USE OF HISTORICALLY FISHLESS HIGH-MOUNTAIN LAKES AND STREAMS BY NEARCTIC RIVER OTTERS *(LONTRA CANADENSIS)* IN CALIFORNIA

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ABSTRACT—In California, River Otters (*Lontra canadensis*) are most commonly associated with food-rich lowland aquatic habitats where they forage primarily on fish and crustaceans. Their distribution in high-elevation montane regions of the state, areas in which fish and crayfish were absent historically, is largely unknown. We compiled occurrence records of River Otters in California from elevations >1100 m, and evaluated them using evidentiary standards. Based on 126 records, we report the widespread presence of River Otters in the Klamath, southern Cascades, and Sierra Nevada mountain ranges, including at elevations exceeding 3000 m. Sixty-three percent of the records met our definition as ''verified'', and the remaining 37% were considered ''unverified''. The distribution of observations through time and habitats in which observations were made were similar between verified and unverified records. River Otter records spanned the period from 1900 to 2010, with 50% occurring between 1991 and 2010. Ninety-three percent of the water bodies with records of River Otters contained nonnative prey (fish and crayfish). Those lacking nonnative prey all supported native prey, including amphibians and reptiles. Based on records that contained River Otter foraging observations, nonnative fishes and crayfish were represented in 89% of the total accounts, and native frogs and invertebrates were represented in 22%. It remains unclear whether River Otters occurred in California's high-elevation water bodies prior to the introduction of fish and crayfish, and additional research is needed to understand the possible influence of nonnative prey in allowing River Otters to expand their distribution in these habitats.

Key words: California, Cascade Range, fishless habitats, introduced prey, Klamath Mountains, *Lontra canadensis*, montane distribution, River Otter, Sierra Nevada, trout stocking

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The River Otter (*Lontra canadensis*) is a large aquatic mustelid endemic to North America north of Mexico (Melquist and others 2003). River Otters are most commonly described as using food-rich aquatic habitats including low-elevation lakes, wetlands, rivers, large streams, and estuaries, where they forage primarily on fish and crustaceans. They also opportunistically take other prey, including mammals, birds, amphibians, reptiles, and insects (Manning 1990; Melquist and others 2003; Studebaker 2008; Penland and Black 2009). River Otters are highly mobile; movements of more than 4 km/d are common, and individuals are known to move up to 42 km/d (Melquist and Hornocker 1983).

In California, the River Otter was abundant historically before it was harvested for fur prior to and during the California gold rush (1848–1855). Commercial trapping was banned in 1961 and California populations have likely increased since then (Schempf and White 1977; Jameson and Peeters 2004). Known distribution in the state includes low-elevation habitats from the Oregon border to central California, including large portions of the Central Valley (Stevens 1906; Grinnell and others 1937; Zeiner and others 1990; Black 2009). In the Central Valley, River Otters are restricted to large river systems and lentic water bodies, with the southernmost record occurring at Tulare Lake in Kings County (Grinnell and others 1937).

Historical accounts of River Otters are rare from the montane, subalpine, and alpine zones of California. For example, River Otters are not mentioned in the comprehensive surveys of vertebrates conducted in Yosemite and Lassen Volcanic National Park regions in the early 1900s (Grinnell and Storer 1924; Grinnell and others 1930). Most of the records used to describe the historical distribution of River Otters in montane California are from large rivers of the foothill regions (see map in Grinnell and others 1937, p 276). The earliest published account noting high-elevation occurrences of River Otters described a dead specimen collected in Yosemite National Park in 1928 (Babcock Lake, elevation 2744 m), and additional unsubstantiated sightings in some of Yosemite's high country lakes and below Lake Eleanor (Russell 1928). In the southern Sierra Nevada, River Otters were reported to be ''scarce'' by Sumner and Dixon (1953), and they noted only 2 second-hand visual records in Sequoia National Park and 2 visual records in Kings Canyon National Park. These 4 records were in the lower reaches of the Kaweah River and Kings River that harbored native fish populations (Moyle and others 1996).

Historically, aquatic habitats in mountainous regions of western North America were primarily fish-free due to steep, rugged terrain that prevented natural colonization of high-elevation lakes and streams from downstream habitats (Pister 2001). In the late 1800s, humans began introducing fishes into these high-elevation ecosystems to create sport fisheries (Bahls 1992; Knapp and others 2001a). Introductions of these aquatic predators have modified the abundance and composition of native biota, both directly by decreasing the abundance of prey species (zooplankton: Knapp and others 2001b; aquatic macroinvertebrates: Carlisle and Hawkins 1998; Knapp and others 2001b; Pope and others 2009; amphibians: Knapp and Matthews 2000; Vredenburg 2004; Pope 2008), and indirectly by creating trophic cascades (Simon and Townsend 2003; Sarnelle and Knapp 2005; Herbst and others 2009; Epanchin and others 2010). For example, lakes in California's Sierra Nevada that contain introduced salmonids are far less likely to support populations of native amphibians compared to lakes without salmonids due to predation (Knapp and Matthews 2000; Knapp 2005). Consequently, a native predator of amphibians, the Mountain Gartersnake (*Thamnophis elegans elegans*; Crother 2008), is also less likely found at lakes with fish because their amphibian prey (*Rana sierra* and *Rana muscosa*) is absent (Matthews and others 2002; Knapp 2005).

