Ecological Engineering 107 (2017) 224–232

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Research Paper

Climbing above the competition: Innovative approaches and recommendations for improving Pacific Lamprey passage at fishways

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ARTICLE INFO

Keywords:
Entosphenus tridentatus
Pacific lamprey
Fish passage
PIT telemetry
Pool-weir
Culvert
Orifices
Delay
Entrainment
Behavior

ABSTRACT

We evaluated the behavior and capabilities of upstream migrating adult Pacific Lamprey using a series of experimental trials in relation to existing and novel fishway designs using Passive Integrated Transponder (PIT) telemetry. Five treatments were evaluated with PIT telemetry of 164 upstream migrating Pacific Lamprey. Experimental treatments included an existing pool and weir fishway, two in-situ modifications of the existing fishway and two treatments designed to provide lamprey-specific routes. The probability of passage success through trials (10 m distance and 1 m elevation gain over 1 night) was related to treatment. The existing pool and weir fishway provided the lowest predicted passage efficiency at 0.44 (95% CI 0.29–0.59), while tube and culvert treatments had perfect efficiencies. For individuals that successfully ascended trials, passage time was also related to treatment. Lampreys ascending the pool and weir structure had the longest predicted passage time at 5.2 h (95% CI 3.96–6.46) while individuals in the tube were the fastest, with a 20-fold reduction in migration time at 0.26 h (95% CI 0.21–0.30). Lamprey ranged from 52 to 66 cm TL, however length did not influence passage success or migration time. Over 200 h of night-time observations were used to improve our understanding of how lampreys pass barriers and where they encounter particular challenges. Our results and observations of lamprey migration behavior confirm that pool and weir fishways and design features common to other fishways types can pose a substantial obstacle to Pacific Lamprey migration. We provide a set of recommendations for behavioral considerations and design features, both beneficial and those that should be avoided at fishways. This study identifies a variety of solutions applicable to a range of obstacles that, if implemented, should significantly improve the opportunity for Pacific Lamprey to pass existing and future man-made structures.

1. Introduction

Anadromy allows fishes to exploit a wide range of resources, often over broad geographic ranges, but is coupled with a unique set of challenges. Along much of the western coast of North America the Pacific plates collide with the North American Plate, creating a rugged interface that drains steep coastal mountain ranges forming gateways between marine and freshwater habitats. Waterfalls, steep cascades and rapids are frequently encountered and provide a riverine architecture that has shaped the evolution of native anadromous fishes (Montgomery, 2000). Anadromous fishes that evolved within this environment have developed adaptive strategies for navigating obstacles to maximize access to upstream freshwater resources (Montgomery, 2000). Anadromous Pacific salmonids (*Oncorhynchus* spp.) are well known for their ability to ascend riverine obstacles by jumping, which facilitates passage beyond impediments and extends their distribution within drainages (Stuart, 2014; Yoshiyama et al., 2001). The proficiency of salmonids to jump has been a crucial component in engineering solutions that facilitate fish passage over man-made obstacles (Clay, 1994). However, the ability to jump is not universal among anadromous fishes.

Pacific Lamprey (*Entosphenus tridentatus*) are the most widely distributed anadromous fish in the Pacific Basin (Ruiz-Campos and Pister, 1995; Ruiz-Campos and Gonzalez-Guzman, 1996; Mecklenburg et al., 2002; Augerot, 2005; Orlov et al., 2008, 2009; Reid and Goodman, 2016a; Renaud, 2008, 2011; Abadía-Cardoso et al., 2016). They span the North Pacific Rim, with marine feeding grounds extending from as far north as the Bering Sea (63.5°N) to as far south as the Revillagigedo Archipelago off México (18.3°N) and the Naka River, Honshu, Japan (36.3°N). Freshwater spawning occurs in most rivers along the Eastern Pacific from the Aleutian Islands as far south as the Río Santo Domingo, Baja California (30.7°N) as well as down to Japan in the western Pacific.

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http://dx.doi.org/10.1016/j.ecoleng.2017.07.041
Received 28 January 2017; Received in revised form 21 July 2017; Accepted 29 July 2017
0925-8574/ Published by Elsevier B.V.

Although Pacific Lamprey lack the ability to jump, they are observed in rivers upstream of natural waterfalls that limit the distribution of even the most athletic of salmonids (Moser and Mesa, 2009; Goodman and Reid, 2012).

While the anadromous Pacific Lamprey is widely distributed and generally sympatric with anadromous salmonids, it takes a different, and arguably more successful, approach to navigating impediments to upstream migration. Pacific Lamprey have evolved the ability to climb, using their suctorial mouths, a rare capability among fishes, and documented in perhaps only one other species of lamprey, *Geotria australis* (Kemp et al., 2009; Reinhardt et al., 2008; Tweed, 1987; Zhu et al., 2011). They typically ascend subaerial, inclined and vertical wetted surfaces with an energetically efficient dyno-climbing behavior (derived from moutaineering terminology), attaching with their suctorial mouth, flexing their body in a waveform, then extending upward and reattaching by means of their mouth (Zhu et al., 2011). During climbing ascents, lampreys typically seek subaerial routes where lower velocities exist outside of primary flow, such as shallow flow or even splash zones, where they are partially or completely out of the water (Miller, 2012; Petersen-Lewis, 2009; Goodman and Reid, this paper). In natural settings, Pacific Lamprey are able to ascend even large obstacles like waterfalls (10 m vertical or greater), a skill which provides access to a range of habitats not accessible by jumping. However, their approach to passing obstacles requires smooth attachment points and rounded surfaces without acute angles, common in natural features, but not typically considered when designing artificial fishways (Keefer et al., 2010).

Globally, lampreys are a growing conservation concern, with over half of the species in the Northern Hemisphere classified as extinct, endangered or vulnerable in at least part of their range (Renaud, 1997). Pacific Lamprey are no exception, with populations declining and their distribution contracting, particularly in the southern extent of their range (Reid and Goodman, 2016a). Habitat loss due to the lack of access to historic habitats, caused by dams and other man-made barriers, has been identified as one of the greatest threats to Pacific Lamprey during their time in freshwater and has substantially curtailed their distribution (Goodman and Reid, 2012). Low passage success has been observed at dams and other man-made obstacles even where fishways exist, highlighting the need to consider lamprey-specific needs (Moser et al., 2002a; Jackson and Moser, 2012). Appropriate strategies and designs for lamprey passage, incorporating the unique climbing abilities of Pacific Lamprey, have only recently been considered (Moser et al., 2015).

