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A Comparison of the Ecology of Resident and Translocated Beavers Used for Passive Restoration in Degraded Desert Rivers

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A COMPARISON OF THE ECOLOGY OF RESIDENT AND TRANSLOCATED BEAVERS USED FOR PASSIVE RESTORATION IN DEGRADED DESERT RIVERS

by

Emma Doden

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Julie K. Young, Ph.D. Co-Major Professor	Phaedra Budy, Ph.D. Co-Major Professor
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ABSTRACT

A Comparison of the Ecology of Resident and Translocated Beavers Used for Passive Restoration in Degraded Desert Rivers

by

Emma S. Doden, Master of Science

Utah State University, 2021

Major Professor: Dr. Julie K. Young
Department: Wildland Resources

Ecosystem engineers influence resource availability and quality in their respective communities. Beavers (*Castor canadensis*) are ecosystem engineers capable of assisting in stream ecosystem restoration; therefore, translocation of nuisance beavers has become a popular method to simultaneously mitigate human-wildlife conflict and restore riparian systems. However, there remains a lack of evidence about the efficacy of such efforts. Few projects monitor beavers post-release and compare behavior to resident beavers, and translocations to desert river systems are rare. We captured, tagged, and monitored 47 beavers which we translocated to desert river restoration sites on the Price and San Rafael Rivers, Utah, USA. We compared translocated beaver site fidelity, survival, dam-building behavior, and space use to 24 resident beavers we also captured and tagged for monitoring. We found high apparent survival (*i.e.,* survived and stayed in the study area) for eight weeks post-release of resident adult beavers (0.85 ± 0.03) and lower apparent survival rates for resident subadult (0.34 ± 0.12), translocated adult (0.37 ± 0.01), and translocated subadult beavers (0.22 ± 0.03). There were significantly more river reaches with dams ($\chi^2 (1, n = 210) = 16.38, p = 5.2 \times 10^{-5}$) after beaver translocations than before translocations, although we were unable to determine which beavers were responsible for dam building. We detected resident adult beavers for a mean maximum distance of 0.86 ± 0.21 (1 Standard Error) km of river. We detected resident subadult (11.00 ± 4.24 km), translocated adult (19.69 ± 3.76 km), and translocated subadult (21.09 ± 5.54 km) beavers for greater mean maximum distances. According to results from coarse-scale, six-month post-release movement models, translocated and resident subadult beavers moved significantly farther from release sites and faster than resident adult beavers. In contrast, all beavers demonstrated similar activity levels according to a fine-scale, short-term movement model, indicating day-to-day activity patterns such as foraging and resting were not substantially altered by translocation. Our findings suggest translocated beavers exhibited survival rates, dam building behavior, and movement patterns most similar to resident subadult beavers during dispersal. Many translocated beavers emigrated from the study sites but may still be providing services in other degraded stretches of river. Nevertheless, translocation directly or indirectly led to additional beaver dams in the restoration sites, the common goal of beaver-assisted restoration. Low site-fidelity, high mortality, and wide-ranging movement patterns should be anticipated when translocating beavers, with multiple releases at targeted restoration sites eventually resulting in some establishment and dam-building. Notably, translocated beavers did not appear to negatively affect resident beaver behavior, indicating they can be used to supplement existing low populations to potentially help reach restoration goals more quickly. As climate change and widespread environmental degradation persist, improving strategies to restore healthy ecosystems, such as beaver-assisted restoration, is fundamental to the conservation of global biodiversity.

(102 pages)

PUBLIC ABSTRACT

A Comparison of the Ecology of Resident and Translocated Beavers Used for Passive Restoration in Degraded Desert Rivers

Emma Doden

Ecosystem engineers are species that create, destroy, modify, or maintain habitat. As ecosystem engineers, beavers have the potential to assist in stream restoration. Translocation is the capture and relocation of an animal to another area. Translocation of nuisance beavers has become a popular method to reduce human-wildlife conflict and restore waterways. However, few projects monitor beavers after release and compare behavior to naturally occurring resident beavers. Translocations to desert rivers are also rare. We captured, tagged, and monitored 47 beavers which we translocated to desert river restoration sites on the Price and San Rafael Rivers, Utah, USA. We compared translocated beaver behavior and activity to 24 resident beavers we also captured and tagged for monitoring. We found high survival rates for resident adult beavers and lower survival rates for resident subadult, translocated adult, and translocated subadult beavers. There were many more river reaches with dams after beaver translocations than before translocations, although we were unable to determine which beavers were responsible for dam building. In general, resident subadult and translocated adult and subadult beavers used ten times longer stretches of river than resident adult beavers. Translocated and resident subadult beavers moved farther from release sites and faster than resident adult beavers in the first six months after release. In contrast, all beavers had similar short-term activity levels, indicating day-to-day activities such as searching for food and resting may not be changed by translocation. Our findings suggest translocated beavers exhibited survival rates, dam building behavior, and movement patterns most similar to resident subadult beavers during dispersal, which is the movement away from the location where a beaver was born. Many translocated beavers left the study sites in search of a suitable area in which to settle, but even those beavers that left the restoration areas may still be benefiting other degraded stretches of river. Further, translocations led to additional beaver dams in the restoration sites, the common goal of beaver-assisted restoration. Low probability of staying near release sites, a high death rate, and wide-ranging movement patterns should be anticipated when translocating beavers. Multiple beaver releases at targeted restoration sites may eventually result in some settlement and dam-building. Resident beavers did not appear to be negatively affected by translocated beavers introduced into the rivers, indicating that translocations can be used to increase low beaver populations to potentially help reach restoration goals more quickly. Improving methods of restoring healthy ecosystems, such as beaver-assisted restoration, is important to maintaining diverse, abundant life globally.

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CHAPTER 1

INTRODUCTION

Ecosystem engineers are species that create, destroy, modify, or maintain habitat (Jones, Lawton, & Shachak, 1994). Examples abound for a variety of taxonomic groups. Termites (*Macrotermes*) create landscape mosaics and affect resource flows by altering soil chemical and physical properties with their mounds and tunnels (Dangerfield, McCarthy, & Ellery, 1998). African elephants (*Loxodonta* spp.) push over trees which can convert woodland to grassland (Haynes, 2012). Tree-excavating birds such as woodpeckers create nesting cavities for other organisms (Robles & Martin, 2013). Ecosystem engineers influence resource availability in their respective communities. Furthermore, because of their ability to alter the abiotic and abiotic interactions in their environment, ecosystem engineers can be harnessed as natural tools for ecosystem restoration (Byers *et al*., 2006; Law *et al*., 2017).

Perhaps one of the most well-known ecosystem engineers is the beaver, of which there are two ecologically similar species (Rosell *et al.*, 2005; American beaver, *Castor canadensis,* and Eurasian beaver, *C. fiber*). In addition to being ecosystem engineers, beavers are classified as keystone modifiers because their dam-building behavior substantially alters the wetland or riverine ecosystem they inhabit (Mills *et al.* 1993, McKinstry, Caffrey, & Anderson 2001). Beaver dams create pools that retain water, nutrients, and sediment, add heterogeneity to lentic and lotic systems, regulate water temperature, and impact riparian vegetation (Naiman, Johnston, & Kelley*,* 1988; Rosell *et al.*, 2005). Water impoundment by dams promotes riparian vegetation establishment, a persistent water source, and a more drought-resistant and fire-resilient ecosystem, also potentially mitigating the effects of climate change in certain areas (Hood & Bayley, 2008; Fairfax & Small, 2018; Fairfax & Whittle, 2020). Invertebrates, reptiles, amphibians, birds, fish, other mammals, and domestic livestock benefit from ecosystems maintained by beavers (Wright, Jones, & Flecker*,* 2002; Baker & Hill, 2003).

Both Eurasian and American beavers were nearly extirpated from most of their ranges across Europe, Asia, and North America before the 1900s due to overharvest, but since then reintroduction, regulation, and natural range expansion have stabilized populations of both species in many areas, although at lower abundances than historically (Baker & Hill, 2003; Halley, Saveljev, & Rosell, 2021). Today, American beaver (hereafter, beaver) populations are estimated only at 1.5-10% of their size relative to European settlement (Baker & Hill, 2003). Streams across the United States changed in the absence of beavers and their dams, many reverting from braided, heterogeneous channels to single incised channels, with degradation exacerbated by human activity (Poff *et al.*, 1997; Pollock, Heim, & Werner, 2003; Polvi & Wohl, 2013). To reverse some of these effects, beavers are translocated as a method to restore degraded systems. But in some areas, beavers are still considered a nuisance species and lethally removed when they cause damage to trees, unwanted flooding, or threaten infrastructure (Siemer *et al.*, 2013).

Restoration projects involving beavers employ various strategies centered around the goal of establishing dams or dam-like structures in the system. Methods include encouraging natural colonization of beavers, mimicking beaver effects by building artificial dam structures, translocating individuals, or a combination of these techniques. Encouraging natural colonization is feasible when there is an existing beaver population nearby, and habitat in the restoration area is attractive to dispersing beavers. However, colonization may not always provide anticipated results or succeed because restoration sites are likely degraded and lower-quality habitat that does not attract beavers (Ritter, Gower, & McNew, 2020). Some restoration projects opt instead to mimic beavers through artificial dam structures, beaver dam analogues (BDAs), or post-assisted log structures (PALS; Pollock *et al.,* 2014), but installation and long-term maintenance of these structures can be costly and time-consuming. Using translocated beavers reduces costs associated with the need for human maintenance and gives an outlet for nuisance beavers. Translocations are carried out independent of or in combination with beaver mimicry structures. In a review of beaver-related restoration projects in the western rangeland streams of the U.S., most projects involved translocations (n = 76 of 97 projects), but success rates tended to be low or uncertain and standardized best management practices were lacking (Pilliod *et al.,* 2018).

Translocation success is especially challenging in extreme environments or low-quality habitat (Armstrong & Seddon, 2008), such as in degraded desert rivers. Many arid systems have become imperiled by simplification, invasive species, altered flow regimes, and climate change (Stromberg, 2001; Mott Lacroix, Tapia, & Springer, 2017), and beavers could play an important part in desert river restoration by storing water and increasing habitat complexity with their dams (Harper, 2001). However, few translocations have occurred and beavers are understudied in desert systems (Gibson & Olden, 2014; Barela & Frey, 2016). Therefore, my study focused on assessing the efficacy of nuisance beaver translocation for passive desert river restoration, primarily for creating and maintaining habitat for imperiled endemic desert fish and other wildlife species. Whereas past beaver translocation efforts have typically been reintroductions to areas without beavers (Woodruff & Pollock, 2018), I assessed whether translocated beavers could be used as a population augmentation strategy with no adverse effects on existing beaver populations. I monitored resident and translocated beavers in the same system to compare their life history traits and behavior.

In Chapter 2, I compared the site fidelity, survival, and dam-building behavior of translocated beavers to that of resident beavers. I expected that translocated beavers would have low site fidelity, survival, and dam-building behavior similar to dispersing resident subadult beavers initially, conducting exploratory movements in search of a mate and suitable site to settle in, but would eventually establish and have similar survival and dam-building behavior as resident adult beavers. A beaver translocation project is considered successful when beavers stay at the targeted site, survive, and build or maintain dams long enough for restoration objectives to be met. Site establishment after translocation may vary depending on resource availability and quality, whether other territorial beavers are already established nearby, stream geomorphology, season, group size, or age (Nolet & Rosell, 1994; Fustec *et al.*, 2001; Ritter *et al.*, 2020). Translocating a mated pair, family unit, or colony may help keep them from dispersing because beavers are a socially monogamous species (Baker & Hill, 2003), but individual beavers released in groups or as mates may still separate after release (Petro, Taylor, & Sanchez, 2015).

Successful translocation establishment also depends on the survival of beavers. Naturally occurring beavers can survive about 10 years in the wild (Müller-Schwarze, 2011; Taylor, Yarrow, & Miller, 2017), but for translocated beavers, mortality is often high immediately following release. Translocated individuals are affected by unnatural stressors related to translocation and being released in an unfamiliar environment without known food sources and shelter from predators, similar to the risks associated with dispersal (Bonte *et al.*, 2012; Teixeira *et al.,* 2007; Dickens, Delehanty, & Romero, 2010). Wolves (*Canis lupus*), coyotes *(Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and bears (*Ursus americanus* and *U. arctos*) most commonly prey upon beavers (Baker & Hill, 2003). Predation appears to be the most common cause of mortality for translocated beavers in the western United States (Pilliod *et al.,* 2018).

The final step towards translocation success in the context of ecological restoration after beavers establish at a targeted site and survive is dam construction. The goal of many translocation projects is to increase the number of dams in the system to initiate process-based restoration and alter degraded systems (Nash *et al.*, 2021; Naiman *et al.* 1988). However, dam-building is limited by geomorphology, including flow regime, discharge and gradient, and vegetation, such as the availability and access to dam-building material (Poff *et al.*, 1977; Macfarlane *et al.* 2017; Petro *et al.*, 2018). In addition, beavers may not build dams if there is adequate existing refuge from predators, areas to cache food, and access to bank dens and lodges

(Żurowski, 1992; Baker & Hill, 2003; Nash *et al.*, 2021). Therefore, encouraging translocated beavers to build dams can still have variable success, and a study in Oregon found no apparent link between dam-building behavior before and after translocation (Petro *et al.* 2015). Artificial dams or woody structures in the system seem to attract beavers to improve upon the structures (MacCracken & Lebovitz, 2005; DeVries *et al.*, 2012; Bouwes *et al.*, 2016), as maintaining an existing structure is more energy-efficient than constructing a new dam.

In Chapter 3, I examined the space use of resident and translocated beavers on multiple spatiotemporal scales, to develop an expectation framework of beaver movement patterns after translocation and how it compares with natural beaver movement patterns. I analyzed space use on a coarse scale, describing resident beaver home ranges in a desert system, and comparing movement patterns and speed of resident and translocated beavers over time. I also analyzed space use at a fine scale, comparing the median distance resident and translocated beavers moved in five minutes as a proxy for activity patterns such as resting and foraging. I expected that translocated beavers would be more active and move farther and more quickly than territorial resident beavers initially, exhibiting space use patterns more like dispersing resident subadult beavers, but would eventually settle into similar movement behavior as resident beavers.

Home range sizes of resident beavers typically average 1.6 to 3.9 km (Breck, Wilson, & Andersen, 2001; Herr & Rosell, 2004; Havens, Crawford, & Nelson, 2013). Dams, the common goal of beaver-assisted restoration, tend to be built by beavers with established home ranges and territories (DeStefano *et al.*, 2006; McClintic *et al.*, 2014; Ritter, 2018) and are not usually built by beavers during dispersal or transience. Instead, these individuals tend to spend their time and energy traveling longer distances in search of a mate and a new site to establish. Before settling into a home range, dispersing subadult beavers typically travel 3.5 to 19.8 km (Beer, 1955; Sun, Müller-Schwarze, & Schulte, 2000; Ritter, 2018), and space use of translocated beavers can vary extensively from 3.3 to 238 km, leading to variable dam-building success (Hibbard, 1958;

McKinstry & Anderson, 2002; Petro *et al.*, 2015). In addition, in our arid system resources may be more patchy, scarce, and unpredictable than temperate environments inhabited by beavers, such as wetlands, waterways through forests, and montane streams (Baker & Hill, 2003), likely impacting beaver space use. Determining the movement behavior of translocated beavers in our understudied desert system can help future efforts identify appropriate areas where beavers can still provide beneficial restoration services even if individuals move considerable distances.

In Chapter 4, I synthesize the findings of my two research chapters into general conclusions regarding the efficacy of beaver translocations for desert river restoration. Though many studies exist regarding natural beaver ecology, there are few studies on translocated beavers or beavers in desert systems, and none comparing resident and translocated beaver ecology. My research provides a framework to set expectations and anticipate unexpected outcomes, ensure existing beaver populations are not negatively affected, and increase the efficacy of future translocations. Beaver translocation success is possible (Woodruff & Pollock, 2018; Brick & Woodruff, 2019), and gaining a greater understanding of the site fidelity, survival, dam building, and space use behavior of translocated beavers can produce more effective and successful future translocation efforts.

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CHAPTER 2

COMPARING LIFE HISTORY TRAITS OF RESIDENT AND TRANSLOCATED BEAVERS USED AS PASSIVE RESTORATION TOOLS IN DEGRADED DESERT RIVERS[1]

ABSTRACT

Wildlife translocation is a popular conservation tool for recovering imperiled species, reducing human-wildlife conflict, and restoring degraded ecosystems. Beaver (American, *Castor canadensis;* Eurasian, *C. fiber*) translocation is used as one method of conflict mitigation, beaver reintroduction, and ecosystem restoration. However, few projects translocate to desert river systems or measure outcomes of translocations by monitoring beavers post-release to compare behavior to resident beavers. We captured, tagged, and monitored 47 American beavers (hereafter, beavers); we then translocated them to two desert rivers in Utah, USA, for desert river restoration. We compared translocated beaver site fidelity, survival, and dam-building behavior to 24 resident beavers that we also tagged and monitored. We found high apparent survival (*i.e.,* survived and stayed in the study area) for eight weeks post-release of resident adult beavers (0.88 ± 0.09; SE), and lower but similar apparent survival rates for resident subadult (0.24 ± 0.34), translocated adult (0.37 ± 0.01), and translocated subadult beavers (0.24 ± 0.12). There were significantly more river reaches with dams (χ^2 (1, n =210) = 16.38, $p = 5.2\text{x}10^{-5}$) after translocations as compared to before beaver translocations, although we were unable to determine which beavers were responsible for dam building. Translocated beavers initially exhibited similar characteristics as resident subadult beavers during dispersal; they were more vulnerable to

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predation and many emigrated from the study sites apparently in search of a suitable area to establish. Even so, translocation directly or indirectly contributed to additional beaver dams in the restoration sites, the common goal of beaver-assisted river restoration. High mortality and low site-fidelity should be anticipated when translocating beavers, but multiple releases at targeted restoration sites may eventually result in establishment and meet conservation objectives for desert rivers.

