# Management and Mother Nature: piping plover demography and condition in response to flooding on the Missouri River

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Management and Mother Nature: piping plover demography and condition in response to flooding on the Missouri River

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**ABSTRACT (ACADEMIC)**

Globally, riparian ecosystems are in decline due to anthropogenic modifications including damming, channelization and the conversion of the floodplain for human use. These changes can profoundly affect riparian species as many have adapted to the historical dynamism of these ecosystems. On the managed Missouri River, an imperiled shorebird, the piping plover (*Charadrius melodus*) uses riverine sandbars to breed. From 2004 to 2009, due to limited breeding habitat and low population numbers, the U.S. Army Corps of Engineers constructed 255 ha of sandbar habitat to benefit piping plovers and least terns (*Sternula antillarum*). During the breeding seasons of 2010 and 2011, historically high flows resulted in the creation of 1,887 ha of suitable sandbar habitat. Our study compared the demographic response and the condition of piping plovers to these anthropogenic and natural habitat creation events.

From 2005–2014 we monitored 1,071 nests, and from those nests we uniquely banded 968 adults and 2,021 piping plover chicks. We obtained 405 egg (clutch) mass measurements, 1,285 mass measurements from 633 adults, and 7,093 mass measurements from 1,996 plover chicks resulting in 3,175 mass measurements from 654 broods of chicks. We also collected 3,347 invertebrate prey samples. We used a random effects logistic exposure model to estimate nest success, a random effects Cormack-Jolly-Seber model in RMARK to estimate pre-fledge chick survival and the

Barker model in RMARK to estimate hatch-year (HY) and after hatch-year (AHY) survival and fidelity to our study area. We then used estimates from these analyses to calculate reproductive output, reproductive output necessary for a stationary population, and population growth (λ). For adult condition and egg (clutch) mass we used generalized linear mixed regression, and for pre-fledge chick growth rates we used a modified Richard's model to estimate the effects of habitat type (pre- vs. post-flood). We also tested for differences in invertebrate prey abundance between habitat types using negative binomial regression.

Our results indicated that AHY survival varied throughout our study and was lowest during the flood (2010 and 2011). We found that nest success, pre-fledge chick survival, reproductive output, and HY survival and fidelity were consistently higher on the flood-created habitat than engineered habitat, leading to sustained population growth after the flooding, as compared to just one year of population growth prior to the flood. Unlike pre-flood engineered habitat, the demographic parameters we measured did not decrease as the post-flood habitat aged. These differences were related to increased sandbar habitat, low nesting densities, and decreased nest and chick predation on the post-flood habitat. Although we hypothesized that increased demographic rates would be reflected by increased piping plover condition following the flood, we found that our measured condition variables (adult mass, clutch mass, and pre-fledge chick growth rates) remained unchanged following the flood. We also found evidence that clutch mass, chick growth rates and invertebrate prey abundance decreased as the post-flood sandbar habitat aged. As the condition of individuals did not appear to contribute directly to the increased demographic rates following the flood,

we suggest that the change in density-dependent predation pressure may explain the discrepancy. As many ecosystems have previously been altered, it's rare that ecologists have the opportunity to compare management practices with natural ecosystem processes. Results from this study suggest that management intervention may not be an equivalent substitute for natural ecosystem processes and provide insight on future management of riparian ecosystem.

## ABSTRACT (PUBLIC)

Worldwide, riverine ecosystems are declining, which has had a negative effect on many species. On the managed Missouri River, a threatened shorebird, the piping plover (*Charadrius melodus*), likes to nest on unvegetated sandbars with saturated, or 'muddy' areas where they, and their chicks can feed on insects. Historically, flooding of the river created new sandbar habitat and scoured vegetation off of existing sandbars. However, the current river management regime, including dams and channelization, means that the river floods less, and over time sandbars become vegetated and eventually erode away.

From 2004 to 2009 the U.S. Army Corps of Engineers built sandbars for piping plovers to use for nesting and raising their chicks. In 2011, the Missouri River flooded as a result of increased mountain snow and spring precipitation. Although devastating at the time, the flood created an abundance of new sandbar habitat for piping plovers to use, nearly ten times more habitat than was available before. To understand what effect the flood and the newly created sandbars had on piping plovers, we collected data on the Missouri River from 2005–2014. We monitored nests to figure out how many

hatched, and used color bands on both adults and chicks to see how many survived throughout the season and over the years. We also weighed piping plover eggs, chicks, and adults and collected insect prey samples.

Following the flood, more nests hatched, more chicks survived to fledging, and more chicks survived from one year to the next than during any of the years prior. This success led to the population of piping plovers nearly doubling each year. Because the flood created so much habitat, piping plovers were still able to successfully hatch nests and raise their chicks, even with the sandbars eroding and vegetating over time. Although we thought that the increase in rates such as survival and population growth, would be reflected by increased egg masses, adult masses, and chick masses, we found that they remained unchanged following the flood. We also found evidence that egg masses and chick masses were related to the amount of insect prey.

Following the flood, less nests and chicks were eaten by predators such as, mink, crow, and great-horned owls, and we think this is a result of decreases in nesting densities which may have made nests and chicks harder to locate. These results indicate that the amount of habitat available to nesting piping plovers is an incredibly important factor in the population growth of this imperiled species.

## DEDICATION

To the piping plovers, especially those that call the Missouri River home.

Photo used with permission of Diane Borden

## ACKNOWLEDGEMENTS

First and foremost, I would like to thank my family and friends, both near and far, for their support throughout my time as a graduate student as well as the last 30 years of life. I would especially like to thank my amazing parents, who have always supported me and pushed me to follow my dreams, even when that dream involved becoming a unicorn when I grew up. I wouldn't be who I am, or where I am today without you. To my far away friends, thank you for your love and encouragement and for understanding that graduate school and piping plovers can sometimes be all consuming (I'm sorry for missing so many things!). To my Blacksburg friends, thank you for being you! And for providing me with beer (and wine) and for always being willing and eager to ride bikes up and down the mountain with me.

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As with most field projects, this work wouldn't have been possible without the blood, sweat, and tears of our crew leaders and research technicians that worked on the Missouri River from 2005–2014. I would especially like to thank those I worked closely with throughout the 2012–2014 field seasons: Audrey Albrecht, Kayla Baker, Hen Bellman, Brandon Boehm, Diane Borden, Alex Brazeal, Roxy Chicalo, Emily Coba, Alex Cook, Gabby Dancourt, Kayla Davis, Lauren Deets, Grace DeRose-Wilson, Diana Duron, Theresa Edwards, Sterling Fulford, Elizabeth Ford, Callie Gesmundo, Clay Graham, Leigh Graziano, Rachel Harris, Eamon Harrity, Chelsea Hawk, Cathy Hughes, Sean Jeffreys, Erica Krygsman, Tiffany Lane, Maddie Leonard, Kelly Lockman, Zoe Long, Andy Lutz, Josiah Maine, Michaela Maine, Jenna May, Lindsey McKinney, Andi Mott, Ryan Munes, Steph Nefas, Brad O'Hanlon Dana Palm, Reid Plumb, Chelsae Radell, Karl Reinhold, Ryan Risher, Sam Robinson, Elsie Shogren, Jamie Smith, Shawn Sullivan, Kelly Surgalski, Fumika Takahashi, Alyx Vogel, Katie Walker, Chelsea Weithman, and Kirsten Wert. To these wonderful humans, thank you for all of your hard work, dedication, and positive attitudes. And above all, thank you for your kindness and friendship, for making me laugh when I needed it most, and for your ability to make long days in the field not really feel like work at all. To say that I couldn't have done it without you would be an understatement. You all rock!

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## Chapter 1



## Chapter 2

## ATTRIBUTION

Below is a brief description of the contributions made by my co-authors for manuscript publication.

**Chapter 1. Demographic response of an imperiled bird suggests that engineered habitat restoration is no match for natural riverine processes**

Jim Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured project funding and provided substantial edits to the manuscript. Meryl Friedrich (Department of Fish and Wildlife Conservation, Virginia Tech) managed our database, collected supplemental piping plover band resighting data, and assisted with fieldwork. Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) provided assistance and edits to the manuscript. Dan Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, managed the field operations from 2005–2011, provided statistical and analytical assistance, and provided substantial edits to the manuscript.

**Chapter 2. Piping Plover body condition and prey abundance on flood-created habitat on the Missouri River, USA**

Jim Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured project funding and provided substantial edits to the manuscript. Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) provided assistance and edits to the manuscript. Dan Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, managed the field operations from 2005–2011, provided statistical and analytical assistance, and provided substantial edits to the manuscript.

## INTRODUCTION

Humans have altered riparian ecosystems worldwide by constructing dams, channelizing rivers, and converting floodplains to agriculture or development. Two-thirds of ocean-bound fresh water is obstructed by greater than 800,000 dams (McCully 1996, Petts 1984). Globally, more than 58% (172 of 292) of all river systems have been regulated and fragmented by dams (Nilsson et al. 2005), including 85 of 139 systems in the Northern Hemisphere alone (Dynesius and Nilsson 1994, Nilsson and Berggren 2000). Numerous habitat changes have been linked to dam installation (Nilsson and Berggren 2000), including the reduction of over-bank flooding, resulting in changes in geomorphology, floodplain connectivity, forest communities (Nilsson and Berggren 2000), and a reduction of sandbar deposition and river meandering (Johnson 1992). River regulation has profound effects on plant and animal species, especially those adapted to the historic dynamism of riparian ecosystems (Lytle and Poff 2004).

Similar to many riverine systems, the Missouri River has undergone numerous anthropogenic changes. The historic Missouri River was dynamic, exhibiting two flow pulses within years that coincided with snow melt in the prairie and Rocky Mountains. (Galat et al. 1998, Galat and Lipkin 2000, Hesse and Mestl 1993). Between 1937 and 1964 the U.S. Army Corps of Engineers constructed six dams on the mainstem of the river and channelized much of the lower Missouri River (USACE 2006), which reduced flood frequency and suppressed flood pulses (Galat et al. 1998, Galat and Lipkin 2000, Hesse and Mestl 1993) and ultimately resulted in a decrease of 96% of Missouri River sandbar habitat (Dixon et al. 2012). This reduction in the flood frequency has led to a decrease in habitat for a suite of species, including piping plovers (*Charadrius* *melodus*), least terns (*Sternula antillarum*), pallid sturgeon (*Scaphirhynchus albus*), and plains cottonwood (*Populus deltiodes;* USFWS 2003 Dixon et al. 2012, Johnson et al. 2015).

This work focused on the piping plover, an imperiled shorebird that breeds in along the Atlantic Coast from Newfoundland to North Carolina, in the Great Lakes, and in the Northern Great Plains from Prairie Canada to Nebraska and winters along the Southeast Atlantic and Gulf Coasts and in the Caribbean (Elliott-Smith and Haig 2004). On the Missouri River, plovers nest on riverine sandbars in open, sparsely vegetated sand or gravel, typically with nearby saturated or moist substrate for foraging and brood rearing (Elliott-Smith and Haig 2004, Catlin et al. 2015). Adult plovers and their precocial young prey on invertebrates that use these habitats (e.g., Diptera, Collembola, Orthoptera; Catlin et al. 2012). In large part due to a decrease in breeding habitat, plovers were placed on the U.S. Endangered Species List in 1986 (USFWS 1985, USFWS 2009).

Beginning in 2004, as a result of low piping plover population numbers, the USACE, in accordance with the U.S. Fish and Wildlife Services biological opinion, began constructing sandbar habitat for breeding piping plovers and least terns (USFWS 2000, USFWS 2003). Research conducted from 2005–2009 focused on comparing piping plover demography and movement on new, ‘engineered’ sandbar habitat to ‘natural’ sandbar habitat that was created by high flows in 1996–1997 (Catlin 2009, Catlin et al. 2011, Catlin et al. 2015). Results indicated that although certain demographic parameters, such as reproductive output, were initially high on engineered sandbars, these rates decreased substantially as the sandbars aged and nesting densities and predation increased, stemming from a loss of suitable habitat due to erosion and vegetation encroachment (Catlin et al. 2015).

During the breeding seasons of 2010 and 2011, flooding occurred on the Missouri River that resulted in the almost complete inundation of sandbar habitat throughout the Missouri River system (USACE 2012). In 2011, due to increased mountain snowpack and spring precipitation, flows from the Gavins Point Dam exceeded 2,831 $m^3/s$ for 85 days with a maximum monthly flow of 4,530 $m^3/s$ reached in July (USACE 2012). The increased flows from the 2011 flood created a substantial amount of new habitat for plovers, terns, and potentially cottonwoods, and the flood was associated with the first documented successful pallid sturgeon spawning in the Missouri River (Delonay et al. 2016, DeLonay et al. 2014). From 2012–2014 we continued the research methods conducted by Catlin et al. 2015 with the goal of understanding how piping plovers responded to the flood-created sandbar habitat. When the Missouri River flooded in 1996–1997, piping plovers experienced a rapid population increase (USACE unpublished data) and we hypothesized a similar response following the 2011 flood. The overall objective of this study was to evaluate the effects of habitat creation, both anthropogenic and natural, on piping plover prey, growth rates, and demography by comparing the flood created habitat to the pre-flood engineered and natural habitat on the Missouri River.

Chapter 1 compares the effect of a large-scale ecosystem management project to a natural, high water event on the demographic responses of piping plovers. The specific objectives of this study were: *i.* compare plover demography (e.g., nest success, survival, fidelity) and population change before and after an historic flood and *ii.* determine the drivers for changes in demographic rates between pre-flood engineered and post-flood naturally-created habitat types.

Because an animal's habitat can have a profound effect the condition and fitness of individuals and the dynamics of populations (Lindström 1999, Reid et al. 2003, Van De Pol et al. 2006), in Chapter 2, we investigated the relationship between several piping plover condition variables (adult mass, egg mass, chick growth), and habitat quality (invertebrate abundance) and quantity (amount of foraging area available) before and after the flood. Previous work indicated that Missouri River plover chick condition (e.g., growth rates, time to fledging, and fledging mass) was positively related to parental quality, egg size, and the availability of foraging habitat, which resulted in both short- and long-term effects on survival (Catlin et al. 2014). Our results from chapter 1 indicated that the flood was followed by increased chick survival, hatch-year survival, fidelity, reproductive output, and population growth. Therefore, we hypothesized that increased demographic rates following the flood would be accompanied by improved habitat quality and an improvement in condition.

As many ecosystems have been previously altered, there generally are not instances where ecologists are able to conduct a natural experiment, such as this study, which allowed us to directly examine current management practices of an imperiled species in comparison to how the system functioned naturally, or prior to human alterations. In this case we ask, how did the sandbar habitat construction by the USACE (current management practice) compare to sandbar habitat creation from flooding (natural process)? This work also represents one of the few studies to focus on the ecological response of birds to altered flow regimes (Poff and Zimmerman 2010), and furthermore, our results provide insight into how to manage habitat for piping plovers. But on a larger scale, results from this study may be applied to imperiled riverine ground-nesting species worldwide and can also be used to underscore the importance of natural ecosystem processes.

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# CHAPTER 1: DEMOGRAPHIC RESPONSE OF AN IMPERILED BIRD SUGGESTS THAT ENGINEERED HABITAT RESTORATION IS NO MATCH FOR NATURAL RIVERINE PROCESSES

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**Demographic response of an imperiled bird suggests that engineered habitat restoration is no match for natural riverine processes**

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**Abstract**

Globally, riparian ecosystems are in decline due to anthropogenic modifications including damming, channelization and the conversion of the floodplain for human use. A major effect of damming is the alteration of habitat through the reduction and timing of flood events, resulting in decreased connectivity with the floodplain, changes in sediment cycling and riparian forest communities, and increased erosion, leading to the reduction of sandbar deposition and river meandering. These changes can profoundly affect riparian species as many have adapted to the historical dynamism of these ecosystems. On the managed Missouri River, an imperiled shorebird, the piping plover (*Charadrius melodus*) uses riverine sandbars to breed. From 2004 to 2009, due to limited breeding habitat and low population numbers, the U.S. Army Corps of Engineers constructed 255 ha of sandbar habitat. During the breeding seasons of 2010 and 2011, historically high flows resulted in the creation of 1,887 ha of suitable sandbar habitat. Our study compared the demographic response of piping plovers to this anthropogenic and natural habitat creation. We found demographic parameters were consistently higher on the flood-created habitat than engineered habitat, leading to increased population growth after the flooding. These differences were related to increased sandbar habitat, low nesting densities, and decreased nest and chick predation. As many ecosystems have previously been altered, it's rare that ecologists have the opportunity to compare management practices with natural ecosystem processes. Results from this study suggest that management intervention may not be an appropriate substitute for natural ecosystem processes and provide insight on future management of riparian ecosystems.

*Keywords: Charadrius melodus*, density dependent, flood, habitat creation, Missouri River, piping plover, riparian ecosystems

## 1. Introduction

Humans have altered riparian ecosystems worldwide by constructing dams channelizing rivers, and converting floodplains to agriculture or development. Two-thirds of ocean-bound fresh water is obstructed by more than 800,000 dams (McCully, 1996; Petts, 1984). Globally, more than 58% (172 of 292) of all river systems have been regulated and fragmented by dams (Nilsson et al., 2005), including 85 of 139 systems in the Northern Hemisphere alone (Dynesius and Nilsson, 1994; Nilsson and Berggren, 2000). Riparian ecosystems provide habitats for numerous communities and species (Naiman et al., 2005; Ward et al., 1999), and are pathways for dispersal and migration (Naiman and Decamps, 1997). Due to their complexity, riparian ecosystems are sensitive to variations in hydrology and often are early indicators of environmental change (Nilsson and Berggren, 2000).

Numerous habitat changes have been linked to dams (Nilsson and Berggren, 2000). Upstream terrestrial habitats are inundated and previously lotic habitats are converted to lentic (Nilsson and Berggren, 2000). Downstream, over-bank flooding often is reduced or shifted temporally, resulting in changes in the system geomorphology, connectivity with the floodplain, forest communities, sediment cycling, and erosion rates (Nilsson and Berggren, 2000). Moreover, dams can reduce sandbar deposition and river meandering (Johnson, 1992). River regulation especially affects plants and animals adapted to the natural dynamism of riparian ecosystems (Lytle and Poff, 2004). Of 165 peer-reviewed papers examining flow alterations and ecological responses, 92% reported degraded values for recorded ecological metrics with only 8% reporting improvements (Poff and Zimmerman 2010). River regulation has been shown to have deleterious effects on plants, fishes, and riparian bird species. Specifically, loss of wetlands and sand and gravel bars due to river regulation has contributed to the decline of shorebird populations worldwide (Caruso, 2006; Claassen, 2004; Katayama et al., 2010; Nebel et al., 2008).

The historic Missouri River was dynamic, exhibiting two flow pulses within years that coincided with snow melt in the Great Plains, and in the mountains (Galat et al., 1998; Galat and Lipkin, 2000; Hesse and Mestl, 1993). Between 1937 and 1964 the U.S. Army Corps of Engineers constructed six dams on the main stem of the river and channelized much of the lower Missouri River (USACE 2006) which reduced flood frequency and suppressed within-year flood pulses (Galat et al., 1998; Galat and Lipkin, 2000; Hesse and Mestl, 1993) and ultimately resulted in a decrease of 96% of Missouri River sandbar habitat (Dixon et al. 2012).