Herein, we investigate behavior and performance of upstream migrating Pacific Lamprey at a series of experimental modifications to an existing fishway. We use Passive Integrated Transponder (PIT) telemetry to track the performance of individuals, coupled with observational studies to evaluate how lampreys approach passage within fishways. The scope of this assessment is limited to behavior of upstream migrating lampreys within fishways and does not evaluate other aspects of fishways that almost certainly affect lamprey migration (i.e. attraction efficiency, downstream migration, etc.). Results are discussed in the context of applying modifications to existing fishways and considerations for incorporating the needs of Pacific Lamprey into new designs.

2. Materials and methods

2.1. Study site

The Eel River in northern California was named after its historically abundant Pacific Lamprey run by European settlers who mistook the abundant lamprey for eels due to their anguilliform bodies. It flows from south to north, entering the Pacific Ocean 150 km south of the Oregon-California border and is the third largest drainage in the state, covering 9540 km^2. The river is known for its unstable geology and highly variable discharge (0.3–21,300 m^3/s; USGS gauge 11477000).

This study was conducted at Cape Horn Dam, located on the Eel River 240 km upstream of the estuary, near the town of Ukiah, California (lat. 39.3861°, long. −123.1164°,WGS84, 463 m). Cape Horn Dam was constructed in 1907 and facilitates one of California's first inter-basin water diversions. The dam is 19 m in height (measured from bedrock base) and is used to divert water from the Eel River into the Russian River through a 3 km long wooden tunnel. The primary uses of the diverted water are agriculture and power generation. Cape Horn Dam is 20 km downstream of the artificial limit to anadromy at Scott Dam, a 42 m high storage facility, which is used to regulate streamflow for the inter-basin diversion and blocks approximately 90 km of anadromous habitat (Venture Tech Network Oregon Inc., 1982).

All passage experiments and observations were conducted at a pool and weir fishway designed to aid salmon in passing Cape Horn Dam. The fishway was constructed in 1922 and was designed to provide upstream passage for Chinook Salmon (*O. tshawytscha*) and steelhead Rainbow Trout (*O. mykiss*). The primary passage features in the ladder are a series of 50 step pools, with each step approximately 25 cm tall and separated by pools of about 2 m in length and 1 m in depth within a mixed cement, bedrock and cobble channel. Steps are formed by wooden board weirs, held in place by vertical u-channels in concrete bulkhead walls.

2.2. Experimental trials

Passive Integrated Transponder (PIT) telemetry was used to evaluate Pacific Lamprey passage in relation to fishway design features. Custom PIT-tag interrogation antennas (hereafter, antenna) were constructed for the study using 3.8 cm diameter polyvinyl chloride (PVC) pipes, as described in Reid and Goodman (2016b) and Steinke et al. (2011). The antennas were 130 × 61 cm and sized to fit within channels separating fishway pools. Available lamprey passage routes in the study reaches all passed through antenna loops and were within 25 cm of antenna housing. Antennas were connected to a centralized multiplex radio-frequency identification transceiver that was run continuously during experimental trials (Biomark FS1001M-Mux).

Migrating Pacific Lampreys were netted while ascending the fishway entrance between April 5 and 7, 2016. Collections were made during a period when numerous lamprey were attempting to ascend the fishway and likely coincided with the peak of migration during that year. Glass encapsulated 12.5 mm PIT tags (Biomark FDX-B HPT12) were implanted to provide a unique identifier when individuals were detected by antennas. Tags were implanted in upstream migrating lampreys on the ventral mid-line below the first dorsal fin and anterior to the anus following Reid and Goodman (2016b). Lampreys that were sexually ripe were not tagged or included in the study due to potential impacts on their reproductive success. After tagging and before experimental trials, lampreys were held for at least 24 h. in perforated plastic barrels (120 l) immersed in the fishway's shaded raceway and transferred to the release site in the afternoon prior to the nocturnal test period where they were kept submerged in the same barrels prior to release. For release, the submerged lid was removed to allow volitional exit from the barrel." We evaluated tag effects on lamprey survival and tag retention in 50 individuals held for a 3-week period and found no mortality or tag loss. Individuals used in the tag retention study were not used in experimental trials discussed below.

We evaluated lamprey performance in five treatments including the existing fishway and four modifications intended to improve lamprey passage (Fig. 1).

1. Pool and weir (Control) – Each board weir raised the water surface elevation approximately 25 cm. Boards were standard dimensional wood (6.5 wide by 130 cm long) with square edges and were held in place by steel u-channels (5 cm deep by 7.6 cm wide). This