INTRODUCTION

Wildlife translocations are valuable conservation tools for recovering imperiled species, reducing human-wildlife conflict, and restoring degraded ecosystems (Germano *et al.*, 2015; Mengak, 2018; Novak, Phelan, & Weber, 2021). Although there have been many successful translocation efforts, challenges arise when moving animals to novel environments (Griffith *et al.*, 1989; Wolf *et al.*, 1996). Animals can leave their targeted release site, experience high rates of mortality, or behave unexpectedly (Mengak, 2018; Berger-Tal, Blumstein, & Swaisgood, 2020). Identifying and finding ways to mitigate these challenges can help improve the success of future translocation efforts, and ultimately aid in wildlife conservation (Fischer & Lindenmayer, 2000; Armstrong & Seddon, 2008).

American and Eurasian beavers (*Castor canadensis* and *C. fiber*) have been translocated for over fifty years after extensive extirpation from much of their historical ranges during the fur trade of the 1700s-1800s (Baker & Hill, 2003; Halley, Saveljev, & Rosell, 2021). Translocations of American beavers (hereafter, beavers) in the United States often focus on removing nuisance individuals from conflict situations where they would otherwise be euthanized and using them as ecosystem engineers for riparian restoration; they may increase the number of dams in the system to initiate process-based restoration and improve degraded systems (Naiman, Johnstson, & Kelley, 1988; Pollock *et al.*, 2014; Pilliod *et al.*, 2018). Beavers provide numerous services such as adding heterogeneity to ecosystems (Wright e*t al.*, 2002), reducing stream channel incision

(Pollock *et al.*, 2014), and promoting drought, climate change, and wildfire resiliency (Hood & Bayley, 2008; Fairfax & Small, 2018; Fairfax & Whittle, 2020), which benefit many other species (Rosell *et al.*, 2005).

Despite the history of using beaver translocations for species and ecosystem conservation, best management practices to ensure beaver establishment are still lacking (Pilliod *et al.*, 2018; Nash *et al.*, 2021). Understanding life history characteristics of existing resident individuals could help inform management practices, yet studies comparing translocated individuals to residents are uncommon (*but see* Pinter-Wollman, Isbell, & Hart, 2009; Baker *et al.*, 2021; Muriel *et al.*, 2021). Successful beaver establishment is defined by long-term residency, survival, and dam building at release sites; however, long-term residency rarely exceeds 50% of individuals released (McKinstry & Anderson, 2002; Petro, 2013; Dittbrenner, 2019; *but see* Albert & Trimble, 2000), survival of translocated beavers can be < 50% (McKinstry & Anderson, 2002; Petro *et al.*, 2015), and there may be no apparent link between dam-building behavior before and after translocations (Petro *et al.* 2015). Thus, successful beaver translocation remains challenging.

Suitable habitat for dam-building, foraging, and evading predators are key components for long-term residency and survival of translocated beavers. Beavers build dams to create pools as refuge from predators, cache food, and access bank dens and lodges, but beavers may not build dams if these needs are already met (Baker & Hill, 2003; Nash *et al.*, 2021). Releasing translocated beavers at artificial or natural woody structures may potentially help them establish at the release site and encourage dam-building behavior (DeVries *et al.,* 2012; Bouwes *et al.,* 2016). Site-specific factors can affect success (*e.g.,* predator density, existing beaver densities, inter-colony interactions, and habitat availability), emphasizing the importance of assessing the suitability of translocation release sites on a case-by-case basis (Petro *et al.*, 2018; Touihri *et al.*, 2018).

Translocation success can be more challenging in extreme environments or low-quality habitat, such as in degraded desert rivers (Armstrong & Seddon, 2008). Desert rivers are integral for the survival of many desert species (Knopf *et al.*, 1988; Kingsford & Thompson, 2006), but are often jeopardized by altered flow regimes, impoundment structures, and invasive species (Stromberg, 2001; Mott Lacroix, Tapia, & Springer, 2017). Beavers could help to mitigate the effects of these alterations and naturally inhabit arid desert rivers already (though dam-building could be restricted by limited availability of woody material), but little is known about their ecology and effects on desert systems (Gibson & Olden, 2014; Barela & Frey, 2016). Further, it is likely some desert rivers have not recovered to maximum beaver capacity since the fur trade, especially with beaver bounties still in some places, and therefore translocations could supplement existing populations.

Our study sought to identify whether nuisance beaver translocation could serve as an effective means of restoration in desert rivers by determining translocation success and comparing the residency, survival, and dam-building behavior of translocated beavers to resident beavers. We defined translocation success as beavers staying, surviving, and building dams within the study areas for at least eight weeks post-release. We expected resident adult beavers would remain in their territories, have high survival rates, and build dams, while resident subadult and translocated beavers would have lower rates of release-site fidelity, survival, and dam-building activity. We expected some would successfully establish in the study sites, and could then potentially serve as an effective tool for creating and maintaining habitat for imperiled endemic desert fish and many other wildlife species, enhancing the effects of resident beavers already in the system.

MATERIALS AND METHODS

Study Area

We conducted our study at three sites along the lower stretches of the Price and San Rafael Rivers, part of the greater Colorado River Basin in east-central Utah, USA. Degradation is caused by simplification, dewatering, and invasive species encroachment especially in the lower river reaches. Several federally endangered or state-sensitive fish species use these rivers (Colorado pikeminnow *Ptychocheilus Lucius*, bonytail chub *Gila elegans*, razorback sucker *Xyrauchen texanus*, bluehead sucker *Catostomus discobolus*, flannelmouth sucker *Catostomus latipinnis*, roundtail chub *Gila robusta*; Bottcher *et al*., 2013; Budy *et al.*, 2015). The first study site was 20.5 kilometers (km) of the Price River near Woodside, UT, where a multi-faceted restoration project is planned. The second study site was 8.1 kms of the San Rafael River at Moonshine Wash near the confluence with the Green River, where tamarisk removal, gravel addition, native tree planting, and installation of beaver dam analogues (BDAs) were completed (Laub, 2015; Laub, 2018). The third field site was 1.5 kms of the San Rafael River near Cottonwood Wash, which experienced a dramatic geomorphic change beginning in 2010 due to a sediment plug, resulting in a rare stretch of in-stream habitat complexity in the otherwise simplified lower San Rafael River (Lyster, 2018). We did not translocate any beavers to this site as a natural colony was already established and actively building dams.

The rivers flow through canyonlands and desert shrublands, with temperatures ranging from -11°C in winter to above 37°C in summer. Annual rainfall averages 21 cm per year (NOAA, 2021a). Dominant riparian vegetation includes a limited mix of native and non-native species: willow (*Salix* spp.), Fremont cottonwood (*Populus fremontii*), common reed (*Phragmites* spp.), as well as tamarisk (live and dead; *Tamarix ramosissima*) and Russian olive (*Elaeagnus angustifolia*). Cattails (*Typha* spp.) were also present at Cottonwood Wash.

Capture, Quarantine, and Tagging

All capture, handling, and monitoring procedures were approved by Utah State University's Institute for Animal Care and Use Committee (No.10128). We responded to nuisance beaver calls in northern, central, and eastern Utah to capture beavers for translocation (Figure 2-1) and captured resident beavers at the Cottonwood Wash and Price River study sites. We captured beavers from May to October of 2019 and 2020 using Hancock/Koro suitcase-style traps, Comstock box traps, or nonlethal cable restraints and held captured beavers at the Utah State University Beaver Ecology and Relocation Center in Logan, Utah, or the field site, providing food and fresh water daily (Campbell-Palmer & Rosell, 2015). We held translocated beavers for at least three days to minimize the spread of disease and aquatic invasive species transmission, following state protocols (Utah Division of Wildlife Resources, 2017; Pilliod *et al.,* 2018).

We processed and fitted beavers with monitoring tags before release. First, we used weight and body size to assign age class (kit < 1 year, subadult = 1-2 years, adult > 2 years; Patric & Webb, 1960) and sexed beavers using anal gland secretion (Schulte, Müller-Schwarze, & Sun, 1995; Woodruff & Pollock, 2018). Then we inserted passive integrated transponder- (PIT-) tags (Biomark APT12 tags; Boise, Idaho, USA) in the tails of all beavers and fit beavers > 9 kg with a remotely downloadable store on-board GPS tag (Africa Wildlife Tracking; Rietondale, Pretoria, South Africa) or a VHF modified ear-tag as tail-mounted transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA; Model #M3530; Rothmeyer, McKinstry, & Anderson 2002; Arjo *et al.,* 2008). Initially, we attached GPS- and VHF-tags with 19 mm neoprene and steel washers, then increased the sizes of washers (neoprene: 38.1 mm, steel: 31.8 mm) in September 2019 to improve transmitter retention (Windels & Belant, 2016). We chemically immobilized and supplemented beavers with oxygen and isoflurane during GPS- or VHF-tag attachment (Roug *et al.,* 2018). We released resident beavers at their capture sites and translocated beavers at

Moonshine Wash near BDAs and unoccupied stretches of the Price River site. The San Rafael River study sites were unsuitable for beaver translocation in 2020 due to extremely low flows (Figure A-1).

Monitoring

We located beavers two to seven times per week via radio-telemetry and GPS locations from May through October 2019 and 2020. We also used semi-permanent and submersible passive integrated antennae (PIA; Biomark; Boise, Idaho, USA) installed in the rivers to passively detect PIT-tags from May 2019 through March 2021 (Figure 2-2). When VHF signals indicated mortality, we recovered the transmitter. If we found a dead beaver, we performed a necropsy to determine the cause of death. If no beaver was present and there were no signs of predation, we recorded the event as a transmitter loss. We searched for beavers that likely left the study sites (*i.e.*, were not regularly detected) for at least two weeks following its last detection and sporadically throughout the remaining field season. To increase detections, we conducted monthly scans along the Green River, one aerial flight, and several river floats on the Price and San Rafael Rivers. We considered beavers detected during these occasions to have temporarily (later detected back in the study area) or permanently (never detected back in the study area) emigrated from the study areas. At the end of the monitoring period (31 March 2021), we classified beavers into different fate categories: unknown, mortality, and alive (detected ≥ five months and within 15 days of the end of the monitoring period).

Dam and Sign Surveys

We conducted sign surveys in June 2019 at Cottonwood and Moonshine Wash, and in August 2019 at the Price River study site, which consisted of walking or floating along the rivers and recording all dams, lodges, burrows, and fresh beaver sign on a handheld GPS unit (Garmin, Chicago, Illinois, USA; Model GPSMAP 78s or 66st). We observed areas of resident beaver activity at Cottonwood Wash and certain stretches of the Price River, but little sign at Moonshine Wash. We censused all existing beaver dams before translocations occurred using sign surveys and satellite imagery (Google Earth Pro, 2019), and then completed a final beaver dam count in October 2020. We categorized beaver dams into four types: resident old, resident new, translocated new, and unknown new. We considered dams new if built after the first beaver dam census at each study site. We considered old and new dams built within a resident adult beaver's 100% MCP home range to be built by that individual. We designated new dams built by translocated beavers when the construction date was known and within 100 m of at least four concurrent locations of a translocated beaver (*similar to methods in* Woodford, Macfarland, & Worland, 2013; Touihri *et al.,* 2018; Matykiewicz *et al.,* 2021). All other new dams encountered we assigned as unknown. Finally, we assigned each observed dam based on its location in the river to its appropriate river reach delineated by the Utah Beaver Restoration Assessment Tool (BRAT; Macfarlane, Wheaton, & Jensen, 2014; Macfarlane *et. al,* 2017).

Data Analysis

We estimated the probability of beavers surviving and remaining in the study area (φ; apparent survival) using Cormack-Jolly-Seber (CJS) models in program MARK with *logit*-link functions to produce maximum likelihood estimates (Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton *et al.*, 1992; White & Burnham, 1999; version 9.0). We estimated apparent survival in the study sites for eight weeks post-release for radio-tagged beavers, split into four groups (*g*): resident adult, resident subadult, translocated adult, and translocated subadult, and three sampling occasions (*t*): weeks 0-1, 2-4, and 5-8, adjusted in MARK for uneven sampling intervals. We used CJS models to estimate φ because a known-fate model was unsuitable with our high rate of unknown fate, and limited analysis to eight weeks post-release since we only monitored most individuals for eight weeks before unknown fate occurred. First, we built a model set with the additive effects of individual covariates on φ: including sex, year released (*Year*), days held in quarantine before release, average discharge and temperature across the time period (NOAA, 2021b; USGS, 2021), maximum temperature the day of release (NOAA, 2021b; USGS, 2021), season, and Omernik level III ecoregion of an individual's origin (Colorado Plateaus, Wasatch and Uinta Mountains, and Central Basin and Range; Omernik, 1987). We did not include study site as a covariate due to small sample size and because sites were correlated with year, as we only released beavers on the San Rafael River in 2019. We constrained models to include ≤ 7 parameters to balance between optimizing model likelihood and avoiding model overparameterization (Burnham & Anderson, 2002). We compared models using an information-theoretic approach with AICc tables adjusted for small sample size (Anderson, Burnham, & White, 1994; Burnham & Anderson, 2002). Using the estimates from the top model with the most support, we multiplied the apparent survival estimated for each time interval to generate apparent survival probability for the entire 8-week period and used the Delta Method to estimate the Standard Error (SE) (White & Burnham, 1999; Ver Hoef, 2012). We considered parameters included in the top model with 95% Confidence Intervals (CI) that overlapped zero to be insignificant (Arnold, 2010).

We used a binomial generalized linear model (GLM) with a *logit*-link function to determine whether the dam capacity per river reach from BRAT was a significant predictor of the probability pre- and post-translocation that ≥ 1 dam was observed in a given river reach at $\alpha = 0.05$. We also performed a χ^2 Goodness of Fit test comparing the post-translocation count of reaches with ≥ 1 dam to the pre-translocation count of reaches with ≥ 1 dam, which served as the expected number of reaches with and without ≥ 1 dam/reach if no changes had occurred due to translocation. We performed all statistical analyses in R Statistical Program (version 4.0.3; R Core Team, 2020, package "nlme", Pinheiro *et al.*, 2021).

RESULTS

We captured and PIT-tagged 24 resident and 47 translocated beavers, with a subset radio-tagged (Table 2-1). Three additional resident beavers died from capture- and processing-related events so we censored them from the dataset. We excluded beaver kits from analyses due to low detection rates.

We never detected resident adult beavers outside of the study areas. One resident subadult beaver temporarily left the Price River study site for 18 days before being detected back in the site. We detected only 6.4% (n = 3 adult beavers) of all PIT-tagged translocated beavers exclusively inside the study areas after eight weeks (Figure A-2). We detected 40.4% (n = 19) of all PIT-tagged translocated beavers outside of the study sites, primarily with PIAs, though the final locations for two of these individuals were back in the study sites.

At the end of the study, there were three out of 24 resident beavers alive: one kit and one subadult at the Price River site and one adult at the Cottonwood Wash site. There were also four out of 47 translocated subadult beavers alive, but all had emigrated from the Price River study site. Unknown fate made up the largest proportion of translocated adult and subadult beavers (n = 13, 81% of resident beavers; n = 30, 73% of translocated beavers), caused by GPS-transmitter failures, transmitter loss, or individuals emigrating outside of the study areas where monitoring was limited. We recovered 11 transmitters pulled out of tails (six resident and five translocated beavers), with a 46% transmitter loss rate before washer improvements, and a 17% transmitter loss rate afterward. We continued to detect two individuals who lost their transmitters with PIAs until the end of the study and therefore included them in the "alive" category. We detected eight mortalities for beavers fitted with radio transmitters, half occurring within the first week post-release. One resident dispersing subadult beaver was killed by a felid (bobcat or mountain lion). Seven translocated beavers died (four adults and three subadults). One translocated beaver died of translocation stress and poor body condition, two died of the combined stressors of sustaining cable-restraint injuries and being released during an unanticipated drought on the Price River. Four translocated beavers were killed, one each by felid, coyote, and black bear, and one too old to distinguish the predator.

Resident adult beavers had significantly higher apparent survival probability "φ" than all other groups (Table 2-2).

We were unable to assess the goodness-of-fit of our models or adjust our overdispersion factor, ĉ, due to problems estimating deviance degrees of freedom with only three encounter periods, meaning our reported SEs are smaller than if we were able to adjust ĉ (*similar to* Pfeiler *et al.,* 2021). For most models, MARK estimated encounter probability p as 1.00 for all time intervals. Estimates of p did not improve after using alternate optimization methods, profile likelihood CIs, and inspecting results after data cloning, but φ appeared largely unaffected by the poor estimation of p. The top model used for estimating apparent survival was $\varphi(g + t + Year)p(.)$. We reported the estimates from this model rather than the model-averaged estimates as nonlinear model-averaging can be problematic (Table 2-3; Table A-1; Cade, 2015; Banner & Higgs, 2017). Significant covariates included group type (resident adults exhibited significantly higher apparent survival than resident subadult and translocated adult and subadult beavers), and year (beavers in 2019 experienced higher apparent survival than those in 2020).

Before beaver translocations began, we observed 23 existing dams in 17 river reaches built by resident beavers in the study areas (six at Cottonwood Wash, 17 on the Price River). We recorded 22 new dams built in 16 previously undammed reaches and four reaches where dams already existed. One dam was built by a translocated beaver (Price River), two by resident beavers (Price River), and 19 by unknown beavers (three at Moonshine Wash, 14 on the Price River; Figure 2-3). The translocated beaver who built a dam was later depredated.