Management of riparian ecosystems can be challenging as often alterations have been made without understanding of natural processes (Nilsson and Berggren, 2000) and only recently have we begun to restore impacted rivers (Nilsson et al., 2007). More commonly, management or restoration of riparian ecosystems is species- or taxa-specific (Clarke et al., 2003; Poff and Zimmerman, 2010), and many studies lack the longevity to fully assess management practices (Clarke et al., 2003; Nilsson et al., 2007). On the Missouri River, the current water management regime has resulted in fewer flood events and has led to a decrease in habitat for a suite of species including piping plovers (*Charadrius melodus*, hereafter, ‘plover’), least terns (*Sternula antillarum*), pallid sturgeon (*Scaphirhynchus albus*), and plains cottonwood (*Populus deltiodes;* (Dixon et al., 2012; Johnson et al., 2015; U.S. Fish and Wildlife Service, 2003). In response, the USACE initiated ecosystem management specifically to recover these species. The USACE created shallow water habitat for sturgeon, and constructed emergent sandbars for plovers and least terns (USFWS 2000, USFWS 2003).

In 2010 and 2011, record high flows on the Missouri River inundated most sandbar habitat (USACE 2012). In 2011, flows from the Gavins Point Dam exceeded 2,831 $m^3/s$ for 85 days with a maximum flow of 4,530 $m^3/s$ reached in July (USACE 2012). This compares to 748 $m^3/s$, the mean July flow from 2005–2009. The increased flows from the 2011 flood created a substantial amount of new habitat for plovers, terns, and potentially cottonwoods, and was associated with the first documented successful pallid sturgeon spawning in the Missouri River since the species was listed (Delonay et al., 2016; DeLonay et al., 2014).

The goal of the study was to compare the demographic response (nest success, survival, fidelity and population changes) of an imperiled shorebird, the piping plover, to the large-scale ecosystem management effort vs. the results of the natural high water event. From 2005–2009 research focused on evaluating demography and movement on this new, ‘engineered’ sandbar habitat relative to ‘natural’ sandbar habitat (Catlin, 2009; Catlin et al., 2015, 2011b). From 2012–2014 we studied how plovers responded to the flood-created sandbar habitat. Our work is one of the few studies of the ecological response of birds to altered river flow regimes (Poff and Zimmerman, 2010) and provides insight into the relative merits of ecosystem management vs. natural processes for plovers. More broadly, these results may be applied to imperiled riverine-nesting shorebird species worldwide, including fifteen species of small plovers and dotterels (Charariinae) that breed on river sandbars on all continents except Antarctica (Fraser and Catlin unpublished data), and used to underscore the importance of natural ecosystem processes for a host of species affected by anthropogenic habitat modifications.

## 2. Material and methods

### *2.1 Study species*

The piping plover (*Charadrius melodus*, hereafter, 'plover') is an imperiled shorebird that breeds in three areas: the Atlantic Coast from Newfoundland to North Carolina, the Great Lakes, and in the Northern Great Plains from Prairie Canada to Nebraska. The species winters on the Southeast Atlantic and Gulf Coasts and in the Caribbean (Elliott-Smith and Haig, 2004). On the Missouri River, plovers nest on riverine sandbars in open, sparsely vegetated sand or gravel substrate with adjacent saturated or moist substrate for foraging and brood rearing (Elliott-Smith and Haig, 2004). In part due to a decrease in breeding habitat, plovers were placed on the U.S. Threatened and Endangered Species List in 1986 (USFWS 1985, USFWS 2009).

### *2.2 Study area*

We studied plovers on the Gavins Point Reach of the Missouri River, which extends 95 km downriver from the Gavins Point Dam (42° 52' N, 97° 29.8' W, Figure 1), from 2005–2014. Newly created sandbars (both engineered and flood created) consisted of high, barren sand nesting areas and low-lying, unvegetated sand and mudflats. As sandbars aged, they were colonized by cottonwood (*Populus* spp.) and willow (*Salix* spp.). Common predators of shorebirds and their nests included American crow (*Corvus brachyrhynchos*), great horned owl (*Bubo virginianus*, Catlin et al. 2011a), American mink (*Neovison vison*), and northern raccoon (*Procyon lotor*, Catlin et al. 2011b).

*2.3 Field methods*

Each breeding season (April–August), we searched sandbars for nests by walking transects through potential nesting habitat and observing plover behavior. We recorded nest locations using Trimble GPS units (Trimble Navigation, Ltd., Sunnyvale, CA) and attempted to check nests every 2–3 days until failure or hatching. We captured adult plovers with drop-door or drop-box traps placed over nests and uniquely marked individuals. We uniquely marked chicks as close to hatch as possible. We attempted to resight or recapture chicks every 2–4 days until they fledged (Hunt et al. 2013; ~25 days) and continued to resight fledged chicks when possible. Throughout each breeding season, we used spotting scopes to resight previously banded plovers and received supplemental color band resighting information from plover breeding, wintering and migratory stop-over locations outside our study area submitted by cooperators.

*2.4 Habitat information*

We calculated sandbar habitat availability using imagery collected during the 2005–2009 and 2012–2014 breeding seasons. Pan-sharpened multispectral QuickBird (satellite) imagery (1m resolution) was collected each year between April and October and classified using Definens Developer Software (L. Strong, U.S. Geological Survey, pers. comm.). We classified habitats into open and sparsely vegetated (< 30% vegetative cover) and vegetated (> 30% vegetative cover) dry or moist sand. The amount of suitable nesting habitat was calculated as the amount of open and sparsely vegetated wet and dry sand on a sandbar. We calculated the maximum number of nests active annually on each sandbar and estimated nesting density as pairs/ha for each sandbar.

*2.5 Analytical methods*

*2.5.1 Modeling approach*

To test hypotheses related to the flood we used models that explained the data in pre-flood conditions (Catlin et al., 2015), and then examined the effects on model fit of adding variables that described post flood conditions or the differences between pre-flood and post flood conditions. By so doing, we examined the effects of flood while controlling for the effects of covariates that were known to affect demographic parameters in the pre flood state (Table 1). In all cases we tested for the effects of the flood by replacing year with pre-flood (2005–2009), flood (2010, 2011) and post-flood (2012–2014). As there were no nests or chicks during flooding in 2010 and 2011, the ‘flood’ variable was only used when modeling adult survival and fidelity. In this study, we refer to three age-classes of plovers: adult or after-hatch-year (AHY, ≥ 1 year post-hatch), hatch-year (HY, hatch to the following breeding season, and pre-fledge chicks (hatch to fledging, ~25 days post-hatch). All survival analyses were performed in Program MARK (White and Burnham, 1999) and run through RMARK (Laake, 2013). Unless otherwise stated, we obtained model-averaged parameter estimates and unconditional standard errors for all real parameters (Burnham and Anderson, 2002). For beta estimates, we provide estimates from the top-ranked model (Cade, 2015). When interpreting the difference between individual estimates, we used several types of evidence including: model ranking, size of the estimate relative to the standard error, model weights, and confidence intervals. We interpreted differences based on these factors and in relationship to other factors in our models and model sets. Means are presented as $\bar{x}$ ± 1 SE unless otherwise noted

*2.5.2 Nest success*

We considered a nest successful if ≥1 egg hatched or if ≥1 egg disappeared without signs of predation or flooding within ± 2 days of the estimated hatch date. We used a random effects, logistic exposure model (Rotella et al. 2000, Stephens et al. 2004, Shaffer 2004) to calculate the daily survival rate (DSR) of nests. We controlled for significant covariates from the pre-flood period (Table 1) as well as a fixed effect for year, a random effect for the interaction between sandbar and year to account for possible dependence among nests (Catlin et al., 2015).

We hypothesized that nest success would be higher on post-flood sandbars due to the increased amount of habitat, however we thought that nest success may decrease as the flood-created sandbar habitat aged due to vegetation encroachment and the predator community becoming aware of nesting colony locations, similar to the trend for engineered habitat found by Catlin et al. 2015. To examine our hypotheses, we started with the global model from Catlin et al. 2015 with the addition of our density variable as nesting densities were substantially lower following the flood. We tested the fit of the global model with a Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow, 2004). We used a stepped approach to modeling; in the first step, we removed variables that were not supported (Table 2). We then tested for the effect of the flood and finally, we added the age of the post-flood sandbar habitat to the model containing the flood variable to examine changes in the effect of flooding over time. We used Akaike's Information Criterion corrected for small sample size (Burnham and Anderson, 2002) to evaluate the effect of each step. If the $AIC_c$ increased after a step, we stopped the process and used the model with the lower $AIC_c$ value.

*2.5.3 Pre-fledge chick survival*

We used the random effects Cormack-Jolly-Seber (CJS) model (Gimenez and Choquet, 2010) to estimate age specific daily survival (Φ) and recapture rate (p) from hatch to fledge (25 days). We modeled age- (days) and year-specific variation in both survival (Φ) and recapture rate (p). We estimated overdispersion using a model that included year- and age- specific variation in apparent survival and resight rate (age × year). We controlled for significant covariates from the pre-flood period (Table 1) and prior to modeling we determined that an individual random effect on resight rate improved the fit of the global model (using $AIC_c$) and all modeling proceeded with the individual random effect on p.

We hypothesized that pre-fledge chick survival would be higher on post-flood sandbars due to the increased amount of habitat and lower densities following the flood, but that the effect of density would decrease as chicks aged and were better able to compete for resources. We began by modeling basic structures for resight rate (p) and survival (Φ). We then used the model with the lowest $AIC_c$ value and repeated this process, adding covariates for engineered sandbars, the age of engineered sandbars, and the interaction between nesting density and chick age to survival (Φ), as well as engineered sandbars and density to resight rate (p) (Catlin et al., 2015). In the final step, we tested for the effects of the flood using the highest ranked model from the previous step.

*2.5.4 True survival and fidelity to the study area*

We estimated plover annual true survival and fidelity to the study area using the Barker (1997) live-dead encounter model, which allowed us to estimate survival unbiased by emigration by using resightings outside of our study area (supplemental resightings) to separate survival from permanent emigration. The parameters of the Barker 1997 model are true survival (S), resight probability (p), reporting rate of dead encounters (r), resight probability during the supplemental period given that an animal survives (R), the probability of being resighted and then dying during the supplemental period (R'), fidelity to the study area (F), and the probability that an individual returns to the study area after emigrating (F'). Because there were no reports of dead plovers outside of our study area, we fixed the reporting rate of dead birds (r) to 0.

We hypothesized that AHY and HY survival and fidelity would be higher due to the increased amount of habitat and lower nesting densities following the flood. We estimated overdispersion using median $\hat{c}$ on a model with year- and age-specific variation in all parameters (except r). We began modeling by testing several reduced structures for p, R, and R’, while setting S, F, and F’ to be fully time (year) and age (AHY vs. HY) dependent. Based on results of prior modeling (Catlin et al., 2015, 2011a) we also included the covariates hatch date and age at banding on HY survival in all models, except when testing for overdispersion. We used the model with the lowest $AIC_c$ and repeated this process for S, F, and F’. Finally, we tested for the effects of engineered sandbars, engineered sandbar age, and nesting density on annual HY true survival and fidelity to the study area and the effects of the flood.

*2.5.5 Reproductive output and population growth (λ)*

We estimated the number of fledged chicks produced per pair to compare the value needed to maintain a stationary population using our year specific estimates of nest success and pre-fledged chick survival for each habitat type (pre-flood natural, pre-flood engineered, post-flood, Appendix A). We used our demographic estimates to calculate reproductive output needed to maintain a stationary population. We followed Cohen and Gratto-Trevor 2011, Catlin et al. 2015 (Appendix A) to estimate the reproductive output needed for a stationary population. To incorporate variance, we obtained the estimate of process variance for AHY survival (Gould and Nichols, 1998; Larson et al., 2000).

## 3. Results

We monitored 1,071 nests and banded 986 AHY plovers and 2,021 pre-fledged chicks from 2005–2014. Chicks were banded at 1.8 (range: 0–24) days of age and had a mean hatch date of 27 June (range: 26 May–04 Aug). The average sandbar density for chicks hatched during the study was 1.16 (range: 0.01–12.75) pairs/ha. Thirty-nine percent of banded AHYs, (389/986) and 11% of banded chicks (222/2,021) were observed outside of the study area during the supplemental period. The amount of available, suitable habitat (Figure 2) varied between years with more habitat available after the flood ($\bar{x}$ = 1,012 ha, range: 887–1103 ha) than before ($\bar{x}$ = 166.45 ha, range: 98–307 ha), which resulted in lower nesting densities (Figure 2) after the flood ($\bar{x}$ = 0.20 pairs/ha, range: 0.11–0.36 pairs/ha) than before ($\bar{x}$ = 1.22 range: 0.74–2.11 pairs/ha).

### *3.1 Nest success*

Overall nest success averaged 0.52 ± 0.02, and nest success was higher on post-flood habitat (0.74 ± 0.025, $n$ = 270) than on pre-flood habitat (0.45 ± 0.016, $n$ = 801). Our top model (Step 3, Table 2) indicated that daily nest survival was positively related to the use of predator exclosures, pre-flood engineered habitat, the date of nest initiation, clutch size, and post-flood habitat (Appendix B). Daily nest survival was negatively related the age of the nest and the age of pre-flood engineered habitat (Appendix B). Our top model did not include nesting density and the age of post-flood sandbars, indicating they were less important in determining plover daily nest survival in our study than the other variables examined.

*3.2 Pre-fledge chick survival*

Pre-fledge chick survival (Φ) to 25 days varied between years throughout the duration of the study and was consistently higher after the flood from 2012–2014 (Table 3). The two highest ranked models ($w_i$ = 0.75) included the interaction between year and age, hatch date, engineered habitat, and the interaction between density and age for daily chick survival (Appendix C). Our top model (Table 4) indicated that daily chick survival was negatively related to hatch date and the age of engineered habitat and positively related to hatching on engineered habitat and the interaction between chick age and density, although the confidence interval included 0 for the effect of engineered habitat and age of engineered habitat (Appendix B). The probability of chick being recaptured or resighted (p) varied by year and chick age (Table 4) and was higher on sandbars with higher nesting densities and on engineered sandbars, although the confidence interval for engineered habitat included 0 (Appendix B).

*3.3 True survival and fidelity to the study area*

AHY true survival (S) averaged 0.76 ± 0.05, and the top model (Table 5) indicated that true survival was highest prior to the flood, lowest during the flood, and intermediate after the flood. There also was some indication that AHY true survival varied by year, as evident by the second ranked model (Appendix D). AHY true survival was higher than HY true survival each year of the study, and HY true survival was highest following the flood (Table 3). HY true survival was positively related to the age of chicks at banding and hatching on engineered habitat and negatively related to hatch date, nesting density (Figure 3), and the age of engineered habitat, although the confidence intervals for age of engineered habitat suggested it was a not significant factor (Appendix B).

Our top model (Table 5) indicated that fidelity to the study area (F) varied by year and was higher for AHY's than for HY's in all years of the study, and HY fidelity was highest from 2013–2014 (Table 3). Fidelity to the study area was lowest for AHYs from 2011–2012 (Table 3) and highest from 2013–2014. The probability of being resighted in our study area (p), subsequently dying during the supplemental period (R'), and that an individual returned to the study area after emigrating (F') did not vary by year and was lower for HY's than for AHY's (Appendix D). The probability of being resighted outside of the study area (R) differed between years and was lower for HYs than for AHYs (Appendix D).

*3.4 Reproductive output and population growth*

The reproductive output needed for a stationary population given observed survival rates was 1.17 chicks fledged per pair (95% CI: 0.74–1.70). Prior to the flood, reproductive output only exceeded that needed for a stationary population in two years, however following the flood, reproductive output was as high or higher than that of engineered habitat and was above that needed for a stationary population in all years (Figure 4). Prior to the flood, calculated λ exceeded one in only one year (Figure 5). Lambda was lowest and substantially less than 1 during the years of the flood when reproductive output was 0 and was highest after the flood, exceeding 1 in all years (Figure 5).

## 4. Discussion

A key mission of the dams on the mainstem of the Missouri River is to control flooding (USACE 2006). A byproduct of managing for flood control has been the dramatic alteration of the ecosystem, leading to decreases in a variety of taxa primarily through habitat loss (Catlin et al., 2015; Dixon et al., 2012; Johnson et al., 2015; U.S. Fish and Wildlife Service, 2003). When the Missouri River dams failed to control flooding in 2010 and 2011 there was extensive damage to human infrastructure (United States Department of Commerce, 2012), but the floodwaters also increased the amount of plover nesting habitat by a factor of 10, contributing to a substantial decline in nesting densities and increases in all measured demographic rates.

Estimates of nest success, pre-fledged chick survival to fledging, and HY annual survival were as high or higher after the flood than before, and unlike prior to the flood, these rates remained high as the sandbar habitat aged. Increased nest, chick, and HY survival following the flood, resulted in high reproductive output and increased population growth. Suitable habitat increased and nesting densities decreased following the flood, and our results indicated that both pre-fledge chick survival and HY survival were density-dependent. On the Missouri River, decreased nesting densities can result in increased availability of foraging habitat for individuals (Catlin et al., 2014, 2013), decreased predation (Catlin et al., 2015), and decreased inter- and intra-species aggression (D. Catlin pers. obs.). Moreover, more plovers double brooded at low densities than at high densities during this study (Hunt et al., 2015). Our results indicate that these fecundity parameters and increased immigration (Catlin et al., 2016) drove the growth of the population following the flood.

The mechanical creation of habitat from 2005–2009 increased reproductive output and contributed to positive population growth for a year following creation. After construction, plovers selected engineered habitat over natural habitat (Catlin et al., 2011b). However, immigration and reproductive rates decreased rapidly as density increased (Catlin et al., 2015). Even with the construction of sandbar habitat, plovers were at or near carrying capacity throughout the pre-flood portion of this study (Catlin et al., 2015). In comparison, the 2011 flood increased the amount of suitable habitat 10-fold, resulting in lower densities and ultimately high population growth. Although habitat decreased between 2013 and 2014, reproductive output remained high, suggesting that the population was below carrying capacity. On average, HY plovers arrive 28 d after AHYs (Catlin, 2009; Catlin et al., 2015), and, with a population near carrying capacity, these individuals may lose the ability to secure a territory and therefore exhibit decreased fidelity to the study area and potentially decreased survival (Catlin et al., 2015). After the flood, annual HY true survival and fidelity to the study area increased.

Across their range, plovers rapidly colonize newly created suitable habitat (Catlin et al., 2015; Cohen et al., 2009; U.S. Army Corps of Engineers, 2006; Wilcox, 1959). Our results indicated that plovers experienced increased reproductive output and population growth on the habitat created by the 2011 flood. Remarkably, these gains in reproductive output were achieved with no predator management, compared to intense predator management on engineered sandbars prior to the flood (Catlin et al. 2015). Nest exclosures (Boettcher et al., 2007; Isaksson et al., 2007; Johnson and Oring, 2002; Neuman et al., 2004; Niehaus et al., 2004) and the predator removal (USFWS 1985, 2009; Cohen et al. 2009, Catlin et al. 2011a) are commonly used to protect plovers. Indeed, the use of exclosures prior to the flood on the Missouri River increased nest success and great horned owl removal increased chick survival in one of two years studied (2008; Catlin et al. 2011a, 2015). Small parcels of habitat and high nesting densities before the flood may have facilitated predation (Burger, 1984; Catlin et al., 2015) prior to the flood. Nests and chicks were still lost to predators following the flood, but predation was substantially reduced, suggesting that plover nest and chick predation was density-dependent during our study. Kruse et al. 2001 suggested that predator efficiency would be reduced in the presence of large, sandbar with large areas of unused nesting habitat. It is also possible that the predators such as mink, raccoon, and coyote experienced decreased survival during the flood, resulting in lower numbers post-flood.

