupied, suggesting that within-talus temperatures are not what excludes pikas from these locations. These findings echo those of Stewart et al. (2017), who found a large, apparently recently extirpated area of former pika occupation north of Lake Tahoe, California, where air temperatures have become increasingly challenging for pikas.

The tendency of researchers to study microclimates—such as subsurface temperatures within talus—only where pikas occur may be responsible for unjustified optimism about pika resilience to climate change (Millar and Westfall 2010, Smith et al. 2016). Varner and Dearing (2014), based on more moderate within-talus temperatures at lower elevations, suggested that lower elevation taluses might even provide better climate change refugia than higher elevations. We found, however, by examining elevations below where pikas currently occur, that pikas have been present in the past at low elevation taluses but appear extirpated there now, despite generally suitable within-talus temperatures. These lower taluses have warmer aboveground climates. Lower and warmer yet, we found no evidence of pika occurrence at all, despite comparable below-talus temperatures, even in taluses that appeared to be within pika dispersal range (e.g., Yosemite Valley, Lovers Leap).

As opposed to within-talus temperatures, aboveground summer temperatures appear more relevant to pika occupancy in our region. Elsewhere we argued that, among available climatic variables, mean summer temperature had mechanistic appeal as an index of chronic summer heat stress (Stewart et al. 2015), and it was a strong explanatory factor in this study as well. Several authors have shown negative correlations of pika activity with ambient aboveground temperature (MacArthur and Wang 1974, Smith 1974, Moyer-Horner et al. 2015, Otto et al. 2015, Stafl and O'Connor 2015). Warm aboveground temperatures may impair pikas' ability to forage or to disperse (Smith 1974, Wilkening et al. 2011), both essential activities contributing to reproductive rate and metapopulation persistence. Heat restricts foraging activity due to pikas' heat sensitivity and limited ability to shed body heat (MacArthur and Wang 1973, Otto et al. 2015). Moyer-Horner et al. (2015), based on a biomechanical heat flux model, estimated that American pika activity generally would be limited by ambient temperatures above about 20°C. Above this temperature, brief bouts of activity (as opposed to resting metabolism) might still be possible, but would generate body heat load that would have to be dissipated quickly to avoid stress and perhaps death. Mathewson et al (2017), exploring further the consequences of the same heat flux model, calculated under a "moderate" climate change scenario (mean western USA temperatures, summer +2.6°C, winter daily minimums +0.8°C) that by the year 2070 the American pika would be extirpated at 53 of 616 sites. A purely associative temperature model (i.e., not incorporating pika morphology, physiology or behavior) under the same conditions projected extirpation at more sites (69 of 616), the difference implying pika resilience—including use of the thermal refuge of talus—would reduce but not eliminate pika range retraction in the face of climate change.

Finding and establishing new territories is a potentially heat-sensitive period in the life of juvenile pikas. Svendsen (1979) reported that subadult American pikas near Gothic, Colorado, before they dispersed to find and establish their own territories, attempted to use "ephemeral home ranges" within their natal talus that sometimes overlapped adult territories. Territorial adults harassed them at times when the adults were active. Svendsen observed that subadults took advantage of times of day when adults were less active—prior to 0700 hours, during midday, and beyond dusk—to have greater use of these areas without harassment. Under conditions of high daytime air temperatures, subadult pikas might be less able to be active aboveground during the warmest midday hours, which could affect their ability to forage and avoid aggression by adults, and therefore to survive through the dispersal phase of their life cycle. In addition, subadult dispersal to new territories sometimes involves movement through areas lacking thermal refugia such as deep talus, and if temperatures are too warm, dispersing individuals may be subjected to stress or mortality during this essential life stage (Smith 1974, Smith et al. 2016).

Within-talus winter cold stress has emerged repeatedly as another possible climate-related factor leading to pika extirpations (Beever et al. 2010, 2011, Erb et al. 2011, Ray et al. 2012, Yandow et al. 2015), but was not strongly supported as an explanation of pika occupancy in our study. Instead, we found colder within-talus temperatures correlated to higher pika occupancy within our scope of study. This correlation must not be taken too literally because pikas can no doubt access more equable places within talus than those where our loggers were placed—warmer during winters and cooler during summers. Nevertheless, low temperatures within talus—below our focal thresholds—were weakly less frequent with increasing mean air temperature and with decreasing elevation, which ran counter to a cold-stress hypothesis to explain the broad absence of pikas at our lowest, warmest sites.

Overall, our results indicate, in agreement with Mathewson et al. (2017), that the thermal refuge provided by talus is likely to be necessary and beneficial to American pikas, but sufficient only to partially offset the ongoing impacts of warming ambient temperatures on waning pika distribution.