We excluded one dam and river reach from analysis because we were unable to determine whether the dam was built before or after beaver translocations occurred. We included

210 total river reaches in analyses. Results from the binomial GLM revealed that BRAT dam capacity was not a significant predictor of the probability of observed reaches having a dam or not for both pre- and post-translocation observations (Table 2-4). However, we did find significantly more river reaches with ≥ 1 dam post-translocation than pre-translocation ($\chi^2_{1, n = 210} = 16.38$, $p = 5.2\text{x}10^{-5}$).

DISCUSSION

Even though individual beaver outcomes are variable, our results suggest translocated beavers can successfully establish residency, survive, and increase the number of dams in desert river systems. To achieve success, we translocated a high number of beavers to compensate for the mobility, mortality, and unpredictable nature of translocated beavers. Translocated beavers initially behaved and had mortality risks similar to dispersing natural subadult beavers, spending time exploring their novel environment before finding a place to establish, sometimes outside of the study sites. Resident adult beavers reliably stayed, survived, and built and maintained dams in the study sites. These patterns suggest adding translocated beavers has minimal to no impact on resident beavers and can be used as a viable population augmentation or restoration strategy when resident populations are below carrying capacity.

Our apparent survival analysis predicted roughly one-third of translocated beavers survived and remained in the study sites for at least eight weeks (56 days). The mean dispersal-settlement time for subadult beavers in Montana was 40.9 days (Ritter, 2018), and because translocated beavers behaved similar to subadult residents in our study system, mean dispersal-settlement time could be a proxy for the expected time translocated beavers need to establish a site. Thus, our survival analysis likely captured all the translocated beavers that established and could have contributed to building new dams within the study sites.

Our resident subadult apparent survival rate was substantially lower than the survival rates reported by other studies (ranging from 0.43 ± 0.12 (SE) to 0.84 ± 0.04; McNew & Woolf, 2005; DeStefano *et al.*, 2006; Ritter, 2018). Similarly, our apparent survival of translocated beavers was also lower than American beavers in Wyoming (0.49 ± 0.07; McKinstry & Anderson, 2002) and Oregon (0.47 ± 0.12; Petro *et al.*, 2015), and Eurasian beavers in the Netherlands (64-67%, Nolet & Baveco, 1996; *but see* Table A-2). Instead, our results resemble establishment rates reported in Wyoming, where only 19% of beavers translocated to degraded streams survived > 180 days, built dams, and stayed within 3 km of their release site (McKinstry & Anderson, 2002).

Due to the limitations of CJS analyses, we were unable to estimate mortality separately from emigration. It is unlikely that our low apparent survival rates are solely attributed to mortality since we only encountered eight mortalities out of 38 radio-tagged resident subadult and translocated beavers. Apparent survival was likely biased low due to unknown fate and emigration from the study areas. In degraded desert rivers, resources are scarce and dynamic (Gibson & Olden, 2014; Barela & Frey, 2016), potentially leading to high rates of emigration if release sites do not have adequate resources for survival or mates nearby. In addition, beavers have an increased risk of predation or starvation during dispersal or translocation while in unfamiliar waters without known lodges, burrows, and foraging resources (Letty, Marchandeau, & Aubineau, 2007; Müller-Schwarze, 2011; Bonte *et al.*, 2012). Predation was the largest cause of mortality for translocated beavers in our study, similar to previous studies (McKinstry & Anderson, 2002; Petro *et al.*, 2015). Translocation-related stressors can also decrease beaver survival, which contributed to the deaths of some of our beavers (Teixeira *et al.,* 2007; Dickens, Delehanty, & Romero, 2010). Nonetheless, our low apparent survival rates for translocated beavers remain an improvement over euthanasia of these nuisance beavers.

We did not observe any resident adult beavers emigrating from the study areas, and their apparent survival rates appeared more comparable to other natural American beaver studies (ranging from 0.76 ± 0.05 to 1.00; McNew & Woolf, 2005; DeStefano *et al.*, 2006; Bloomquist &

Nielsen, 2010; Maenhout, 2013), and a Eurasian beaver study in Norway (0.87 ± 0.02 for dominant adults; Campbell *et al.*, 2012). Despite inhabiting an arid system, our resident adult beavers may have comparable survival to other studies in less harsh climates because in our study sites low beaver population densities could limit fatal disease transmission (Cross *et al.*, 2009), there may be low predator densities (Menge & Sutherland, 1987), and there was no beaver harvest. Our high resident adult apparent survival rate exemplifies the suitability of our study sites for beavers, indicating that once translocated beavers establish a territory like resident adult beavers, they will survive and provide services to the system.

We observed several new dams post-translocation, suggesting that translocation efforts increased restoration services in the rivers despite being in dynamic, wood-limited systems. In our regulated rivers, monsoons and flash floods still occur and dams can get blown out (Andersen & Shafroth, 2010), with high stream power and limited availability of woody material inhibiting long-lasting dams (DeVries *et al.*, 2012; Persico & Meyer, 2013; Barela & Frey, 2016). At least one dam was built by a translocated beaver and eight other new dams were built where we did not document resident beavers on the Price River; all appeared likely to be able to withstand high flows. At Moonshine Wash where we did not document any resident beaver presence, three new partially spanning dams were built during drought in July 2020. These partial dams at only 0.5 meters high were unlikely to withstand high flows, but the impacts of beaver dams on in-stream habitat complexity continue even in the process of and after blowing out or breaching (Demmer & Beschta, 2008; Pollock *et al.*, 2014). We also anecdotally observed that partially spanning artificial structures provided habitat improvements, albeit effects were local. Two of the three dams were within 30 meters of BDAs, suggesting that beaver translocation may be more effective when artificial structures are provided, as Bouwes *et al.* (2016) demonstrated that BDA installation led to an overall increase in dams in Oregon.

Our observed pre- and post-translocation reaches with dams were not well-predicted by the dam capacity model, BRAT. Because BRAT predicts the maximum capacity of dams and not beavers on the landscape (Macfarlane *et al.*, 2017), there could be other factors limiting beaver dams in the area. Only 1% of the estimated BRAT dam capacity in the Price River watershed was fulfilled by beavers in a survey conducted by Macfarlane *et al.* (2017), and therefore these rivers are likely below their maximum beaver capacity. In addition, beavers may be fulfilling their safety and food accessibility requirements without needing to construct dams (Nash *et al.*, 2021). Especially in 2019 when discharges in our rivers were above historical averages, water depths may have been naturally sufficient for travel and cover. We found a significant increase in the number of river reaches with dams post-translocation as compared to pre-translocation, suggesting that translocated beavers built many of these new dams, or influenced resident beavers to construct more dams.

Translocation establishment success can be strongly related to the number of individuals released (Morris *et al.*, 2021). We translocated 39 individuals to the Price River and eight to Moonshine Wash in 21 separate release efforts, leading to establishment success in at least one site (Price River). Beavers are a territorial, socially monogamous species (Baker & Hill, 2003), so the number of individuals in a given release effort may be limited to beavers captured from the same colony or opposite-sex pairs, but previous American beaver studies have tied success to the release of several individuals, often in multiple release efforts (McKinstry & Anderson, 2002; Petro *et al.*, 2015; Brick & Woodruff, 2019). Persistent release efforts have also contributed to the successful translocation establishment of Eurasian beavers (Dewas *et al.*, 2012; Halley *et al.*, 2021).

No published studies have compared the ecology of resident beavers to that of translocated beavers in the same system. Though our study had limited inference from challenges associated with long-term monitoring and small sample size, it represents novel comparative research in an understudied desert system. Simultaneously monitoring resident beavers alongside translocated beavers allowed us to directly compare the site fidelity, survival, and dam building behavior of the two groups. In general, translocation projects do not expect every individual to successfully establish at targeted sites (Berger-Tal *et al.*, 2020), but comparing translocated and resident individuals can help set expectations, ensure existing populations are not negatively impacted, mitigate unexpected outcomes, and increase the efficacy of future translocations. This strategy could be useful to translocation of any species, beyond American or Eurasian beaver translocation. In our study, translocating beavers resulted in an increase in beaver dams with no apparent change in behavior of resident beavers, indicating translocations can augment the number of dams built by resident beavers. This finding could be beneficial for other beaver-assisted restoration projects since supplemental translocations could more quickly reach restoration goals.

Beavers were historically widespread and abundant in the northern hemisphere, impacting virtually every low-gradient, small-order stream with their dams (Naiman *et al.*, 1988; Pollock, Heim, & Werner, 2003). Invasive species encroachment, altered flow regimes, simplification, and climate change limit recovery of historical function of rivers on a landscape scale, and long-term, watershed-level management can be challenging to implement (Bennett *et al.*, 2016). However, this approach may be necessary instead of localized reach-level efforts to restore structure and function to degraded rivers and induce population-level responses in imperiled species tied to these ecosystems (Bernhardt & Palmer, 2011; Bennett *et al.*, 2016; Bouwes *et al.*, 2016). Therefore, translocation establishment success should not be limited to small, targeted sites and should instead be expanded, possibly even to include all waterways in a watershed. Provided that potential for human-wildlife conflict is addressed and minimized, this larger-scale perspective of success permits higher tolerance for movement of translocated beavers away from release sites since even those individuals who emigrated from release sites could still be providing restoration services in degraded areas. With an adaptive expectation for success, beaver translocation can be an effective restoration tool and simultaneously give nuisance beavers a second chance (Pilliod *et al*., 2018; Nash *et al.*, 2021). Translocation remains a high-impact conservation strategy for rivers when challenges are recognized and mitigated.

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TABLES AND FIGURES

Table 2-1. The number of resident and translocated beavers PIT-tagged and released in study sites on the Price River and at Cottonwood Wash and Moonshine Wash on the San Rafael River, Utah, USA from May-October 2019 and 2020. Numbers in parentheses indicate the number of individuals radio-tagged (GPS- or VHF-tag) in addition to being PIT-tagged.

Study Site	Resident Adult	Resident Subadult	Resident Kit	Translocated Adult	Translocated Subadult	Translocated Kit
Cottonwood Wash	2 (2)	1	0	0	0	0
Moonshine Wash	0	0	0	5 (5)	3 (3)	0
Price River	8 (7)	5 (3)	8	16 (16)	17 (11)	6
Total	*10*	*6*	*8*	*21*	*20*	*6*

Table 2-2. Apparent survival probability estimates (the probability an individual survived and stayed in the study area) from Cormack-Jolly-Seber models of beavers monitored for eight weeks post-release, May-October 2019 and 2020, in study sites on the Price River and at Cottonwood Wash and Moonshine Wash on the San Rafael River, Utah, USA.

Group Type	Sample Size	Apparent Survival Probability (φ)	1 Standard Error
Resident adult	9	0.88	0.09
Resident subadult	3	0.24	0.31
Translocated adult	21	0.37	0.10
Translocated subadult	14	0.24	0.12

Table 2-3. AICc output adjusted for small sample-size of Cormack-Jolly-Seber models estimating apparent survival probability for beaver detections within three study sites in a desert ecosystem of Utah, USA, for eight weeks post-release, May-October 2019 and 2020.

Model[a]	Number of parameters	AICc	ΔAICc	AICc Weight	Model Likelihood	Deviance
φ(g + t + Year) p(.)	7	89.48	0.00	0.30	1.00	73.78
φ(g) p(.)	5	91.21	1.73	0.13	0.42	80.33
φ(g + t) p(.)	6	91.77	2.29	0.10	0.32	78.52
φ(g + t + Av8WkDis) p(.)	7	92.22	2.74	0.08	0.25	76.52
φ(g + t + Sex) p(.)	7	92.55	3.07	0.07	0.22	76.85
φ(g + t + SeasSum) p(.)	7	93.25	3.77	0.05	0.15	77.55
φ(g + t + DaysHeld) p(.)	7	93.29	3.81	0.04	0.15	77.60
φ(g + t + SeasSpr) p(.)	7	93.54	4.06	0.04	0.13	77.85
φ(g * t) p(.)	7	93.90	4.42	0.03	0.11	78.20
φ(g + t + MaxTmpRel) p(.)	7	93.96	4.48	0.03	0.11	78.26
φ(.) p(.)	2	94.03	4.55	0.03	0.10	89.86
φ(g+ t + Av8WkTmp) p(.)	7	94.16	4.68	0.03	0.10	78.46
φ(g + t + EcoB) p(.)	7	94.18	4.70	0.03	0.10	78.48
φ(g + t + EcoM) p(.)	7	94.22	4.73	0.03	0.09	78.52
φ(t) p(.)	3	95.15	5.67	0.02	0.06	88.81

[a] *Key: g – group type (resident adult, resident subadult, translocated adult, translocated subadult); t – sampling occasion, Year – year released, 2019 or 2020; Av8WkDis – mean 8-week discharge; Sex – female or male; SeasSpr – spring season; SeasSum – summer season; DaysHeld – days held in quarantine; MaxTmpRel – maximum temperature on day of release; Av8WkTmp – mean 8-week temperature; EcoB – Central Basin & Range ecoregion; EcoM –Wasatch & Uinta Mountains ecoregion; "." – null model. See Table A-1 for more information.*

Table 2-4. Parameter estimates for two binomial generalized linear models using the expected number of dams in a given river reach from the Utah Beaver Restoration Assessment Tool (BRAT; Macfarlane, Wheaton, & Jensen, 2014; Macfarlane *et al.,* 2017) to predict observed river reaches with ≥ 1 beaver dam before beaver translocations occurred (“pre-translocation”), and after beaver translocations occurred (“post-translocation”) in the Price and San Rafael Rivers, Utah, USA, May-October 2019 and 2020.

Parameter	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**p-value**
Pre-translocation ~ BRAT				
Estimated dam capacity from BRAT	-0.32	-0.91	0.27	0.28
Post-translocation ~ BRAT				
Estimated dam capacity from BRAT	0.02	-0.35	0.39	0.93

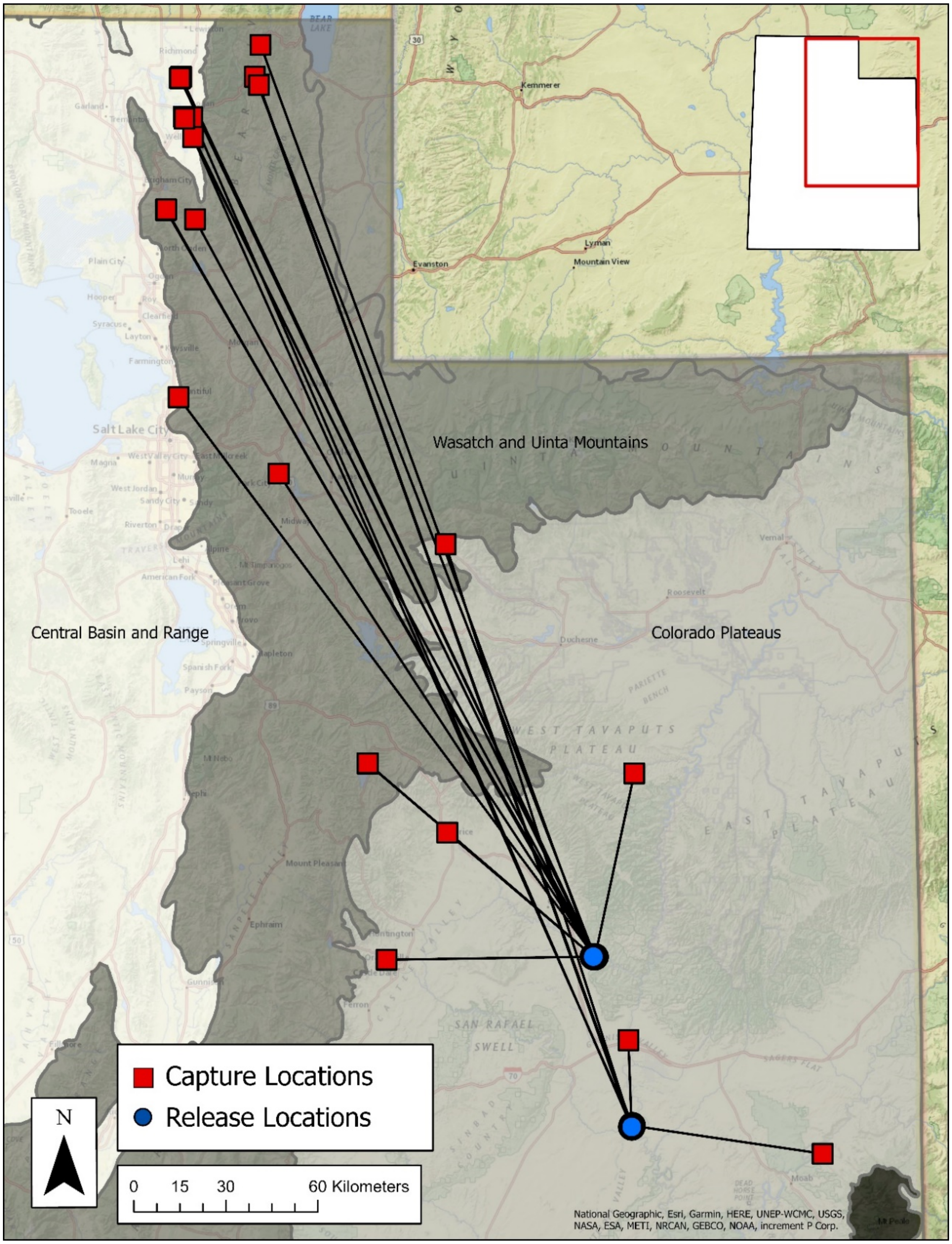


Figure 2-1. Capture and release locations of translocated beavers. Beavers were captured in three Omernik Level III ecoregion types in Utah (Omernik, 1987; delineation used by the U.S. Environmental Protection Agency). Release sites are on the Price River east of Woodside and the San Rafael River at Moonshine Wash, Utah, USA.