On the other hand, species that prey on fish may have increased in distribution and abundance in response to the expansion of their prey into these naturally fishless high-elevation habitats. Facilitation of native species by nonnative species has only recently received much attention (Rodriguez 2006), but its influence on species distributions may be far-reaching. For example, in high-elevation lake habitats of the Klamath Mountains (California), Pope and others (2008) provided evidence that the Oregon Gartersnake (*Thamnophis atratus hydrophilus*), a fish predator, has expanded its range due to the introduction of nonnative fish. In Montana, the introduction of Kokanee (*Oncorhynchus nerka*) to

several lakes and streams positively affected Bald Eagle (*Haliaeetus leucocephalus*), Grizzly Bear (*Ursus arctos*), and River Otter populations as a new abundant prey source (McClelland and McClelland 1986; Spencer and others 1991). The influence of introduced fish on the distribution of River Otters in montane regions of California remains unknown.

The primary objective of this study was to use historical and current records to describe the distribution of River Otters in 3 high-elevation mountain ranges of California: Klamath Mountains, Southern Cascades, and Sierra Nevada. Most aquatic habitats in these ranges were historically fishless, but now contain widespread fish populations due to more than a century of stocking. We also provide limited information on the prey of River Otters in these high elevation habitats.

METHODS

Study Area

The Klamath Mountains, Southern Cascades, and Sierra Nevada are largely contained within national forests and national parks (Fig. 1). Most aquatic habitats above 1100 m in these ranges historically lacked fish and crayfish populations, but now support several salmonid species (primarily Brook Trout (*Salvelinus fontinalis*), Rainbow Trout (*Oncorhynchus mykiss*), Golden Trout (*Oncorhynchus mykiss aquabonita*), Brown Trout (*Salmo trutta*)), and introduced crayfish (*Pacifastacus* spp.) (Pister 2001). Within the study mountain ranges, fish stocking was discontinued in national parks in the early 1990s, but continues in lakes and streams on national forest lands.

The Klamath Mountains of northern California encompass an extensive mixed conifer-subalpine region reaching 2750 m elevation, with high levels of biotic diversity and endemism (Coleman and Kruckeberg 1999; DellaSala and others 1999). The range contains hundreds of lakes and ponds, and a large fraction is protected in 5 wilderness areas. The Southern Cascades range in California is largely of volcanic origin, and its southernmost extent lies within Lassen Volcanic National Park (LVNP). The California portion of this mountain range reaches 3187 m and contains relatively few lakes. However, LVNP is an exception, with >50 lakes and hundreds of ponds in mixed-conifer and subalpine zones. The Sierra Nevada is the tallest mountain range in the conterminous United States (4421 m), the majority of which is protected in 13 national forest wilderness areas and 3 national parks. This range contains thousands of lakes and ponds in the mixed-conifer, subalpine, and alpine zones.

Between 1995 and 2008, more than 95% of all lentic habitats within the Klamath Mountains (>1000), Southern Cascades (825), and Sierra Nevada (>12,000) were surveyed to describe the distribution of native amphibians, aquatic reptiles, and introduced fish (for example, Knapp and others 2003; Knapp 2005; Welsh and others 2006; California Department of Fish and Wildlife [CDFW], unpubl. data). As a result of these surveys, the contemporary distribution of fish, amphibians, and aquatic reptiles (potential River Otter prey) in these mountain ranges is exceptionally well known.

Data Acquisition

To document the distribution of River Otters in the 3 ranges, we gathered occurrence records from all known sources, including the peer-reviewed scientific literature, books, published and unpublished reports, wildlife observation databases, incidental unpublished sightings made by field biologists, and via internet searches. We conducted searches of the relevant scientific literature and included several journals with relatively limited circulation: California Fish and Game (1900–2009), Yosemite Nature Notes (1922–1985), and Yosemite (formerly Yosemite Nature Notes; 1985–2009). We also included 3 unpublished reports that described the distribution of River Otters in California (Kirk 1975; Gould 1977; Schempf and White 1977), and 3 wildlife observation databases maintained by staff at Sequoia-Kings Canyon, Yosemite, and Lassen Volcanic National Parks (National Park Service 2008, 2009a, 2009b). Incidental River Otter sightings were obtained from field biologists who made their observations while conducting surveys in high-elevation aquatic environments across the 3 mountain ranges. We conducted internet searches to find images and other descriptions of River Otters in the 3 ranges. For recent sightings (1975 to 2010) and all internet-based records, we attempted to contact the observers directly to obtain verification and supplementary information. For all River Otter records that we retrieved, only those made at elevations of