The effects of dams on avian species is relatively undocumented (Poff and Zimmerman, 2010), but what is known indicates that, similar to other taxa, the presence of dams have been reported to negatively impact species. Throughout the Upper Waitaki Basin of New Zealand, several species including the critically endangered black stilt (*Himantopus novaezelandiae*), the threatened wrybill (*Anarynchus frontalis*), the black-fronted tern (*Chidonias albostriatus*), and the banded dotterel (*Charadrius bicinctus*) breed in a braided river ecosystem negatively affected by hydroelectric dams (Caruso, 2006; Cruz et al., 2013). In Japan, dam construction and flood regulation on the Tama River resulted in the loss of gravel bar habitat and the invasion of exotic plants, ultimately affecting breeding long-billed plovers (*Charadrius placidus,* Katayama et al. 2010). Along the Mekong River in Cambodia, sandbar nesting species such as the river lapwing (*Vanellus duvaucelii*) and little ringed plover (*Charadrius dubuis*) are negatively affected by the Yali Falls dam (Claassen, 2004). Similar to the Missouri River, managers of the Upper Waitaki Basin (Caruso, 2006) and the Tama River (Katayama et al., 2010) have successfully used habitat management (e.g., vegetation removal, wetland and gravel bar creation) to increase nesting pairs and success (Caruso, 2006; Katayama et al., 2010). Although successful, management practices, such as these, are expensive and often difficult to maintain long-term (Caruso, 2006; Catlin et al., 2015).

## 5. Conclusions

Traditionally management and restoration of riparian ecosystems has focused on small geographic areas or a small number of species, generally due to financial and practical constraints (Clarke et al., 2003). Such approaches may not account for underlying geomorphic riverine processes, tend not to be self-sustaining, and require continued management input (Clarke et al., 2003). Management on the Missouri River has largely been narrowly focused on a few species including piping plovers, least terns, and pallid sturgeon. Previous plover research on the Missouri River has provided managers with recommendations for optimizing habitat creation (Catlin et al. 2015), but concluded that plovers will not reach a stage where management actions are no longer necessary unless we dramatically alter the way we manage our rivers or allow flooding to occur.

Rather than restoration focused on single taxon or habitat, managers should attempt to restore a dynamic, variable system that reflects reference systems, and channel geometry that changes with natural flow variability (Palmer et al., 2005; Wohl et al., 2015). Reintroducing key aspects of the natural flow regime may lead to successful restoration of riparian ecosystems (Jansson et al., 2007). However, recreating a self-sustaining natural system requires understanding of underlying processes, flow regimes (Clarke et al., 2003), and conditions prior to anthropogenic alterations (Nilsson and Berggren, 2000). On the Missouri River, the hydrographic record extends to the late 1800's, well before dam construction (Hesse and Mestl, 1993), providing a measure of natural conditions that may allow for mimicking the historic flow regime including within season pulses and increased flows every 4–6 years (Hesse and Mestl, 1993).

The challenge to restoring natural ecosystem processes is competition for river resources, including space in the floodplain, which is increasingly used for non-floodplain depended uses. Since 1977, it has been the policy of the United States government to discourage development in flood plains (Executive Order 11988), but this policy seems to have had minimal effects. Until we remove developments from the floodplains of the world and return to natural hydrographs, it will be difficult to restore these systems and the species that depend on them, and we will be left with potentially less effective practices and more expensive, often single-species approaches to conservation.

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## TABLES

Table 1. Covariates and expected relationships used in modeling nest success, pre-fledged chick apparent survival, and HY true survival and fidelity. Catlin et al. 2015 provided the basis for the expected relationships as well as the justification for the addition of covariates to our demographic models.

| **Covariate**[a] | **Nest success** | **Pre-fledge apparent chick survival (Φ)** | **Pre-fledge chick recapture rate (p)** | **HY true survival ($S_{HY}$)** | **HY fidelity to the study area ($F_{HY}$)** |
|---|---|---|---|---|---|
| Pre-flood engineered habitat | + | + | + | + | + |
| Pre-flood engineered habitat age | - | - | NA | - | - |
| Age (days) | - | NA | NA | + | + |
| Date | + | - | NA | - | - |
| Nest density[b] | - | - | - | - | - |
| Nest exclosure | + | NA | NA | NA | NA |
| Clutch size | + | NA | NA | NA | NA |

[a] Variables used in our demographic models: Pre-flood engineered habitat–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Pre-flood engineered habitat age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Age–for nest success this

refers to the age (days) since nest initiation and for HY true survival and fidelity this refers to the age (days since hatch) at banding, Date–for nest success this refers to a standardized (April 20 as 0) date of nest observation and for pre-fledge chick survival and HY survival and fidelity this refers to the standardized (May 20 as 0) hatch date, Nest density–variable for the number of pairs/ha on a sandbar, Nest exclosure–a categorical variable representing the presence or absence of a nest exclosure, Clutch size–number of eggs in a clutch.

[b] Although Catlin et al. 2015 did not detect a relationship between nesting density and nest success or survival and fidelity parameters, we retained the variable because densities post-flood were far lower than those prior to the flood.

Table 2. Model selection for a random effects logistic exposure model for nest success of piping plovers on the Gavins Point Reach of the Missouri River from 2005–2014.

| Step[a] | Model[b] | AICc[c] | Likelihood | Step Description |
|---|---|---|---|---|
| 1 | yr + exclosure + date + age + clutch size + engineered + engineered age + density + random effect | 4356.7 | 4324.6 | Global model obtained from Catlin et al. 2015 with the addition of the density variable, as nesting densities were substantially lower following the flood. |
| 2 | yr + exclosure + date + age + clutch size + engineered + engineered age + random effect | 4355.4 | 4325.4 | Step 1 with the nesting density variable removed as was not supported. |
| 3[d] | pre-flood + post-flood + exclosure + date + age + clutch size + engineered + engineered age + random effect | 4351.7 | 4333.7 | Step 2 with pre-flood and post-flood in place of individual years. |
| 4 | pre-flood + post-flood + exclosure + date + age + clutch size + engineered + engineered age + post-flood age + random effect | 4353.4 | 4333.4 | Step 3 with the addition of the nested effect of the age of the post-flood habitat. |

[a] The staged approach used when modeling nest success.

[b] Variables used in the models: Pre-flood–a categorical variable for the pre-flood portion of our study (2005–2009), Post-flood–a categorical variable for the post-flood portion of our study (2012–2014), Yr–a categorical variable for year (2005–2009, 2012–2014), Exclosure–a categorical variable representing the presence or absence of a nest exclosure, Date–a

standardized (April 20 as 0) date of nest observation, Age–the age (days) since nest initiation, Clutch size–number of eggs in a clutch, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Post-flood age–the age (years since creation) of post-flood habitat (this is a nested effect that only affects post-flood habitat), Density–variable for the number of pairs/ha on a sandbar, Random effect–sandbar×year to account for the dependence of nests on a given sandbar in a given year.

[c] Akaike's Information Criterion corrected for small sample size.

[d] The top ranked model.

Table 3. Estimated demographic parameters for piping plovers on the Gavins Point Reach of the Missouri River, 2005–2014.

| Year | Nest success[a] | Apparent pre-fledge chick survival (Φ)[b] | AHY true survival ($S_{AHY}$)[c] | HY true survival ($S_{HY}$)[c] | AHY fidelity ($F_{AHY}$)[c] | HY fidelity ($F_{HY}$)[c] |
|---|---|---|---|---|---|---|
| 2005 | 0.50 ± 0.02 | 0.66 ± 0.05 | 0.83 ± 0.04 | 0.23 ± 0.03 | 0.94 ± 0.02 | 0.74 ± 0.07 |
| 2006 | 0.48 ± 0.01 | 0.32 ± 0.03 | 0.81 ± 0.03 | 0.17 ± 0.03 | 0.87 ± 0.03 | 0.52 ± 0.08 |
| 2007 | 0.49 ± 0.02 | 0.15 ± 0.02 | 0.80 ± 0.02 | 0.18 ± 0.03 | 0.95 ± 0.02 | 0.75 ± 0.10 |
| 2008 | 0.47 ± 0.02 | 0.56 ± 0.04 | 0.77 ± 0.03 | 0.17 ± 0.03 | 0.95 ± 0.02 | 0.75 ± 0.06 |
| 2009 | 0.34 ± 0.01 | 0.28 ± 0.03 | 0.68 ± 0.03 | 0.06 ± 0.02 | 0.92 ± 0.02 | 0.64 ± 0.09 |
| 2010[d] | - | - | 0.72 ± 0.03 | - | 0.89 ± 0.03 | - |
| 2011[d] | - | - | 0.75 ± 0.05 | - | 0.76 ± 0.05 | - |
| 2012 | 0.78 ± 0.02 | 0.63 ± 0.04 | 0.72 ± 0.05 | 0.49 ± 0.04 | 0.93 ± 0.03 | 0.64 ± 0.07 |
| 2013 | 0.76 ± 0.02 | 0.70 ± 0.03 | 0.78 ± 0.03 | 0.43 ± 0.04 | 0.98 ± 0.02 | 0.88 ± 0.08 |
| 2014[e] | 0.71 ± 0.02 | 0.61 ± 0.02 | - | - | - | - |

[a] Nest success was calculated using a random effects logistic exposure model (Rotella et al. 2000, Stephens et al. 2004, Shaffer 2004).

[b] Apparent pre-fledge chick survival (Φ) was calculated using a random effects Cormack-Jolly-Seber model (Gimenez and Choquet, 2010).

[c] $S_{AHY}$, $S_{HY}$, $F_{AHY}$, $F_{HY}$ were calculated using a Barker (1997) model.

[d] 2010 and 2011 represent years where flooding inundated nesting habitat and resulted in no nests hatching or chicks surviving.

[e] Estimates for $S_{AHY}$, $S_{HY}$, $F_{AHY}$, and $F_{HY}$ in the final year of the study (2014) were not estimable.

Table 4. Model selection steps for a random effects Cormack-Jolly-Seber model (Gimenez and Choquet, 2010) of apparent survival (Φ) to fledging and resight rate (p) for piping plover chicks on the Gavins Point Reach of the Missouri River prior to flooding (2005–2009) and following the flood (2012–2014). An individual random effect was estimated for p in each model.

| Step[a] | Φ[b] | p[b] | k[c] | AICc[d] | Step Description |
|---|---|---|---|---|---|
| 1 | Age × yr | age × yr | 217 | 23673.93 | Modeling basic structures for Φ and p. |
| 2 | Age × yr + hatch + engineered + engineered age + density × Age | age × yr + engineered + density | 224 | 23620.98 | Using the top model from step 1 we added the covariates for hatch, engineered habitat, the age of engineered habitat and the interaction between density and chick age to Φ. We also added the covariates for engineered habitat and density to p. |
| 3[e] | Age × yr + hatch + engineered + engineered age + density × Age | age × yr + engineered + density | 224 | 23620.98 | Using the top model from step 2 we tested for the effects of the flood on Φ by replacing year with pre- and post-flood. |

[a] The step in the model-selection procedure we used when modeling pre-fledge chick survival (Appendix C).

[b] Variables used in the models: Age–age of the chick in days since hatch (linear trend), age–age of the chick in days since hatch (categorical), Yr–a categorical variable for year (2005–2009, 2012–2014), Hatch–the standardized (May 20 as 0) hatch date, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Density × Age–variable representative of the interaction of nesting density (pairs/ha on a sandbar) and the age of a chick (linear trend).

[c] Number of parameters in the model.

[d] Akaike's Information Criterion corrected for small sample size and over dispersion ($\hat{c}$ = 1.06).

[e] The top ranked model.

Table 5. Model selection steps for a Barker (1997) model of true survival (S), resight probability ($p^a$), reporting rate of dead encounters (r), the probability of being resighted during and surviving the supplemental period ($R^a$), the probability of being resighted and then dying during the supplemental period ($R'^a$), the fidelity of individuals of individuals to the study area (F), and the return rate of individuals that have emigrated (F') for after hatch year (AHY) and hatch year (HY) piping plovers on the Gavins Point Reach of the Missouri River, 2005–2014. We fixed the reporting rate of dead individuals (r) to 0 for all models as there were no reports of dead individuals during the supplemental period and removed it below.

| **Step**[b] | **S**[c] | **F**[c] | **F'**[c] | **k**[d] | **AICc**[e] | **Step Description** |
|---|---|---|---|---|---|---|
| 1 | Age × yr + HY(band age + hatch) | Age × yr | Age × yr | 74 | 10298.19 | Modeling reduced structures for p, R, R', while setting S, F, F' to be fully time (year) and age (AHY vs. HY) dependent as well as the covariates for hatch date and age at banding on HY survival. |
| 2 | Age × yr + HY(band age + hatch) | Age + yr | Age | 52 | 10233.97 | Using the top model from step 1 we modeled reduced structures for S, F, F'. |
| 3[f] | Age × (post-flood + flood) + HY(band age + hatch + engineered + engineered age + density) | Age + yr | Age | 41 | 10212.78 | Using the top model from step 2 we added the covariates for engineered habitat, the age of engineered habitat and nesting density for HY S and F. We also tested for the effects of the flood on S and F by replacing year with pre- and post-flood. |

[a] The top model from each step was the same for these variables: resight rate (p) = Age, the probability of being resighted during and surviving the supplemental period (R) = Age × yr, the probability of being resighted and then dying during the supplemental period (R’) = Age.

[b] The step in the model-selection procedure we used when modeling true survival (S), resight probability (p), reporting rate of dead encounters (r), the probability of being resighted during and surviving the supplemental period (R), the probability of being resighted and then dying during the supplemental period (R’), the fidelity of individuals of individuals to the study area (F), and the return rate of individuals that have emigrated (F’; Appendix D).

[c] Variables used in the models: Age–variable for a difference between hatch-year (HY) and after hatch year (AHY) piping plovers, HY()–indicated the variables within the parentheses only affect HY piping plovers, Band age–age (in days) of banding since hatch, Hatch–the standardized (May 20 as 0) hatch date, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Density–variable representative of the nesting density (pairs/ha on a sandbar), Yr–a categorical variable for year (2005–2014), Post-flood–a categorical variable for the post-flood period (2012–2014), Flood–a categorical variable for the flood (2010, 2011).

[d] Number of parameters in the model.

[e] Akaike’s Information Criterion corrected for small sample size and over dispersion ($\hat{c}$ = 1.13).

[f] The top model from our final modeling step.

## FIGURES

Figure 1. Map of the Missouri River showing the location of our study area on the Gavins Point Reach, downstream of the Gavins Point Dam.

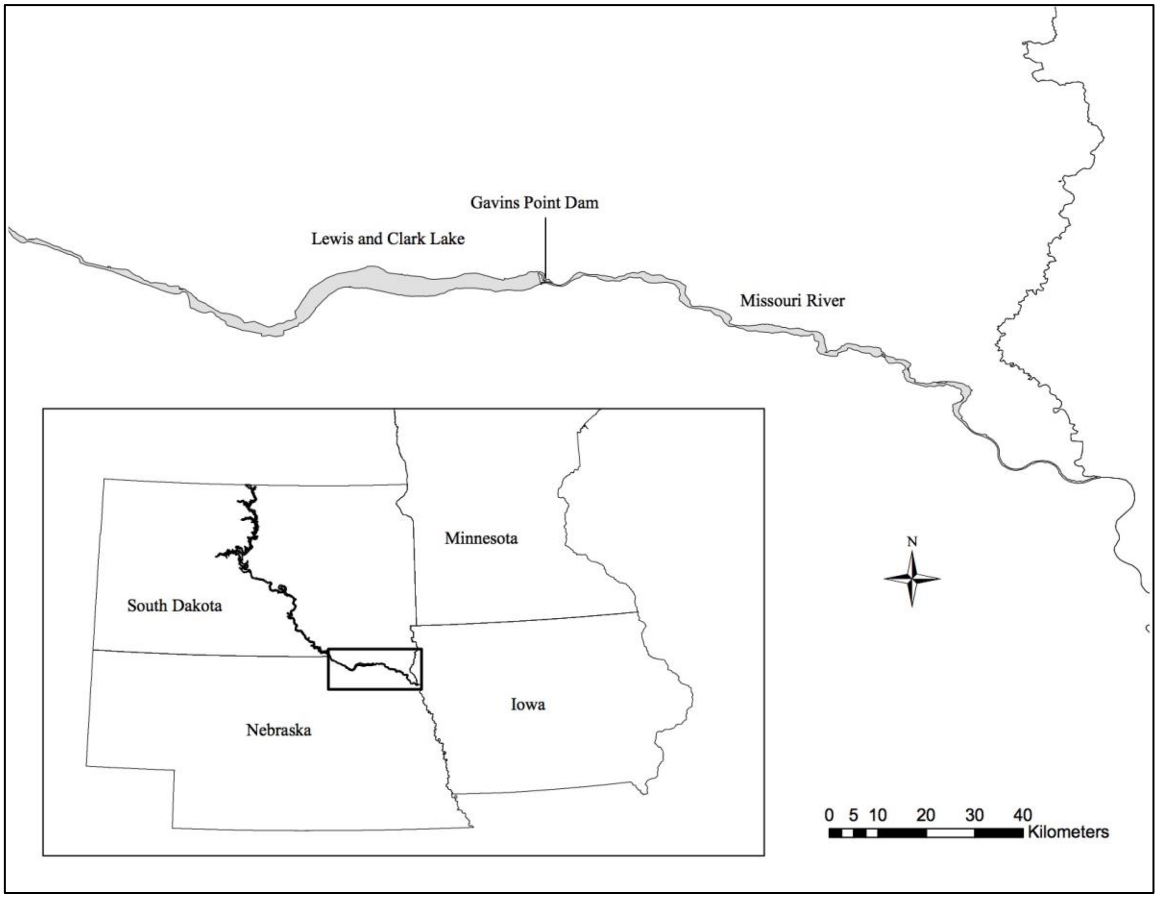


Figure 2. The amount of suitable nesting habitat (<30% vegetated wet and dry sand) indicated by the grey bars and mean piping plover nesting density indicated by the black dots, on the Gavins Point Reach of the Missouri River, 2005–2014. Flooding covered all available nesting habitat in 2010 and 2011. Error bars represent 1 SE.

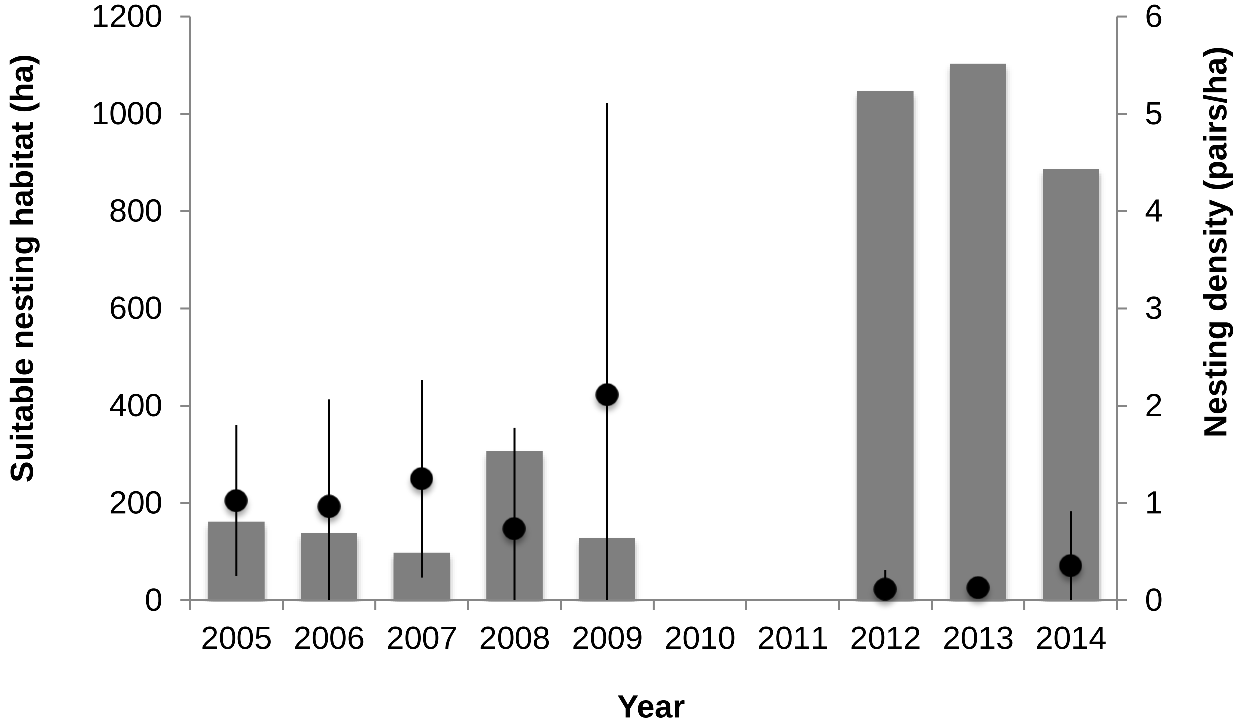


Figure 3. Survival of hatch-year (HY) piping plover chicks (from hatch to the following breeding season) in relationship to nesting density. Estimates are from chicks that hatched on the Gavins Point Reach of the Missouri River prior to flooding, 2005–2009 (pre-food engineered and pre-flood natural habitat) and following the flood, 2012–2014 (post-flood natural habitat). Estimates and standard errors are derived from model average parameter estimates and unconditional standard errors from models of HY survival. Error bars represent 95% confidence intervals.