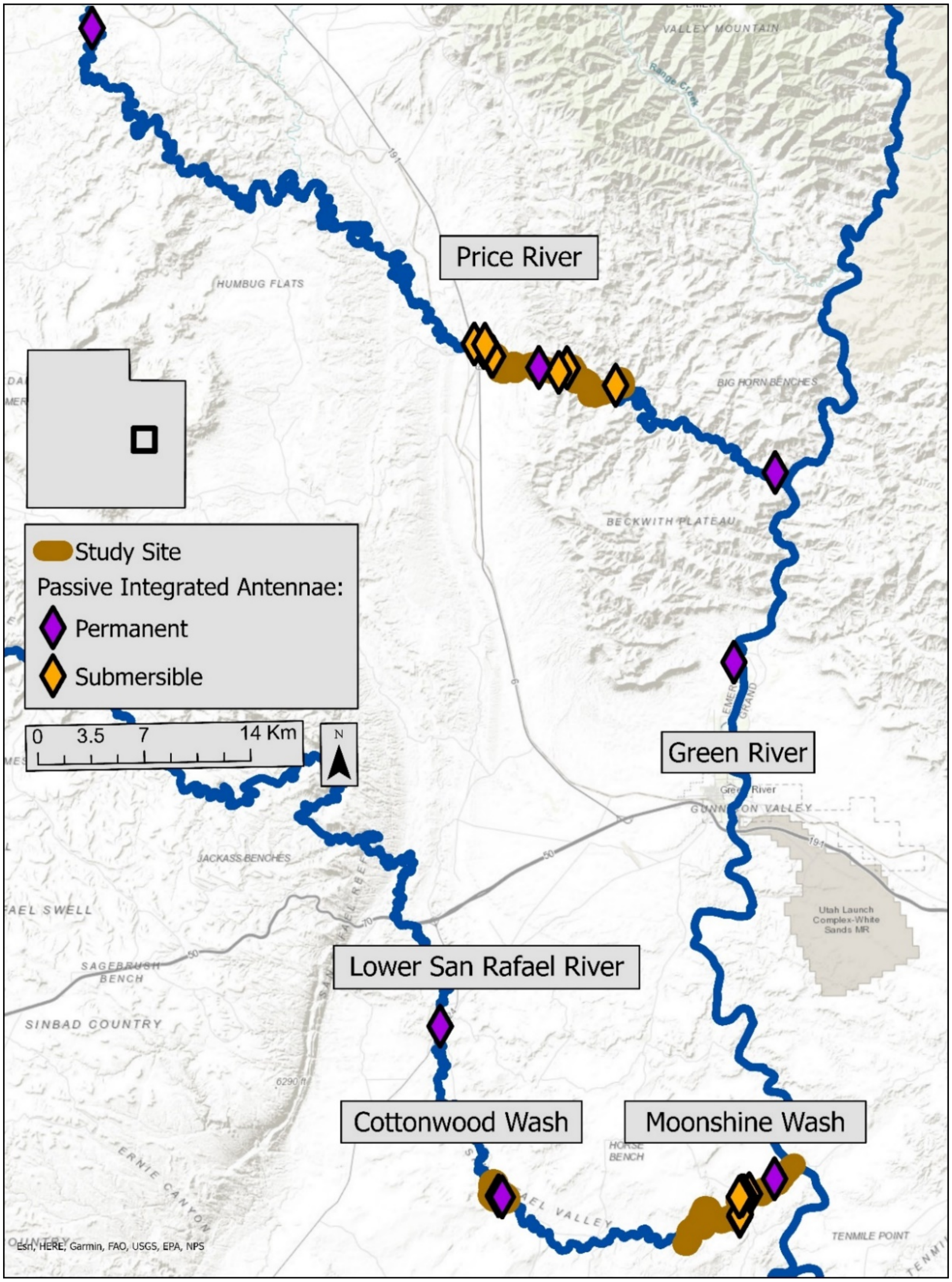
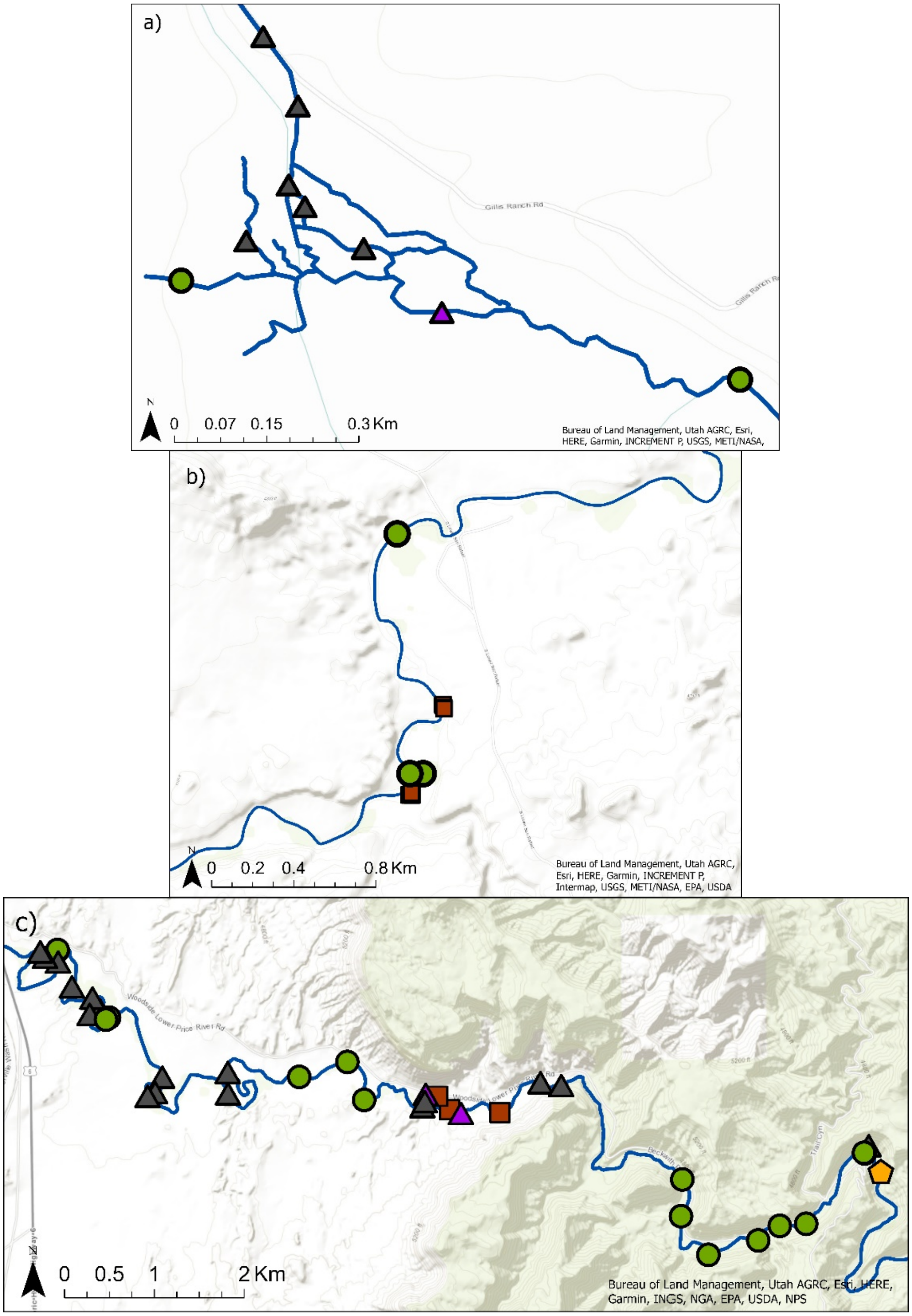


Figure 2-2. The three study sites for our study comparing resident and translocated beaver ecology in east-central Utah, USA: one on the Price River, and two on the lower San Rafael River at Cottonwood Wash and Moonshine Wash. Permanent and submersible "wagon wheel" passive integrated antennae (PIA) locations are included. All locations where submersible wagon wheels were deployed are shown but submersible PIAs were moved several times throughout the study and none remained in one location for the entire study.



Bureau of Land Management, Utah AGRC, Esri, HERE, Garmin, INCREMENT P, USGS, METI/NASA,

Bureau of Land Management, Utah AGRC, Esri, HERE, Garmin, INCREMENT P, Intermap, USGS, METI/NASA, EPA, USDA

Bureau of Land Management, Utah AGRC, Esri, HERE, Garmin, INGS, NGA, EPA, USDA, NPS

Figure 2-3. Beaver dams observed in relation to translocated beaver release sites at Cottonwood Wash (a) and Moonshine Wash (b) on the San Rafael River, and at the Price River (c) study sites, in Utah, USA, May-October 2019 and 2020.[a]

[a] *Key (by beaver type and dam category): Purple triangle – resident new dam, dark gray triangle – resident old dam, green circle – unknown new dam, yellow pentagon – translocated new dam; red square.*

CHAPTER 3

MOVEMENT PATTERNS OF RESIDENT AND TRANSLOCATED BEAVERS AT MULTIPLE SPATIOTEMPORAL SCALES IN DESERT RIVERS[2]

ABSTRACT

Wildlife translocations can dramatically alter animal movement behavior, so identifying common movement patterns post-translocation can help set expectations and anticipate behavior in future translocation efforts. Beavers (*Castor canadensis*) are frequently translocated to mitigate human-wildlife conflict and simultaneously used as an ecosystem restoration tool; however, little is known about naturally occurring beaver ecology or translocated beaver behavior in desert rivers where resources are patchy, scarce, and dynamic. We identified space-use patterns to develop an expectation framework of beaver movement behavior for future beaver-assisted restoration efforts. We captured, tagged, translocated, and monitored 41 beavers in desert river restoration sites on the Price and San Rafael Rivers, Utah, USA, and compared their space use to 16 resident beavers that we also tagged and monitored. Resident adult beavers were detected a mean maximum distance of 0.86 ± 0.21 river km (1 SE), while resident subadult (11.00 ± 4.24 km), translocated adult (19.69 ± 3.76 km), and translocated subadult (21.09 ± 5.54 km) beavers were detected at greater mean maximum distances. Coarse-scale movement models up to six months post-release showed translocated and resident subadult beavers moved substantially farther from release sites and faster than resident adult beavers, while fine-scale, short-term movement models showed similar activity levels for median distance traveled over 5-minute

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intervals. Low river discharge and high NDVI (vegetation greenness) had negative effects on coarse-scale movement patterns, while nighttime sampling and NDVI had positive effects on fine-scale movement patterns. Our findings suggest day-to-day activity patterns such as foraging and resting were largely unaltered by translocation, but translocated beavers exhibited movement behavior most similar to dispersal by resident subadults. Understanding translocated beaver movement behavior in desert systems can help future efforts identify appropriate sites where the potential for unintended conflict is minimized, and beavers still provide beneficial restoration services.

INTRODUCTION

Animal movement behavior, such as natal dispersal, migration, territoriality, and predator avoidance, serves a large role in the life history and ecological processes of a species (Nathan, 2008). However, when animals undergo involuntary movement such as translocation to an unfamiliar area, their natural movement behavior can be substantially altered (Heidinger *et al.*, 2009; Le Gouar, Mihoub, & Sarrazin, 2012). Some individuals may exhibit homing behavior, even when released extremely long distances from their place of origin (Dickens, Delehanty, & Romero, 2010). Translocated individuals may be forced to settle in lower-quality habitats (Burns, 2005), disperse if territorial resident conspecifics already occupy high-quality habitat (McNicol *et al.*, 2020), or move away from their release sites in search of mates (Mihoub *et al.*, 2011). In addition, animals may be translocated in response to human-wildlife conflict, but they can once again become problem individuals if released in an area that is too small to account for long-range movements or has inadequate resources (Weilenmann *et al.*, 2010; Le Gouar *et al.*, 2012). Identifying common movement patterns post-translocation can help to set expectations and anticipate behavioral responses in future translocation efforts, and ultimately guide management.

Beaver (American beaver, *Castor canadensis,* and Eurasian beaver, *C. fiber*) translocation is a popular method of human-wildlife conflict mitigation and ecosystem restoration. Once overexploited during the fur trade of the 1700s and 1800s (Baker & Hill, 2003; Halley, Saveljev, & Rosell, 2021), beaver populations have now recovered in some areas and come in close contact with humans, causing unwanted flooding, damaging trees, and jeopardizing infrastructure. Translocation provides an alternative method to lethal control by removing beavers from conflict situations and allowing them to potentially play a role in restoration initiatives. American and Eurasian beavers are ecologically similar (Rosell *et al.*, 2005), and as ecosystem engineers, both species can significantly alter the system they inhabit, primarily through dam building (Mills, Soulé, & Doak, 1993). Beaver dams retain water and mitigate the effects of drought, add heterogeneity to stream channels, impact riparian vegetation, and benefit many other species (Naiman, Johnstson, & Kelley, 1988; Rosell *et al.*, 2005; Pollock *et al.*, 2014). However, retaining translocated beavers at a targeted site and encouraging the initiation of passive restoration through dam-building can be challenging, and translocated individuals may not behave similarly to naturally occurring beavers, at least initially (Pilliod *et al.*, 2018; Nash *et al.*, 2021).

Beavers are central-place foragers, and dams are most commonly built by territorial colonies to create pools as cover near their lodge or burrow for predator avoidance and transport of wood (DeStefano *et al.*, 2006; McClintic *et al.*, 2014a; Ritter, 2018). Typically, beavers will not build dams during natal dispersal or transience. Home range of established beavers typically covers 1.6 to 3.9 river kilometers (Breck, Wilson, & Andersen, 2001; Herr & Rosell, 2004; Havens, Crawford, & Nelson, 2013), while dispersing subadult beavers typically travel 3.5 to 19.8 km before settling (Beer, 1955; Sun, Müller-Schwarze, & Schulte, 2000; Ritter, 2018). Autonomous displacement recorded for translocated beavers ranges widely from 3.3 to 238 km, leading to variable dam-building success (Hibbard, 1958; McKinstry & Anderson, 2002; Petro, Taylor, & Sanchez, 2015).

The ecology of naturally occurring beavers is understudied in desert rivers, and few translocations have occurred in such systems (Gibson & Olden, 2014; Barela & Frey, 2016). Beavers could play a vital role in desert rivers, sustaining water and increasing habitat complexity with their dams, especially because many arid systems have become imperiled by altered flow regimes and drought, habitat simplification, invasive species, and climate change (Harper, 2001; Stromberg, 2001; Mott Lacroix, Tapia, & Springer, 2017). With multiple releases to degraded sites, translocation can serve as an effective restoration tool in desert rivers (*see Chapter 2*), but beaver space use may be different in degraded arid systems where resources may be more patchy, scarce, and unpredictable than in other environments where the majority of beaver studies have occurred (Gibson & Olden, 2014; Barela & Frey, 2016). Degraded desert rivers with altered hydrographs have increased xeroriparian or upland desert habitat extending right to the river (Stromberg *et al.*, 2007), including vast thickets of tamarisk (*Tamarix* spp.; Nagler *et al*, 2018). These areas do not provide any palatable vegetation for beavers to forage, are rarely sources of building material, and may not be used by beavers especially if they encompass large stretches of river (Lesica & Miles, 2004; Barela & Frey, 2016). In contrast, riparian zones containing leafier, greener willow and cottonwood are used by beavers (Nagler *et al.*, 2004; Barela & Frey, 2016), so vegetation greenness may be an important indicator of beaver space use in desert systems, and may aid in determining the best release sites for beavers.

We compared space use of resident and translocated American beavers (hereafter, beaver) on multiple spatiotemporal scales. We expected that translocated beavers would initially be more active and move farther and more quickly than territorial resident beavers, but then eventually settle into similar movement patterns as resident beavers. A better understanding of the movement patterns of translocated beavers in this novel system can help develop an expectation framework of beaver movement behavior for future beaver-assisted restoration efforts in desert systems.

MATERIALS AND METHODS

Study Area

We conducted our study in desert tributaries of the Green River, along the lower stretches of the Price River and San Rafael River in east-central Utah, USA. Simplification, aggradation, dewatering, and invasive species encroachment have degraded the lower reaches of these rivers (Walker & Hudson, 2004; Bottcher, 2009). We selected the 20.5-km study site on the Price River near Woodside, Utah, USA, and the 8.1-km study site at Moonshine Wash on the San Rafael River near the confluence with the Green River, Utah, USA because there were ongoing restoration projects. Invasive tamarisk removal, gravel bar additions, native tree planting, and beaver dam analogue (BDA) construction had been completed at Moonshine Wash, with beaver translocations included as a passive restoration technique at both sites (Laub, 2015 & Laub, 2018). The third field site was a 1.5-km stretch near Cottonwood Wash on the San Rafael River, which we selected because it is a unique, complex stretch of river that developed after a sediment plug in 2010 slowly formed a braided system in the otherwise simplified and degraded river (Lyster, 2018). A resident beaver colony was already established there, so we did not translocate any beavers to this site but used it to study resident beaver movement patterns.

Both rivers flow through redrock desert, canyonlands, and desert shrubland. Willow (*Salix* spp.), Fremont cottonwood (*Populus fremontii*), common reed (*Phragmites* spp.), tamarisk (live and dead; *Tamarix ramosissima*), and Russian olive (*Elaeagnus angustifolia*) make up the majority of riparian vegetation, with cattails (*Typha* spp.) also growing at Cottonwood Wash. Typical temperatures range from 37°C in the summer to -11°C in the winter, and there is little rainfall, averaging 21 cm per year (NOAA, 2021).