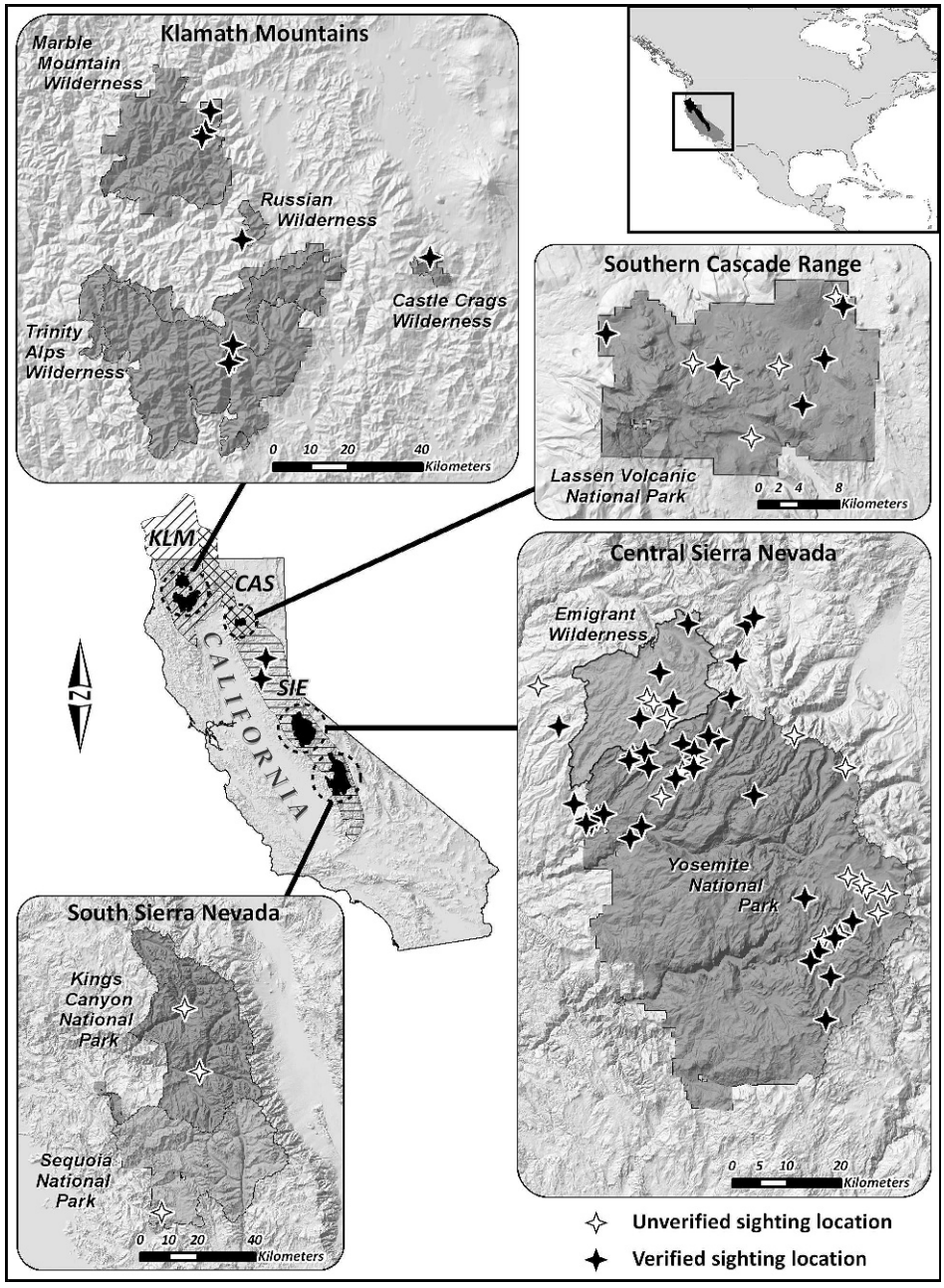

FIGURE 1. Locations of verified and unverified River Otter (*Lontra canadaensis*) observations in high-elevation regions of California from 1900 to 2010 (KLM = Klamath Mountains, CAS = Southern Cascades, SIE = Sierra Nevada). Two sightings in the Sierra Nevada that are shown on the California base map are located outside the areas displayed on the inset maps.

TABLE 1. Records of River Otters (*Lontra canadensis*) using high-elevation habitats in California (1900–2010), categorized by evidentiary standard and region.

	Evidentiary standard[a]						
	Verified			Unverified			Total
Region	1	2	3	4	5	6	
Klamath Mountains	3	4	1	0	0	0	8
Southern Cascades	1	8	9	12	1	0	31
Sierra Nevada	6	39	8	17	16	1	87
Totals	10	51	18	29	17	1	126
Percent of total	7.9	40.5	14.3	23.0	13.5	0.7	

[a] See Evidentiary Standards subsection in Methods for definition of categories.

>1100 m were included in our analyses. We used this elevation threshold to distinguish between habitats that generally lacked fish and crayfish historically (Pister 2001) and those at lower elevations that originally contained 1 or more native fish species.

Evidentiary Standards

Anecdotal occurrence data are often used to describe the distribution of species (Ferrier 2002), especially those that are rare or elusive (Aubry and Houston 1992; Frey 2006; Aubry and others 2007). Using anecdotal occurrence data can be problematic because of inaccuracies and biases inherent in this type of data, but these issues can be at least partially overcome by using evidentiary standards that rank the validity of observations (McKelvey and others 2008). We developed an evidentiary standard [adapted from Aubry and Houston (1992), Frey (2006), and McKelvey and others (2008)] that used 6 criteria to describe the reliability of each River Otter occurrence record. These criteria were as follows: 1 = River Otter specimen or diagnostic photograph; 2 = detailed River Otter sighting by an experienced observer, including tracks, scat, or slides (e.g., path or trace down embankment to waterway); 3 = detailed River Otter sighting by an observer with limited qualifications who was subsequently interviewed by an expert resulting in diagnostic characteristics; 4 = detailed River Otter sighting by observer with unknown qualifications; 5 = River Otter sighting without any description; 6 = observation of tracks, scat, or slides (but lacking diagnostic photographs) by observer with unknown qualifications. After assigning a score to each occurrence record, we grouped them into 2 categories based on the reliability criteria: categories 1 to 3 were considered verified (highly reliable), and categories 4 to 6 were considered unverified (less reliable).

Habitat Use and Diet

To describe the physical habitats associated with each River Otter observation, we determined the water body type (lake, reservoir, marsh, stream, upland) and elevation for each record. The presence of potential native and nonnative prey species was determined for each site using historical fish stocking records (Elliot and Loughlin 1992; CDFW, unpubl. data) and recent survey data acquired from aquatic vertebrate species surveys (Knapp and Matthews 2000; Knapp 2005; Welsh and others 2006; Fellers and others 2008; CDFW, unpubl. data). We summarized diet information for the subset of occurrence records that contained detailed foraging accounts. Finally, we visually examined scats to identify prey remains. In 1 case, DNA analysis of bone fragments was used to identify vertebrate prey species using standard DNA extraction (Ausubel and others 1995; Kearney and Stuart 2004) and DNA amplification (Vences and others 2005) techniques. All diet information was collected opportunistically and likely under represents the full complement and relative frequency of prey items. These data, however, represent the best River Otter diet information currently available for high-elevation habitats.