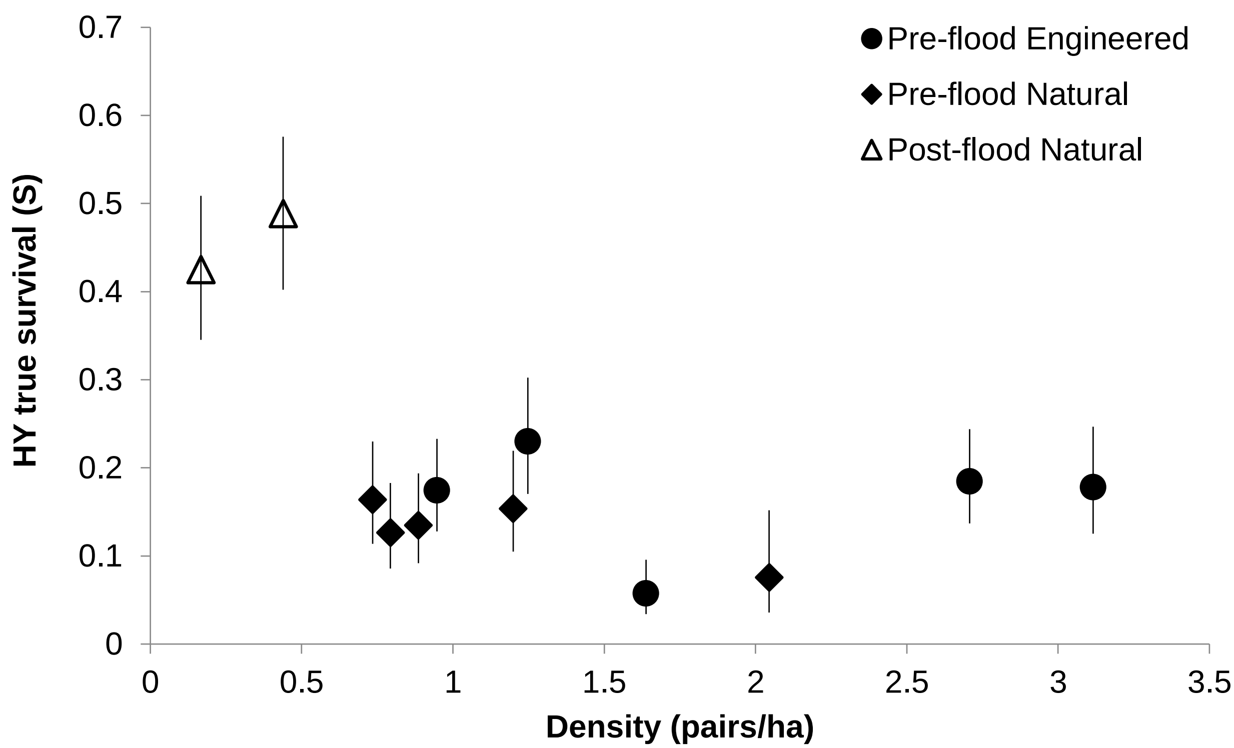


Figure 4. Estimated piping plover reproductive output on the Gavins Point Reach of the Missouri River prior to flooding, 2005–2009 (pre-flood engineered and pre-flood natural habitat) and following flooding, 2012–2014 (post-flood natural habitat). The estimated reproductive output needed for a stationary population is indicated by the grey line and the 95% confidence limits by the dashed grey lines. Error bars represent 95% confidence intervals.

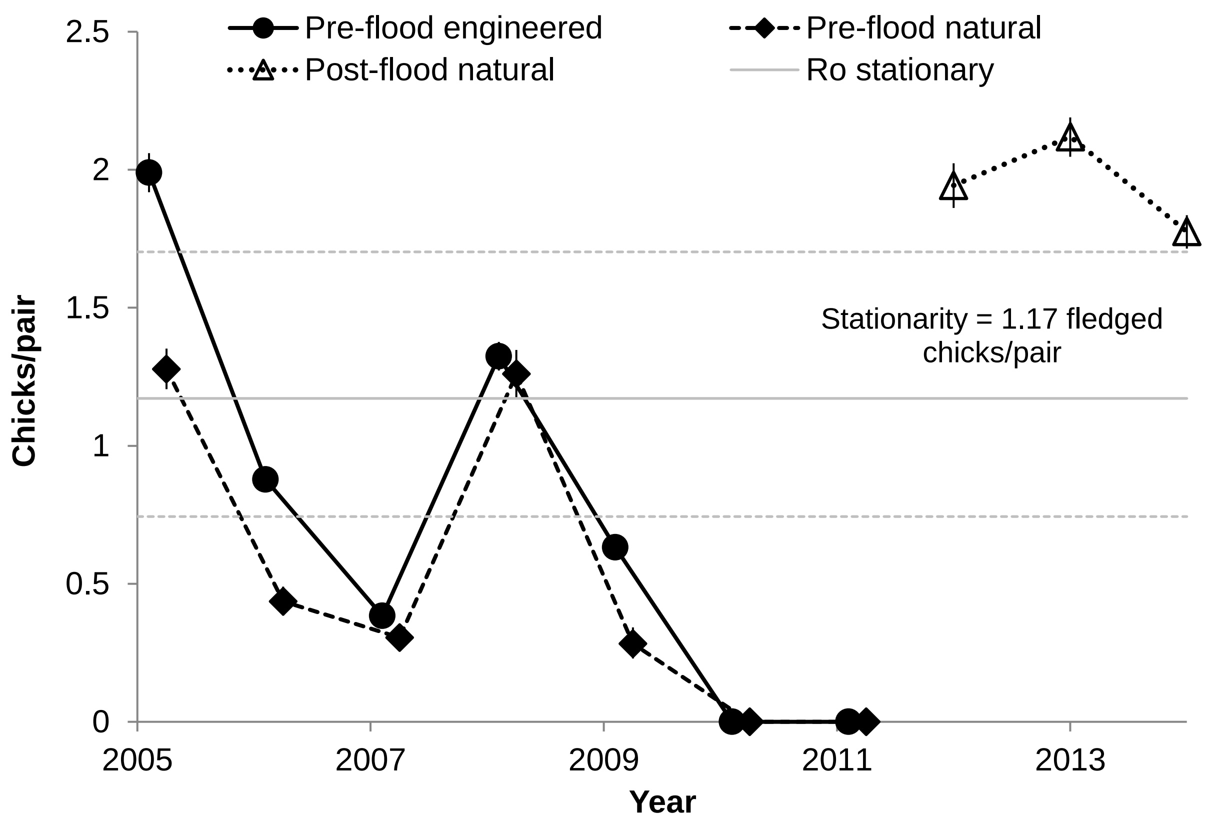
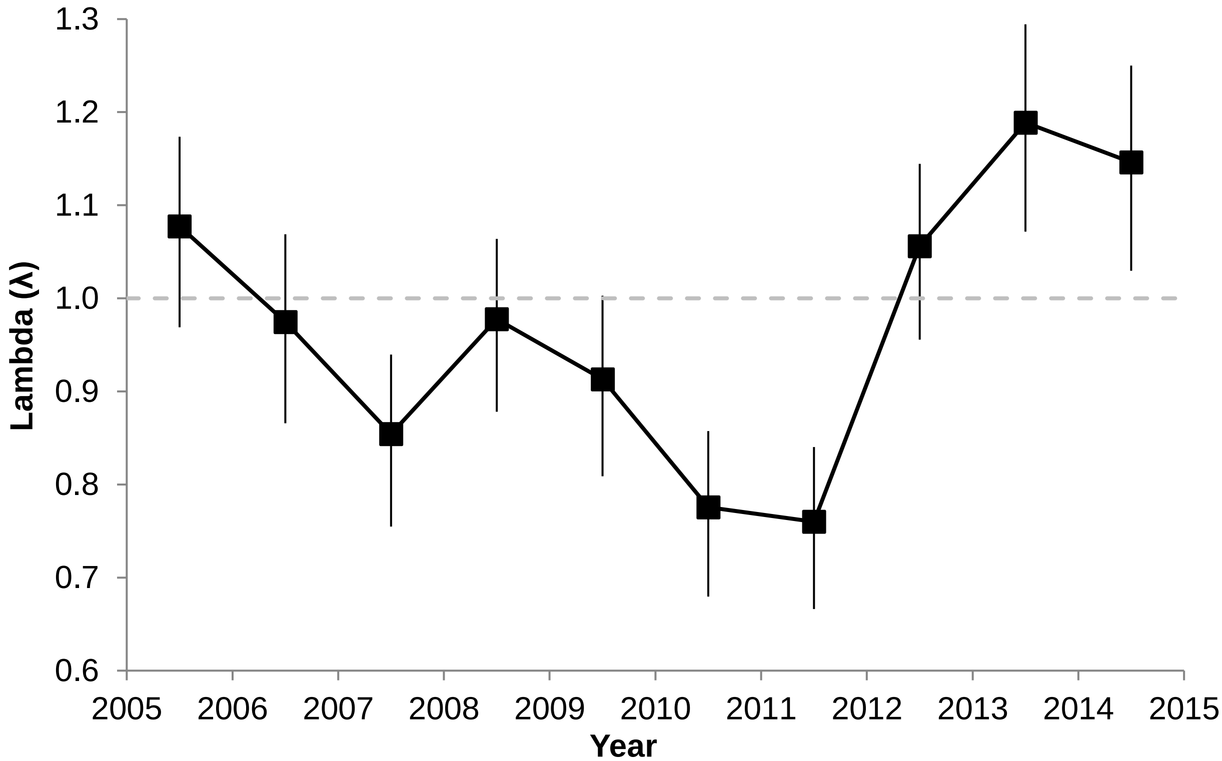


Figure 5. Estimated population growth of piping plovers nesting on the Gavins Point Reach of the Missouri River, 2005–2014. Population growth (λ) was derived from our demographic models. The dashed line represents stationarity (λ=1) and error bars represent 95% confidence intervals.



## SUPPLEMENTAL MATERIAL

Appendix A. Equations used to calculate nest success, hatch-year (HY) post-fledge survival, reproductive output (Ro), and population growth (λ) for piping plovers on the Gavins Point Reach of the Missouri River 2005–2009, 2012–2014.

### 1. Nest success

$$\mathrm{DSR_i} = \frac{e^{\beta_0 + \sum_j \beta_j x_{ij}}}{1 + e^{\beta_0 + \sum_j \beta_j x_{ij}}}$$

i: represents day

j: represents the covariates

$\beta_j$ represents the coefficient of covariate j

### 2. HY post-fledge survival

$$S_{postfledge} = {}^{S_{HY}}/_{\varphi_{prefledge}}$$

$S_{HY}$: represents HY true survival (directly estimated from our analyses)

$\Phi_{prefledge}$: represents apparent survival of chicks from hatching to fledging (directly estimated from our analyses)

### 3. Reproductive output

$$\text{Chicks pair}^{-1}{}_{\text{i,t}} = \text{CS} \times \text{FS}_{\text{i,t}} \times \varphi_{\text{prefledge i,t}}$$

i: represents the habitat type (pre-flood natural, pre-flood engineered, post-flood)

t: represents year

CS: represents clutch size (3.73, mean size of completed clutches in our study; Catlin et al. 2015)

FS: represents the probability that a female successfully hatched a nest in a given year. In the Great Lakes, the estimated re-nesting probability was 50% (Claassen et al., 2014), however we didn't have re-nesting probabilities for our population. We used Cowardin and Johnson 1979 equation for female success to account for nesting attempts following nest failure:

$$\text{Female Success (FS)} = \text{Nest Success} \times e^{(1\text{-Nest Success})2}$$

$\Phi_{prefledge}$: the survival of chicks from hatching to fledging (directly estimated from our analyses)

**4. Popultion growth (λ)**: to calculate the reproductive output needed for a stationary population, we set λ=1 and solved the equation for B (assuming $B_t$=$B_{t-1}$).

$$\lambda = \text{S}_{\text{AHY}} + \text{RP}B_t\text{S}_{\text{postfledge}} + \text{R}(1 - \text{P})B_{t-1}\text{S}_{\text{AHY}}\text{S}_{\text{postfledge}}$$

λ : represents the population growth rate from year t to t+1

$S_{AHY}$: represents the true survival for AHY birds (directly estimated from our study)

$S_{postfledge}$: represents post-fledging survival (derived from our study)

R: represents the sex ratio at hatch (0.5; Cohen and Gratto-Trevor 2011)

P: represents the probability that a returning HY bird will breed in its first year (0.68; Gratto-Trevor et al. 2010, Cohen and Gratto-Trevor 2011)

B: represents the birth rate (Ro, number of fledged chicks produced per pair, derived from our study)

Appendix B. β estimates and 95% confidence intervals from the top-ranked models for nest success, pre-fledge chick survival and resight or recapture rate, and hatch year (HY) annual true survival (S) for piping plovers on the Gavins Point Reach of the Missouri River from 2005–2009, 2012–2014.

Table 1. β estimates and 95% confidence intervals from the top-ranked model for the effect of variables on daily survival rate (DSR) for piping plover nests on the Gavins Point Reach of the Missouri River from 2005–2009, 2012–2014.

| **Variable**[a] | **Estimate** | **SE** | **Estimate/SE**[b] | **Lower 95% CI** | **Upper 95% CI** |
|---|---|---|---|---|---|
| Intercept | 2.067 | 0.202 | 10.23 | 1.668 | 2.466 |
| Post-flood | 1.598 | 0.212 | 7.54 | 1.180 | 2.015 |
| Exclosure | 0.740 | 0.134 | 5.53 | 0.476 | 1.003 |
| Date | 0.009 | 0.003 | 2.89 | 0.003 | 0.014 |
| Age | −0.011 | 0.006 | −1.67 | −0.023 | 0.002 |
| Clutch size | 0.274 | 0.041 | 6.73 | 0.194 | 0.354 |
| Engineered | 1.329 | 0.310 | 4.29 | 0.718 | 1.940 |
| Engineered age | −0.414 | 0.120 | −3.46 | −0.650 | −0.178 |
| Sandbar × Year | 0.549 | 0.136 | 4.03 | 0.280 | 0.817 |

[a] Variables used in the models: Post-flood–a categorical variable for the post-flood portion of our study (2012–2014), Exclosure–a categorical variable representing the presence or absence of a nest exclosure, Date–a standardized (April 20

as 0) date of nest observation, Age–the age (days) since nest initiation, Clutch size–number of eggs in a clutch, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Sandbar×year–A random effect to account for the dependence of nests on a given sandbar in a given year.

[b] Size of effect relative to SE.

Table 2. β estimates and 95% confidence intervals from the top-ranked model for the effects of individual covariates on apparent survival (Φ) and resight or recapture rate (p) from a random effects Cormack-Jolly-Seber analysis of pre-fledged piping plover chicks on the Gavins Point Reach of the Missouri River from 2005–2009, 2012–2014.

| Parameter | Variable[a] | Estimate | SE | Estimate/SE[b] | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|
| Apparent survival (Φ) | Hatch | −0.022 | 0.003 | −6.858 | −0.028 | −0.015 |
| | Engineered | 0.017 | 0.141 | 0.123 | −0.260 | 0.295 |
| | Engineered age | −0.081 | 0.049 | −1.667 | −0.176 | 0.014 |
| | Density × Age | 0.013 | 0.006 | 2.318 | 0.002 | 0.025 |
| Recapture rate (p) | Engineered | 0.104 | 0.110 | 0.953 | −0.110 | 0.319 |
| | Density | 0.088 | 0.030 | 2.932 | 0.029 | 0.147 |

[a] Variables used in the models: Hatch–the standardized (May 20 as 0) hatch date, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Density × Age–variable representative of the interaction of nesting density (pairs/ha on a sandbar) and the age (days since hatch) of a chick (linear trend).

[b] Size of effect relative to SE.

Table 3. β estimates and 95% confidence intervals from the top-ranked model for the effect of individual covariates on hatch year (HY) annual true survival (S) for piping plovers on the Gavins Point Reach of the Missouri River from 2005–2009, 2012–2014.

| Parameter | Variable[a] | Estimate | SE | Estimate/SE[b] | Lower 95% CI | Upper 95% CI |
|---|---|---|---|---|---|---|
| True survival (S) | Hatch | −0.046 | 0.006 | −7.733 | −0.057 | −0.034 |
| | Band age | 0.114 | 0.031 | 3.686 | 0.053 | 0.175 |
| | Engineered | 0.710 | 0.240 | 2.964 | 0.240 | 1.179 |
| | Engineered age | −0.215 | 0.110 | −1.949 | −0.432 | 0.001 |
| | Density | −0.227 | 0.099 | −2.305 | −0.421 | −0.034 |

[a] Variables used in the models: Hatch–the standardized (May 20 as 0) hatch date, Band age–age (in days) of banding since hatch, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Density–variable representative of the nesting density (pairs/ha on a sandbar).

[b] Size of effect relative to SE.

Appendix C.