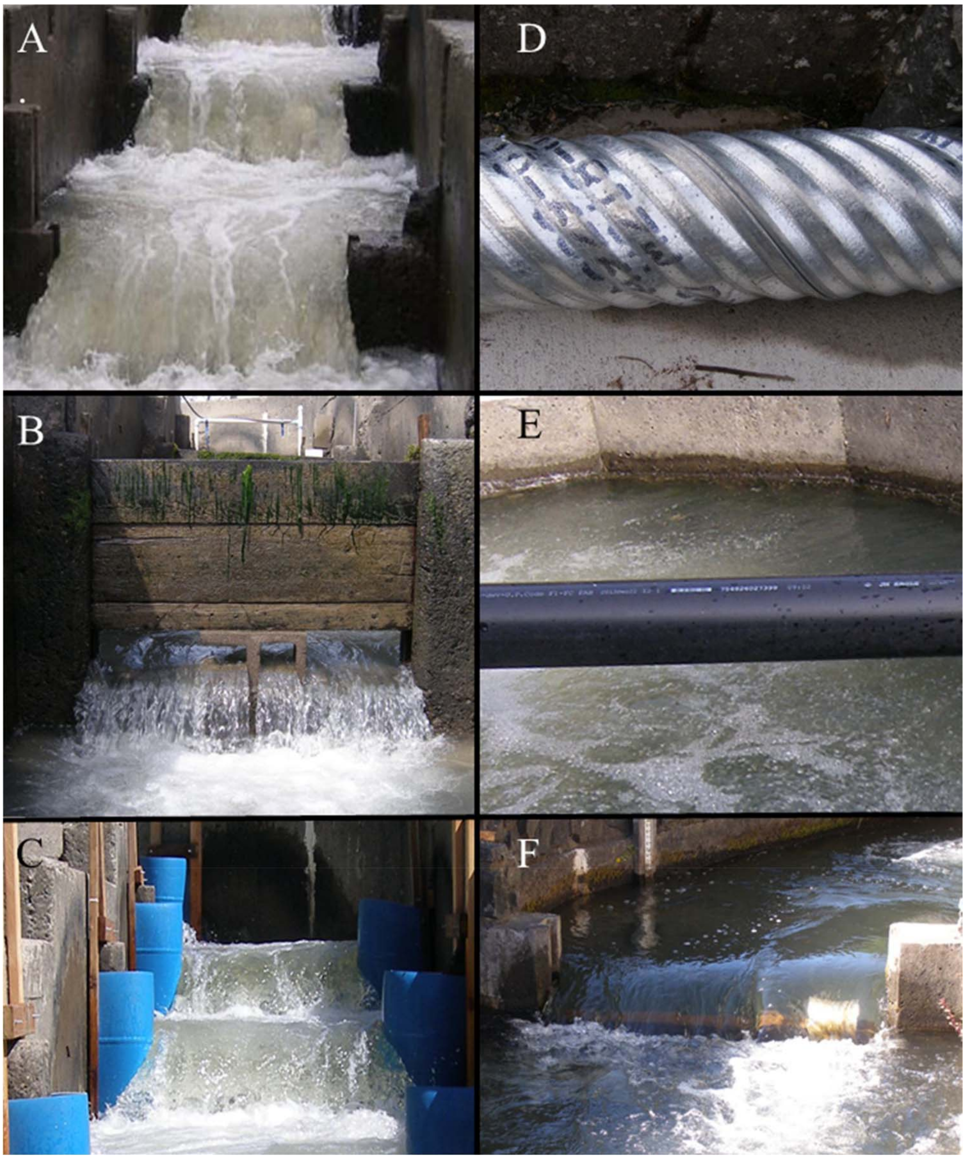

Fig. 1. Experimental treatments tested for passage performance. A indicates Control, B Gap, C Bulkhead, D Culvert, E Tube, F Inverted U. The Gap treatment is shown while the ladder water level has been dropped in order to show the modification that would otherwise be underwater. Image scale varies by treatment and weir boards are 130 cm (A,B,C and F), Culvert (D) is 16.5 cm diameter and Tube (E) is 10 cm diameter.

represents the existing conditions at the fishway. Velocities over the weirs varied from 0.92 to 1.18 m/sec and water depths from 20 to 24 cm in the test reach.

2. Bottom gap (Gap) – Boards were raised off the bottom of the fishway by 10 cm to create a passage corridor for lampreys to travel along the bottom. Each weir had a single flat concrete step rising 15 cm above the downstream pool floor and beginning approximately 10 cm downstream of the weir boards. Velocities through the bottom gaps ranged from 1.74 to 2.25 m/sec in the test reach.
3. Rounded bulkhead (Bulkhead) – A smooth, semi-rigid plastic sheet (0.65 cm thick) was wrapped around weir bulkheads and fit over weir boards that separated each pool, covering vertical angular edges and u-channels to provide a rounded, continuous surface intended to facilitate climbing around bulkheads either while submerged or along the water surface. Velocities ranged from 1.03 to 1.33 m/sec and water depth ranged from 21 to 24 cm over the board between the bulkheads. During the development of the bulkhead setup, lampreys often moved into gaps between bulkhead walls and the plastic wraps and then held. Before trials, we modified the design by filling gaps to eliminate holding areas.
4. Culvert – 16.5 cm diameter galvanized culvert, with spiral corrugations of 0.6 cm amplitude and 3.8 cm wavelength. Water depth in the culvert was about 1 cm and flow rate was about 13 l/min.
5. Tube – 10 cm inner diameter rigid, black Acrylonitrile Butadiene Styrene (ABS, Schedule 40) pipe. Water depth in the pipe was about 1 cm and flow rate was about 13 l/min.

We executed experimental trials to compare lamprey passage performance among treatments. All trials were conducted in a 10 m section of the fishway that gained 1 m in elevation over 10 m length. We established antennas at the upstream and downstream of the test section and no alternate routes were available for lampreys to ascend this section of the ladder (Fig. 2). Each trail was initiated at dusk and terminated the following morning at sunrise. Trials of Control, Gap and Bulkhead treatments were executed sequentially (one trial per night) in a single section of the fishway and included a series of four weirs and pools. These trails were executed by placing 50 fish into the pool immediately downstream of the test section. Culvert and Tube treatments were tested sequentially, each tested by placing 31 fish within an immersed 10 cm inner diameter flexible polyvinyl chloride tube immediately downstream of the first antenna and restricted from migrating downstream by a net. In all trials, lampreys were provided a holding area downstream of the lowest antenna and volitional access to the test section. To participate in the experiment, tagged lampreys were

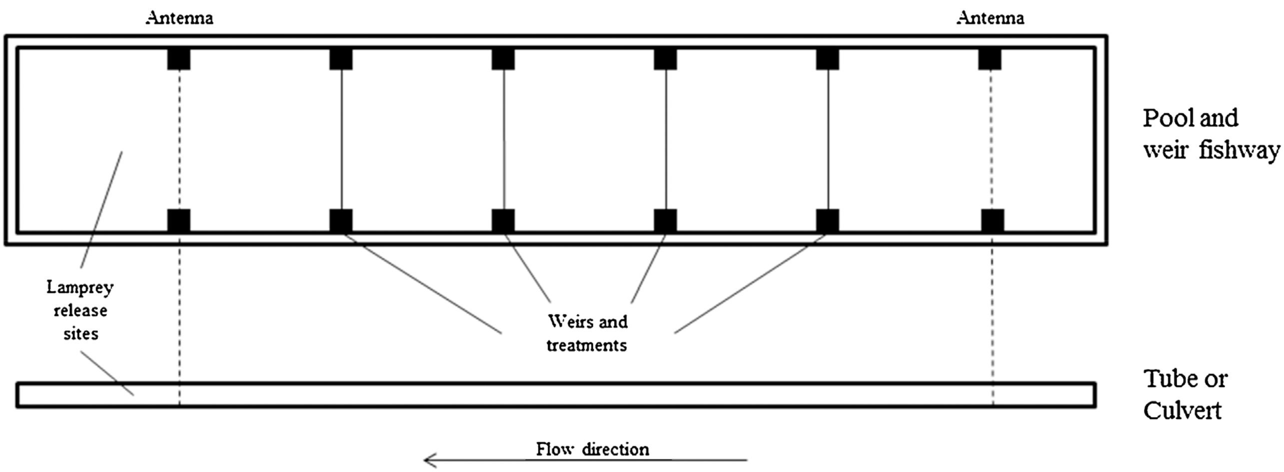

Fig. 2. Plan view of the experimental fishway treatments used to test Pacific Lamprey passage performance. Pool and weir fishway treatments included Control, Gap, Bulkhead.