To determine existing resident beaver activity before translocations, we conducted sign surveys at Cottonwood and Moonshine Wash in June 2019 and at the Price River study site in August 2019. Surveys entailed walking, wading, or floating along the rivers and marking all lodges, burrows, dams, and fresh beaver sign such as foraging, slides, and scent mounds on a handheld GPS unit (Garmin, Chicago, Illinois, USA; Model GPSMAP 78s or 66st). We observed evidence of resident beaver activity at Cottonwood Wash and in several stretches of the Price River, but few signs at Moonshine Wash.

Capture, Quarantine, and Tagging

All procedures including animal capture, handling, tagging, and monitoring were approved by Utah State University's Institute for Animal Care and Use Committee (No.10128). We responded to nuisance calls in northern, central, and eastern Utah to capture beavers for translocation. We captured resident beavers at the Price River and Cottonwood Wash study sites. We captured nuisance and resident beavers from May to October of 2019 and 2020 using Hancock/Koro suitcase-style traps, Comstock box traps, and nonlethal cable restraints. We held translocated beavers for at least three days to accommodate quarantine protocols (Utah Division of Wildlife Resources, 2017; Pilliod *et al.,* 2018), at the Utah State University Beaver Ecology and Relocation Center in Logan, Utah, or the field site, providing them with tree cuttings, root vegetables, rodent pellets, and fresh water daily (Campbell-Palmer & Rosell, 2015). Beavers were held an average of 4.4 ± 1.3 days before release.

We chemically immobilized beavers, supplemented with oxygen and isoflurane to process translocated and resident beavers (Roug *et al.,* 2018). During processing, we assigned an age class based on weight and body size (subadult = 1-2 years, adult > 2years; Patric & Webb, 1960) and sexed beavers using anal gland secretion (Schulte, Müller-Schwarze, & Sun, 1995; Woodruff & Pollock, 2018). We categorized beavers into four "state" categories: resident adult (RA), resident subadult (RS), translocated adult (TA), and translocated subadult (TS). Due to small sample size, we were unable to include sex to further split these state categories. All beavers received a passive integrated transponder- (PIT-) tag (Biomark APT12 tags; Boise, Idaho, USA) inserted in the tail. We also fitted adult and subadult beavers > 9 kg with tail-mounted transmitters (Rothmeyer, McKinstry, & Anderson 2002; Arjo *et al.,* 2008). Transmitters were either a remotely downloadable store on-board GPS tag (Africa Wildlife Tracking; Rietondale, Pretoria, South Africa) or a VHF modified ear-tag (Advanced Telemetry Systems, Isanti, Minnesota, USA; Model #M3530). Initially we secured GPS- and VHF-tags with neoprene (19 mm) and steel (19 mm) washers, then in September 2019 we increased the sizes of washers (neoprene: 38.1 mm, steel: 31.8 mm), which improved transmitter retention (Windels & Belant, 2016).

We released resident beavers at their capture sites, at Cottonwood Wash (2019) and in the Price River (2019 and 2020). We released translocated beavers in unoccupied portions of the Price River study site both years, but only released translocated beavers near BDAs at Moonshine Wash in 2019, since drought in 2020 caused extremely low flows in the San Rafael River study sites, making them unsuitable for translocation.

Monitoring

We tracked beavers two to seven times per week via GPS locations and radio-telemetry using homing-in or triangulation techniques from May through October 2019 and 2020. We also used semi-permanent and submersible passive integrated antennae (PIA; Biomark; Boise, Idaho, USA) in the rivers to passively detect PIT-tags from May 2019 through March 2021. Some beavers emigrated from the study sites, so we scanned along the Green River monthly, conducted one aerial flight, and floated the Price and San Rafael Rivers several times to attempt to locate these individuals. We only included live detections in analyses, and assumed that all PIA detections were of live beavers.

We also conducted hour-long, fine-scale movement monitoring sessions on a weekly to bi-monthly basis per individual. First, we triangulated the individual to get a general location and positioned ourselves perpendicular to that point along the river. From this location, we took a bearing every five minutes to approximate the beaver's movement patterns in the river.

Depending on terrain and vegetation, we were 10-320 m from the river during monitoring sessions.

Home Range Analysis

To generate beaver locations from triangulations, we input at least three telemetry bearings ≤ 30 minutes apart into "Location of A Signal" (LOAS, version 4.0, Ecological Software Solutions, Sacramento, CA) using Maximum Likelihood Estimation. We only included LOAS locations < 200 m from the river with < 10 ha error ellipse in analyses. We calculated linear home ranges for resident beavers with ≥ 15 locations (Sauer, Ben-David, & Bowyer, 1999; Blundell, Maier, & Debevec, 2001). First, we combined all GPS, triangulation, homing-in, and PIA locations, only including locations ≥ 24 hours apart for a given individual to minimize autocorrelation between consecutive locations. To avoid skewing home range estimations to PIA locations, we only included PIA detections during the period we radio-tracked a given individual. For each individual we estimated their home range, or the area used by an individual during normal day-to-day activities (Burt, 1943, Powell, 2000), and core use areas, the portion of the home range used the most by the individual (Powell, 2000). To generate these estimations, we fit 95% (home range) and 50% (core use) Minimum Convex Polygons (MCPs) using package "adehabitatHR" in program R (Calenge, 2006, version 0.4.18). We reported home range and core use lengths as the one-dimensional length of river contained within the 95% and 50% MCPs, respectively. We also determined transient (temporary) and permanent establishment sites of translocated beavers, which we defined as areas with ≥ 3 consecutive locations within the mean 100% MCP home range size of our resident beavers, used for ≥ 7 days for transient sites, and ≥ 91 days for permanent sites (*see methods in* Woodford, Macfarland, & Worland, 2013; Matykiewicz *et al.,* 2021). All data are reported as $\bar{x}$ ± 1 Standard Error.

Coarse-Scale Movement Analyses

We used three methods to compare coarse-scale movement patterns among translocated and resident beavers. All locations ≥ 2.5 hours apart for a given individual were used for these analyses. First, we used package "riverdist" in Program R to snap the most up- and down-stream locations for each beaver to the closest vertex (spaced 0.5 m apart) of our river network shapefile and calculate the maximum river distance detected for all resident and translocated beavers (Tyers, 2016, version 0.15.3; R Core Team, version 4.0.3, 2020). Second, we used "riverdist" to calculate the distance each beaver location was from the individual's release site (in km), only including individuals with ≥ 3 locations within the first 6 months post-release, as we detected very few individuals longer than this. Third, we calculated the step length (in m) between consecutive points using "riverdist", including only step lengths > 0 m, ≤ 91-day step durations, and individuals with ≥ 2 step lengths.

To statistically analyze the latter two measurements, we constructed two log-log linear regression mixed models to assess differences in displacement from release ($distance\ from\ release\ site \sim time\ since\ release$) and the distance from one observed location to the next ($step\ length \sim step\ duration$) between resident and translocated adult and subadult beavers, and the influence of several covariates on these differences. The log-log regressions are needed here to account for the theoretically expected non-linear relationship between displacement and time (*for further details see* Street, Avgar, & Börger, 2017). For $ln(distance\ from\ release)$, our global model included the following fixed effects: state category (RA, RS, TA, or TS), $ln(time\ since\ release)$, the interaction between state category and $ln(time\ since\ release)$, whether the location was a PIA detection or not (as opposed to GPS or telemetry locations), year released, site released, days held in quarantine, whether the individual was part of a group of beavers or not (family or pair), sex, discharge category, and normalized difference vegetation index of the previous location (NDVI). Individual ID was included as a random effect on both the intercept and $ln(time\ since\ release)$. For $ln(step\ length)$, our global model included the following fixed effects: state category, $ln(step\ duration)$, whether the starting location was a PIA detection or not, the (scaled) number of days since release, year released, site released, days held in quarantine, whether the individual was part of a group of beavers or not (family or pair), sex, discharge category, and NDVI at the start of the step. Individual ID was included as a random effect on both the intercept and $ln(step\ duration)$.

We categorized discharge (high, medium, or low; cubic feet per second (cfs)) based on median historical average discharge (87.2 cfs) for the lower Price and San Rafael Rivers, using 66 and 84 years of data respectively (USGS, 2021a). We included all discharges from 0 to 30.9 cfs in the "low" category, discharges from 31.0 to 142.9 cfs in the "medium" category, and all discharges greater than 143.0 cfs in the "high" category.

We used NDVI as a greenness index of standing plant biomass at beaver locations (Pettorelli *et al*., 2011; Neumann *et al.,* 2015). NDVI is an effective measure of suitable beaver habitat because tamarisk thickets and desert habitat have lower NDVI than cottonwood, willow, and riparian zones favored by beavers (Lesica & Miles, 2004; Nagler *et al*., 2004; Barela & Frey, 2016). The NDVI values at the start of a given step were used because the habitat quality at this "starting" location should influence a beaver's inclination to move far. For example, an area of high NDVI indicates high greenness, a proxy for higher quality habitat, which a beaver is likely to spend more time in than an area of low NDVI, which indicates low greenness and a proxy for poor quality habitat, which a beaver will spend less time in (*similar to* Avgar *et al*., 2013; McClintic *et al*., 2014b). Over 95% of beaver locations used in analyses had a location error < 900 m^2, so we downloaded 30 x 30 m resolution Landsat 8 Operational Land Imager Surface Reflectance scenes with < 15% cloud cover for NDVI derivation. We ordered scenes through USGS Earth Explorer (USGS, 2021b) and NDVI calculations from the Earth Science Processing

Architecture platform (USGS, 2017). We generated seasonal mean NDVI pixel values using the "Mosaic to New Raster" tool in ArcGIS Pro (ESRI, 2021; version 2.8.0; Redlands, CA, USA). In our rivers, discharge and NDVI typically follow seasonal patterns, so we did not include season as an additional covariate.

Mixed effects log-log linear models were fitted using package "nlme" in program R (Pinheiro *et al.,* 2013; version 3.1.152). To select the best models based on Akaike's Information Criterion corrected for small sample size (AICc), we employed backward stepwise variable selection to identify the most parsimonious models (within ΔAICc ≤ 2 of the models with the lowest AICc value) in package "MuMIn" in program R (Barton, 2009; version 1.43.17). We fitted models using maximum likelihood through the model selection procedure but then refitted the best models using restricted maximum likelihood. We confirmed normality using diagnostic plots of the best model residuals.

Fine-Scale Movement Analysis

We estimated the beaver's location in the river using the "Bearing Distance to Line" and "Intersect" tools in ArcGIS Pro (ESRI, 2021; version 2.8.0; Redlands, CA, USA) from the bearings taken during fine-scale (five minutes between consecutive observations) movement monitoring sessions. We assumed beavers were in the river for all locations. Using these estimated points, we calculated the step length between consecutive points in "riverdist" using the same methods as described above. Lastly, we calculated the median five-minute step length (in meters) for each sampling session. We were unable to include individual step length in analysis because our sample size was too small to include nested random effects of sampling session within Beaver ID.

We used a log-linear regression mixed model to compare the fine-scale movement rates (median five-minute step lengths) of resident adult and translocated adult and subadult beavers, and the influence of several covariates on these movement patterns. We included the following covariates as fixed effects: state category, year released, days held in quarantine, whether the individual was part of a group of beavers or not (family or pair), sex, time of day (day- or night-time sampling session), discharge category, mean NDVI calculated from all 5-minute steps in a sampling session, study site, and $ln(days\ since\ release)$. We included individual ID as a random effect on the intercept. We categorized daytime as 06:00-17:59 hours and nighttime as 18:00-05:59 hours. We employed stepwise variable selection with the same methods as above to reduce to the final model, using residual diagnostic plots to confirm normality.

Comparing Coarse- and Fine-Scale Model Relationships

To determine whether the variation in the models attributed to individual beavers was similar at different spatiotemporal scales, we compared random effects from our coarse-scale displacement and step length models with those from our fine-scale movement rate model. We extracted values for the Best Linear Unbiased Predictions (BLUPs) of the random effect of Beaver ID from each of the three final models with package "nlme" (Pinheiro *et al.,* 2013; version 3.1.152). Then we calculated pairwise Spearman Rank Correlation coefficients in Program R for all pairwise combinations of BLUPs, only including BLUPs for individual beavers that appeared in both respective models (Spearman, 1904; R Core Team, 2020; version 4.0.3). If individual-based variation in movement is consistent across scales, we would expect a strong positive correlation between individual BLUPs.

RESULTS

We captured and PIT-tagged 16 resident beavers; three at Cottonwood Wash and 13 on the Price River (10 adults, 6 subadults). We fitted twelve of these beavers with radio transmitters (9 adults, 3 subadults). We captured and PIT-tagged 41 translocated beavers; we translocated eight to Moonshine Wash on the San Rafael River and 33 to the Price River (21 adults, 20 subadults). We fitted 35 translocated beavers (21 adults, 14 subadults) with radio transmitters. We censored three additional resident beavers from analyses because they died from capture- or processing-related events. We released 36 translocated beavers (76.5%) as family groups or as pairs formed during quarantine.

We estimated the mean 95% MCP home range for resident adult beavers as 0.44 ± 0.07 km (n = 8), and the mean core 50% MCP area as 0.18 ± 0.05 km (n = 8). We were unable to assess differences in home range size between sexes or sites due to small sample size. In addition, we were unable to radio-track any resident subadult or translocated beavers long enough to observe home range establishment and subsequently collect enough locations for home range estimation.

On average we detected resident subadult and translocated beavers over tenfold longer stretches of river than resident adult beavers (Table 3-1). The time passed between an individuals' most up- and downstream locations was an average of 54.1 ± 31.5 days for resident adult beavers, 35.9 ± 30.1 days for resident subadult beavers, 38.1 ± 23.6 days for translocated adult beavers, and 40.6 ± 12.1 days for translocated subadult beavers. We detected 41.4% of all translocated adult and subadult beavers (n = 17) > 20 km from their release site (Figure 3-1). Eleven translocated beavers (four adults at the Price River, two adults at Moonshine Wash, and five subadults at the Price River) settled in transient resting sites within the study areas for an average of 16.2 ± 2.7 days before moving to other areas. We did not observe any transient resting sites for resident subadult beavers. Four translocated beavers (two adults, two subadults) permanently settled outside the study areas; three near the confluence of the Green and Price Rivers, and one subadult beaver farther downstream closer to the town of Green River (Figure 3-1). We detected these beavers for an average of 134.8 ± 7.5 days with PIAs at these settlement sites.

Based on the displacement model, we observed distinct differences in the relationship between the distance and time since release resident adult beavers and resident subadult or translocated beavers traveled from their release sites in the first six months post-release ($\alpha = 0.05$;

Table 3-2). *Low discharge* and high *NDVI* at a given previous location negatively influenced coarse-scale displacement. *Beaver ID* as a random effect appeared to substantially improve model fit (marginal $R^2 = 0.45$, conditional $R^2 = 0.87$). Resident adult beavers remained at shorter distances from their release sites throughout time, while the other beaver state categories traveled much farther distances from their release sites when all other covariates were held constant (Figure 3-2).

For the step length model, 97.6% of step lengths (603 steps out of 618 total) included in the analysis were < 6 months post-release, similar to the timeframe used for the coarse-scale displacement model. Based on the step length model, we observed differences between the speed of resident adult beavers and resident subadult or translocated beavers (Table 3-2). *Low discharge*, *Moonshine Wash study site*, and high *NDVI* at the start of a given step negatively influenced speed, while *PIA detections* were associated with higher speed. Similar to the displacement model, *Beaver ID* as a random effect appeared to improve model fit (marginal $R^2 = 0.35$, conditional $R^2 = 0.51$). Resident beavers appeared to move more slowly than the other beaver state categories, though all state categories exhibited gradual deceleration in increasing step duration when all other covariates were held constant (Figure 3-3).

Conversely, the fine-scale movement rate model indicated that translocated beavers' median distance moved was slightly less than resident adult beavers during 5-minute sampling intervals, though the 95% Confidence Intervals (CI) of *state category* overlapped zero (Table 3-2; Figure A-3). We did not detect any resident subadults long enough to conduct these fine-scale movement monitoring sessions, and we excluded Cottonwood Wash from this analysis because we only monitored one individual on a fine-scale at this site. *Time of day* (day vs. night) was an important parameter explaining fine-scale beaver movement patterns, with beavers moving more at night. Including *Individual ID* as a random effect in the fine-scale movement rate model did not improve model fit (marginal $R^2 = 0.37$, conditional $R^2 = 0.37$). *Mean NDVI* for a given sampling session was positively associated with fine-scale beaver movement rate.

Spearman correlation coefficients between BLUPs were consistently positive and had moderate magnitude ($\rho = 0.30$ to 0.57) when comparing individual intercepts among all three models, and when comparing the time-related BLUPs between the displacement and step length models (Figure 3-4). Based on our pairwise comparisons of BLUPs it appears that the variation attributed to individual beavers is repeatable at multiple spatiotemporal scales, suggesting in general those individuals which moved the farthest and fastest on a coarse scale were also the most active on a fine scale.

DISCUSSION

Our findings suggest translocated beavers exhibited movement behavior most similar to dispersing resident subadult beavers, likely moving through their new environment in search of a mate and a suitable site to establish. Based on the displacement and step length models we estimated that in the first six months post-release, translocated beavers moved no differently than resident subadult beavers, and all moved substantially farther and faster than resident adult beavers, who already had established territories and therefore had no need for exploratory movement patterns. However, based on our fine-scale movement rate model, we observed no difference in median distance moved between translocated and resident adult beavers during a short time span, suggesting day-to-day activity patterns such as foraging and resting were not greatly impacted by dispersal or translocation. These results suggest that although translocated beavers typically had wide-ranging movement patterns, they still retained some natural behaviors, and once establishing a home range they may eventually behave similarly to resident adult beavers with regard to movement patterns, the most likely individuals to build dams and contribute to ecosystem restoration.