RESULTS

We collected 126 records of River Otters observed at high-elevation water bodies in the 3 study mountain ranges, dating from 1900 to 2010 (Fig. 1, Appendix). The Sierra Nevada had the greatest number of records (87), followed by the Southern Cascades (31), and the Klamath Mountains (8) (Table 1, Fig. 1). Of the 126

TABLE 2. Records of River Otters (*Lontra canadensis*) in high-elevation habitats in California, categorized by record verification status, time period, and presence of nonnative prey.

		Verified		Unverified	
Time Period	# Records (%)	# Records	# NN prey[a]	# Records	# NN prey[a]
1900–1930	5 (4.1)	1	1	4	4
1931–1960	11 (8.9)	5	5	6	6
1961–1990	45 (36.6)	14	13	31	28
1991–2010	62 (50.4)	57	53	5	5
Total	123	77	72	46	43

[a] # NN prey = number of River Otter records at sites with nonnative prey. Three records at water bodies for which we lacked nonnative prey information were omitted.

records, 79 (63%) were categorized as ''verified'' (Table 1, Appendix) and 47 (37%) were ''unverified''. Ten records (8%) provided indisputable physical evidence of River Otters (score = 1); 2 of these were collected specimens and 8 were photographed individuals showing diagnostic characteristics. Each of the 3 mountain ranges contained 1 to 6 indisputable records (Table 1), with the earliest occurring in Yosemite National Park in 1928. Of the 47 unverified records, nearly all occurred within the geographic range of verified records for the 3 mountain ranges (Fig. 1). The only exceptions were 4 early records from Sequoia and Kings Canyon National Parks, 2 from 1910 and 2 from 1941. In addition, 19 of the unverified records (40%) were recorded at water bodies having at least 1 additional verified record (Appendix). The vast majority of both verified and unverified records (92% and 77%, respectively) were from the period 1961 to 2010, and the remaining observations were made during 1900 to 1961 (Table 2). Forty-two percent of all records were from the most recent decade (2001 and 2010).

The majority of River Otter records (both verified and unverified) occurred at lentic water bodies (lake, reservoir, or marsh; Table 3). The remaining records were from streams (9 records) or upland habitat (1 record; Table 3). Several lakes and reservoirs had multiple records; for example, Butte Lake in LVNP (Southern Cascades) had 21 River Otter records between 1966 and 2007 (Appendix). River Otter observations in the 3 mountain ranges occurred over a wide elevation range, with the mean elevation of both verified and unverified records increasing from north to south (Table 3). Seven observations (4 verified, 3 unverified) were made at elevations exceeding 3000 m, and the highest verified record was from a lake at 3150 m in Yosemite National Park (Appendix).

Of the 114 records of River Otters that included a specific date of observation (Appendix), nearly all occurred during the summer months (June–September; verified = 84%, unverified = 85%). An additional 4 records occurred in fall (October), 1 in winter (January), and 13 in spring (March–May). Of the records

TABLE 3. Habitats used by River Otters (*Lontra canadaensis*) in the 3 study mountain ranges, based on (A) verified records (1928–2010), and (B) unverified records (1900–2009). The Klamath Range had no localities with unverified records.

Region	# Localities[a]	Lake (%)	Reservoir (%)	Marsh (%)	Stream (%)	Elevation[b] (range)
(A)						
Klamath Range	8	8 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	1851 (1682–2107)
Southern Cascades	5	4 (80.0)	0 (0.0)	1 (20.0)	0 (0.0)	1900 (1782–2012)
Sierra Nevada	30	23 (76.7)	5 (16.7)	0 (0.0)	2 (6.7)	2354 (1100–3150)
Totals (%)	43	35 (81.4)	5 (11.6)	1 (2.3)	2 (4.6)	2207 (1100–3150)
(B)						
Southern Cascades	7	5 (71.4)	0 (0.0)	1 (14.3)	1 (14.3)	1924 (1707–2042)
Sierra Nevada	27	14 (58.3)	5 (20.8)	0 (0.0)	8 (33.3)	2420 (1304–3288)
Totals (%)	34	19 (55.9)	5 (14.7)	1 (2.9)	9 (26.5)	2308 (1304–3288)

[a] Localities with multiple records were included only once. In the Sierra Nevada, 3 verified records and 1 unverified record that lacked specific locality information were omitted.
[b] Average elevation in meters.

that provided a reliable count of individual River Otters (95; Appendix), 62% were of single animals, 16% were of 2, 12% reported 3, 6% reported 4, and 4% reported 5 individuals. Three records identified family groups with 2 pups in each group. Another record identified 2 pups without adult individuals. Two den sites were also identified, 1 at a lake in the Klamath Mountains at 1856 m elevation and another at a lake in the Sierra Nevada at 2263 m.

Nearly all River Otter records (verified and unverified) occurred at water bodies containing nonnative fishes, crayfish, or both (Table 2). For the 123 records for which presence of fish and crayfish was known, 115 (93%) occurred at water bodies containing nonnative fishes and 27 (22%) occurred at water bodies containing nonnative crayfish. All early records (1900–1960) occurred at sites harboring nonnative prey (Table 2). Only 8 of the 123 records (7%) occurred at water bodies that did not contain nonnative fish or crayfish, and all of these water bodies supported populations of native amphibians and reptiles and were near lakes containing fish (average distance: 2.8 km, range: 0.5–16.0 km).