required to migrate from their release site past the downstream antenna. Lampreys that did not pass the downstream antenna were not included in the analysis. All trials were conducted between April 6 and 10, 2016. Over the study period, streamflow was a consistent 0.31 m^3/s within the fishway, and the daily mean water temperature ranged from 10.0 to 10.2 °C (California Data Exchange Center Station ID ELP).

Performance was evaluated as 1) the probability of successful passage once a lamprey entered past the lower antenna (passage success), and 2) the time necessary to pass through an experimental treatment (migration time). An individual was considered to successfully pass a treatment if it was detected at the lower antenna and the upper antenna within the same trial (one night). We considered passage times greater than one night to be unsuccessful due to the excessive migration delay that would result from passing dams such as Cape Horn Dam. An initial exploration of the probability of passage success as a function of treatment type revealed that all lampreys successfully ascended the Tube and Culvert treatments. Therefore analysis of passage success was limited to Control, Bulkhead and Gap fishway treatments. The analysis of passage success by treatment type and lamprey length was investigated using a binomial general linear model (GLM) with a logit link function (Zuur et al., 2009). For individuals that were successful in passing a treatment type, migration time was calculated as the time of the first detection at the upper antennal minus the time of the last detection at the lower antenna. For fish that successfully ascended a treatment, we evaluated the effect of treatment and lamprey length on migration time. Initial data exploration identified a positively skewed distribution supporting the use of GLM with a gamma distribution and inverse link function (Zuur et al., 2009). All statistical modeling was conducted in R (R Core Team, 2015).

Not all fish released below study section attempted to move upstream, these individuals were considered non-participants and were not included in analyses. However, they were used to assess overall behavior within the fishway. To avoid potential bias in our analyses associated with repeat migrations, analyses were limited to initial ascents of a test section in the first test period by each individual.

2.3. Behavioral observations

Extensive qualitative observations were made by the authors during the development and execution of experimental trials, representing over 200 night-time hours viewing lamprey migration behavior at the facility, as well as many hours along the fishway in daytime. Observations of lamprey behavior were used in the development of the treatments, as well as interpretation of results in relation to behavior when navigating obstacles. These observations, while not all were quantified, are of considerable interest and valuable for the purpose of designing fishways that incorporate both behavior and capabilities in their design. A compilation of these observations is presented in the Results section.

2.3.1. Inverted U

Vertical inverted u-shaped fittings (Inverted U) were installed on all weirs in the fishway prior to the development of the treatments reported here. The stainless steel fittings were 15 cm wide, with a 21 cm diameter (10 cm radius curvature) and were placed over weir boards, extending down into the water on upstream and downstream sides of the weirs (Fig. 1). While lampreys used them in the absence of other modifications, our observations deemed them of limited benefit at improving passage in their initial configuration. For that reason, they were not formally tested, although we frequently observed their use by lampreys during general activities along the fishway outside the test reach.

2.3.2. Burst-swimming

We estimated burst swimming success at a single un-modified weir where lampreys appeared to have considerable difficulty passing. Burst swimming was monitored by a single observer with an unobstructed view positioned 1 m directly above the weir. All observations were made on 11 May 2016 with a daily mean water temperature of 13.4 °C. We tallied the first 100 burst-swim attempts or lampreys attempting to ascend from one pool to the next and reached at least to the top of the board weir. Of these attempts those that passed into the upstream pool were considered successful and those that were swept downstream, a failure. At this weir, the water column velocity was 1 m/s (1.5–1.9 BL/s), and depth of the overflow was 15 cm with a 15 cm drop between the top of the weir and pool below. The horizontal distance of flow path from the surface of the lower pool to a position where a lamprey could swim down into the upper pool was approximately 1.5 m.

3. Results

3.1. Experimental trials

A total of 164 individuals participated in experimental trials. Participation was 82% for Control, 64% for Gaps, 58% for Bulkhead and 100% for both Culvert and Tube. Length of lampreys that participated in the experiments ranged from 52 to 66 cm TL (mean = 59.43) and did not vary among treatment types (AOV, $P > 0.426$).

The probability of lampreys successfully passing a trial varied by treatment type, but not an individual's length (Table 1). All individuals challenged in the Tube and Culvert treatments participated and were successful in passing their respective trials (Fig. 3). The probability for

Table 1
Explanitory variable parameter estimates for the final GLM model predicting probability of passage success by treatment and lamprey length. Estimates are in logit-link scale. ** indicates strong evidence for parameter effect.

Parameter	Estimate	SE	z value	Pr(> |z|)	
Control	0.864	4.400	0.196	0.844	
Gap	0.236	0.475	0.497	0.619	
Bulkhead	1.403	0.539	2.603	0.009	**
Length	−0.019	0.074	−0.253	0.801	

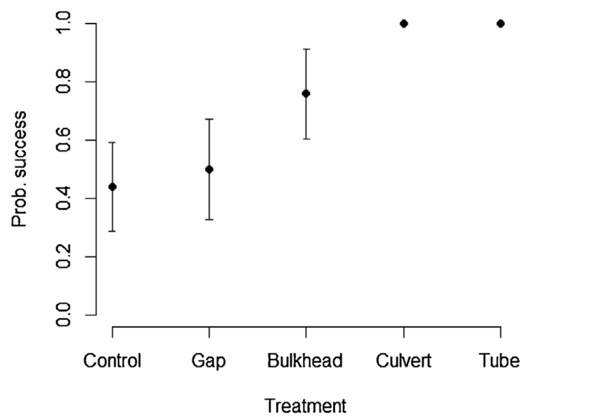

Fig. 3. Migration success and predicted probability of migration success of Pacific Lamprey ascending experimental trials by treatment. Lampreys participating in the Culvert and Tube treatments had perfect passage success and therefore the values are not predicted. Error bars indicate 95% confidence intervals for Control, Gap and Bulkhead treatments.

successful passage of the Bulkhead modification was 0.76 (95% confidence interval [CI]: 0.92–0.60) and significantly greater than Control which had a passage probability of 0.43 (95% CI: 0.29–0.59). We found no significant difference between the Control and Gap treatments ($P = 0.619$). Lamprey length did not have a significant effect on passage success ($P = 0.801$).