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**Appendix I.**—Study sites.

| Site | Latitude ($^0$) | Longitude ($^0$) | Years | Elevation (m) | Pika Status |
|---|---|---|---|---|---|
| Deadman M | 39.6254 | -120.5495 | 2010-2012 | 1923 | Present |
| Sardine L. Uppr. | 39.6086 | -120.6310 | 2011-2012 | 1861 | NoSign |
| Sierra Buttes | 39.5997 | -120.6402 | 2011-2012 | 2225 | NoSign |
| Sierra City NE | 39.5760 | -120.6220 | 2011-2012 | 1489 | NoSign |
| Hwy.80 nr.border | 39.4368 | -120.0288 | 2011-2012 | 1662 | NoSign |
| Carpenter Ridge | 39.4170 | -120.3183 | 2011-2012 | 2595 | Present |
| Donner W_14 | 39.3219 | -120.4100 | 2010-2013 | 2008 | OldSign |
| Donner E | 39.3140 | -120.3233 | 2010-2012 | 2187 | Marginal |
| Cisco Butte NW | 39.3101 | -120.5632 | 2011-2012 | 1911 | NoSign |
| Hwy.89 Bridge 6 | 39.2279 | -120.2005 | 2011-2012 | 1880 | OldSign |
| Mt. Watson 2 | 39.1875 | -120.1877 | 2011-2012 | 2267 | OldSign |
| Mt. Watson 1 | 39.1844 | -120.1855 | 2011-2012 | 2248 | OldSign |
| Big Bear | 39.1619 | -120.1825 | 2011-2012 | 2022 | OldSign |
| Eagle Fls. 4 | 38.9537 | -120.1134 | 2010-2013 | 1905 | OldSign |
| Eagle Fls. 20 | 38.9473 | -120.1172 | 2011-2012 | 2150 | OldSign |
| Eagle Fls. 15 | 38.9470 | -120.1197 | 2011-2012 | 2108 | Present |
| EagleFls_100 | 38.9467 | -120.1248 | 2010-2012 | 2157 | Marginal |
| Eagle Lk. | 38.9414 | -120.1245 | 2010-2012 | 2160 | Present |
| Velma Lk. Lower | 38.9409 | -120.1459 | 2010-2012 | 2382 | OldSign |
| Mt. Tallac | 38.9048 | -120.0984 | 2010-2013 | 2933 | Present |
| Heather Lk. Blw, S | 38.8755 | -120.1294 | 2010-2012 | 2363 | Present |
| Heather Lk. | 38.8745 | -120.1365 | 2010-2012 | 2454 | Present |
| Heather Lk. Below | 38.8727 | -120.1244 | 2010-2013 | 2311 | Present |
| Echo Lk. S | 38.8331 | -120.0561 | 2010-2012 | 2336 | Present |
| Pyramid Ck. E | 38.8285 | -120.1223 | 2011-2012 | 2126 | Marginal |
| Twin Bridges NNE | 38.8282 | -120.1166 | 2011-2012 | 2364 | Marginal |
| Pyramid Ck. SE2 | 38.8267 | -120.1212 | 2011-2012 | 2060 | Marginal |
| Hogback LL3 | 38.8050 | -120.1375 | 2011-2012 | 1781 | OldSign |
| American R., S fork | 38.8028 | -120.1392 | 2011-2012 | 1778 | OldSign |
| Lovers Leap 2 | 38.8007 | -120.1358 | 2011-2012 | 1838 | OldSign |
| Hwy.89 WM | 38.7926 | -119.9671 | 2011-2012 | 2352 | OldSign |
| Carson R. W | 38.7633 | -119.8519 | 2011-2012 | 1870 | Marginal |
| Round Top | 38.6435 | -119.9891 | 2010-2012 | 2348 | Present |
| Mosquito Lk. NW | 38.5189 | -119.9203 | 2011-2012 | 2530 | Marginal |
| Pacific Gr. Summ. 10 | 38.5147 | -119.9074 | 2010-2012 | 2452 | OldSign |
| Calif. Falls N | 37.9176 | -119.4379 | 2011-2012 | 2396 | Present |
| McGee Lk. | 37.9014 | -119.4311 | 2011-2012 | 2471 | Present |
| HalfDome,CloudsR | 37.7589 | -119.5284 | 2011-2013 | 1394 | OldSign |
| Bunnell Pt. | 37.7454 | -119.4652 | 2011-2013 | 2092 | OldSign |
| Bunnell Crossing | 37.7428 | -119.4607 | 2011-2013 | 2020 | OldSign |
| Moraine Dome | 37.7412 | -119.4763 | 2011-2013 | 1956 | OldSign |
| Merced Lk. Camp | 37.7410 | -119.4098 | 2011-2013 | 2227 | Marginal |
| Nevada Fall, Tr.Blw. | 37.7269 | -119.5354 | 2011-2013 | 1641 | OldSign |
| Vernal Fall Tr. | 37.7265 | -119.5539 | 2011-2013 | 1360 | OldSign |
| El Capitan SW | 37.7233 | -119.6543 | 2011-2013 | 1278 | NoSign |
| Bridalveil E | 37.7206 | -119.6448 | 2011-2013 | 1208 | OldSign |

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## INFORMATION FOR CONTRIBUTORS

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| S. Osborn | California Department of Fish and Wildlife |
| L. Patterson | California Department of Fish and Wildlife |
| E. Tennant | California Department of Fish and Wildlife |
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| J. Villepique | California Department of Fish and Wildlife |
| G. Zimmerman | US Fish and Wildlife Service–Sacramento |

**Front.**—Great horned owl (*Bubo virginianus*) nestling. Photo by Sarah Peterson/USGS

**Back.**—American pika (*Ochotona princeps*). Photo © Ron Wolf.

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