Table 1. Model ranking results for a random effects Cormack-Jolly-Seber model (Gimenez and Choquet, 2010) of apparent survival (Φ) and resight rate (p) for pre-fledge piping plover chicks on the Gavins Point Reach of the Missouri River, 2005–2009 and 2012–2014. An individual random effect was estimated for p in each model.

| **Φ**[a] | **p**[a] | **k**[b] | **AICc**[c] | **ΔAICc** | **w*i*** |
|---|---|---|---|---|---|
| Age × year + hatch + engineered + engineered age + density × Age | age × year + engineered + density | 224 | 23620.98 | 0.00 | 0.44 |
| Age × year + hatch + engineered + density × Age | age × year + engineered + density | 223 | 23621.61 | 0.63 | 0.32 |
| Age × year + hatch + engineered + engineered age | age × year + engineered + density | 222 | 23623.38 | 2.41 | 0.13 |
| Age × year + hatch + engineered | age × year + engineered + density | 221 | 23623.79 | 2.81 | 0.11 |
| Age × year + hatch + density × Age | age × year + engineered + density | 222 | 23635.76 | 14.78 | 0.00 |
| Age × year + hatch | age × year + engineered + density | 220 | 23638.08 | 17.10 | 0.00 |
| Age × year | age × year | 217 | 23673.93 | 52.95 | 0.00 |
| Age + year | age × year | 210 | 23681.74 | 60.77 | 0.00 |
| age + year | age × year | 233 | 23689.01 | 68.03 | 0.00 |
| year | age × year | 209 | 23702.89 | 81.92 | 0.00 |
| Age × post-flood + hatch + engineered + engineered age + density × Age | age × year + engineered + density | 212 | 23723.94 | 102.97 | 0.00 |
| Age × year | age + year | 49 | 23833.49 | 212.51 | 0.00 |
| Age + year | age + year | 42 | 23836.53 | 215.55 | 0.00 |
| year | age + year | 41 | 23863.56 | 242.59 | 0.00 |
| Age | age × year | 203 | 23876.74 | 255.77 | 0.00 |
| age × year | age × year | 393 | 23878.54 | 257.57 | 0.00 |
| age | age × year | 226 | 23894.42 | 273.44 | 0.00 |
| . | age × year | 202 | 23913.85 | 292.87 | 0.00 |
| Age × year | age | 42 | 24019.39 | 398.41 | 0.00 |
| Age + year | age | 35 | 24024.16 | 403.19 | 0.00 |

| | | | | | |
|---|---|---|---|---|---|
| year | age | 34 | 24041.12 | 420.15 | 0.00 |
| Age | age + year | 35 | 24079.20 | 458.22 | 0.00 |
| . | age + year | 33 | 24107.33 | 486.36 | 0.00 |
| Age | age | 28 | 24254.18 | 633.21 | 0.00 |
| age + year | Age × year | 49 | 24267.11 | 646.13 | 0.00 |
| . | age | 26 | 24273.96 | 652.98 | 0.00 |
| Age × year | Age × year | 33 | 24286.81 | 665.83 | 0.00 |
| Age + year | Age × year | 26 | 24290.27 | 669.30 | 0.00 |
| age + year | Age + year | 42 | 24346.59 | 725.62 | 0.00 |
| age + year | year | 41 | 24367.09 | 746.12 | 0.00 |
| Age × year | Age + year | 26 | 24373.52 | 752.55 | 0.00 |
| Age + year | Age + year | 19 | 24374.10 | 753.12 | 0.00 |
| Age × year | year | 25 | 24386.84 | 765.87 | 0.00 |
| Age + year | year | 18 | 24389.90 | 768.93 | 0.00 |
| year | Age × year | 25 | 24410.59 | 789.62 | 0.00 |
| age | Age × year | 42 | 24463.42 | 842.44 | 0.00 |
| Age | Age × year | 19 | 24481.24 | 860.27 | 0.00 |
| year | Age + year | 18 | 24485.68 | 864.70 | 0.00 |
| age × year | Age × year | 217 | 24491.76 | 870.78 | 0.00 |
| year | year | 17 | 24516.15 | 895.17 | 0.00 |
| age + year | Age | 35 | 24563.86 | 942.89 | 0.00 |
| age × year | Age + year | 210 | 24565.96 | 944.99 | 0.00 |
| Age × year | Age | 19 | 24583.42 | 962.45 | 0.00 |
| Age + year | Age | 12 | 24588.02 | 967.05 | 0.00 |
| Age × year | . | 18 | 24590.61 | 969.63 | 0.00 |
| age × year | year | 209 | 24592.52 | 971.55 | 0.00 |
| age + year | . | 34 | 24593.00 | 972.02 | 0.00 |
| Age + year | . | 11 | 24597.29 | 976.32 | 0.00 |
| age | Age + year | 35 | 24598.55 | 977.57 | 0.00 |
| age | year | 34 | 24619.20 | 998.22 | 0.00 |
| . | Age × year | 17 | 24626.71 | 1005.73 | 0.00 |
| Age | Age + year | 12 | 24628.89 | 1007.91 | 0.00 |
| Age | year | 11 | 24645.87 | 1024.90 | 0.00 |
| year | Age | 11 | 24685.42 | 1064.44 | 0.00 |
| year | . | 10 | 24705.92 | 1084.94 | 0.00 |
| . | Age + year | 11 | 24770.85 | 1149.87 | 0.00 |

| | | | | | |
|---|---|---|---|---|---|
| age × year | Age | 203 | 24795.41 | 1174.43 | 0.00 |
| age | Age | 28 | 24801.33 | 1180.35 | 0.00 |
| age × year | . | 202 | 24804.39 | 1183.41 | 0.00 |
| . | year | 10 | 24807.61 | 1186.63 | 0.00 |
| age | . | 27 | 24817.30 | 1196.32 | 0.00 |
| Age | Age | 5 | 24830.97 | 1209.99 | 0.00 |
| Age | . | 4 | 24842.51 | 1221.53 | 0.00 |
| . | Age | 4 | 24960.71 | 1339.73 | 0.00 |
| . | . | 3 | 24989.80 | 1368.83 | 0.00 |

[a] Variables used in the models: Age–age of the chick in days since hatch (linear trend), age–age of the chick in days since hatch (categorical), Yr–a categorical variable for year (2005–2009, 2012–2014), Hatch–the standardized (May 20 as 0) hatch date, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Density × Age–variable representative of the interaction of nesting density (pairs/ha on a sandbar) and the age of a chick (linear trend).

[b] Number of parameters in the model.

[c] Akaike's Information Criterion corrected for small sample size and over dispersion ($\hat{c}$ = 1.06).

Appendix D.

Table 1. Model ranking results for a Barker (1997) model of true survival (S), resight probability (p), reporting rate of dead encounters (r), the probability of being resighted during and surviving the supplemental period (R), the probability of being resighted and then dying during the supplemental period (R'), the fidelity of individuals of individuals to the study area (F), and the return rate of individuals that have emigrated (F') for piping plovers on the Gavins Point Reach of the Missouri River, 2005–2014. We fixed the reporting rate of dead individuals (r) to 0 for all models as there were no reports of dead individuals during the supplemental period and removed it below.

| **S**[a] | **p**[a] | **R**[a] | **R'**[a] | **F**[a] | **F'**[a] | **k**[b] | **AIC$_c$**[c] | **ΔAIC$_c$** | **w*i*** |
|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + yr | age | 41 | 10219.177 | 0.000 | 0.160 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered) | age | 49 | 10219.855 | 0.678 | 0.114 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 50 | 10220.092 | 0.915 | 0.101 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 49 | 10220.449 | 1.272 | 0.085 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(density) | age | 42 | 10220.985 | 1.808 | 0.065 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + yr | age | 40 | 10221.186 | 2.009 | 0.059 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 50 | 10221.452 | 2.275 | 0.051 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + yr + HY(engineered) | age | 48 | 10221.692 | 2.515 | 0.045 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 51 | 10222.125 | 2.948 | 0.037 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 50 | 10222.420 | 3.243 | 0.032 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + yr | age | 40 | 10222.925 | 3.748 | 0.025 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + yr + HY(density) | age | 41 | 10222.962 | 3.785 | 0.024 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 49 | 10223.288 | 4.111 | 0.020 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered) | age | 48 | 10223.365 | 4.187 | 0.020 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 48 | 10223.485 | 4.308 | 0.019 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 44 | 10223.658 | 4.481 | 0.017 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 49 | 10223.763 | 4.586 | 0.016 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + yr | age | 46 | 10223.857 | 4.680 | 0.015 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(density) | age | 41 | 10224.403 | 5.226 | 0.012 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + density) | age | 49 | 10224.524 | 5.347 | 0.011 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + yr + HY(engineered) | age | 47 | 10224.541 | 5.364 | 0.011 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + yr | age | 39 | 10225.036 | 5.859 | 0.009 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 49 | 10225.495 | 6.318 | 0.007 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 50 | 10225.693 | 6.515 | 0.006 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + yr + HY(density) | age | 47 | 10225.728 | 6.551 | 0.006 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + yr | age | 48 | 10225.932 | 6.754 | 0.005 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered) | age | 41 | 10226.236 | 7.059 | 0.005 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 48 | 10227.149 | 7.972 | 0.003 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 43 | 10227.365 | 8.188 | 0.003 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + yr | age | 47 | 10227.618 | 8.440 | 0.002 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + yr + HY(density) | age | 49 | 10227.780 | 8.603 | 0.002 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 47 | 10227.895 | 8.717 | 0.002 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + yr | age | 45 | 10228.398 | 9.221 | 0.002 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 48 | 10228.531 | 9.354 | 0.001 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + yr + HY(density) | age | 48 | 10229.438 | 10.261 | 0.001 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + yr | age | 47 | 10229.443 | 10.266 | 0.001 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + yr + HY(density) | age | 46 | 10229.790 | 10.613 | 0.001 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + yr + HY(engineered) | age | 46 | 10229.830 | 10.653 | 0.001 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 42 | 10229.947 | 10.770 | 0.001 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 49 | 10230.559 | 11.381 | 0.001 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + yr + HY(engineered + density) | age | 47 | 10230.742 | 11.565 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + yr + HY(engineered) | age | 47 | 10230.779 | 11.601 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + yr | age | 39 | 10230.834 | 11.657 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + yr + HY(density) | age | 48 | 10230.973 | 11.796 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + yr + HY(engineered) | age | 41 | 10231.344 | 12.167 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + yr + HY(engineered + density) | age | 48 | 10231.659 | 12.482 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 43 | 10231.959 | 12.782 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + yr + HY(density) | age | 40 | 10231.968 | 12.791 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + yr | age | 53 | 10232.852 | 13.675 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + yr + HY(engineered) | age | 54 | 10232.855 | 13.678 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 42 | 10233.132 | 13.954 | 0.000 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 55 | 10233.163 | 13.986 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr + HY(engineered) | age | 53 | 10233.852 | 14.674 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr | age | 52 | 10233.967 | 14.790 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered) | age | 55 | 10234.062 | 14.885 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr | . | 51 | 10234.072 | 14.894 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + yr + HY(engineered + density) | age | 55 | 10234.180 | 15.002 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 54 | 10234.273 | 15.096 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + yr + HY(engineered) | age | 40 | 10234.396 | 15.219 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + yr + HY(density) | age | 54 | 10234.696 | 15.519 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(density) | age | 55 | 10234.743 | 15.565 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + yr | age | 54 | 10234.885 | 15.708 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + yr + HY(engineered) | age | 55 | 10234.888 | 15.711 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age × yr | age | 58 | 10235.031 | 15.854 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 56 | 10235.160 | 15.983 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + yr + HY(density) | age | 40 | 10235.236 | 16.059 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + density) | age | 56 | 10235.465 | 16.288 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + yr + HY(density) | age | 55 | 10235.503 | 16.325 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + yr | age | 53 | 10235.655 | 16.478 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 44 | 10235.697 | 16.520 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 56 | 10235.727 | 16.549 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr + HY(density) | age | 53 | 10235.811 | 16.634 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr + HY(engineered + density) | age | 54 | 10235.900 | 16.723 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered) | age | 56 | 10235.903 | 16.726 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + yr | age | 55 | 10235.916 | 16.739 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 56 | 10236.027 | 16.850 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 55 | 10236.238 | 17.061 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + yr + HY(engineered) | age | 54 | 10236.336 | 17.159 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + yr | age | 46 | 10236.580 | 17.403 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 55 | 10236.666 | 17.489 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 57 | 10236.738 | 17.561 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 57 | 10236.845 | 17.667 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 45 | 10237.005 | 17.828 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 56 | 10237.106 | 17.928 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 57 | 10237.157 | 17.980 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 57 | 10237.186 | 18.008 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + yr + HY(density) | age | 54 | 10237.398 | 18.221 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 55 | 10237.545 | 18.368 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(density) | age | 56 | 10237.756 | 18.578 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + yr + HY(density) | age | 47 | 10237.783 | 18.606 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 48 | 10237.815 | 18.638 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 40 | 10238.218 | 19.041 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 46 | 10238.426 | 19.249 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 53 | 10238.581 | 19.404 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 56 | 10238.618 | 19.441 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 45 | 10239.249 | 20.072 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 47 | 10239.304 | 20.127 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 58 | 10239.552 | 20.375 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 53 | 10239.599 | 20.422 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + yr + HY(density) | age | 39 | 10239.857 | 20.680 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 47 | 10239.908 | 20.731 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 41 | 10239.979 | 20.802 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 46 | 10240.053 | 20.876 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + yr + HY(engineered) | age | 40 | 10240.129 | 20.952 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + yr | age | 54 | 10240.177 | 21.000 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 47 | 10240.450 | 21.273 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 48 | 10240.574 | 21.396 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 48 | 10240.645 | 21.467 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 53 | 10240.677 | 21.500 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 46 | 10240.807 | 21.630 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + yr + HY(engineered + density) | age | 41 | 10241.000 | 21.823 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + yr + HY(engineered + density) | age | 40 | 10241.105 | 21.927 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 41 | 10241.230 | 22.053 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 54 | 10241.370 | 22.193 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 47 | 10241.407 | 22.230 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 53 | 10241.944 | 22.767 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 42 | 10241.979 | 22.802 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 44 | 10242.056 | 22.879 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 48 | 10242.073 | 22.896 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 49 | 10242.080 | 22.903 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 43 | 10242.093 | 22.916 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 | age | 54 | 10242.177 | 22.999 | 0.000 |

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| | | | | + yr9) + HY(post-flood + flood + engineered) | | | | | |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 54 | 10242.403 | 23.226 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 55 | 10242.642 | 23.465 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 55 | 10242.766 | 23.589 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 53 | 10242.902 | 23.725 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 54 | 10243.297 | 24.120 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 46 | 10243.307 | 24.130 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 52 | 10243.711 | 24.534 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 48 | 10243.716 | 24.539 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 55 | 10243.927 | 24.750 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 46 | 10243.943 | 24.765 | 0.000 |

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| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 56 | 10244.097 | 24.920 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 45 | 10244.295 | 25.118 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 47 | 10244.406 | 25.229 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr | age + yr | 60 | 10244.413 | 25.236 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 49 | 10244.634 | 25.457 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | . | 43 | 10244.846 | 25.669 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 49 | 10244.947 | 25.769 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 47 | 10245.141 | 25.964 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 52 | 10245.184 | 26.007 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 49 | 10245.350 | 26.173 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 48 | 10245.436 | 26.259 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 45 | 10245.542 | 26.365 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 50 | 10245.555 | 26.378 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 48 | 10245.571 | 26.394 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 50 | 10245.612 | 26.435 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 51 | 10245.646 | 26.469 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 47 | 10245.658 | 26.481 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 46 | 10245.773 | 26.596 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 52 | 10246.071 | 26.894 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 49 | 10246.352 | 27.175 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 52 | 10246.370 | 27.193 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 58 | 10246.470 | 27.293 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 41 | 10246.613 | 27.436 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 47 | 10246.729 | 27.552 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 48 | 10246.989 | 27.812 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 50 | 10247.114 | 27.937 | 0.000 |

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| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 54 | 10247.122 | 27.945 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 51 | 10247.170 | 27.993 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 54 | 10247.197 | 28.020 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 59 | 10247.660 | 28.483 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 59 | 10247.786 | 28.609 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 53 | 10248.092 | 28.915 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 47 | 10248.299 | 29.122 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 48 | 10248.337 | 29.160 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 59 | 10248.510 | 29.333 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 46 | 10248.714 | 29.537 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 57 | 10248.820 | 29.643 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 54 | 10248.894 | 29.717 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + | age | 55 | 10248.933 | 29.756 | 0.000 |

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| | | | | flood + engineered + engineered age + density) | | | | | |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 60 | 10249.070 | 29.893 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 48 | 10249.190 | 30.013 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 45 | 10249.539 | 30.362 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) | age | 47 | 10249.654 | 30.477 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 60 | 10249.672 | 30.495 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 60 | 10249.694 | 30.517 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 48 | 10249.839 | 30.662 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 47 | 10249.959 | 30.782 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 49 | 10250.073 | 30.896 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 58 | 10250.241 | 31.063 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 49 | 10250.412 | 31.235 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 58 | 10250.536 | 31.359 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 48 | 10250.570 | 31.393 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 | age | 44 | 10250.741 | 31.564 | 0.000 |

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| | | | | + yr9) + HY(post-flood + flood) | | | | | |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 59 | 10250.815 | 31.638 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 51 | 10250.845 | 31.668 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 61 | 10250.864 | 31.687 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 46 | 10250.907 | 31.729 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | age | 44 | 10250.956 | 31.778 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 52 | 10251.092 | 31.914 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 41 | 10251.460 | 32.283 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 49 | 10251.688 | 32.511 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 59 | 10251.753 | 32.576 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 50 | 10251.906 | 32.729 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 50 | 10252.291 | 33.114 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 40 | 10252.295 | 33.118 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 42 | 10252.377 | 33.200 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + | age | 53 | 10252.419 | 33.242 | 0.000 |

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| | | | | engineered age + density) | | | | | |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 53 | 10252.475 | 33.298 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 51 | 10252.674 | 33.497 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 42 | 10252.894 | 33.717 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 53 | 10253.033 | 33.855 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 41 | 10253.136 | 33.959 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 51 | 10253.176 | 33.999 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 54 | 10253.177 | 34.000 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | age | 51 | 10253.340 | 34.163 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 42 | 10253.545 | 34.368 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 43 | 10253.594 | 34.417 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 43 | 10253.705 | 34.528 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 41 | 10253.807 | 34.630 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 52 | 10254.350 | 35.173 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 42 | 10254.440 | 35.263 | 0.000 |