Similar to the probability of passage success, we found evidence for the influence of treatment on migration time and no evidence for an effect of lamprey length (Table 2). We found overwhelming evidence supporting that all treatments reduced migration time over the Control treatment (Fig. 4). Tube had the shortest predicted migration time, with lampreys ascending the treatment in under 0.26 h. (95% CI: 0.21–0.30), a 20 fold improvement over Control estimated at 5.24 h. (95% CI: 3.97–6.50). Lamprey length did not have a significant effect on migration time ($P = 0.585$).

Some 67% of tagged individuals moved downstream and out of the fishway after being released and were not documented re-entering the fishway. Some had participated in the tests and failed, others never attempted the test, and others had successfully passed the test reach but had encountered difficulty passing an upstream weir or challenge (e.g. barrier nets used in other projects).

Table 2
Explanitory variable parameter estimates for final GLM model predicting migration time by treatement and lamprey length. Estimates are in the inverse-link scale. *** indicates overwhelming evidence for parameter effect.** indicates strong evidence for parameter effect.

Parameter	Estimate	SE	z value	Pr(> |z|)	
Control	0.433	0.442	0.980	0.329	
Gap	0.215	0.058	3.697	< 0.001	***
Bulkhead	0.835	0.116	7.204	< 0.001	***
Culvert	1.857	0.192	9.653	< 0.001	***
Tube	3.724	0.366	10.173	< 0.001	***
Length	−0.004	0.007	−0.548	0.585	

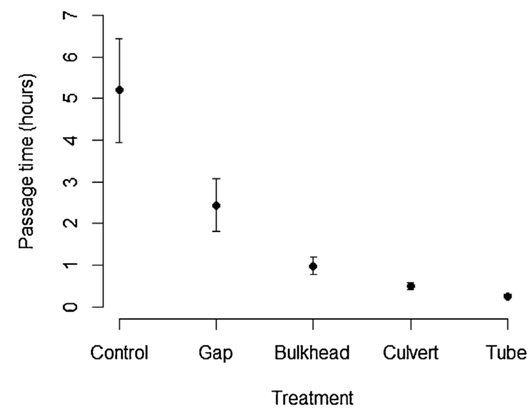

Fig. 4. Predicted passage times of Pacific Lamprey ascending experimental trials by treatment. Error bars indicate 95% confidence intervals.

3.2. Behavioral observations

3.2.1. Inverted-U

Observations of lampreys using the Inverted U were made during general activities along the ladder, when the authors were walking along the fishway and would incidentally note a lamprey trying to pass the weir using the Inverted U. The Inverted U fittings had been placed in high velocity flow regions toward the center of the weir to avoid interference with the vertical u-channels, but this presented a number of challenges. Lampreys had difficulties finding the ramps in the high flows and spent considerable time searching. Also, once on the Inverted U fittings, individuals often moved to the edge, where they lost suction, or were swept off the side of the vertical ramps by currents, causing them to fall back to the previous pool. The radius of curvature (10 cm) of the Inverted Us also appears to be problematic based on our observations. Once an individual's head had passed the apex, the propulsive force vector of the tail and body (upward) was opposite the desired swim direction of the head (downward), greatly reducing their ability to pass the velocity barrier and reach calm water upstream and below the top of the weir.

3.2.2. Burst-swimming

Lampreys sometimes attempted to burst-swim upstream through the flow coming over weirs. Of the 100 burst-swim attempts that were specifically observed and quantified, 95% failed to make the ascent into the next pool. This failure rate is conservative, since we did not include individuals who failed to reach even to the weir board while in mid-water and also excluded individuals attached to the board weir that tried to start a swim from a hanging position but were swept downstream as soon as they entered the flow. No successful attempts were observed by lamprey starting a burst-swim attempt when initially attached to the top of the board weir. Burst swimming was used in what appeared to be a last resort when a weir was difficult to pass.

3.2.3. Activity patterns

Lampreys were primarily active at night. While antennas were monitored we observed 74% of 10,017 PIT tag detections from sunset to sunrise (20:00 and 06:00). Although some individuals were observed in the daytime, this was primarily at weir steps where there was no structural cover in the pool. During the day lampreys in the fishway sought out structural cover (e.g. cracks, gravel, overhangs) and also used net-traps and pens in the fishway for other objects as cover, moving in and out through apertures. In the absence of cover, lampreys huddled together or balled up in low-energy corners or under the weir overflow.

When climbing, lampreys were generally not notably disturbed by the presence of observers or lighting (i.e. flashlights, overhead lighting). During collecting by hand or dipnet from the weirs and bulkhead walls, lampreys did not immediately drop off when disturbed, but if there was considerable jostling of the attached lampreys or a few of them had been removed, climbing activity would often stop at that location for about 5 min before resuming. Lampreys tended to climb in areas where other lampreys were concentrated and followed routes that had been successfully followed by preceding individuals.

3.2.4. Climbing

Lampreys typically climbed to pass obstructions in moderate and high velocity areas where swimming was not effective (see Burst Swimming above). In the fishway, this involved moving around or over bulkhead walls, typically partially or completely out of water, or up vertical wooden weir walls. Lampreys also used climbing behavior to move up inclined tubes and culverts, which contained only partial flow (about 1 cm deep). Angular surfaces, such as 90° wall edges, metal lips or vertical u-channels were very difficult to pass, as were dry surfaces, all of which broke or limited suction. When climbing vertically on wooden walls, progress was blocked by jets at horizontal cracks between boards, where suction was lost and the force of the jet prevented the lamprey from moving its head past the crack. Within about 2/3′s body length of the water surface, lampreys were able to swim upward on a vertical surface to reach a suitable attachment surface. Once out of the water, climbing required consistent reattachment surfaces, or the lamprey would drop back. Climbing progress appeared to be most effective along a straight path that avoided orthogonal propulsion vectors, where posterior body movements were propelling the body in a different direction than the head, such as encountered at the apex of the Inverted U or going over the top of a wall.