Klamath Mountains

The 8 records of River Otters in the Klamath Mountains were all verified (Fig. 1), were of single animals, and occurred at lakes located at elevations up to 2107 m (Table 3). All observations were recent (1999 to 2010), perhaps due to the fact that unlike in the Southern Cascades and Sierra Nevada, no long-term wildlife observation databases are available for the Klamath Mountains. All water bodies with observations of River Otters contained nonnative salmonids, and 7 of these also supported native amphibians and the Common Gartersnake (*Thamnophis sirtalis*).

Southern Cascades

The 31 records of River Otters in the Southern Cascades (1962 to 2007) were all from LVNP; 18 were verified and 13 were unverified (Fig. 1). Verified observations were made at 4 lakes and 1 marsh, with the highest elevation being at 2012 m (1 lake, 1 marsh; Table 3). Unverified records also existed for upland and stream habitats (Table 3). Over half of the records (58%) were recent (2001 to 2007), and 26% occurred prior to 1970. Most records were of 1 or 2 animals, but a group of 5 was observed at Butte Lake in 2005. All water bodies with observations of River Otters contained nonnative salmonids, and 2 lakes also contained nonnative crayfish. Seven of the 9 water bodies also supported native amphibians and the Common Gartersnake.

Sierra Nevada

In the Sierra Nevada, 53 River Otter records were verified and 34 were unverified ($n = 87$, Table 1). Most of the records were from in and around Yosemite National Park and the Emigrant Wilderness (Stanislaus National Forest; Fig. 1). Most records were from lakes, but additional sightings were from reservoirs and streams (Table 3). The highest verified record was from a lake at 3150 m elevation (Table 3). Categorization of sightings by decade indicated that the period 2001 to 2010 had the greatest number of sightings and at least 4 sightings were documented in each decade since 1950. Fourteen sightings were documented prior to 1950, including the earliest record in 1900. At several sites, River Otters were documented multiple times (Appendix), with the largest number of records being from Lake Eleanor (16), a relatively low-elevation reservoir in Yosemite National Park. Eight of the 87 River Otter sightings were at fishless lakes, and all of these lakes contained native amphibians and the Mountain Gartersnake. Family groups of 3 to 5 individuals were observed on 19 occasions at 14 water bodies. Two unverified records separated by 5 d identified 2 River Otter pups at Lake Eleanor, and another verified record identified 2 River Otter pups at Fraser Lake.

Foraging Observations

We found 18 records that documented diet information for River Otters in these high-elevation habitats. Foraging observations were recorded from all 3 mountain ranges, including at 11 lakes, 1 stream, and 2 reservoirs. Of the 18 records, 17 came from water bodies containing introduced fish (7 of these water bodies also contained introduced crayfish) and 14 records came from water bodies containing native prey. Nine records were observations of River Otters actively foraging, 7 were from scats, and 2 were from partially consumed prey remains found at

locations at which River Otters were concurrently observed. Based on the 18 records, River Otters foraged primarily on nonnative prey (16 records), including fish (13 records) and crayfish (4 records). Native prey items were represented in 4 of the foraging records. Of these, 3 observations were scats that contained the remains of only native prey or both native and nonnative prey, and 1 was an observation of the remains of approximately 25 Sierra Nevada Yellow-legged Frogs (*Rana sierrae*) along the lakeshore where an individual River Otter was observed foraging. Two scats from different lakes contained the remains of large-bodied aquatic insects, including *Aeshna* spp. (Odonata) larvae, adult *Lethocerus* spp. (Hemiptera), and adult *Notonecta* spp. (Hemiptera). Frog remains also were identified in 2 scat samples. One sample from the Sierra Nevada contained bones that were identified using mtDNA (by A Baker, Humboldt State University) as Sierran Treefrog (*Pseudacris sierra*). The second sample (from the Klamath Mountains) contained bones that were visually identified (by J Reiss, Humboldt State University) as being from Cascades Frogs (*Rana cascadae*) and salmonid fishes.

Discussion

Previous descriptions of the distribution of River Otters in California suggested this species was found almost exclusively in low elevation habitats (Grinnell and others 1937; Schempf 1977). Our compilation of River Otter sightings provides documentation of their long-term and widespread occurrence in high elevation aquatic habitats of the Klamath Mountains, Southern Cascades, and Sierra Nevada after widespread fish stocking was initiated in these regions. Verified and unverified records provided similar depictions of River Otter distributions and habitat use in the 3 study mountain ranges, indicating their presence primarily in lakes, and some individuals occurring at elevations exceeding 3000 m. The lack of verified River Otter records south of Yosemite National Park (we found only 4 unverified records for this area) leaves uncertain their historical or contemporary occurrence in the southern Sierra Nevada, including Sequoia and Kings Canyon National Parks.

No River Otter occurrence information is available prior to 1900 for any of the 3 study mountain ranges. Consequently, it remains difficult to determine whether the current River Otter distribution is an accurate reflection of their historical distribution. If River Otters did in fact occur at high elevations in the 3 study ranges historically, it is puzzling that the intensive survey efforts conducted in the Yosemite and Lassen regions in the early 1900s (Grinnell and Storer 1924; Grinnell and others 1930) failed to detect them. We suggest 3 possible explanations for the absence of River Otters in these early surveys and their widespread occurrence today. First, it is possible that River Otters were in fact present at high elevations in the 3 mountain ranges, but these early survey efforts were not extensive or intensive enough to detect them. The fact that no River Otters were detected during the survey of all 3200 lentic water bodies in Yosemite National Park conducted from 2000 to 2002 (Knapp 2005), despite the known presence of River Otters in this area, provides support for this possibility. Sierra Nevada Yellow-legged Frogs and Cascades Frogs were very abundant prior to fish introductions (Grinnell and Storer 1924; Grinnell and others 1930), and it is possible that they could have supported high-elevation River Otter populations, at least during summer months. Our observations that River Otters in fishless habitats are apparently subsisting at least in part on amphibians and large invertebrates lends some support to this possibility. Second, in California heavy trapping of River Otters occurred in the mid-1800s, with harvest continuing until trapping was banned in 1961. This could have eliminated River Otters from much of their previous range by the early 1900s, when the 1st extensive vertebrate surveys were conducted (Grinnell and Storer 1924; Grinnell and others 1930). Under this scenario, the widespread presence of River Otters today across all 3 mountain ranges would be evidence of post-trapping recovery. Third, River Otters may have been very rare in the high-elevation portions of the 3 ranges historically because of the limited availability of fish prey, but expanded their distribution into these habitats following the widespread introduction of fish and crayfish. The fact that most River Otter sightings in the 3 study mountain ranges were made at habitats containing fishes, and that in these habitats fish appear to be an important dietary component, lends some support to this possibility and merits additional discussion.