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| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 46 | 10254.884 | 35.706 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 60 | 10254.980 | 35.803 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 47 | 10254.989 | 35.812 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 47 | 10255.031 | 35.853 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) | age | 45 | 10255.049 | 35.872 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + yr + HY(engineered + engineered age + density) | age | 42 | 10255.113 | 35.936 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 44 | 10255.141 | 35.964 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 43 | 10255.169 | 35.992 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 60 | 10255.171 | 35.994 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 47 | 10255.268 | 36.090 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 46 | 10255.681 | 36.504 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + juv × (post-flood + flood) | age | 46 | 10255.834 | 36.657 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 48 | 10255.887 | 36.710 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 39 | 10256.609 | 37.432 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 61 | 10256.683 | 37.506 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) | age | 53 | 10256.715 | 37.538 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 41 | 10256.847 | 37.669 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 40 | 10256.973 | 37.796 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 41 | 10257.050 | 37.873 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) | age | 40 | 10257.345 | 38.168 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 40 | 10257.544 | 38.367 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 41 | 10257.584 | 38.406 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 54 | 10257.982 | 38.805 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) | age | 54 | 10258.011 | 38.834 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 54 | 10258.015 | 38.837 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 42 | 10258.195 | 39.018 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 42 | 10258.440 | 39.263 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 54 | 10258.751 | 39.574 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 41 | 10258.774 | 39.597 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 55 | 10259.068 | 39.891 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 55 | 10259.137 | 39.960 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 53 | 10259.159 | 39.982 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 55 | 10259.289 | 40.112 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 55 | 10259.368 | 40.191 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 42 | 10259.796 | 40.619 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 55 | 10259.920 | 40.743 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 55 | 10259.995 | 40.818 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 55 | 10260.051 | 40.874 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 43 | 10260.063 | 40.886 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 54 | 10260.317 | 41.140 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 54 | 10260.392 | 41.215 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 56 | 10260.440 | 41.263 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 48 | 10260.570 | 41.393 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 48 | 10260.738 | 41.561 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr | age × yr | 68 | 10260.756 | 41.579 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 56 | 10260.778 | 41.601 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) | age | 53 | 10260.778 | 41.601 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 56 | 10260.779 | 41.601 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | age + yr | 52 | 10260.975 | 41.798 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 54 | 10260.980 | 41.803 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 56 | 10261.076 | 41.899 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 56 | 10261.166 | 41.989 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 56 | 10261.172 | 41.995 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 56 | 10261.193 | 42.016 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 47 | 10261.439 | 42.262 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 49 | 10261.470 | 42.293 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 55 | 10261.945 | 42.768 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 54 | 10262.071 | 42.894 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 55 | 10262.075 | 42.898 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 55 | 10262.132 | 42.955 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 57 | 10262.214 | 43.037 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 39 | 10262.321 | 43.144 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 57 | 10262.353 | 43.176 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 40 | 10262.671 | 43.494 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 57 | 10262.693 | 43.516 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 57 | 10262.783 | 43.606 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) | age | 38 | 10263.012 | 43.835 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + juv × (post-flood + flood) | age | 52 | 10263.070 | 43.893 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 40 | 10263.071 | 43.894 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age + yr | . | 45 | 10263.164 | 43.987 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 40 | 10263.385 | 44.208 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 56 | 10263.695 | 44.518 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) | age | 39 | 10263.815 | 44.638 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 41 | 10263.954 | 44.777 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 58 | 10264.159 | 44.982 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 39 | 10264.211 | 45.034 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age) | age | 41 | 10264.398 | 45.221 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + density) | age | 41 | 10264.496 | 45.319 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + juv × (post-flood + flood) + HY(density) | age | 53 | 10264.539 | 45.362 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | 42 | 10264.794 | 45.617 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered) | age | age × yr | age | age + juv × (post-flood + flood) + HY(engineered) | age | 40 | 10265.422 | 46.245 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | . | 50 | 10266.132 | 46.955 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + yr | age | 59 | 10268.138 | 48.961 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | . | 37 | 10268.865 | 49.688 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age + yr | age | 53 | 10268.865 | 49.688 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age × yr | age + yr | 66 | 10269.502 | 50.325 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | age | 51 | 10270.319 | 51.142 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age + yr | age | 46 | 10270.642 | 51.465 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | age | 58 | 10272.942 | 53.765 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | . | . | 42 | 10273.810 | 54.633 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | age | 38 | 10275.069 | 55.892 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | age | 45 | 10275.942 | 56.765 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | . | age | 43 | 10276.948 | 57.771 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | age × yr | 60 | 10277.275 | 58.098 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age + yr | age + yr | 54 | 10278.328 | 59.151 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | . | age | 50 | 10281.287 | 62.109 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | . | 44 | 10282.077 | 62.900 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | age + yr | 46 | 10283.242 | 64.065 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | age | 45 | 10286.523 | 67.346 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | . | age + yr | 51 | 10286.736 | 67.559 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | . | . | 36 | 10293.182 | 74.005 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age + yr | age × yr | 62 | 10294.639 | 75.462 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age × yr | age | 65 | 10294.946 | 75.769 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | . | age | 37 | 10297.162 | 77.984 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age × yr | age × yr | 74 | 10298.188 | 79.011 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age × yr | age | 59 | 10301.725 | 82.548 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age × yr | age + yr | 60 | 10301.917 | 82.740 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | . | age × yr | 59 | 10303.031 | 83.854 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | age + yr | 53 | 10304.259 | 85.082 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | . | age + yr | 45 | 10304.950 | 85.772 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age | age | age × yr | age × yr | 67 | 10306.909 | 87.732 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age + yr | age | age × yr | age × yr | 68 | 10307.551 | 88.374 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | age × yr | 54 | 10310.858 | 91.681 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered) | age | 42 | 10317.889 | 98.712 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age × yr | age × yr | 68 | 10318.260 | 99.083 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + engineered age) | age | 43 | 10318.871 | 99.694 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age + density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 43 | 10319.163 | 99.986 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | . | age | 44 | 10320.328 | 101.151 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age × yr | . | 57 | 10321.798 | 102.621 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 42 | 10321.942 | 102.765 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(engineered + engineered age) | age | age × yr | age | age + yr + HY(engineered + density) | age | 42 | 10322.644 | 103.467 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + yr + HY(engineered + density) | age | 41 | 10324.812 | 105.635 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | age | 52 | 10325.994 | 106.817 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + yr | age | 38 | 10328.862 | 109.685 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 | age | 52 | 10329.476 | 110.299 | 0.000 |

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|---|---|---|---|---|---|---|---|---|---|
| | | | | + yr9) + HY(post-flood + flood) | | | | | |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 46 | 10329.622 | 110.445 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + yr + HY(engineered) | age | 39 | 10330.213 | 111.036 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 45 | 10330.337 | 111.160 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age × yr | . | 51 | 10330.504 | 111.327 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 46 | 10330.966 | 111.788 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) + HY(density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 47 | 10331.338 | 112.161 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age × yr | age | 52 | 10332.538 | 113.361 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + density) | age | 53 | 10334.088 | 114.911 | 0.000 |
| HY(bandage + hatch) + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9 + yr10) + juv + HY(post-flood + flood + engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood) | age | 52 | 10334.719 | 115.542 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 59 | 10335.276 | 116.099 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 60 | 10335.976 | 116.799 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 45 | 10336.149 | 116.972 | 0.000 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 60 | 10336.287 | 117.110 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 58 | 10336.404 | 117.227 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 45 | 10336.490 | 117.312 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 60 | 10336.550 | 117.373 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 46 | 10336.909 | 117.732 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 59 | 10337.238 | 118.061 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 60 | 10337.316 | 118.139 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 59 | 10337.539 | 118.362 | 0.000 |
| HY(bandage + hatch) + juv + juv × (post-flood + flood) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 44 | 10337.654 | 118.477 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 61 | 10337.662 | 118.484 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + | age | 61 | 10337.700 | 118.523 | 0.000 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | flood + engineered + engineered age) | | | | | |
| HY(bandage + hatch) + juv × yr + HY(engineered) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 61 | 10337.723 | 118.546 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 61 | 10338.004 | 118.827 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 61 | 10338.295 | 119.117 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered) | age | 61 | 10338.456 | 119.279 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 60 | 10339.038 | 119.861 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 62 | 10339.388 | 120.210 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + density) | age | 62 | 10339.428 | 120.251 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age) | age | 62 | 10339.620 | 120.443 | 0.000 |
| HY(bandage + hatch) + juv × yr + HY(engineered + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 62 | 10339.726 | 120.549 | 0.000 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv × yr + HY(engineered + engineered age + density) | age | age × yr | age | age + AHY:(yr2 + yr3 + yr4 + yr5 + yr6 + yr7 + yr8 + yr9) + HY(post-flood + flood + engineered + engineered age + density) | age | 63 | 10341.210 | 122.033 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | age | age × yr | 61 | 10341.642 | 122.465 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | age + yr | . | age × yr | age × yr | 66 | 10345.585 | 126.408 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age | age | age × yr | age × yr | 60 | 10355.314 | 136.137 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | . | . | age × yr | age × yr | 58 | 10362.918 | 143.741 | 0.000 |
| HY(bandage + hatch) + juv + yr | age | age × yr | age | . | age × yr | 53 | 10366.793 | 147.616 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | age | age | age × yr | age × yr | 66 | 10369.036 | 149.859 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | age + yr | age | age × yr | age × yr | 67 | 10369.817 | 150.639 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | . | age | age × yr | age × yr | 59 | 10371.500 | 152.323 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | age + yr | 59 | 10372.072 | 152.895 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | age × yr | age | age × yr | age × yr | 73 | 10373.738 | 154.561 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age + yr | . | age × yr | age × yr | 67 | 10380.545 | 161.367 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age | . | age × yr | age × yr | 66 | 10381.240 | 162.063 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | . | age × yr | age × yr | 73 | 10386.008 | 166.831 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age × yr | age | age | age × yr | 67 | 10388.404 | 169.226 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | age | . | age × yr | age × yr | 65 | 10395.496 | 176.319 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | age | . | age × yr | age × yr | 58 | 10398.581 | 179.404 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | age × yr | . | age × yr | age × yr | 72 | 10400.606 | 181.429 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age × yr | . | 43 | 10405.764 | 186.587 | 0.000 |
| HY(bandage + hatch) + juv × yr | age | age | . | age × yr | age × yr | 59 | 10413.360 | 194.183 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age + yr | . | 37 | 10413.975 | 194.798 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age + yr | age | 38 | 10414.636 | 195.459 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age × yr | age + yr | 52 | 10414.753 | 195.575 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age × yr | age | 51 | 10414.944 | 195.767 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age × yr | age | 44 | 10417.136 | 197.958 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age + yr | age | 45 | 10423.497 | 204.320 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | age | age | age × yr | age × yr | 59 | 10429.737 | 210.559 | 0.000 |
| HY(bandage + hatch) + juv × yr | . | . | age | age × yr | age × yr | 58 | 10432.305 | 213.128 | 0.000 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| HY(bandage + hatch) + juv × yr | . | . | . | age × yr | age × yr | 57 | 10432.381 | 213.204 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age + yr | age + yr | 46 | 10433.109 | 213.932 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age × yr | age × yr | 60 | 10443.358 | 224.180 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age + yr | age × yr | 54 | 10449.377 | 230.200 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | . | 36 | 10463.334 | 244.157 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | age | 37 | 10463.900 | 244.723 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | . | 29 | 10467.046 | 247.869 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | age | 30 | 10467.282 | 248.105 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | age | 44 | 10471.226 | 252.049 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | age + yr | 45 | 10471.575 | 252.398 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | age | 37 | 10476.856 | 257.679 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | age + yr | 38 | 10480.616 | 261.439 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | age × yr | 53 | 10486.135 | 266.958 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | . | . | 28 | 10488.887 | 269.709 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | . | age | 29 | 10492.671 | 273.494 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | . | age | 36 | 10497.662 | 278.485 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | age | age × yr | 46 | 10499.646 | 280.469 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | . | age + yr | 37 | 10502.411 | 283.234 | 0.000 |
| HY(bandage + hatch) + juv | age | age × yr | age | . | age × yr | 45 | 10518.631 | 299.454 | 0.000 |
| . | age | age × yr | age | age × yr | . | 40 | 10808.829 | 589.652 | 0.000 |
| . | age | age × yr | age | age × yr | age | 41 | 10811.415 | 592.238 | 0.000 |
| . | age | age × yr | age | age + yr | . | 34 | 10817.950 | 598.773 | 0.000 |
| . | age | age × yr | age | age + yr | age | 35 | 10818.807 | 599.630 | 0.000 |
| . | age | age × yr | age | age × yr | age + yr | 49 | 10845.692 | 626.515 | 0.000 |
| . | age | age × yr | age | age + yr | age + yr | 43 | 10856.350 | 637.173 | 0.000 |
| . | age | age × yr | age | age × yr | age × yr | 57 | 10861.234 | 642.057 | 0.000 |
| . | age | age × yr | age | age × yr | age | 48 | 10864.651 | 645.473 | 0.000 |
| . | age | age × yr | age | age + yr | age × yr | 51 | 10871.928 | 652.751 | 0.000 |
| . | age | age × yr | age | age + yr | age | 42 | 10876.009 | 656.832 | 0.000 |
| . | age | age × yr | age | age | . | 26 | 11020.862 | 801.685 | 0.000 |
| . | age | age × yr | age | age | age | 27 | 11022.880 | 803.702 | 0.000 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| . | age | age × yr | age | age | age | 34 | 11037.023 | 817.846 | 0.000 |
| . | age | age × yr | age | age | age + yr | 35 | 11039.046 | 819.869 | 0.000 |
| . | age | age × yr | age | age | age × yr | 43 | 11055.255 | 836.078 | 0.000 |
| . | age | age × yr | age | age | age | 34 | 11157.101 | 937.924 | 0.000 |
| . | age | age × yr | age | age | . | 33 | 11162.115 | 942.938 | 0.000 |
| . | age | age × yr | age | . | age | 26 | 11187.096 | 967.919 | 0.000 |
| . | age | age × yr | age | . | . | 25 | 11191.371 | 972.194 | 0.000 |
| . | age | age × yr | age | . | age + yr | 34 | 11234.776 | 1015.599 | 0.000 |
| . | age | age × yr | age | age | age + yr | 42 | 11236.591 | 1017.413 | 0.000 |
| . | age | age × yr | age | age | age | 41 | 11245.903 | 1026.725 | 0.000 |
| . | age | age × yr | age | . | age × yr | 42 | 11250.979 | 1031.802 | 0.000 |
| . | age | age × yr | age | age | age × yr | 50 | 11252.837 | 1033.660 | 0.000 |
| . | age | age × yr | age | . | age | 33 | 11293.884 | 1074.707 | 0.000 |

[a] Variables used in the models: Age–variable for a difference between hatch-year (HY) and after hatch year (AHY) piping plovers, HY()–indicated the variables within the parentheses only affect HY piping plovers, Band age–age (in days) of banding since hatch, Hatch–the standardized (May 20 as 0) hatch date, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Density–variable representative of the nesting density (pairs/ha on a sandbar), Yr–a categorical variable for year (2005–2014), Post-flood–a categorical variable for the post-flood period (2012–2014), Flood–a categorical variable for the flood (2010, 2011).

[b] Number of parameters in the model.

[c] Akaike's Information Criterion corrected for small sample size and over dispersion ($\hat{c}$ = 1.13).

# CHAPTER 2: PIPING PLOVER BODY CONDITION AND PREY ABUNDANCE ON FLOOD-CREATED HABITAT ON THE MISSOURI RIVER, USA

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RRH: *Hunt et al.* • Piping Plover condition

PIPING PLOVER BODY CONDITION AND PREY ABUNDANCE ON FLOOD-CREATED HABITAT ON THE MISSOURI RIVER, USA

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ABSTRACT.---Habitat quality can have a profound effect on the condition and fitness of individual birds and on population demography. We investigated the effects of habitat metrics on the condition of Piping Plovers (*Charadrius melodus*) nesting on Missouri River sandbars from 2005–2014. We measured adult mass, egg mass, and pre-fledged chick growth rates. The amount of breeding habitat was variable throughout our study, and increased substantially following flooding in 2011, resulting in increased demographic rates such as reproductive output and hatch-year survival, compared to the pre-flood period. We hypothesized that condition would be related to habitat quality (invertebrate prey abundance) and that increased demographic rates throughout the post-flood period would, at least in part, be related to increased condition. However, we found there was no difference in condition (egg mass, pre-fledge chick growth, adult mass) between pre- and post-flood habitat types. We also found that egg mass and pre-fledge chick growth may be related to invertebrate prey abundance as these variables increased initially following the flood but decreased as the flood-created habitat aged. As the condition of individuals did not appear to contribute directly to the increased demographic rates following the flood, we suggest that the change in density-dependent predation pressure may explain the increase. Although the demographic effects of the flood were positive for plovers, it is important to understand the effects of habitat on the condition of individuals, and the short- and long-term consequences of these effects that may ultimately contribute to demography.

*Keywords.--- Charadrius melodus*, condition, growth rates, habitat, Missouri River, prey abundance

Habitat quality affects the condition and fitness of individuals and the dynamics of populations (Lindström 1999, Reid et al. 2003, Van De Pol et al. 2006). As ecosystems are altered, habitat may be degraded with resulting indirect consequences such as changes in predation pressure, and changes in prey availability, which affect species (Schekkerman et al. 2008, Kentie et al. 2013). For migratory birds, the effects of habitat degradation may be compounded by the variety of habitats they use throughout their annual cycle (Webster et al. 2002), and habitat quality at one stage may influence habitat selection (Gunnarsson et al. 2005) and reproductive success (Norris et al. 2004) at another. The effects of habitat quality can begin early in development; coupled with environmental conditions and parental quality, habitat quality can affect the condition of pre-fledge chicks and influence their survival. The combination of egg size and parental quality can affect chick size at hatching and subsequent short-term survival (Bolton 1991, Blomqvist et al. 1997, Catlin et al. 2014). Precocial chicks, in particular, may experience increased impacts of early conditions because they must move and forage immediately after hatching (Metcalfe and Monaghan 2001).

Prey abundance is an important component of habitat quality, affecting pre-fledge growth rates, time to reach fledging, fledging mass, and survival to fledging (Kersten and Brenninkmeijer 1995, Loegering and Fraser 1995, Park et al. 2001, Schekkerman et al. 2002, 2008, Pearce-Higgins and Yalden 2004, Kentie et al. 2013). For shorebird chicks, the ability to thermoregulate is primarily related to body mass (Visser and Ricklefs 1993), and reductions in food intake may lead to the stagnation of growth sooner than with other taxa (Schekkerman and Visser 2001). Shorebird chicks need to forage continually and therefore have a decreased potential to save energy, such that shorebird chicks operate within fairly narrow energetic margins (Schekkerman and Visser 2001). However, it is not only starvation that may affect chicks reared in low quality habitat, but also behaviors related to hunger that may make them more vulnerable to predation (Hunt and Hunt 1976). For example, precocial chicks in lower quality habitat may allocate more time to foraging in areas where they are more likely to be detected by predators and, if they are of lower condition, may not have the ability to evade predation (Kosztolányi et al. 2007, Schekkerman et al. 2008, Kentie et al. 2013).

The short-term effects of natal condition are relatively well documented, but reduced condition during development can have further, long-lasting effects on the individual and its fitness (Lindström 1999, Metcalfe and Monaghan 2001). Habitat quality and natal condition can affect the probability of survival in the first year of life (Kentie et al. 2013, Catlin et al. 2014) and also chronic effects on adult survival, recruitment, habitat selection, and reproductive output (Cam et al. 2003, Reid et al. 2003, Van De Pol et al. 2006, Catlin et al. 2014). To examine the links among habitat quality, natal condition, and demography, we investigated the relationship between habitat and condition in a species experiencing a rapid population increase on a large, highly altered river system.

The Piping Plover (*Charadrius melodus,* hereafter, 'plover') is a migratory shorebird that breeds on the Atlantic Coast, the Great Lakes, and prairie rivers and alkali lakes of the Great Plains (Elliott-Smith and Haig 2004). On the Missouri River, plovers use riverine sandbars that consist of unvegetated and sparsely vegetated sand and cobble for nesting with adjacent moist substrate used for foraging (Catlin et al.

2015). Adult plovers and their precocial young prey on invertebrates (e.g., Diptera, Collembola, Orthoptera; Catlin et al. 2012) that use these habitats.

We investigated the relationship between several plover condition (adult mass, egg mass, chick growth), and habitat quality (invertebrate abundance) and quantity (amount of foraging area available) before and after an historic flood event. Previous work indicated that Missouri River plover chick condition (e.g., growth rates, time to fledging, and fledging mass) was positively linked to parental quality, egg size, and the availability of foraging habitat, which resulted in both short- and long-term effects on survival (Catlin et al. 2013, Catlin et al. 2014). The flood was followed by increased chick survival, hatch-year survival, fidelity, reproductive output, and population growth (Chapter 1), therefore we hypothesized that increased demographic rates following the flood would be accompanied by improved habitat quality and an improvement in condition.

## METHODS

### Study Area

We studied plovers on sandbars throughout the Gavins Point Reach of the Missouri River from 2005–2014 (Fig. 1). Historically, the Missouri River had a more dynamic flow regime, with relatively frequent floods that created and maintained sandbar habitat through sediment deposition and vegetation scouring (Hesse and Mestl 1993, U.S. Fish and Wildlife Service 2009). However, six dams along the mainstem and a strict water management regime have reduced flood frequency, which in turn, reduced habitat quantity through erosion and vegetation encroachment (U.S. Fish and Wildlife

Service 2009). In response, the U.S. Army Corps of Engineers (USACE) began constructing sandbars on the Missouri River for plovers and Least Terns (*Sternula antillarum*) in 2004, and from 2005–2009, we studied the effectiveness of these sandbars by examining survival, reproductive output, and movement (Catlin et al. 2015). In 2010 and 2011, unplanned flooding created more than 1000 ha of unvegetated sandbar habitat (Fig. 2) that was used by breeding plovers from 2012–2014. Newly created sandbars (both engineered and flood-created) were almost entirely unvegetated bare sand, however vegetation increased through time as the sandbars aged and throughout the breeding seasons (Catlin et al. 2015).