3.2.5. Exploratory behavior

Lampreys varied their behavior in response to passage challenges, seeking alternate routes over or around a barrier. At a difficult weir, individual lampreys would be observed trying to climb past the bulkhead wall, dropping off and seeking different paths over the same weir when they encountered difficulties. Individuals who had passed a section of the fishway but encountered a barrier (e.g. especially difficult step or one of the net-traps used in other projects) usually dropped back down the fishway, sometimes making multiple trips up the same reach. In some instances, tagged lampreys that had failed a particular experimental test reach or had dropped entirely out of the fishway were encountered in the fishway after the completion of trials. At a particular step, downstream of the test section, that typically overflowed slightly out of the ladder when a large intermediate pool backed up, lampreys followed overland paths directly over the wet bedrock/concrete to pass weirs before reentering the fishway further upstream.

3.2.6. Impingement and entrainment

Pacific Lamprey were found, often dead, stuck in gaps, cracks and holes in boards where high velocity downstream flow had sucked them in, but where their body didn't fit through, had become lodged sideways, or was wrapped in other trapped debris. The high velocities near the holes exceeded their ability to burst-swim out of the zone of entrainment. These localized velocity features often occurred where the lampreys, on passing a weir, would swim towards the bottom expecting a low-velocity refuge on the upstream side of the weir or would engage in midwater searching behavior along the upstream weir face in otherwise relatively calm water. Similarly, at weirs with bottom gaps (experimental treatment, or caused by unseated boards, eroded bottom, or stuck debris) lampreys which passed over a weir and swam to the bottom appeared to be entrained by high-velocity, near-bottom flows that sucked them downstream before they could attach to the bottom and hold position. Even larger gaps, which lamprey might have passed, often contained enough entrained debris (e.g. sticks and rocks) that lamprey became entangled and could not extricate themselves in the high velocities. Similarly, during near-surface searching behavior within a pool, individuals that approached the outflow were often swept back over the downstream weir, negating their previous efforts to enter the pool.

4. Discussion

Problems with traditional weir and pool fishways − Our results support a growing body of literature indicating that fishways can be a substantial obstacle for upstream migration of adult lampreys (Moser et al., 2002a; Keefer et al., 2009; Foulds and Lucas, 2013). The weir and pool fishway was designed specifically to facilitate adult salmonid passage, as are most fishways in the Northwest, and Pacific Lamprey were not considered in its design. Lamprey passage efficiency has been found to vary within and among fishways and likely relate to with site-specific operations or design features (Keefer et al., 2013). Therefore the findings of our control (weir and pool) treatment may not be directly applicable to other fishways. However, several features common in fishways create difficulties for Pacific Lamprey attempting to ascend. These include high midwater velocities over the weirs, u-channels, acute angles and edges on potential climbing attachment surfaces, as well as gaps and orifices creating narrow high velocity jets that either form velocity barriers or entrain lampreys, transporting them further downstream.

Design flow velocities over weirs are typically higher than critical swimming speeds for lamprey (U_{crit} 0.86 m/s; Mesa et al., 2003), preventing them from using swimming as a viable approach to moving through most fishways. This is strongly supported by our estimation of 95% failed attempts to burst swim past a single weir at flow velocities of 1 m/s. This result is likely related to a combination of factors besides strict velocity, including complex turbulence at weir drops, extended swim path (ca. 1.5 m), and relatively low temperatures (ca. 10 °C) during observations. Kirk et al. (2016) found Pacific Lamprey successfully passed a single experimental weir (0.33–1.0 m length) without attachment at 1.2 m/s. They do not provide water temperatures. However, others have found that swimming performance and passage probabilities increased substantially at higher temperatures (Keefer et al., 2013). Regardless, the study fishway has fifty similar weirs to pass, and even were velocities somewhat lower than U_{crit}, they would likely represent a major challenge. When lampreys attempted to climb around existing weirs, they typically encountered sharp corners on concrete bulkheads or weir boards, angular vertical U-channels, and dry surfaces, all of which impede attachment and the use of climbing behavior (Moser and Mesa, 2009). In our experimental trials, less than half of the tested lampreys passed the 5-weir unmodified control treatment within one night, and those that did took over 5 h to do so. The test section represents approximately 1/15th of the total elevation change to pass the dam, which likely acts as a substantial filter preventing lamprey from reaching upstream habitats, although some do, based on Pacific Lamprey ammocoete populations above the dam (Keefer et al., 2009).

Passage capabilities of Pacific Lamprey may vary throughout a migration season, dependent on temperature, a factor which was not assessed in this study. Passage efficiency of Pacific Lamprey has been shown to vary with water temperature at Bonneville Dam on the Columbia River, with peak performance at higher water temperatures (15–18° C), well above those evaluated in this study (Keefer et al., 2013). This indicates that passage at Cape Horn Dam may improve later in the migration season, a factor that should be evaluated in future studies of the facility. Regardless, the passage efficiency estimates from this study are applicable to a time of peak lamprey migration at Cape Horn Dam, and we would recommend that designs accommodate lampreys throughout the expected range of temperatures encountered during a migration season.

All experimental treatments formally evaluated in this study outperformed the Control in one or both passage metrics. The Tube outperformed all other treatments, with perfect passage success and a 20-fold reduction in migration time when compared to the unmodified weirs. Other studies have documented successful improvement in passage with lamprey specific fishways (e.g. Moser et al., 2011) however; our study represents the first use of smooth round-section tubing for the passage of Pacific Lamprey with broad applicability to improve passage at a wide range of man-made obstacles or fishways. Our experimental treatments included a 10 m tube with 10% slope. Future studies are planned to expand our understanding of the applicability of this treatment, including the effect of tube length, tube diameter and slope on the performance metrics. Benefits of this treatment for implementing passage at fishways include the use of materials that are readily available, low cost, and applicable to a variety of structure types. By providing a lamprey specific passage route, this treatment has minimal impact to the function and hydraulics of existing structures or hydrodynamic design criteria for new fishways. Assessments of approaches for guiding lamprey from the river into the tube are planned and critical to the successful implementation of this design.