The facilitation of native species by nonnative species is a widespread phenomenon and can

have cascading effects across trophic levels and reconfigure community structure (Rodriguez 2006). One way in which this facilitation can occur is via trophic subsidy, such as when nonnative prey expand the resource base of native predators. An example of facilitation via a trophic subsidy is the response by the Oregon Gartersnake (*T. atratus hydrophilus*) to the introduction of nonnative trout into historically fishless aquatic habitats in the Klamath Mountains. Pope and others (2008) suggested the Oregon Gartersnake, a species that preys on fish and amphibians and generally occurs at lower elevations, expanded its range into high-elevation areas following nonnative trout introductions. In high-elevation habitats the Oregon Gartersnake also feeds on Cascades Frogs, and perhaps as a consequence lake basins with the Oregon Gartersnake had significantly lower Cascades Frog densities than did basins lacking the Oregon Gartersnake (Pope and others 2008). Therefore, the introduction of trout likely facilitated the population expansion by the Oregon Gartersnake which subsequently suppressed populations of the alternate prey, amphibians. A very similar scenario could be associated with the presence of River Otters in California's montane habitats.

River Otters are rarely found in habitats that lack fish or crayfish, likely due to the importance of these taxa as prey. A review of 48 studies on River Otter diets in North America (Melquist and others 2003) indicated that at least 90% of the studies reported fish and 88% reported crayfish in River Otter diets. More than half of these studies also recorded the presence of amphibians in River Otter diets, but amphibians nonetheless constituted a small proportion of the overall diet (Melquist and others 2003). When abundant, amphibians were occasionally consumed in large quantities, such as during warm months when amphibians are most active (McDonald 1989). If the introduction of trout and crayfish into montane lakes and streams facilitated the expansion of River Otters into these high elevation habitats, River Otters would likely consume not only nonnative prey but also large-bodied native species, including amphibians, reptiles, and invertebrates. Alternatively, if River Otters were highly selective toward nonnative fish and crayfish prey, then native species could possibly benefit from local reductions of nonnative predators as observed in experimental fish removal studies (see: Vredenburg 2004; Pope 2008). Because 3 out of the 4 River Otter scat samples collected by this study contained both native and nonnative prey, we cannot rule out the possibility that River Otters are opportunistic predators in these high-elevation habitats.

The extent to which the presence of River Otters could produce cascading trophic effects on native prey species is likely a function of River Otter density and prey selection; both remain largely unknown for montane regions of California and the western US in general. River Otters have high metabolic rates for land mammals (Iverson 1972), and the resulting high prey biomass consumed by River Otters can represent a large fraction of their prey's annual production, with the potential to strongly influence trophic dynamics (Mack 1985; Dekar and others 2010). Given the widespread practice of trout stocking across the western US, and the presence of River Otters across this landscape, the possible facilitation of River Otter populations by nonnative trout would likely not be restricted to California. With the declining status of many montane amphibian populations in the western US, additional research should focus on exploring the ecological implications of predator-prey interactions between River Otters and their native and nonnative prey.

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APPENDIX

Descriptions of the 126 River Otter observations from high-elevation regions of California used in the current study. Cells lacking information are labeled ND for no data available.

Region	Site Name	Water body	Elev.	X[a]	Y[a]	Non-native[b]	Native[c]	Month	Year	# Otters	Score[d]	Source[e]
Klamath	"L"[f]	Lake	1991	−123.01	40.98	Y	Y	October	2005	1	1	This study
Klamath	Campbell	Lake	1756	−123.10	41.53	Y	Y	June	2010	1	1	This study
Klamath	Canyon Creek[f]	Lake	1735	−123.03	40.97	Y	Y	August	2008	1	2	This study
Klamath	Castle	Lake	1682	−122.38	41.23	Y	Y	Summer	2003	1	1	UC Davis
Klamath	Cliff	Lake	1863	−123.11	41.52	Y	Y	July	2010	1	2	This study
Klamath	Golden Russian	Lake	1856	−122.98	41.27	Y	Y	August	2001	1	2	USFS
Klamath	Little Southfork[f]	Lake	1817	−123.01	41.02	Y	Y	July	1999	1	2	This study
Klamath	Lower Wrights[f]	Lake	2107	−123.09	41.58	Y	ND	July	2009	1	3	This study
Cascades	Bathtub	Lake	1912	−121.30	40.57	Y	Y	July	1967	1	4	LVNP
Cascades	Butte[f]	Lake	1844	−121.29	40.56	Y	Y	July	1966	1	4	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	June	1967	2	4	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	July	1967	1	4	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	July	1967	1	4	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	June	1968	1	3	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	1972	1	4	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	1974	1	4	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	1978	1	4	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	July	2003	1	3	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	2003	1	3	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	2003	1	3	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	Sept	2003	1	3	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	July	2004	1	2	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	July	2005	5	1	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	2005	4	2	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	2006	1	2	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	2006	1	2	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	July	2007	1	2	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	July	2007	2	3	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	2007	1	3	LVNP
Cascades	Butte	Lake	1844	−121.29	40.56	Y	Y	August	2007	1	3	LVNP
Cascades	Hat	Lake	1963	−121.46	40.51	Y	ND	July	2006	1	4	LVNP
Cascades	Horseshoe	Lake	2012	−121.34	40.47	Y	ND	July	2006	1	4	LVNP
Cascades	Horseshoe	Lake	2012	−121.34	40.47	Y	ND	July	2006	1	2	LVNP
Cascades	Manzanita	Lake	1782	−121.57	40.53	Y	Y	July	2001	1	3	LVNP
Cascades	Snag	Lake	1852	−121.31	40.51	Y	Y	Sept	1976	1	2	LVNP
Cascades	Twin	Lake	1992	−121.36	40.51	Y	Y	June	1962	1	4	LVNP