Field Methods

During the breeding season (April–August) from 2005–2014, we located plover nests by searching suitable (unvegetated and sparsely vegetated dry and wet sand) nesting habitat and by observing adult behavior. We floated eggs upon nest discovery to determine initiation date and weighed eggs (± 0.1g) as soon after clutch completion as possible. We trapped adult plovers using traps placed over nests during incubation and uniquely marked and weighed (± 0.1g) all captured individuals. We sexed adult individuals based on plumage characteristics (Gratto-Trevor et al. 2010) and behavior. We uniquely marked chicks as close to hatch as possible and attempted to recapture them every 2–3 days until they were able to fly (approximately 25 days; Hunt et al. 2013). We recorded the chick mass (± 0.1g) each time they were handled.

We sampled invertebrate prey abundance in plover foraging habitat using paint-stirrers coated in Tanglefoot Insect Trap Coating (The Tanglefoot Company, Grand

Rapids, MI, USA) approximately every two weeks during the chick-rearing period (June–August) on randomly selected sandbars (Catlin et al. 2012). During each sampling attempt, we placed two transects extending from one shoreline of the sandbar to the other, perpendicular to the river flow. The first transect was placed randomly along the shoreline. We then placed a second transect 50 m upstream, parallel to the first. We sampled in saturated and moist sand and mud (Le Fer et al. 2008a, Le Fer et al. 2008b, Catlin et al. 2012). The two transects consisted of 2–4 samples each, depending on the presence of wet substrates on each transect. At the center of each habitat type we placed two paint-stirrers (one placed horizontally and one vertically) in the sand for 30 min. When we collected the paint-stirrers, we counted and identified organisms to Order. To prevent bird injury, we placed wire cages around the samples (Le Fer et al. 2008a, Le Fer et al. 2008b, Catlin et al. 2012).

Analytical Methods

*Habitat Information*.---We determined landcover types and estimated nesting density. We calculated habitat availability using land classification coverage's made from data collected during the 2005–2014 breeding seasons. Pan-sharpened multispectral QuickBird (satellite) imagery (2005–2009, 2012–2014) was collected each year between April and October and classified using Definens Developer Software (L. Strong, U.S. Geological Survey, pers. comm.). Habitats were classified into open and sparsely vegetated (< 30% vegetative cover) dry sand, open and sparsely vegetated moist sand, and vegetated (> 30% vegetative cover). The amount of suitable foraging habitat was calculated as the amount (ha) of sparsely vegetated moist sand on a sandbar. We calculated the maximum number of nests simultaneously active on each sandbar and divided by the hectares of foraging habitat (moist sand) to estimate the foraging density (pairs/ha) for each sandbar.

*Modeling approach*.--- To determine the effects of habitat type and age on adult mass, egg mass, chick growth rates, and invertebrate prey abundance, we evaluated the following three models for each:

1. A model including yearly variation as well as covariates for pre-flood habitat type (engineered vs. natural), the age of pre-flood engineered habitat (years from construction) and additional covariates specific to each condition variable and invertebrate prey abundance (global model).
2. A model without time variation that included all other covariates (null model).
3. A model that replaced yearly variation with pre- (2005–2009) and post-flood (2012–2014) as well as the age of post-flood habitat (years since flood) and all other covariates (post-flood model).

We used AICc to rank models (Burnham and Anderson 2002) and analysis of deviance (Skalski 1996) to determine the amount of variation accounted for by the post-flood model. Analysis of deviance tests the significance of the regression coefficients on the basis of the relative distance between likelihood extremes and the proposed regression model (Skalski 1996); it assesses the proportion of temporal variation in our data that was explained by simpler, ecologically relevant parameters, assuming that with large sample sizes, such as ours, fully time variable models could achieve the best, if ecologically less relevant, model fit.

*Adult mass*.---For adult plovers we used an individual's mass as an index of their condition (Catlin et al. 2014). We used generalized linear mixed regression to estimate the effects of habitat type and the age of engineered and post-flood habitat on male and female condition. We used a random effect of individual to control for repeated measures of individuals throughout the study.

*Egg mass*.---Although we attempted to measure eggs as soon after completion as possible, clutches were weighed at various times following completion (range: 0–24 days). We used simple linear regression to estimate the total clutch mass at the time of completion. We used generalized linear mixed models to examine the effects of habitat type and the age of engineered and post-flood habitat on the mass of a clutch at the time of completion.

*Chick growth rates.*---We analyzed the change in mass of chicks as a function of age (days since hatch) using non-linear mixed models. In addition to comparing habitat types and ages, we used covariates to control for the effects of hatch date, foraging density, and year (Catlin et al. 2013, Catlin et al. 2014). We used the following parameterization of the Richards model as the functional form for models:

$$\mathrm{mass} = \mathrm{A} \times [1 + (\mathrm{M} - 1)\mathrm{e}^{\frac{-\mathrm{R} \times (\mathrm{Age} - \mathrm{T})}{\mathrm{M}^{\mathrm{M}/_{1-\mathrm{M}}}}}]^{1/_{1-\mathrm{M}}}$$

where *A* is the asymptotic value, *T* is the inflection point, *R* is the rate of growth, and *M* is the shape parameter (Tjørve and Tjørve 2010). Each of the parameters could be simultaneously modeled as a linear function of multiple covariates (Catlin et al. 2013, Catlin et al. 2014) to test hypotheses about the effect of habitat type and environmental variables on the different components of growth. We controlled for the non-independence of multiple measurements from individuals and broods by averaging the mass within each brood for each age (days since hatch) and added a random effect for brood in the equation for the asymptote (*A*). To reduce the number of estimates and improve model convergence, we added covariates only to the linear equations for the asymptote (*A*) and the growth rate parameter (*R*) in all models.

*Prey Abundance.*---We tested for differences in invertebrate prey abundance between pre-flood natural habitat, pre-flood engineered habitat, and post-flood habitat and among ages of pre-flood engineered habitat and post-flood habitat using negative binomial regression. In addition to comparing habitat types, we also used covariates to control for the effects of date, temperature, wind speed, and year when we analyzed the data from the samples (Catlin et al. 2012). We included a random effect for sandbar × year in all of our models, as prey abundance samples on the same sandbar in the same year may not have been independent from one another. We assessed goodness of fit for the model including all fixed-effects (no random effect) and used the Pearson Chi-squared value divided by the degrees of freedom to control for overdispersion in our analysis (correction: 1.22).

## RESULTS

### Adult mass

We obtained 1,285 mass measurements from 633 AHY plovers from 2005–2014. Of these, 302 (48%) were female and 331 (52%) were male. The global model, which included yearly variation and all covariates, was ranked highest (Table 1), and as the null model was ranked above the post-flood model, we were unable to perform the analysis of deviance. However, as we were most interested in evaluating the effects of the flood-created habitat on pre-fledge growth rates, we present the estimates and explanations for the post-flood (third ranked) model (Table 1). We found no difference between masses when comparing pre-flood habitat types (engineered vs. natural, β = 0.40 ± 0.29, $t$ = 1.38, $P$ = 0.17) nor as engineered habitat aged (β = 0.10 ± 0.12, $t$ = 0.81, $P$ = 0.42). We also found no difference between adult masses when comparing pre- to post-flood habitat types, (β = 0.30 ± 0.34, t = 0.88, $P$ = 0.38) or as the post-flood habitat aged (β = 0.06 ± 0.18, $t$ = 0.32, $P$ = 0.75). Female mass averaged 51.39 ± 0.16g prior to the flood and 50.89 ± 0.20g following the flood. Male mass averaged 51.06 ± 0.16g prior to the flood and 51.19 ± 0.20g following the flood.

Egg mass

We obtained egg mass measurements from 405 plover nests from 2006–2014. Of these, 256 (63%) were from the pre-flood portion of our study and 149 (37%) were from the post-flood portion of our study. The global model, which included yearly variation and all covariates, was ranked highest (Table 2), and the post-flood model accounted for 51% of the temporal variation in the global model ($F$ = 2.78, $P$ = 0.013), and therefore, we present the estimates and explanations for the post-flood (second ranked) model (Table 2). We found no difference between clutch masses on pre-flood habitat types (engineered vs. natural, β = 0.14 ± 0.32, $t$ = 0.45, $P$ = 0.65), as engineered habitat aged (β = –0.01 ± 0.12, $t$ = 0.05, $P$ = 0.96) or between pre- and post-flood habitat (β = –0.48 ± 0.44, $t$ = –1.11, $P$ = 0.27). However, average clutch masses decreased as the post-flood habitat aged (β = –0.71 ± 0.24, t = –3.01, $P$ = 0.003). On average clutches were 37.06 ± 0.11g prior to the flood and 36.58 ± 0.17g after the flood. Following the flood, clutch mass averaged 38.07 ± 0.48g, 36.72 ± 0.29 g, and 36.28 ± 0.22g at 0, 1, and 2 years after the flood, respectively.

Chick growth rates

We collected 7,093 mass measurements from 1,996 plover chicks, resulting in 3,175 mass measurements from 654 broods from 2005–2014. On average, chicks in our study hatched on 28 June (range: 26 May–4 Aug) with a mean foraging density of 5.34 ± 0.34 nests/ha of wet habitat. Mean foraging density was 8.78 ± 1.68 nests/ha prior to the flood, and 3.27 ± 0.86 nests/ha following the flood. The masses of chicks increased with age from hatch to 25 days (Fig. 3). The global model, which included yearly variation and all covariates, was ranked highest (Table 3), and the post-flood model accounted for 36% of the temporal variation in the global model ($F = 7.33$, $P < 0.001$) and therefore, we present the estimates and explanations for the post-flood (second ranked) model (Table 3).

There was no difference in asymptotic mass and growth rates between pre-flood habitat types (natural vs. engineered, Table 4). Pre-flood asymptotic mass, growth rates, and shape parameter didn't differ from that of post-flood, but chicks reached their inflection point ($T$) approximately 3 days earlier prior to the flood than after ($\beta = -2.96$, Table 4). Growth rates on pre-flood engineered sandbars increased as the habitat aged ($\beta = 0.001$, Table 4). Conversely, the growth rates appeared to decrease as the post-flood habitat aged ($\beta = -0.004$, Table 4). Chicks that hatched earlier had a higher asymptotic mass and rate of growth than those hatching later, and chicks experiencing higher foraging habitat density had lower asymptotic masses than those that experienced lower densities (Table 4).

### Prey Abundance

We collected 3,347 invertebrate prey samples from 2005–2014. The global model, which included yearly variation and all covariates, was ranked highest (Table 5), and the post-flood model accounted for 28% of the temporal variation described by the global model ($F$ = 15.6, $p$ = 0.0005). As above, we used the post-flood (second ranked) model to investigate the effects of the flood (Table 5).

Pre-flood natural habitat prey abundance was higher ($\bar{x}$ = 7.88 ± 0.69) than the pre-flood engineered habitat ($\bar{x}$ = 4.47 ± 0.52) but similar to post-flood habitat ($\bar{x}$ = 7.44 ± 0.76; Table 6). There was some evidence that invertebrate abundance increased as pre-flood engineered habitat aged, conversely, invertebrate abundance decreased as the post-flood habitat aged (Table 6, Fig. 4a). Invertebrate abundance was positively correlated with temperature and date and negatively correlated with wind speed (Table 6). The amount of foraging habitat available varied throughout the study (Fig. 2) and was higher on pre-flood engineered habitat as compared to post-flood habitat (Fig. 4b). Mean foraging habitat appeared to decrease as both pre-flood engineered and post-flood sandbar habitat aged (Fig. 4b).

## DISCUSSION

Contrary to our expectations, plover condition (adult mass, egg mass, chick growth rates) was similar prior to- and following the flood. Although the mass and eggs of chicks appeared to increase in the first year following the flood (2012), we detected a decreasing trend in condition as the post-flood habitat aged. Adult mass was unaffected by habitat type or age, but clutch mass did decrease as the post-flood habitat aged. This finding agrees with life-history theory such that in unpredictable conditions, such as the Missouri River, parents of relatively long-lived species ought to maximize their own survival at the cost of low reproductive output (Hirshfield and Tinkle 1975). Moreover, we found that chick growth decreased as post-flood sandbar habitat aged in this study, despite improved survival (Chapter 1).

In a variety of avian species, chick condition is positively related to habitat quality in terms of prey abundance (Kersten and Brenninkmeijer 1995, Loegering and Fraser 1995, Park et al. 2001, Schekkerman et al. 2002, 2008, Pearce-Higgins and Yalden 2004, Kentie et al. 2013), and we found a similar trend for plovers on the Missouri River. While prey abundance may have increased slightly as the pre-flood engineered habitat aged, and although clutch mass did not change as the engineered habitat aged, we found that pre-fledged growth rates increased as engineered habitat aged. Conversely, we found that although prey abundance was high in the first year following the flood (2012), it decreased as post-flood sandbars aged, which was similar to the trend observed in both clutch mass and growth rates so we infer that habitat quality may have affected these condition variables. Although we detected a decreasing trend in condition and prey abundance as the post-flood habitat aged and not while pre-flood habitat aged, it is also possible that with just 3 years of data following the flood, we were unable to parse out environmental variation from this trend.

For a number of shorebird species, chick condition and survival can be positively related to parental quality and egg size as well as habitat quality (Kersten and Brenninkmeijer 1995, Loegering and Fraser 1995, Blomqvist et al. 1997, Pearce-Higgins and Yalden 2004, Ruthrauff and McCaffery 2005, Kosztolányi et al. 2007, Schekkerman et al. 2008, Kentie et al. 2013) even into the first-year and beyond (Kentie et al. 2013, Catlin et al. 2014). Despite improved demographic rates, such as reproductive output and hatch-year survival, in this population following the flood (Chapter 1), we found no differences in condition prior to and following the flood. While condition can have short-term effects on demography, plover reproductive output in this system appears to be driven by density-dependent predation (Catlin et al. 2015).

Predation pressure was substantially higher from 2005–2009 compared to 2012–2014. Prior to the flood a high proportion nests (Catlin et al. 2011*b*) and chicks (Catlin et al. 2011*a*) were lost to predators. Additionally, predator management techniques used before the flood (Catlin et al. 2015) were not used after, and yet reproductive output and HY true survival were higher (Chapter 1). Predator communities living on sandbars or the floodplain may have experienced increased mortality through displacement (Yeager and Anderson 1944) or increased mortality of their prey (Blair 1939, Andersen et al. 2000, Chamberlain et al. 2003) during the flood events. It also possible that the flood-created sandbar habitat was an unknown environment for predators, and low nesting densities following the flood may have made pre-fledged chicks harder to locate (Burger 1984, Catlin et al. 2015), such that predation was density-dependent. Black-tailed Godwit (*Limosa limosa*) chicks reared in lower quality habitat were of lower condition and were at a higher risk of mortality through both starvation and predation

(Schekkerman et al. 2008, Kentie et al. 2013). Similarly, Kosztolányi et al. 2007 suggested that Kentish Plovers (*Charadrius alexandrinus*) of higher mass (better condition) would be more able to evade attacking predators. Although the condition of pre-fledged chicks decreased as the flood-created sandbar habitat aged, continued high survival to fledge and hatch-year survival following the flood suggest that predation pressure remained low.

Deficiencies in nutrition during early development can have long-term consequences on future fitness (Metcalfe and Monaghan 2001), and these cohorts of lower quality may ultimately affect the dynamics of a population (Albon et al. 1992, Lindström 1999). For example, Eurasian Oystercatchers (*Haematopus ostralegus*) reared in higher quality habitat had higher lifetime fitness than those reared in lower quality habitat, potentially affecting life-history decisions up to ten years later (Van De Pol et al. 2006). Similarly, for Red-billed Chough (*Pyrrhocorax pyrrhocorax*), the quality of a cohort's natal environment was positively correlated with juvenile survival, recruitment into the breeding population, breeding longevity, and number of offspring fledged (Reid et al. 2003).

Plover condition variables such as egg mass and chick growth rates could be related to habitat quality as measured by invertebrate prey abundance as well as the age of breeding adults. However, contrary to many previous studies, we did not see similar trends in short-term demographic rates (e.g., reproductive output and hatch-year survival) and condition variables, which we attributed to the change in density-dependent predation pressure during the post-flood portion of our study. With ecosystems such as the Missouri River, continuing to be managed and altered, it is important to understand the effects of habitat on the condition of individuals, and the short- and long-term consequences of these effects that may ultimately contribute to the dynamics of populations.


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## TABLES

Table 1. Model selection for a generalized mixed linear regression used to evaluate the effect of flooding on adult mass of adult piping plovers on the Gavins Point Reach of the Missouri River, 2005–2009, 2012–2014.

| Model[a] | *k*[b] | AIC*c*[c] | Deviance |
|---|---|---|---|
| yr + sex + engineered + engineered age + μ | 11 | 6397.7 | 6393.7 |
| post-flood + post-flood age + sex + engineered + engineered age + μ | 5 | 6524.6 | 6520.6 |
| sex + engineered + engineered age + μ | 3 | 6523.1 | 6519.1 |

[a] Variables used in the models: Yr–a categorical variable for year (2005–2009, 2012–2014), Sex–a categorical variable for piping plover sex, Post-flood–a categorical variable for the post-flood portion of our study (2012–2014), Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Post-flood age–the age (years since creation) of post-flood habitat (this is a nested effect that only affects post-flood habitat), Random effect–variable to control for repeated measurements of individuals throughout the study.

Table 2. Model selection for a generalized mixed linear regression used to evaluate the effect of flooding on piping plover egg (clutch) mass on the Gavins Point Reach of the Missouri River, 2006–2009, 2012–2014.

| Model[a] | *k*[b] | AIC*c*[c] | Deviance |
|---|---|---|---|
| yr + engineered + engineered age | 9 | 1654.3 | 1652.3 |
| post-flood + post-flood age + engineered + engineered age | 5 | 1664.9 | 1662.9 |
| engineered + engineered age | 3 | 1676.3 | 1674.3 |

[a] Variables used in the models: Yr–a categorical variable for year (2005–2009, 2012–2014), Post-flood–a categorical variable for the post-flood portion of our study (2012–2014), Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Post-flood age–the age (years since creation) of post-flood habitat (this is a nested effect that only affects post-flood habitat.

Table 3. Model selection results for a modified Richard's growth curve (Tjørve and Tjørve, 2010) used to evaluate the effect of flooding on the growth rates (mass) of pre-fledged piping plover chicks on the Gavins Point of the Missouri River, 2005–2009, 2012–2014. To reduce the number of estimates and improve model convergence, we added covariates only to the linear equations for the asymptote (*A*) and the growth rate parameter (*R*) in all models.

| Model[a] | *k*[b] | AIC*c*[c] | Deviance |
|---|---|---|---|
| yr + hatch + engineered + engineered age + density + μ | 42 | 13538 | 13453 |
| post-flood + post-flood age + hatch + engineered + engineered age + density + μ | 22 | 13696 | 13652 |
| hatch + engineered + engineered age + density + μ | 14 | 13865 | 13853 |

[a] Variables used in the models: Yr–a categorical variable for year (2005–2009, 2012–2014), Post-flood–a categorical variable for the post-flood portion of our study (2012–2014), Hatch–the standardized (April 20 as 0) hatch date, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Post-flood age–the age (years since creation) of post-flood habitat (this is a nested effect that only affects post-flood habitat), Density–variable for the number of pairs/ha of foraging habitat on a sandbar, Random effect–variable to control for repeated measurements of a single brood (only used in the linear equation for the asymptote (*A*)).

[b] Number of parameters in the model.

[c] Akaike's Information Criterion corrected for small sample size.