The Culvert also performed well in our tests and have similar advantages to the straight tubes. This represents the first formal evaluation of lamprey passage performance within a culvert. Culverts can be fish passage impediments and reduce connectivity of riverine fish communities (Favaro et al., 2014) and have been considered a potential threat to Pacific Lamprey that could interrupt or block access to upstream habitats (Moser and Mesa, 2009). Our results demonstrate that lampreys can ascend corrugated culverts during low flow conditions by climbing, as demonstrated by perfect passage success in our experimental trials. Corrugation design has been hypothesized to create difficulties for climbing Pacific Lamprey, with shorter wave length corrugations suggested to challenge lampreys due to the tighter corrugation curves and limitations in oral disk flexibility and/or attachment capabilities (Moser and Mesa, 2009; Stillwater Sciences, 2014). In this study, the tested corrugation amplitude and width were less than that in culverts typically used in larger streams suitable for Pacific Lamprey (Taylor and Love, 2003). Nevertheless, we saw no evidence for a corrugation effect on passage success. We did observe a significant increase in migration time in comparison to the Tube, suggesting that corrugations somewhat increase migration time, which may be due to reduced climbing attachment efficiency or increased turbulence. However, it is also possible that some of the increased transit time may be due to a simple function of longer travel distance over the corrugations versus along a straight, smooth path in the Tube. In our case, the surface distance following the corrugations would be about 18% longer than a straight line smooth surface. Regardless, migration time in Culvert was still a substantial improvement over all other treatments, except Tube, and had 100% success rate. Furthermore, our results are likely a conservative estimate of corrugation effect, since culverts in most perennial streams within the distribution of Pacific Lamprey would have larger corrugation widths and broader curves (Stillwater Sciences, 2014).

Our results suggest lampreys can readily ascend corrugated culverts under low-flow conditions; however instream applications may still be obstacles to lamprey migration. At typical culvert installations, entrance conditions at the mouth of a culvert may have a substantial influence on lamprey passage success, particularly when the entry is perched and requires the ability to jump to enter the culvert. In addition, baffles are commonly installed as a low cost measure to improve fish passage at culverts; many include sharp angled structures installed along the bottom intended to diffuse velocities (Favaro et al., 2014), but may be an additional challenge for lampreys. The effect of higher streamflows, gradient and baffle designs on lamprey passage have not been assessed and should be further evaluated to elucidate the potential influence of culverts on lamprey distribution.

Bulkhead was the top performing within-fishway treatment tested in this study and outperformed the Control in both passage success and migration time metrics. This treatment was designed to provide a continuous, wetted attachment surface for climbing around weirs at or above the water surface. The benefit of the design is corroborated by previous studies that improved passage efficiencies by rounding bulkheads and orifice entries (Moser et al., 2002b; Keefer et al., 2010). If implemented as a design feature in new construction, designs could easily be altered to meet target velocities for midwater fishes.

Gap outperformed Control for migration time but not passage success and was the poorest performing modification evaluated. The design was intended to promote burst-attach movement along the bottom under the weir boards. Burst-attach swim mode which is used by lampreys in higher velocities (above approximately 0.6 m/s) involves attachment to the surface followed by short burst-swimming to advance incrementally upstream against the flow (Keefer et al., 2010). However, water velocities near the bottom gaps (1.74–2.25 m/sec) reached levels that have been shown to increase attached holding behavior and approached velocities found to be a limit for burst-attach movement (2.5–3.0 m/s; Keefer et al., 2009; Kirk et al., 2016). The vertical step just downstream of each weir-bottom gap may have added to the challenge for lampreys attempting to ascend this modification; however the step was rounded, extended 15 cm below the weir, extended lateral beyond the high velocity area and did provide an opportunity for attachment prior to the primary velocity challenge. Even when passable, high velocity pathways requiring burst-attach swimming may extract a high energetic cost to the individual, particularly when encountered repetitively in a fishway. The high velocities through the bottom gaps also eliminated resting areas at the bottom of pools between weirs and apparently entrained lampreys that had successfully entered the upstream pool, flushing them back downstream.

Previous studies have suggested that Pacific Lamprey passage capabilities are related to body length. Keefer et al. (2009) observed smaller Pacific Lamprey to have shorter migration distances and ascend fewer fishways during their migration up the Columbia River. They suggested that passage capabilities might be related to length. However, in experimental assessments, our study and the results of Kirk et al. (2016) found no support for an effect of body size on the ability of lampreys to ascend obstacles. Therefore, we suggest the findings of Keefer et al. (2009) can be explained by other factors, such as size-dependent energy reserves limiting long-distance migrations or maturation state (Kirk et al., 2016).

4.1. Recommendations

Successful design of passage facilities for Pacific Lamprey will ultimately include consideration of the behavior of the species, as well as its physical capabilities, and the needs of other species that use the fishway. Every facility will have its unique constraints and characteristics. Many fish passage facilities are already established along migration routes used by Pacific Lamprey. Unfortunately, many are actually unintended barriers to lamprey passage. In our experience, a crucial component of early design planning for retrofitting existing structures should be observation of lampreys attempting to use the existing facility: their timing, abundance, holding areas, and existing pathways (successful and unsuccessful), as well as an assessment of existing design or structural features which impede passage or may cause lamprey mortality. Based on the results of this study and experience gained during on-site observations, we provide the following considerations for designing or modifying fishways to improve passage success and migration time for Pacific Lamprey:

4.1.1. Behavioral considerations

- Preferred locomotion in low velocity water (< 0.6 m/s) is efficient anguilliform swimming, typically near the bottom where velocities are lowest (Reid and Goodman, 2016a, 2016b). A roughened bottom thickens the boundary flow region and decreases velocities.
- Preferred locomotion to pass high velocities or physical barriers is either 1) burst-attach swimming along a wall at, or just above, the surface, where water drag is substantially lower, or 2) subaerial

climbing to pass around barriers.