APPENDIX. Continued.

Region	Site Name	Water body	Elev.	X[a]	Y[a]	Non-native[b]	Native[c]	Month	Year	# Otters	Score[d]	Source[e]
Cascades	Dersch	Marsh	2012	−121.44	40.50	Y	Y	August	2006	1	2	LVNP
Cascades	Hot Springs	Stream	1707	−121.40	40.44	Y	Y	August	1991	2	4	LVNP
Cascades	Summit	Upland	2042	−121.42	40.49	ND	ND	July	1967	1	5	LVNP
Sierra	Babcock	Lake	2744	−119.40	37.76	Y	ND	August	1928	1	1	Russell 1928
Sierra	Benson	Lake	2311	−119.52	38.01	Y	ND	July	1992	1	3	This study
Sierra	Benson	Lake	2311	−119.52	38.01	Y	ND	Sept	1992	2	3	YNP
Sierra	Blue Canyon	Lake	3067	−119.66	38.30	Y	ND	ND	1963	ND	3	CDFW
Sierra	Buck	Lake	2537	−119.74	38.16	Y	Y	ND	1971	4	4	Schempf 1977
Sierra	Cathedral	Lake	2831	−119.42	37.84	Y	ND	August	1942	1	2	YNP
Sierra	Cathedral	Lake	2831	−119.42	37.84	Y	ND	June	1950	1	2	YNP
Sierra	Chain of Lakes	Lake	2733	−119.56	38.24	Y	ND	August	2005	2	2	This study
Sierra	Clear	Lake	2109	−119.94	38.13	Y	ND	ND	1965	ND	3	CDFW
Sierra	Crown	Lake	2886	−119.44	38.11	Y	Y	Summer	2009	1	4	This study
Sierra	Edith	Lake	1924	−119.75	38.06	Y	ND	June	1974	ND	3	Schempf 1977
Sierra	Edna	Lake	3095	−119.38	37.64	Y	ND	August	2006	1	1	YNP
Sierra	Edna	Lake	3095	−119.38	37.64	Y	ND	ND	2006	1	2	YNP
Sierra	Emeric	Lake	2846	−119.38	37.78	Y	ND	August	1975	1	4	YNP
Sierra	Evelyn	Lake	3150	−119.32	37.80	Y	ND	Sept	1974	ND	5	YNP
Sierra	Evelyn	Lake	3150	−119.32	37.80	Y	ND	Sept	1975	1	2	YNP
Sierra	Fraser	Lake	2815	−119.70	38.17	Y	Y	July	1999	3	2	This study
Sierra	Frog	Lake	2548	−119.71	38.14	Y	Y	ND	1972	ND	5	Schempf 1977
Sierra	Inferno	Lake	2419	−119.76	38.08	N	Y	June	2010	ND	2	This study
Sierra	Kuna	Lake	3288	−119.25	37.85	Y	ND	July	1972	ND	5	YNP
Sierra	Leighton	Lake	2523	−119.77	38.14	N	Y	ND	1963	ND	5	Schempf 1977
Sierra	Leighton	Lake	2523	−119.77	38.14	N	Y	June	2007	1	2	CDFW
Sierra	Little Bear	Lake	2298	−119.78	38.08	N	Y	August	1977	2	4	YNP
Sierra	Long	Lake	2653	−119.75	38.17	Y	Y	ND	1963	ND	5	Schempf 1977
Sierra	Lower Sardine	Lake	1757	−120.63	39.61	Y	ND	July	2009	5	1	This study
Sierra	Mahan	Lake	2379	−119.68	38.05	N	Y	June	1981	3	4	YNP
Sierra	Merced	Lake	2197	−119.41	37.74	Y	Y	July	2002	1	2	YNP
Sierra	Merced	Lake	2197	−119.41	37.74	Y	Y	July–Aug	2003	1	2	YNP
Sierra	Merced	Lake	2197	−119.41	37.74	Y	Y	June–July	2004	1	2	YNP
Sierra	Merced	Lake	2197	−119.41	37.74	Y	Y	July–Aug	2004	1	2	YNP
Sierra	Otter	Lake	2715	−119.65	38.09	Y	Y	Sept	1975	2	2	YNP
Sierra	Otter	Lake	2715	−119.65	38.09	Y	Y	August	1982	4	4	YNP
Sierra	Peninsula	Lake	2298	−119.68	38.10	N	Y	July	1992	3	2	YNP
Sierra	Peninsula	Lake	2298	−119.68	38.10	N	Y	July	2002	4	2	YNP
Sierra	Roosevelt	Lake	2217	−119.54	38.30	Y	Y	May	1999	1	3	This study
Sierra	Roosevelt[f]	Lake	2217	−119.54	38.30	Y	Y	July	2001	2	2	CDFW

APPENDIX. Continued.