Resident adult beavers remained in small stretches of river throughout time (a mean linear river distance of 0.86 ± 0.21 km between a given individual's most upstream and downstream locations), suggesting they had established home ranges. We calculated linear home ranges that can provide accurate estimates of the area used by semi-aquatic mammals in riverine environments (Blundell, *et al.*, 2001; Sauer *et al.*, 1999; Ahlers *et al.*, 2010). Common home range estimators such as minimum convex polygon (MCP) and kernel density estimators would overestimate beaver home ranges by including unused desert habitat (Andersen & Shafroth, 2010; Gibson & Olden, 2014). Mean home range (0.44 ± 0.07 km) and core use (0.18 ± 0.05 km) sizes of our resident adult beavers were smaller than other studies using similar methods of linear home range estimation. For example, Eurasian beavers in Norway had a mean 95% linear home range size of 3.6 ± 1.6 km (Graf *et al.*, 2016). For American beavers in the Green River in northwestern Colorado, farther upstream from our study, mean 95% linear home range size was 2.19 ± 0.46 km (1 SE; Breck *et al.*, 2001). In Illinois, mean linear 95% home range size was 1.8 ± 0.3 km (1 SE) in smaller streams, and 3.6 ± 0.5 km in larger rivers, and the investigators suggested resources may be less widely dispersed in smaller rivers (Havens *et al.*, 2013). Our small home range sizes could be due in part to our smaller stream size, similar to a small creek in Oregon, where mean linear home range size was 1.56 ± 0.71 km (1 SE; Maenhout, 2013).

Resource availability in a given season may also affect home range size (Bloomquist, Nielsen, & Shew, 2012; McClintic *et al.*, 2014b; Korbelová *et al.*, 2016), an effect which may be intensified in a desert ecosystem. We monitored most individuals in the summer when temperatures were at extreme highs and localized food resources were available, both potentially contributing to reduced movements. In addition, we tracked many beavers during drought periods when river discharges were low, increasing the difficulty of predator evasion for movements far from the safety of a burrow or lodge. Home range size of beavers can also be limited by high population density (Busher, Warner, & Jenkins, 1983), but it is unlikely this was a factor in our study. Based on the sign surveys we conducted, as well as those conducted by Macfarlane *et al.* (2017), beaver density remained extremely low even with the addition of translocated beavers at our study sites. Finally, we had limited sample size for most of our home range estimates (< 30 locations for 62.5% of individuals), and therefore our estimates may not have captured the full length of river that our beavers used.

Resident subadult and translocated beavers moved farther from their release sites than resident adult beavers, supported by the displacement model. We acknowledge that spatiotemporal autocorrelation exists due to our use of sequential observations in this model, but it serves as an effective demonstration of the considerably larger distances traveled by dispersing subadult and translocated beavers compared to resident adult beavers, even soon after release. The linear river distances between a given resident subadult or translocated individual's most upstream and downstream locations were similar to or larger than movement patterns recorded in other studies (RS, 11.00 ± 4.24 km; TA, 19.69 ± 3.76 km; TS, 21.09 ± 5.54 km). In Montana, mean dispersal-settlement distance for American beavers was 10.9 ± 3.1 km (Ritter, 2018), and in Oregon, it was 16.17 ± 9.34 km (Maenhout, 2013), while mean dispersal distance of Eurasian beavers in Norway was 4.5 ± 5.4 km (Mayer, Zedrosser, & Rosell, 2017). All four of the resident subadult beavers in our study dispersed following release; three moved > 9 km, and though one only moved 2.38 km, its movements were from its natal colony to another colony, an indication of successful dispersal (Sun *et al.*, 2000). It is possible that capture and handling could have induced these dispersal events (Kukalová, Gazárková, & Adamík, 2013), but a study in Norway observed no change in short-term Eurasian beaver space use post-capture and -tagging, though only dominant adults were included in the study and effects may be different for other age classes (Graf *et al.*, 2016). In other studies, translocated beavers also tended to travel similar distances as compared to dispersing subadult beavers, with mean distances moved such as 14.6 ± 2.1 km in North Dakota (Hibbard, 1958), 7.4 straight-line km for beavers released in streams in Wisconsin

(Knudsen & Hale, 1965), and > 10 km from their release sites for 51% of translocated beavers in Wyoming (McKinstry & Anderson, 2002). Conversely, in Oregon translocated beavers only moved a mean distance of 3.3 ± 0.2 km from their release sites, indicating their model-based method of release-site selection may have identified high-quality habitat which encouraged beavers to stay (Petro *et al.*, 2015). Translocated individuals may also roam much further than naturally dispersing individuals. Along with our study, where translocated beavers moved up to 101.8 km, beavers have been reported to move 238 km in North Dakota (Hibbard, 1958) and 76.2 km in Wisconsin (Knudsen & Hale, 1965).

Resources may be patchier and more unpredictable in desert rivers, causing dispersers to travel long distances to find an area to establish with sufficient resources for survival (Gibson & Olden, 2014; Barela & Frey, 2016). In addition, in our rivers with low beaver density (Macfarlane *et al.*, 2017), individuals may have to travel farther to find a mate. After one week post-release, we observed no translocated beavers who were released as a pair or family group in close proximity to each other, indicating that translocated beavers likely were searching for new mates after release. Low beaver densities also result in more unoccupied territories and fewer aggressive encounters with conspecifics, allowing resident subadult and translocated beavers to be choosier about selecting high-quality sites to establish (DeStefano *et al.*, 2006) and reducing “social resistance” effects (Armansin *et al.*, 2020). Some of our translocated beavers used temporary settlement sites centered around a discovered burrow or hiding place as a known safety refuge from which to conduct exploratory movements, which has been documented in dispersing subadult beavers as well (Sun *et al.*, 2000; McNew & Woolf, 2005; Ritter, 2018).

Our results from the step length model demonstrated that resident subadult and translocated beavers also appeared to move more quickly than resident adult beavers. Notably, one translocated beaver moved 30.7 km in 2.37 days. When prey species are in an area of suitable resources and cover, they tend to move more slowly to reduce their encounter rate with predators, as opposed to when prey are in areas in which resources are poor or perceived predation risk is high, they tend to move more quickly to minimize the time spent in the risky area (Prokopenko, Boyce, & Avgar, 2017; Dickie *et al.*, 2020). Resident adult beavers were likely already established in the best quality habitat, spending more time in concentrated areas of high resource availability with a known place of safety nearby, therefore moving more slowly to reduce their encounter rates with predators. This pattern is similar to a study of woodland caribou (*Rangifer tarandus caribou*) in Ontario, Canada in which higher forage quality and availability and summertime refuge habitat for calves were linked to decreased movement rates (Avgar *et al.*, 2013). Though there are no aquatic predators of beavers in our system besides river otters (*Lontra canadensis*), which were extremely rare in our rivers and seldom prey upon beavers (Reid e*t al.*, 1994), the fact that resident subadult and translocated beavers were in an unfamiliar environment may have heightened their perceived predation risk, causing them to move faster. Similarly, wolverines (*Gulo gulo luscus*) in Alberta were found to move more quickly near roads with increasing traffic, mimicking a natural response to increasing predation risk (Scrafford *et al.*, 2018). In Alabama, beavers moved faster in wetlands the farther they moved from their lodge, likely to minimize the increasing predation risk from alligators the farther away they moved from known cover (McClintic *et al.*, 2014a). In addition, resident subadult and translocated beavers likely moved through areas of poor habitat during dispersal, moving quickly through the areas unsuitable for foraging or rest, comparable to a study in Cyprus where Eleonora's falcons (*Falco eleonorae*) flew over unsuitable habitat more quickly during migration (Hadjikyriakou *et al.*, 2020).

Fine-scale movement behavior did not differ strongly by beaver state category, suggesting environmental factors had a larger effect on median distance moved in five minutes. In general, beavers exhibit crepuscular or nocturnal activity patterns as a predator avoidance strategy (Swinnen, Hughes, & Leirs, 2015). Translocation or dispersal did not appear to alter this behavior; all beavers moved less during the day, likely resting in burrows or lodges to insulate against the extreme desert temperatures (Buech, Rugg, & Miller, 1989). During dispersal or translocation, beavers must still forage and rest to survive, and our fine-scale movement patterns suggest that these short-term behaviors remained similar to resident adult beavers behaving naturally. We note that there is likely some error in our estimation of the true location of beavers during fine-scale monitoring since we used single bearings to estimate locations, but the error 88remained generally the same at various sampling distances from the river based on calibration tests using stationary test transmitters, and therefore this bias appeared fairly uniform across sampling sessions.

In both coarse-scale models (displacement and step length), including individual ID as a random effect improved model fit, by 42% for the displacement model and 16% for the step length model, suggesting there was some variation in coarse-scale movement behavior among individuals. Individual ID did not improve model fit for the fine-scale movement rate model, perhaps indicating that short-term beaver activity patterns were less variable among individuals (conditional and marginal R^2 values were 0.37). For the fine-scale movement rate model, we were unable to provide repeated sampling for some individuals and had small sample size (n = 21 individuals), which could be contributing factors to the lack of model fit as well.

Low discharge appeared to cause beavers of all state categories to remain closer to release sites and move more slowly (displacement and step length models). Some studies of dispersing subadult beavers have reported that the predominant direction of travel is downstream (Leege, 1968; Sun *et al*., 2000), and 66.3% of our translocated and resident subadult beavers' final detections were downstream of their release sites. When traveling downstream, beavers would have to exert more energy to travel long distances at low discharge as opposed to when flows are higher and faster and the river itself would push them downstream. Beavers may also perceive a higher predation risk when discharge is low and deep pools for underwater travel in the river are scarce, leading them to spend more time hiding than moving.

In addition, the results from our coarse-scale models suggest that higher vegetation greenness (NDVI) also decreased beaver displacement and speed. Though we were unable to conduct a habitat selection analysis or use more detailed habitat covariates (*e.g.,* Wang, McClintic, & Taylor, 2019), this pattern indicates NDVI could be used as a quick and simple habitat metric for translocated beaver release site selection by identifying areas with long stretches of high greenness, which may encourage beavers to stay closer to and move away more slowly from release sites. Conversely, higher vegetation greenness (NDVI) appeared to result in increased fine-scale median distance moved, potentially explained by beavers foraging at night in areas with higher NDVI (mean 0.36 ± 0.02 NDVI for all nighttime sessions), therefore being more active in the greener areas, and resting during the day in areas with lower NDVI (mean 0.30 ± 0.03 NDVI for all daytime sessions). We were however unable to include a *time of day* and *mean NDVI* interaction term in our fine-scale model due to small sample size.

An individual's personality, shaped in part by the abiotic and inter- and intraspecific interactions an individual is exposed to over its lifetime, can contribute to individual variation in movement behavior (Shaw, 2020). However, rarely has consistent individual variation in movement tendencies been correlated across spatial scales (Spiegel *et al.*, 2017). Based on our BLUPs comparisons between our displacement, step length, and fine-scale movement rate models, it appears that there may be some link in individual beaver movement patterns across spatiotemporal scales. By determining which translocated individuals are more or less active on a fine-scale post-release, which takes little time and effort to monitor, restoration projects can potentially anticipate which beavers will quickly move long distances and not contribute to restoration efforts at targeted sites, and which beavers will successfully stay near release sites long-term. However, given we observed only moderate correlations and used BLUPs and not modeling to compare individual behavior at multiple spatiotemporal scales, further research is needed to investigate these inferences (Hadfield *et al.*, 2010).

To our knowledge, this study is the first to compare naturally occurring resident beaver movement behavior to translocated beaver movement behavior in the same system and is one of few studies of naturally occurring beaver movement ecology in desert systems (Gibson & Olden, 2014). Though translocated beavers tended to move more similarly to dispersing resident subadult beavers overall, the displacement from release model shows a gradual leveling-off for these state categories, suggesting these individuals will eventually establish a home range similar to resident adult beavers and may subsequently build dams which contribute to restoration. Releasing beavers at lower river discharges and areas of high vegetation greenness may encourage them to stay nearer to release sites, though these factors should be considered in the context of existing release site selection recommendations to increase establishment success (Pollock *et al*., 2018; Ritter, 2018; Brick & Woodruff, 2019). For example, previous studies have also observed increases in beaver dams near structural features such as BDAs installed in rivers (Bouwes *et al.*, 2016), and these structures create deep pools which help improve translocation success (Pollock *et al*., 2018).

Translocation is an important alternative to the lethal removal of nuisance beavers, and our study shows that targeted restoration sites should have large surrounding buffer areas where beavers can establish without becoming nuisance animals. Gaining a better understanding of beaver movement behavior post-translocation can help to set realistic expectations and increase the success of beaver-related restoration. Determining translocated beaver movement behavior in desert systems by using resident beavers as baselines of comparison can help future efforts identify appropriate sites where the potential for unintended conflict is minimized and beavers provide beneficial restoration services. This comparative technique could also be applied to

Eurasian beaver restoration monitoring in Europe and Asia, as well as to better inform translocation outcomes for other species as well.

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TABLES AND FIGURES

Table 3-1. The mean linear river distances (km) between resident and translocated adult and subadult beavers' most upstream and downstream locations in the Price, San Rafael, and Green Rivers in east-central Utah, USA. Beavers were monitored via PIT-, VHF-, and GPS-tags from May 2019 to March 2021.

State Category	n	Mean	1 Standard Error	Minimum	Maximum
Resident adult	9	0.86	0.21	0.13	2.19
Resident subadult	4	11.00	4.24	2.38	22.66
Translocated adult	21	19.69	3.76	2.63	58.3
Translocated subadult	19	21.09	5.54	0.3[†]	101.8

[†] *Mortality event < 3 days post-release*

Table 3-2. Fixed effects estimates from three movement models of resident adult (RA), resident subadult (RS), translocated adult (TA), and translocated subadult (TS) beavers monitored via PIT-, VHF-, and GPS-tags in desert rivers in east-central, Utah, USA, from May 2019 to March 2021. Models were fitted to each of three response variables: displacement (distance from release; marginal $R^2 = 0.45$, conditional $R^2 = 0.87$, n = 1107), step length (distance from one observed location to the next; marginal $R^2 = 0.35$, conditional $R^2 = 0.51$, n = 618), and fine-scale movement rate (median 5-minute step length; marginal $R^2 = 0.37$, conditional $R^2 = 0.37$, n = 68).

Parameter	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
Coarse-scale displacement			
Low discharge	-0.12	-0.2376	-0.0024
NDVI (previous location)	-0.53	-0.8828	-0.1772
Ln(Time since release)	-0.05	-0.2068	0.1068
(RS + TA + TS)*Ln(Time since release)	0.46	0.3032	0.6168
Coarse-scale step length			
(RS + TA + TS)	2.23	1.4656	2.9944
PIA detection	0.47	0.0976	0.8424
Site (Moonshine Wash)	-1.00	-1.9212	-0.0788
Low discharge	-0.70	-1.2292	-0.1708
NDVI (start of step)	-1.59	-3.0796	-0.1004
Time since release (scaled)	-0.71	-0.9452	-0.4748
Ln(Step Duration)	0.52	0.3436	0.6964
Fine-scale movement rate			
(TA + TS)	-0.49	-1.0192	0.0392
Time of Day (Night)	0.80	0.2904	1.3096
Mean NDVI	3.31	1.3696	5.2504
Ln(Time Since Release)	-0.26	-0.4756	-0.0444

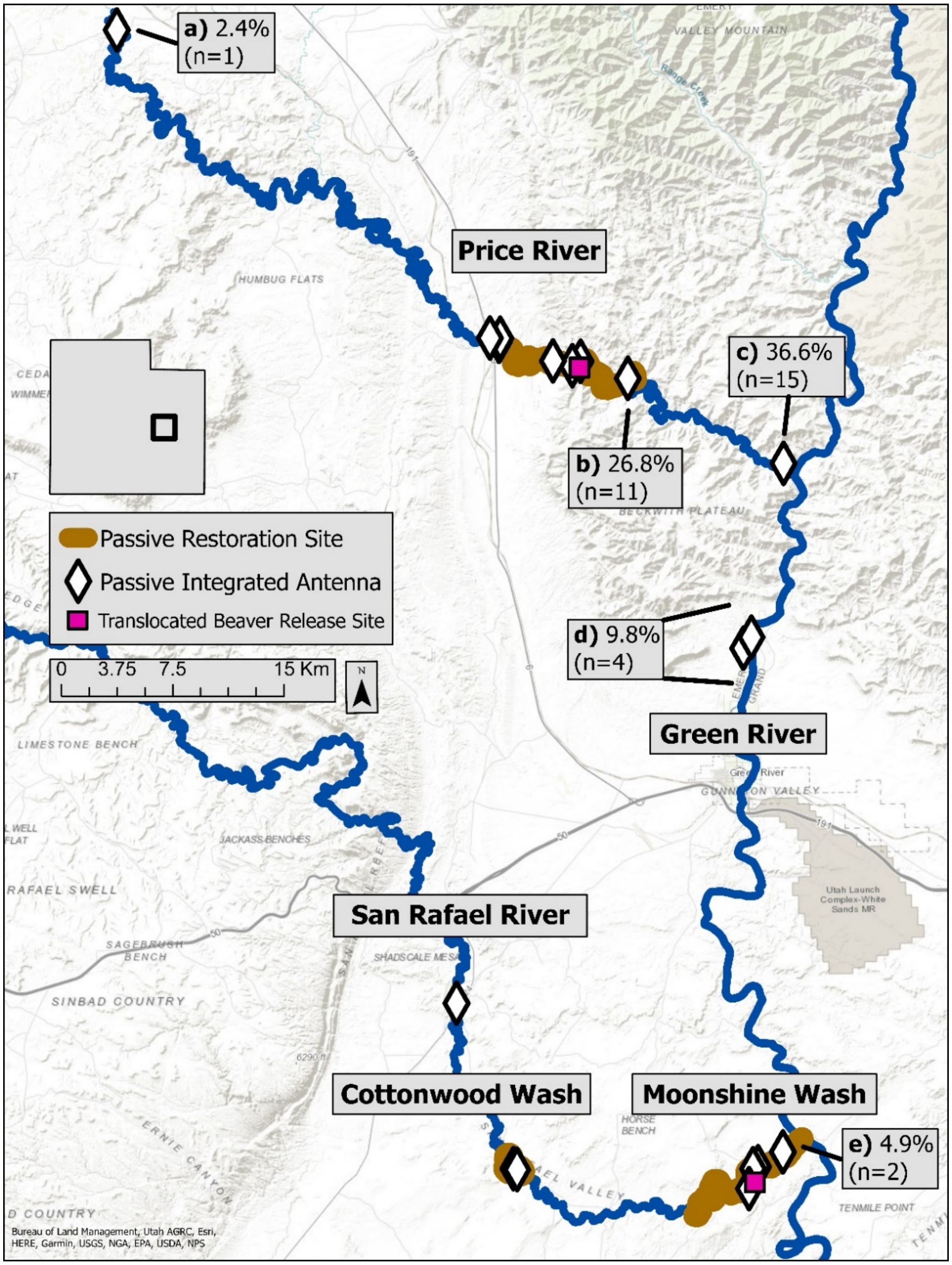

Figure 3-1. Study sites on the Price River east of Woodside and on the lower San Rafael River at Cottonwood Wash and Moonshine Wash in east-central Utah, USA. Inset text boxes labeled with letters represent the proportion and number of translocated beavers detected at certain passive integrated antennae (PIA)[†].