- In unavoidable high-velocity flows, when a smooth surface is available (e.g. along the bottom or on a wall), Pacific Lamprey will use a burst-attach locomotion mode to move forward. However, this behavior is strenuous and only feasible for short distances. It is typically initiated at velocities over 0.6 m/s and becomes substantially less effective at higher velocities (2.4–3.0 m/s) and under turbulent conditions (Keefer et al., 2010; Kirk et al., 2016).
- Upon passing a barrier, lampreys typically swim down into deeper, presumably calmer water.
- Activity is primarily nocturnal, with lampreys seeking cover during day-time. Therefore, they may not be seen during day, under-representing actual activity at a fishway.
- When presented with a passage challenge, searching behavior allows lampreys to locate pathways without high attraction flows. We observed Pacific Lamprey exhibiting considerable exploratory behavior, both locally within a pool and broadly in the fishway, often heading back downstream when a difficult challenge was encountered. Similar searching behavior has been noted at the large Columbia River dams when approaching obstacles to migration (Kirk and Caudill, 2016).

4.1.2. Preferred design features

- Midwater velocities under 0.6 m/s, preferably with near-bottom velocities approaching zero or under 0.1 m/s. Near-bottom velocities can be reduced by increasing surface roughness, while still allowing attachment surfaces.
- Smooth, wetted surfaces, with shallow flow or spray zones that provide wet climbing attachment surfaces, allowing lampreys to climb around velocity barriers.
- Large radius curves at corners (≥10 cm) to provide a continuous surface for reattaching during climbing without angular features.
- Extended platform space beyond corners (horizontal or vertical) to avoid conflicting direction of body propulsion. Once an individual's head has passed a curve, the propulsive force vector of the tail and body (upward) is no longer aligned with the head direction, making climbing more difficult. Continuing the horizontal platform above a climb out at about 90° to a full body length (ca. 60 cm) allows the lamprey to align its body before redirecting itself into the subsequent pool.
- In proximity to high velocity areas, the edges of climbing surfaces should incorporate a low fence to keep lampreys from inadvertently falling off. Climbing often involves lateral searching as well as vertical climbing and the climb path is inherently irregular, with reattachment points off the center-line of movement.
- In consideration to inherently different approaches that lampreys use to pass physical and velocity barriers, it is worth considering a dedicated pathway for lampreys that avoids the need to adapt existing fishway features designed for other fishes. Such a route can often be established at relatively low cost and has the benefit of specifically meeting the needs of lampreys. A separate pathway can also more easily incorporate lamprey-oriented monitoring equipment.
- If a separate pathway is established for lampreys, it may be worthwhile to adapt the entry of the fishway to prevent entry by lamprey, avoiding wasted energetic cost expended in attempting to pass or explore the main fishway. This will ultimately reduce the time spent by lampreys searching for a more suitable pathway.

4.1.3. Design features to avoid

- Gaps and orifices, either in or along bottom of weir, which can entrain and trap lampreys with high velocity near-field flows. Gaps can also entrain debris which reduces aperture size and can entangle entrained lampreys, preventing them from passing downstream.
- Sharp corners and edges that break suction, force lampreys off the climbing surface or prevent reattachment. This includes u-channels used for retaining weir boards and angular lips on walls.
- Grates or porous surfaces that prevent suction attachment.
- Gaps and orifices, either in or along bottom of weirs that produce high velocity pathways requiring extended burst-attach swimming. These can cause extended attachment times or approach the limits of burst-attach capabilities, while increasing energy expenditures.
- High velocity corridors without alternative routes suitable for lamprey passage.
- It is important to note that a single feature that prevents passage at any point along the pathway can render a fishway ineffective for lamprey. This can be as minor as a single 1 m reach exceeding 1 m/s without attachment points, a U-channel imbedded in the wall and bottom in higher velocity, or a 2 cm angle-iron lip at the top of a climbing surface.
- Fishway designs should promote through-passage by lampreys by minimizing areas suitable for holding (e.g. complex cover, burrowing substrate and off-channel refuges). Adult Pacific Lamprey have been observed holding and even over-summering in the Cape Horn fishway. Onsite fishway management staff also observe adult Pacific Lamprey emerging from fishway pools annually during late summer fishway dewatering and maintenance. Sometimes individuals do not appear until several days after lowering water levels and typically in locations where sand and gravels accumulate or where cracks in the concrete exist (S. Harris, California Department of Fish and Wildlife, personal communications). Apparently, these individuals are over-summering to spawn the following spring, as they are observed outside of the typical spring migration period.

4.2. Conclusions

Anthropogenic barriers that restrict upstream movement has been recognized as one of the primary threats to migratory lamprey populations worldwide. Improving connectivity to reaches above barriers returns lampreys to their historical range and increases available spawning and rearing habitat. It can also improve population resilience though access to the broader riverscape, including greater dispersion of spawning and rearing areas, increased diversity of habitat, improved water quality conditions and typically cooler temperatures at higher elevations and varied aquatic species assemblages (Fausch et al., 2002). The return of lampreys to upstream reaches also reestablishes their lost ecological roles, including as sediment engineers, bioturbators, filter feeders, cyclers of primary productivity, prey and transporters of marine nutrients (Close et al., 2002). However, the majority of existing fishways, which are generally designed for other species, perform poorly for lamprey. Incorporation of the needs of lamprey into existing and future fishways will alleviate this threat and help ensure the long-term survival of these species. The lamprey behaviors, passage performance at design elements, and recommendations to improve upstream passage at barriers developed in this study are directly applicable to other locations and other fishway types. Although not all lampreys share the climbing ability of Pacific Lamprey, many of the issues addressed here can be applied to other at-risk migratory lampreys as well.

Acknowledgements

Many individuals contributed to the success of this project. In particular, we would like to thank Scott J. Harris from California Department of Fish and Wildlife on the ground support of this project and Pacific Gas and Electric Company for use of the experimental facility. Kurt Steinke of U.S. Fish and Wildlife Service was instrumental in assisting with the constructing the telemetry antennas. Jen Edgar and Amanda Ekstrand from California Department of Fish and Wildlife and Vincent DiMarzo from the Wiyot Tribe provided field assistance. This manuscript benefited from the thoughtful reviews of Chris Caudill of the University of Idaho and other anonymous reviewers. This project was improved by discussions with Nicholas A. Som and Nicholas J. Hetrick of the U.S. Fish and Wildlife Service. This project was funded by the U.S. Fish and Wildlife Service Region 8. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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