Region	Site Name	Water body	Elev.	X[a]	Y[a]	Non-native[b]	Native[c]	Month	Year	# Otters	Score[d]	Source[e]
Sierra	Ruth	Lake	2987	−119.57	38.17	Y	Y	June	2001	1	2	CDFW
Sierra	Tilden[f]	Lake	2710	−119.60	38.10	Y	Y	July	1938	4	2	Whitney 1939
Sierra	Unknown	Lake	ND	ND	ND	ND	ND	ND	1927	ND	2	YNP
Sierra	Unknown	Lake	ND	ND	ND	ND	ND	Summer	1932	11	2	Borell 1933
Sierra	Unnamed[f]	Lake	ND	ND	ND	Y	ND	July	1938	ND	4	YNP
Sierra	Unnamed[f]	Lake	2972	−119.36	37.78	N	Y	July	1975	2	2	YNP
Sierra	Unnamed[f]	Lake	2263	−119.79	38.07	Y	Y	Summer	2007	5	1	This study
Sierra	Upper Lewis	Lake	2910	−119.72	38.22	Y	ND	August	2003	2	3	This study
Sierra	Vernon	Lake	2001	−119.72	38.01	Y	Y	June	1977	1	4	YNP
Sierra	Washburn	Lake	2319	−119.37	37.71	Y	ND	June	2003	1	2	YNP
Sierra	Washburn	Lake	2319	−119.37	37.71	Y	ND	Summer	2004	1	4	YNP
Sierra	Wilma	Lake	2420	−119.64	38.07	Y	Y	July	1951	3	4	YNP
Sierra	Wilma	Lake	2420	−119.64	38.07	Y	ND	April	1987	ND	2	YNP
Sierra	Cherry	Reservoir	1433	−119.91	38.00	Y	ND	January	2005	ND	2	YNP
Sierra	Eleanor[f]	Reservoir	1420	−119.88	37.97	Y	Y	ND	1927	ND	4	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	April	1957	ND	5	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	May	1974	ND	5	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	April	1977	1	4	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	June	1983	2	2	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	June	1986	ND	2	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	October	1986	ND	2	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	Sept	1987	2	4	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	Sept	1987	3	4	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	June	1989	1	4	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	April	1993	1	2	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	Summer	2005	3	2	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	Summer	2006	3	2	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	Summer	2007	3	2	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	July	2007	1	2	YNP
Sierra	Eleanor	Reservoir	1420	−119.88	37.97	Y	Y	Summer	2008	3	2	YNP
Sierra	Hetch Hetchy	Reservoir	1153	−119.79	37.94	Y	ND	April	1949	ND	2	YNP
Sierra	Hetch Hetchy	Reservoir	1153	−119.79	37.94	Y	ND	April	1997	1	2	YNP
Sierra	Hetch Hetchy	Reservoir	1153	−119.79	37.94	Y	ND	May	2005	1	3	YNP
Sierra	Pinecrest	Reservoir	1713	−119.98	38.20	Y	ND	ND	1979	4	4	Schempf 1977
Sierra	Poore[f]	Reservoir	2200	−119.53	38.31	Y	Y	August	1954	5	2	Laughlin 1955
Sierra	Sugar Pine	Reservoir	1100	−120.79	39.13	Y	ND	July	2006	3	1	This study
Sierra	Falls Creek	Stream	2329	−119.69	38.04	Y	ND	August	1977	2	2	YNP
Sierra	Falls Creek[f]	Stream	2346	−119.65	38.06	Y	ND	October	1979	2	1	YNP
Sierra	Falls Creek	Stream	2346	−119.65	38.06	Y	ND	July	1981	3	4	YNP

APPENDIX. Continued.

Region	Site Name	Water body	Elev.	X[a]	Y[a]	Non-native[b]	Native[c]	Month	Year	# Otters	Score[d]	Source[e]
Sierra	Grace Meadow	Stream	2542	−119.62	38.11	Y	ND	March	2001	ND	2	YNP
Sierra	Jack Main Cyn	Stream	ND	ND	ND	Y	ND	March	2003	2	2	YNP
Sierra	Kaweah, South Fk	Stream	1304	−118.74	36.35	Y	ND	March	1941	ND	5	Sumner and Dixon 1953
Sierra	Kaweah, South Fk	Stream	1304	−118.74	36.35	Y	ND	April	1941	ND	5	Sumner and Dixon 1953
Sierra	Kings	Stream	1524	−118.58	36.79	Y	ND	ND	1910	ND	5	Sumner and Dixon 1953
Sierra	Merced, Lyell Fk	Stream	2691	−119.29	37.85	Y	ND	June	1900	ND	5	YNP
Sierra	Merced, Lyell Fk	Stream	2716	−119.27	37.82	Y	ND	August	1971	ND	5	YNP
Sierra	Merced, Lyell Fk	Stream	2673	−119.30	37.87	Y	ND	July	1973	ND	5	YNP
Sierra	Simpson Meadow	Stream	1807	−118.63	36.97	Y	ND	ND	1910	ND	5	Sumner and Dixon 1953
Sierra	Tuolumne	Stream	2657	−119.33	37.88	Y	ND	June	1948	ND	6	YNP
Sierra	Virginia Canyon	Stream	2980	−119.34	38.06	Y	ND	October	1972	ND	5	YNP
Sierra	Vogelsang	Stream	3081	−119.35	37.78	Y	ND	August	1980	ND	5	YNP

[a] Coordinate system is WGS84.
[b] Nonnative prey present at location during time of River Otter observation.
[c] Native prey documented at location.
[d] Evidentiary category.
[e] Observation data source — CDFG: California Department of Fish and Game; LVNP: Lassen Volcanic National Park; USFS: US Forest Service; YNP: Yosemite National Park.
[f] River Otter foraging observation.