[†] *Distance each PIA is from a given translocated beaver release site: a) 101 km from Price River release site, b) 7 km from Price River release site, c) 29 km from Price River release site, d) 47 km from Price River release site and 58 km from Moonshine Wash release site, e) 5 km from Moonshine Wash release site.*

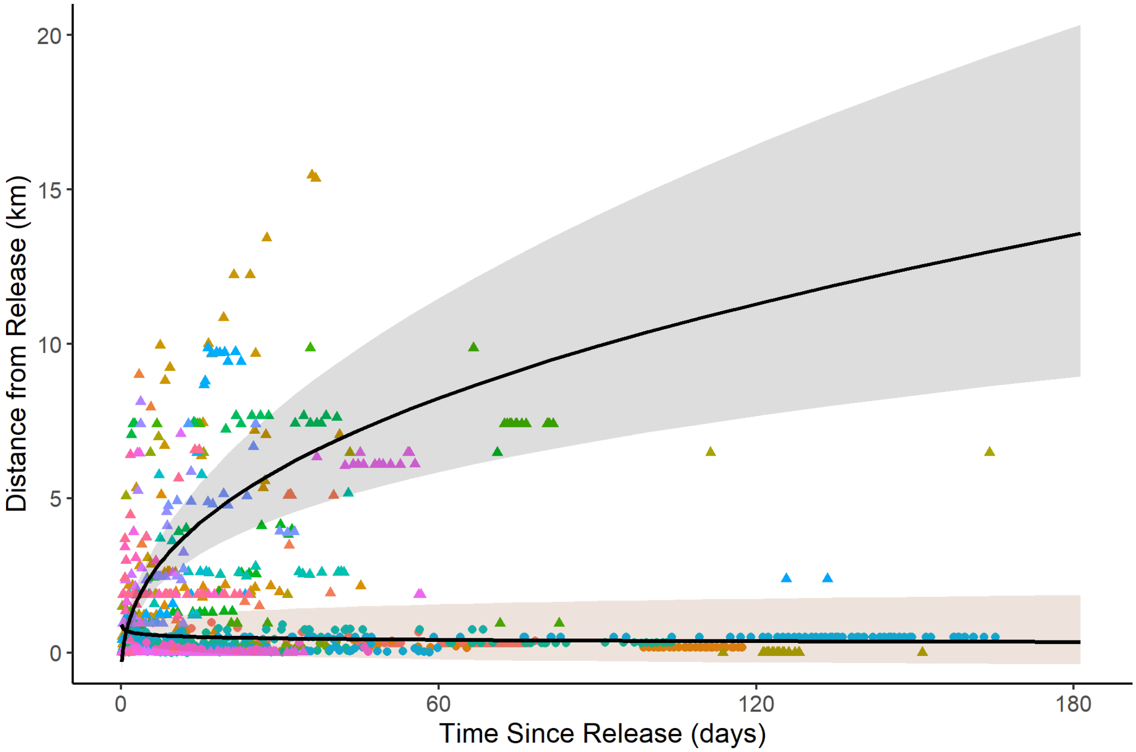

Figure 3-2. Relationship between distance from release (displacement) and time since release for beavers monitored in desert rivers, east-central Utah, USA. Circles represent observations of resident adult beavers, and triangles represent observations of resident subadult, translocated subadult, or translocated adult beavers. The coloration of points denotes individual beavers. Lines and 95% Confidence Intervals (brown = resident adult beavers, gray = all other beavers) are back-transformed predicted values only including the fixed effects of a log-log regression linear mixed model. We held all other covariates constant for visualization purposes: low discharge and mean NDVI.

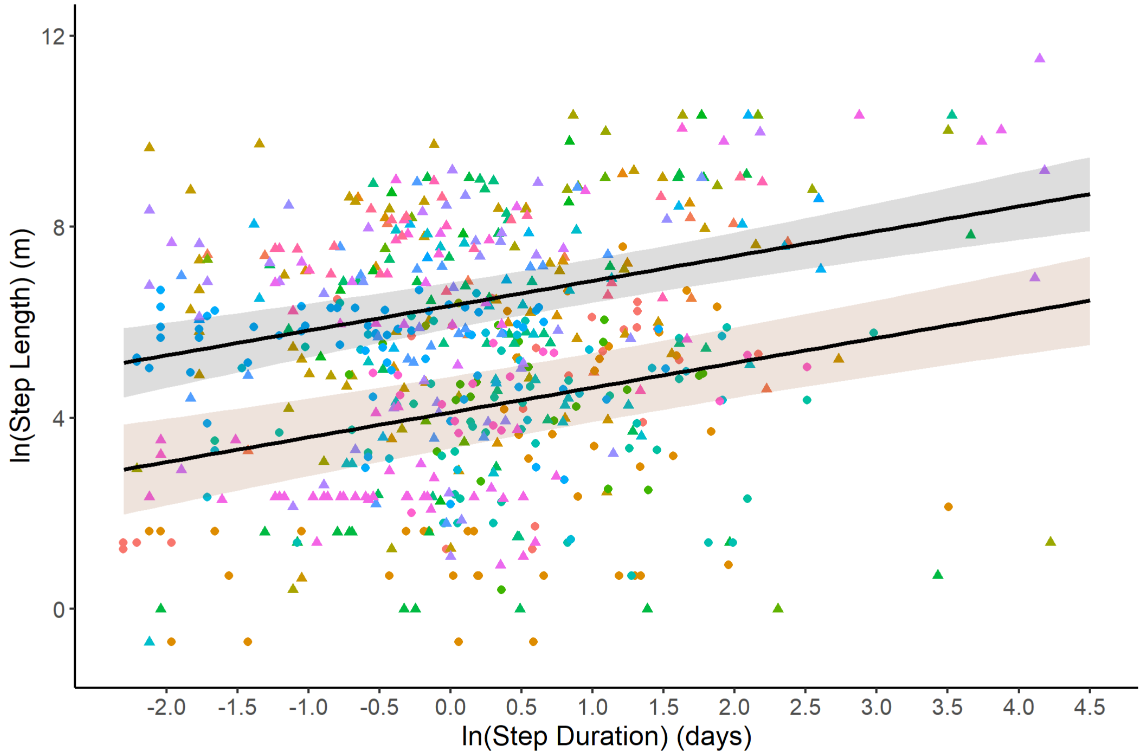

Figure 3-3. Relationship between $ln(step\ duration)$ and $ln(step\ length)$ for beavers monitored in desert rivers, east-central Utah, USA. Circles represent observations of resident adult beavers, and triangles represent observations of resident subadult, translocated subadult, or translocated adult beavers. The coloration of points denotes individual beavers. Lines and 95% Confidence Intervals (brown = resident adult beavers, gray = all other beavers) are predicted values including only the fixed effects of a log-log regression linear mixed model. We held all other covariates held constant for visualization purposes (low discharge, Price and Cottonwood study sites, PIA detections only, mean time since release, and mean NDVI).

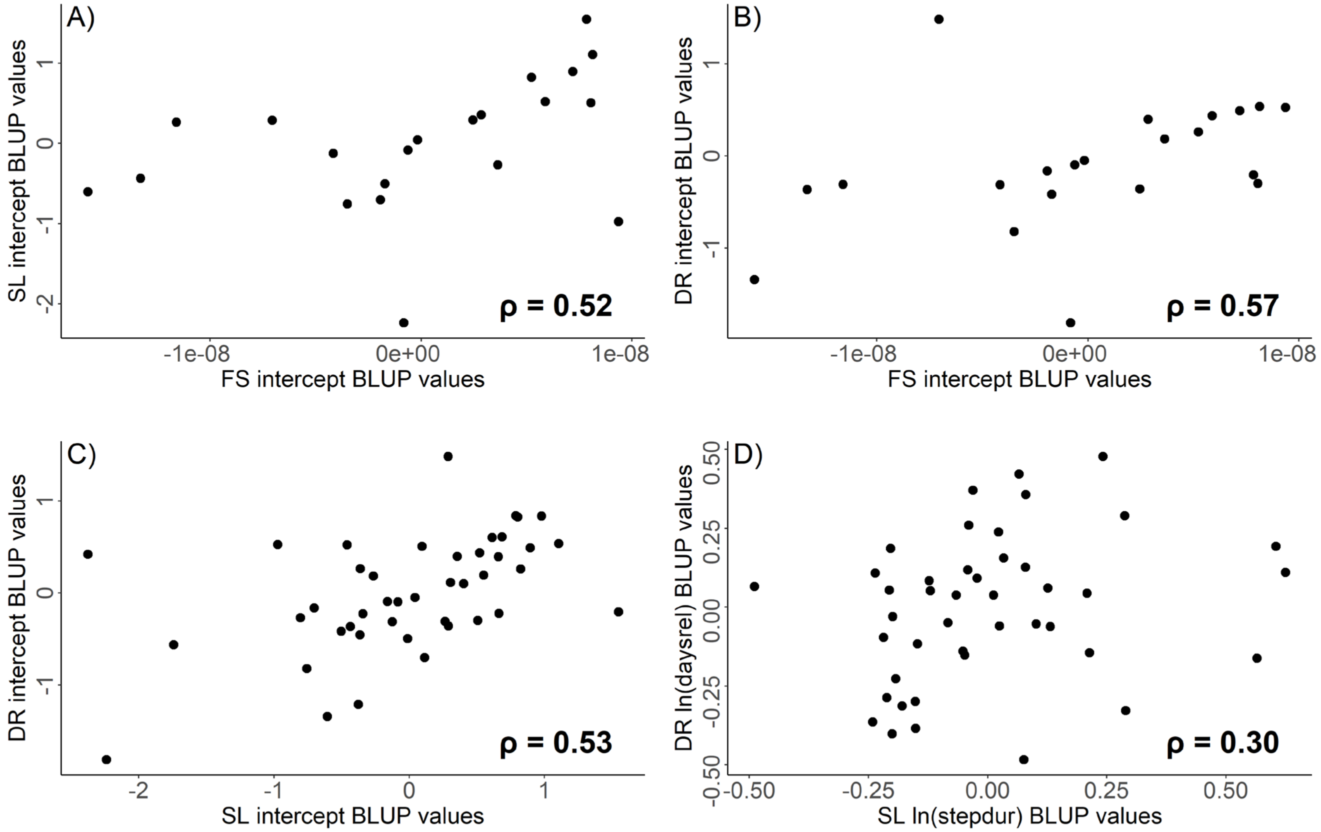

Figure 3-4. Pairwise comparisons between Best Linear Unbiased Predictions (BLUPs) of individual beavers monitored in desert rivers in east-central Utah, USA and included as random effects in 3 movement models: fine-scale movement (FS), step length (SL), and displacement from release (DR). Spearman Rank Correlation coefficients, ρ, are displayed in the lower-right of each figure[†].

[†] ***A)*** *SL intercept BLUPs~ FS intercept BLUPs,* ***B)*** *DR intercept~ FS intercept,*
C) *DR intercept~ SL intercept,* ***D)*** *DR ln(days since release)~ SL ln(step duration)*

CHAPTER 4

CONCLUSIONS

This study provides insight into the ecology of resident and translocated beavers in desert river restoration sites. I captured, tagged, and monitored 47 nuisance beavers that were translocated and released in 21 separate efforts to the Price and San Rafael Rivers, Utah. I compared their site fidelity, apparent survival, dam-building behavior, and movement patterns to 24 resident beavers. Beavers were split into four “state” categories for analyses: resident adult, resident subadult, translocated adult, and translocated subadult (kits were excluded due to limited monitoring abilities). Results show that translocated beavers had survival rates and behaved like resident subadult beavers during dispersal. Initially translocated beavers had low site fidelity, low survival, and did not build dams. They also moved long distances through the rivers, likely in search of a mate and a suitable place to establish similar to beavers during natural dispersal events. These movements indicate that restoration efforts should select sites where even when beavers move far away from their release location, they can still provide beneficial services to the system and will not be subject to human-wildlife conflict.

Despite difficulties with long-term monitoring limiting my ability to identify individuals due to transmitter loss and failure, it appeared that some translocated beavers may have eventually established in the study areas and built dams. These individuals likely settled into similar patterns as resident adult beavers who had higher site fidelity, higher survival, built dams, and used small sections of river. As dam-building is the goal of most beaver-assisted restoration, those individuals that remained at targeted restoration sites, survived, and built dams would be considered part of successful restoration efforts. Thus, when multiple beavers are translocated in several release efforts, it appears that translocation can be used as a passive river restoration tool and can supplement existing low populations with no apparent negative effects on resident beavers in desert rivers.

In Chapter 2, I focused specifically on comparing translocated and resident beaver site fidelity, survival, and dam-building behavior. I monitored beavers via radio-telemetry, GPS locations, and Passive Integrated Antennae (PIAs) from May 2019-March 2021. I used Cormack-Jolly-Seber (CJS) models to estimate the apparent survival, or the probability of surviving and remaining in the study sites, of beavers for at least eight weeks post-release. My resident subadult and translocated adult and subadult beaver apparent survival rates (0.24 ± 0.34; 1 Standard Error, 0.37 ± 0.01, and 0.24 ± 0.12, respectively) were lower than the survival rates reported in other studies of naturally dispersing beavers (*e.g.* 0.76 ± 0.05 for females and 0.55 ± 0.07 for males, Bloomquist & Neilsen, 2010; 0.82, 0.710-0.96 (95% C.I.), DeStefano *et al.*, 2006; 0.84, 0.76-0.93 (2016) and 0.67, 0.65-0.69 (2017), Ritter, 2018) as well as translocated beavers (*e.g.* 0.49 ± 0.07, McKinstry & Anderson, 2002; 0.47 ± 0.12, Petro *et al.*, 2015; 64-67%, Nolet & Baveco, 1996). My estimates are lower likely due to the limitations of my CJS analyses; I was unable to estimate mortality separately from emigration from the study sites. Beavers had high rates of emigration from my study sites (38.3% of translocated beavers were detected outside of the study sites; n = 18), and I observed only eight mortalities out of 38 radio-tagged resident subadult and translocated beavers. Unsurprisingly, resident subadult and translocated beavers had significantly lower apparent survival than my resident adult beavers because they are more vulnerable to predation, starvation, and translocation or dispersal-related stressors (Letty, Marchandeau, & Aubineau, 2007; Müller-Schwarze, 2011; Bonte *et al.*, 2012). My resident adult apparent survival rates (0.88 ± 0.09) were more comparable to other studies (*e.g.,* 0.76 ± 0.05 for females and 0.87 ± 0.04 for males, Bloomquist & Nielsen, 2010; 0.88, 0.75-1.00, DeStefano *et al.*, 2006; 0.78 ± 0.14, Maenhout, 2013; 0.87 ± 0.02 for dominant adults, Campbell *et al.*, 2012) likely because none of these individuals emigrated from the study sites. The high apparent survival of my resident adult beavers could indicate that once translocated beavers establish and adjust to their new desert system, these individuals will also have similar high survival, an indication of successful translocation.

I conducted beaver dam surveys to determine the number of river reaches with beaver dams in the study sites before and after translocation. I compared these observations with the expected maximum dam capacity per river reach in my study sites from the Beaver Restoration Assessment Tool with a binomial generalized linear model. I also compared the number of river reaches with ≥ 1 dam pre- and post-translocation using a χ^2 Goodness of Fit test. I observed significantly more river reaches with beaver dams post-translocation as compared to pre-translocation, showing that translocation efforts may have increased restoration services in the rivers despite being in dynamic, wood-limited desert rivers (DeVries *et al.*, 2012; Persico & Meyer, 2013; Barela & Frey, 2016). Nevertheless, the number of river reaches containing observed beaver dams was not well-predicted by the maximum dam capacity from the Beaver Restoration Assessment Tool (BRAT; Macfarlane *et al.,* 2017). Only 1% of the Price River watershed's BRAT dam capacity was fulfilled by beaver dams in a survey conducted by Macfarlane *et al.* (2017), so it appears that these rivers are far below their maximum beaver capacity. Therefore, translocations could help to supplement the low existing population and increase the overall number of dams in the rivers.

In Chapter 3, I compared the space use of resident and translocated beavers at multiple spatiotemporal scales. I used telemetry, GPS, and PIA detections to develop coarse-scale movement models comparing the displacement from release site and the speed (step length) of beaver state categories. According to my displacement and step length models, which generally modeled movement patterns in the first six months post-release, translocated beavers moved no differently than resident subadult beavers. However, translocated and resident subadult beavers moved substantially farther and faster than resident adult beavers who maintained home ranges. The mean maximum distance detected for resident adult beavers was 0.86 ± 0.21 km, for resident subadult beavers was 11.00 ± 4.24 km, for translocated adult beavers was 19.69 ± 3.76 km, and for translocated subadult beavers was 21.09 ± 5.54 km. In desert rivers, resources may be patchy, scarce, and unpredictable, leading dispersers to travel long distances in search of a mate and a site with sufficient resources for survival to establish (Gibson & Olden, 2014; Barela & Frey, 2016). When moving through unfamiliar waters during dispersal, these resident subadult and translocated beavers likely have heightened perception of predation risk and encounter areas of poor-quality habitat, leading them to move more quickly than resident adult beavers established in areas of high resource availability with known places of escape from predators. High vegetation greenness (NDVI) and low river discharge (< 31 cubic feet per second in my rivers) appeared to decrease beaver displacement and speed for all state categories. These factors could be considered when selecting release site locations and the timing of translocation in desert rivers, where perhaps areas of high NDVI may have enough resources to encourage translocated beavers to stay nearby, and low discharge makes it more difficult for beavers to quickly move away from release sites. However, when applying river discharge and NDVI to release site selection of future translocation efforts, these factors should be considered within the context of existing research specifically on maximizing beaver-related restoration success (Pollock *et al*., 2018; Ritter, 2018; Brick & Woodruff, 2019). In addition, it should be noted that extremely low discharge such as in drought may lead to death (2 out of 8 observed mortalities in my study were due in part to release during drought), so fluctuations in river discharge should be carefully assessed before releasing translocated beavers.

In addition to monitoring coarse-scale movement patterns of beavers in the first six months post-release, I also conducted fine-scale movement monitoring sessions by estimating a beaver's location in the river every five minutes over an hour. With these fine-scale data, I was able to model the median distance a beaver moved in five minutes as a proxy for activity level (*i.e.,* active vs. not active). There were no differences in the median distance moved between resident adult and translocated beavers in the fine-scale movement rate analysis. This result suggests that though translocated beavers may have had wide-ranging coarse-scale movement patterns, some behaviors regarding day-to-day activity patterns such as foraging or resting were unaltered by translocation. For example, time of day (day vs. night) was an important predictor of median distance moved for all state categories, indicating that even translocated beavers remained most active at night and moved less during the day, likely resting in burrows or lodges to insulate against the intense desert heat (Buech, Rugg, & Miller, 1989).

To my knowledge, I conducted the first comparative study of resident and translocated beaver ecology in the same system. In addition, my study was conducted in desert rivers, a relatively novel system in which little beaver research has been conducted (Gibson & Olden, 2014). More research is needed to expand upon the findings of my study, ideally with fewer logistical challenges constraining the length of monitoring and sample size to explore the long-term effects of beaver translocation. The relationship between translocation success and in-stream structures in desert rivers should also be explored, as beaver dam analogues and other structures improve site fidelity and encourage dam building (Bouwes *et al.*, 2016, Pollock *et al.*, 2018).

Translocation can considerably alter an individual's natural behavior and life history traits, and I investigated these changes in translocated beavers to help set a framework of realistic expectations and anticipate unexpected outcomes after translocation. The mobility, mortality, and unpredictable nature of translocated beavers must be accounted for to achieve translocation success. Establishment in localized areas may require the release of many individuals in multiple release efforts for a subset of individuals to eventually establish, but success should not be limited to the small-scale reach level. Instead, translocation success should be expanded to include those beavers who survived, established, and built dams long distances from their release site, as a landscape-level approach is necessary to achieve widespread, long-lasting restoration of degraded waterways (Bernhardt & Palmer, 2011; Bennett *et al.*, 2016). I found that adding translocated beavers into my rivers resulted in no apparent changes to the behavior and life history traits of resident beavers, suggesting that translocations can be used to augment dam-building in populations below carrying capacity to reach restoration goals more quickly. In addition, regardless of whether individuals contribute to restoration efforts or not, translocation remains an effective tool for human-beaver conflict mitigation when release sites are selected that allow for the long-distance movement patterns of some individuals.

Climate change and environmental degradation are worldwide threats to biodiversity, and as desert rivers undergo increasing periods of drought and dewatering, the animals that rely on perennial water for survival in these arid environments are threatened (Mott Lacroix, Tapia, & Springer, 2017). Using effective methods to sustain water in these systems even during drought is increasingly important (Stromberg, 2001), and beaver dams can have large contributions to drought mitigation (Hood & Bayley, 2008; Fairfax & Small, 2018). Improving our understanding of desert beaver ecology and beaver translocations in desert systems can help to increase the efficacy of beaver-related restoration, and ultimately contribute to ecosystem-wide conservation efforts in these imperiled arid systems.

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APPENDICES

APPENDIX A. SUPPLEMENTARY TABLES

Table A-1. Key to parameter codes used for AICc table of eight-week Cormack-Jolly-Seber models of apparent survival probability for resident and translocated beavers in the desert Price and San Rafael Rivers of Utah, USA, May-October 2019 and 2020.

Parameter name	Parameter code	Parameter type	Description
φ	Phi	Probability	Apparent survival
p	p	Probability	Encounter/Detection
Group Type	g	Categorical	Resident adult, resident subadult, translocated adult, translocated subadult
Sex	Sex	Categorical	Female or male
Year	Year	Categorical	2019 or 2020
Ecoregion	EcoB	Categorical	Central Basin and Range
	EcoM	Categorical	Wasatch and Uinta Mountains
	N/A	Categorical	Colorado Plateaus
Season	SeasSpr	Categorical	Spring
	SeasSum	Categorical	Summer
	N/A	Categorical	Fall
Mean 8 Week Discharge	Av8WkDis	Continuous	Mean discharge for each individual’s first 8 weeks post-release
Mean 8 Week Temperature	Av8WkTmp	Continuous	Mean temperature for each individual’s first 8 weeks post-release
Maximum Temperature on Release	MaxTmpRel	Continuous	Maximum temperature on each individual’s day of release
Days Held in Quarantine	DaysHeld	Continuous	Number of days held in quarantine prior to release
Null	.	N/A	Null model with no covariates included to estimate φ or p

Table A-2. Kaplan-Meier survival estimates for resident and translocated beavers in the Price and San Rafael Rivers, Utah, USA, up to eight weeks post-release. Beavers were not separated by age class due to small sample size. In my study, I experienced high rates of transmitter failure, transmitter loss, and emigration to areas of limited detection so this analysis is not truly "known-fate", an assumption of Kaplan-Meier estimators. Nevertheless, I included this appendix to further support my explanation that my low apparent survival rates from the Cormack-Jolly-Seber analysis for resident subadult and translocated beavers are attributed to high emigration and not just high mortality of these individuals.

Group Type	n	Survival Rate	1 Standard Error	Lower 95% CI	Upper 95% CI
Resident	10	0.900	0.095	0.732	1.00
Translocated	35	0.710	0.102	0.536	0.940

APPENDIX B. SUPPLEMENTARY FIGURES

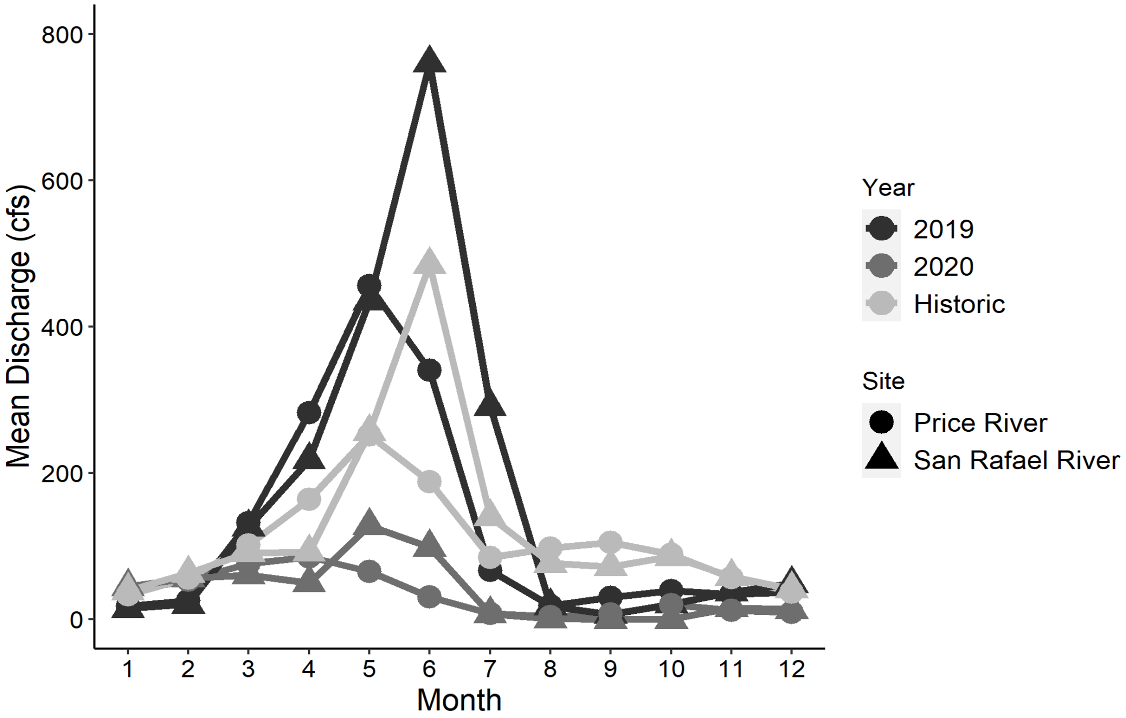

Figure A-1. Mean monthly discharge (cubic feet per second) for the Price River at Woodside and the San Rafael River at Hatts Ranch, Utah, USA. Lines illustrate each year of the study (2019 and 2020) and the historical mean monthly discharge at each site (October 1909 – September 2021 for the San Rafael River and October 1946 – September 2021 for the Price River; USGS 2021).

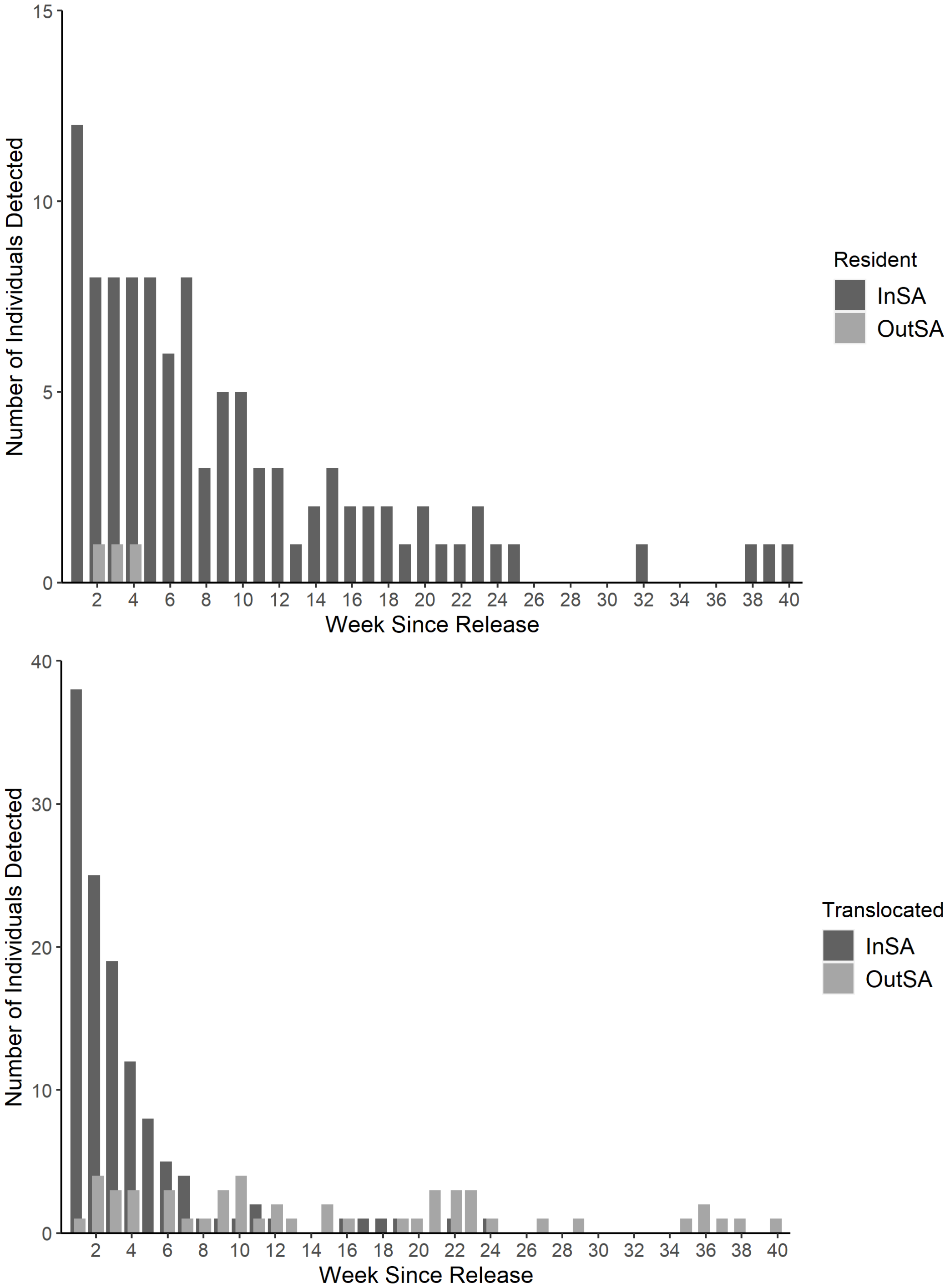

Figure A-2. The number of individuals detected each week post-release in ("InSA") and out ("OutSA") of three study sites for resident beavers (top) and translocated beavers (bottom) on the Price and San Rafael Rivers, Utah, USA.

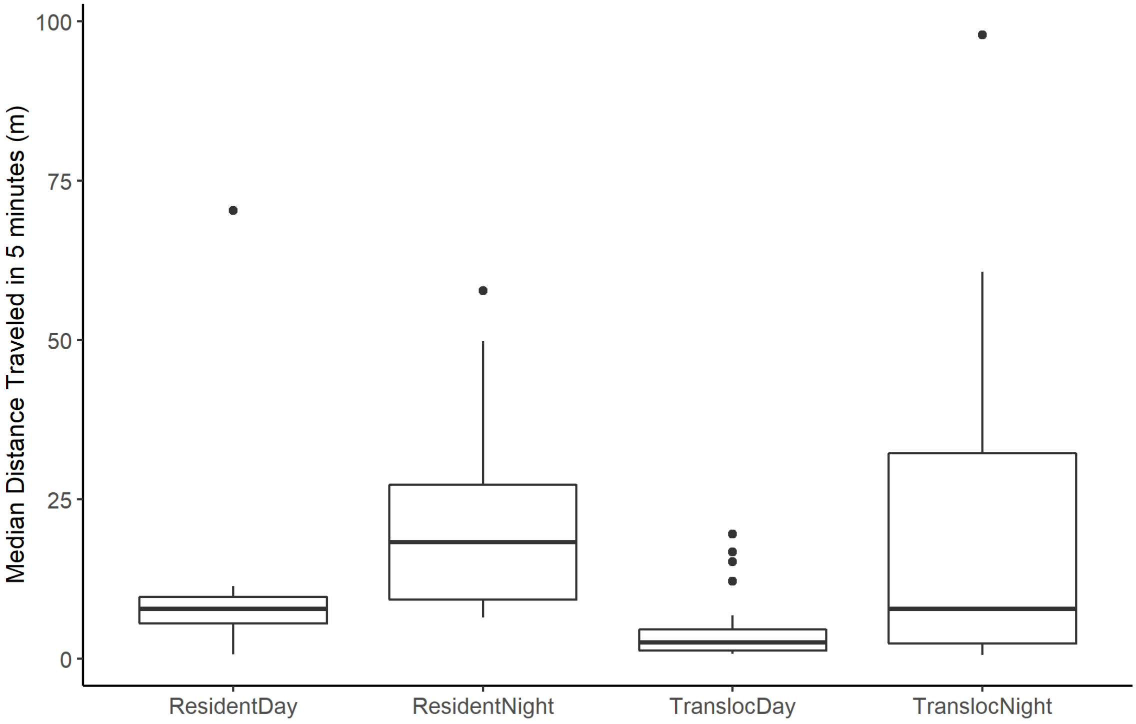

Figure A-3. Median distance (m) resident and translocated beavers traveled in 5 minutes during hour-long sampling sessions in the Price, San Rafael, and Green Rivers, Utah USA. Observations are separated by beaver group type (“Resident” or “Transloc”) and time of day (“Day” or “Night”).