Table 4. Parameter estimates from a modified Richard's growth curve (Tjørve and Tjørve, 2010) for the effects on environmental variables of the growth (mass) of pre-fledge piping plover chicks hatched on the Gavins Point Reach of the Missouri River, 2005–2009, 2012–2014. The post-flood model accounted for 36% of the temporal variation ($F = 7.33$, $P < 0.001$) of the global model and therefore present the parameter estimates from the second-ranked model that included the post-flood and post-flood age variables.

| Growth parameter | Variable[a] | Estimate | SE | Pr > \|t\| | Lower 95% | Upper 95% |
|---|---|---|---|---|---|---|
| Asymptote (*A*) | Engineered | 0.490 | 0.817 | 0.5484 | −1.1132 | 2.0941 |
| | Engineered age | −0.158 | 0.321 | 0.6220 | −0.7891 | 0.4722 |
| | Post-flood | 1.467 | 1.719 | 0.3937 | −1.9081 | 4.8422 |
| | Post-flood age | −0.686 | 0.970 | 0.4798 | −2.5903 | 1.2189 |
| | Density | −0.199 | 0.030 | <0.0001 | −0.2593 | −0.1397 |
| | Hatch | −0.095 | 0.019 | <0.0001 | −0.1321 | −0.0582 |
| Inflection point (*T*) | Post-flood | −2.964 | 0.485 | <0.0001 | −3.9164 | −2.0113 |
| | Post-flood age | 1.896 | 0.344 | <0.0001 | 1.2214 | 2.5712 |
| Growth rate (*R*) | Engineered | −0.000 | 0.001 | 0.8348 | −0.0015 | 0.0012 |
| | Engineered age | 0.001 | 0.001 | 0.0305 | 0.0001 | 0.0010 |
| | Post-flood | 0.002 | 0.003 | 0.4686 | −0.0031 | 0.0067 |
| | Post-flood age | −0.004 | 0.001 | 0.0088 | −0.0066 | −0.0001 |
| | Density | −0.000 | 0.000 | 0.0541 | −0.0001 | 0.0000 |
| | Hatch | −0.000 | 0.000 | 0.0037 | −0.0001 | −0.0000 |
| Shape parameter (*M*) | Post-flood | −0.665 | 0.362 | 0.0672 | −1.3767 | 0.04709 |
| | Post-flood age | 0.190 | 0.232 | 0.4126 | −0.2657 | 0.6465 |

[a] Variables used in the models: Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Post-flood–a categorical variable for the post-flood portion of our study (2012–2014),

Post-flood age–the age (years since creation) of post-flood habitat (this is a nested effect that only affects post-flood habitat), Density–variable for the number of pairs/ha of foraging habitat on a sandbar, Hatch–the standardized (April 20 as 0) hatch date.

Table 5. Model selection results for a negative binomial regression used to evaluate the effect of flooding on the piping plover invertebrate prey abundance on sandbar habitat on the Gavins Point of the Missouri River, 2005–2009, 2012–2014.

| Model[a] | $k$[b] | AIC$c$[c] | Deviance |
|---|---|---|---|
| yr + temperature + wind speed + date + engineered + engineered age + μ | 12 | 20296 | 20266 |
| post-flood + post-flood age + temperature + wind speed + date + engineered + engineered age + μ | 6 | 20312 | 20292 |
| temperature + wind speed + date + engineered + engineered age + μ | 4 | 20318 | 20302 |

[a] Variables used in the models: Yr–a categorical variable for year (2005–2009, 2012–2014), Post-flood–a categorical variable for the post-flood portion of our study (2012–2014), Temperature–a continuous variable to account for the effect of temperature (ºC) on invertebrate prey catch rate, Wind speed–a continuous variable to account for the effect of wind speed (km/hr) on invertebrate prey catch rate, Date–The standardized (June 1 as 0) date when the sample was collected, Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat), Post-flood age–the age (years since creation) of post-flood habitat (this is a nested effect that only affects post-flood habitat), Random effect–sandbar×year to account for the samples on the same sandbar in a given year not being independent of each other.

[b] Number of parameters in the model.

[c] Akaike's Information Criterion corrected for small sample size.

Table 6. Parameter estimates from a negative binomial regression for the effects of environmental variables on the abundance of piping plover invertebrate prey on the Gavins Point Reach of the Missouri River, 2005–2009, 2012–2014. The post-flood model accounted for 28% of the temporal variation ($F$ = 15.6, $p$ = 0.0005) of the global model and therefore present the parameter estimates from the second-ranked model that included the post-flood and post-flood age variables.

| Variable[a] | Estimate | SE | Pr > \|t\| | Lower 95% | Upper 95% |
|---|---|---|---|---|---|
| Intercept | 0.4875 | 0.1683 | 0.0046 | 0.1538 | 0.8213 |
| Temperature | 0.0609 | 0.0056 | <.0001 | 0.0499 | 0.0719 |
| Wind speed | -0.0256 | 0.0044 | <.0001 | -0.0344 | -0.0168 |
| Date | 0.0094 | 0.0011 | <.0001 | 0.0072 | 0.0116 |
| Engineered | -0.7524 | 0.1963 | 0.0002 | -1.1416 | -0.3632 |
| Engineered age | 0.1144 | 0.0779 | 0.1453 | -0.0402 | 0.2690 |
| Post-flood | -0.0107 | 0.1835 | 0.9535 | -0.3746 | 0.3532 |
| Post-flood age | -0.2779 | 0.1257 | 0.0292 | -0.5272 | -0.0287 |

[a] Variables used in the models: Temperature–a continuous variable to account for the effect of temperature (ºC) on invertebrate prey catch rate, Wind speed–a continuous variable to account for the effect of wind speed (km/hr) on invertebrate prey catch rate, Date– The standardized (June 1 as 0)date when the sample was collected,  Engineered–a categorical variable for engineered sandbar habitat created by the USACE from 2005–2009 (vs. natural), Engineered age–the age (years since creation) of engineered habitat (this is a nested effect that only affects engineered habitat),

Post-flood–a categorical variable for the post-flood portion of our study (2012–2014), Post-flood age–the age (years since creation) of post-flood habitat (this is a nested effect that only affects post-flood habitat).

## FIGURES

Figure 1. Map of the Missouri River showing the location of our study area on the Gavins Point Reach, downstream of the Gavins Point Dam, 2005–2014.

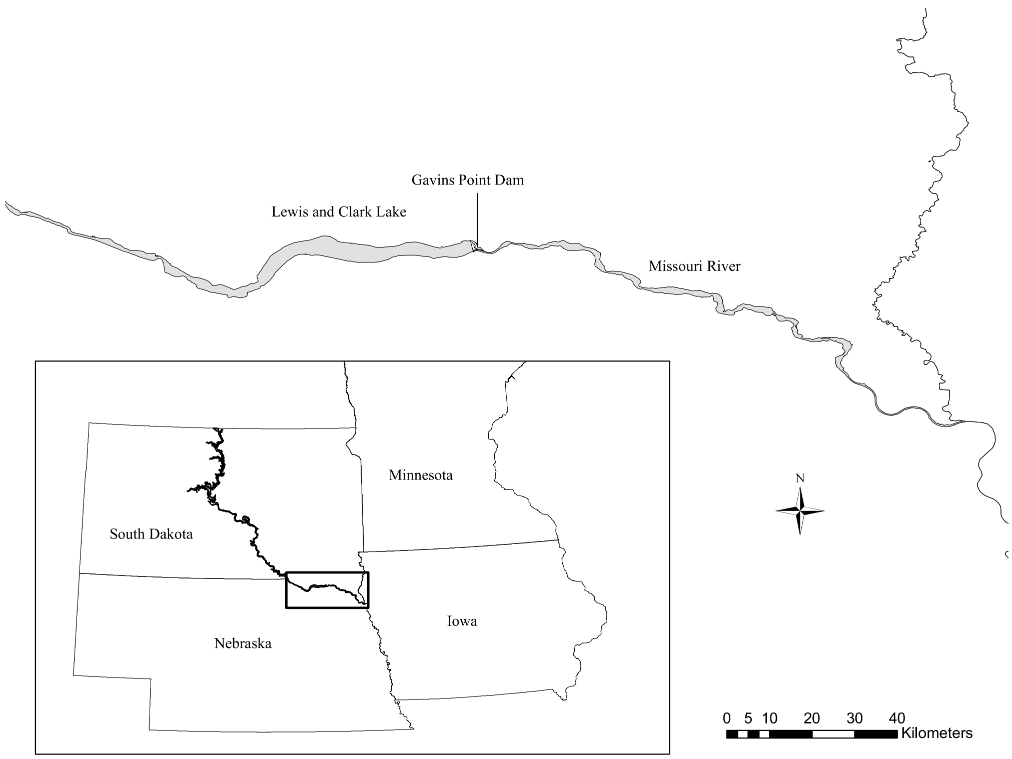


Figure 2. The amount of suitable sandbar habitat (< 30% vegetated wet and dry sand) available for use by piping plovers on the Gavins Point Reach of the Missouri River, 2005–2014. Flooding covered all available habitat in 2010 and 2011.

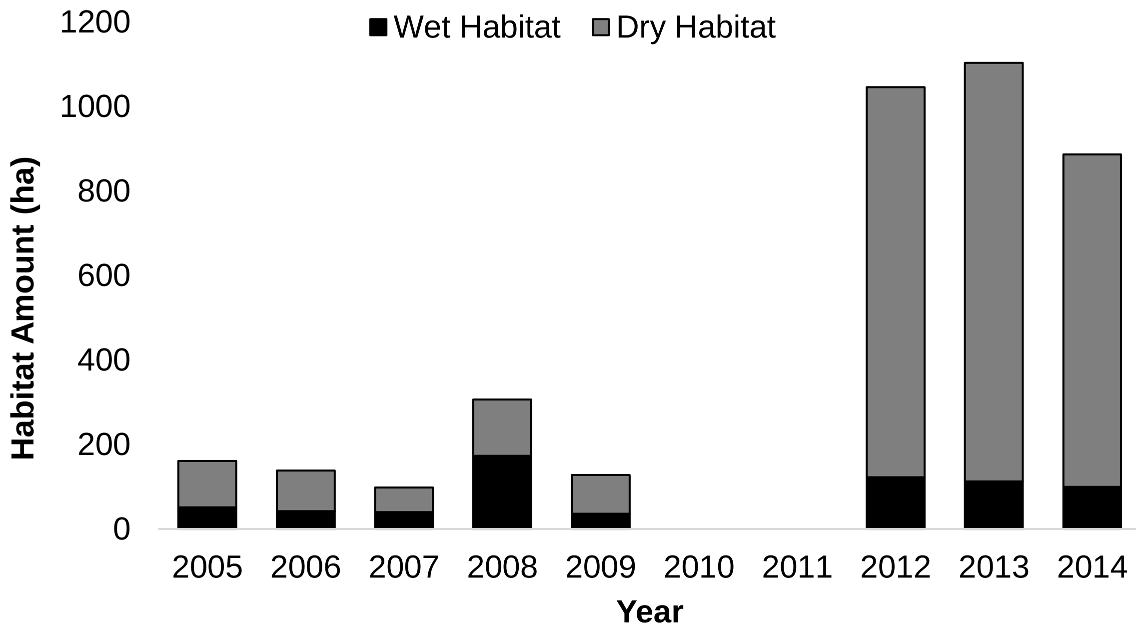


Figure 3. Predicted average growth curves for pre-fledged piping plover chick mass hatched on pre- and post-flood sandbar habitat on the Gavins Point Reach of the Missouri River, 2005–2009, 2012–2014. The pre-flood curve includes both engineered and natural sandbar habitat. We used a modified Richard's growth curve including the following parameters; the asymptotic value (*A*), the inflection point (*T*), the rate of growth (*R*), and the shape parameter (*M*) to estimate these curves (Tjørve and Tjørve, 2010).

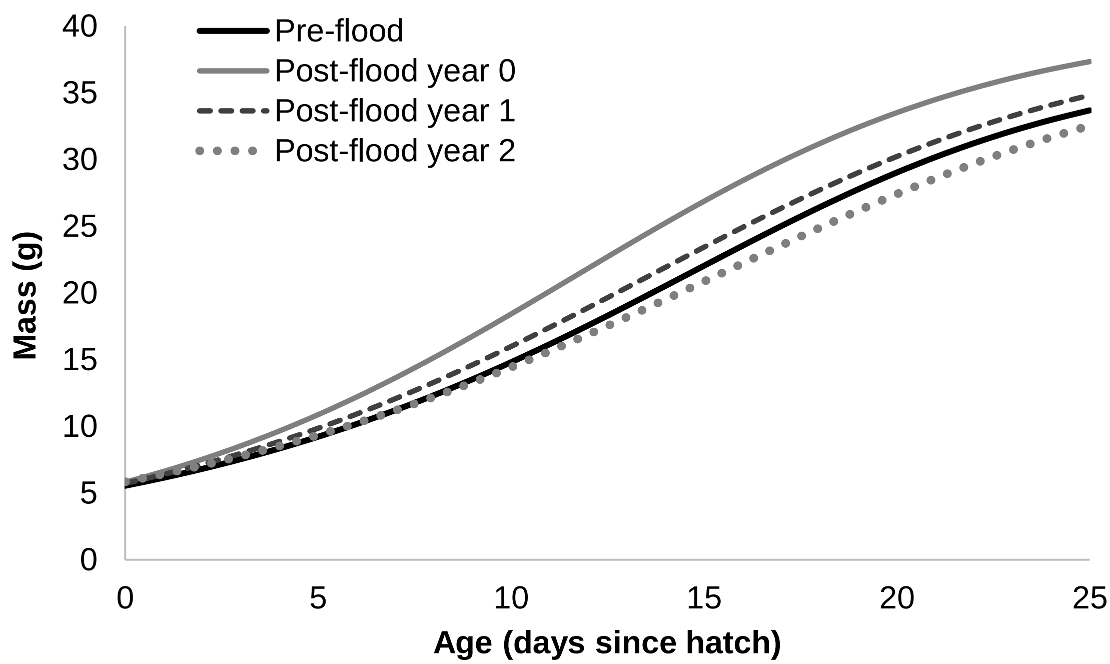


Figure 4a. Predicted invertebrate prey abundance available on pre-flood natural sandbar, pre-flood engineered sandbars, and post-flood sandbars for piping plovers on the Gavins Point Reach of the Missouri River, 2005–2014. Pre-flood natural sandbars ranged from years 8–12 throughout our study. Error bars represent ± 1 SE.

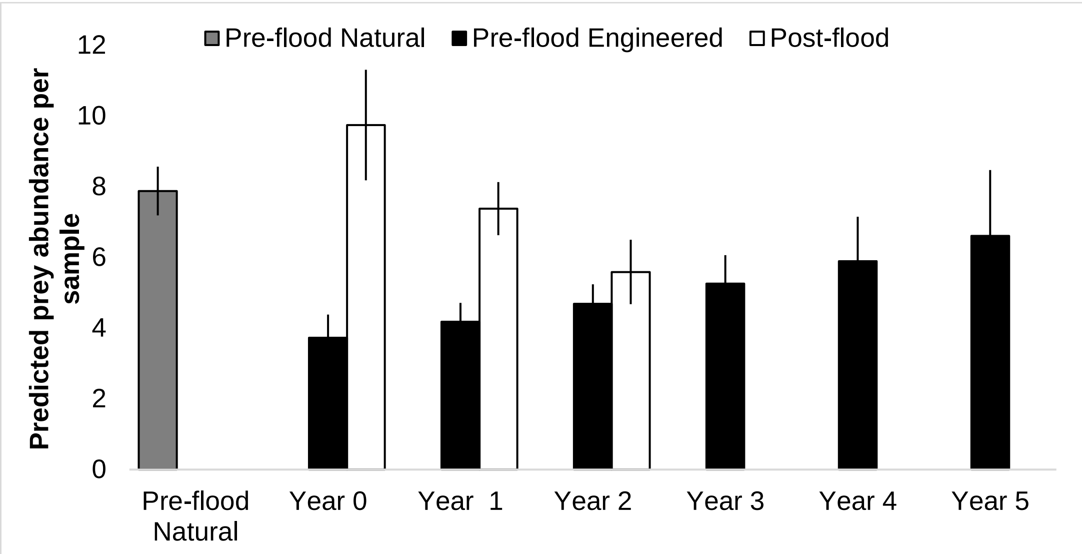
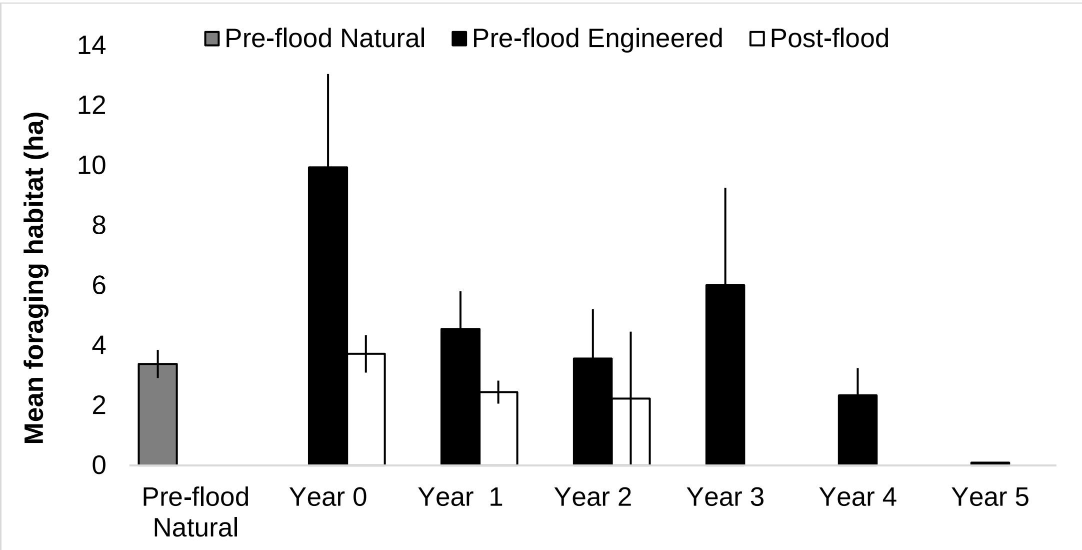


Figure 4b. The mean foraging (wet) habitat available on pre-flood natural, pre-flood engineered, and post-flood for piping plovers on the Gavins Point Reach of the Missouri River, 2005–2014. Pre-flood natural sandbars ranged from years 8–12 throughout our study. Error bars represent ± 1 SE



## CONCLUSION

In 2010 and 2011 flooding occurred on the Missouri River, resulting in near complete inundation of sandbar habitat throughout the Missouri River system (USACE 2012). In 2011, due to increased mountain snowpack and spring precipitation, flows from the Gavins Point Dam exceeded 2,831 $m^3/s$ for 85 days with a maximum monthly flow of 4,530 $m^3/s$ reached in July, the most water released since the Gavins Point Dam became operational in 1957 (USACE 2012). Although piping plover reproductive output was nil and adult survival decreased slightly, the flooding increased the amount of plover nesting habitat by a factor of 10. This increase in habitat contributed to declines in nesting densities and increases in all measured piping plover demographic rates. Estimates of nest success, chick survival, and hatch year (HY) annual survival were as high, or higher after the flood than before. Moreover, unlike after the construction of habitat prior to the flood, where rates increased for only one year (Catlin et al. 2015), these rates remained high for 3 years as the sandbar habitat aged. With increased suitable habitat and decreased nesting densities following the flood, our results indicated that high fecundity and immigration (Catlin et al. 2016) drove the growth of the population.

Across their range, piping plovers rapidly colonize newly created suitable habitat (Wilcox 1959, U.S. Army Corps of Engineers 2006, Cohen et al. 2009, Catlin et al. 2015). The mechanical creation of habitat from 2005–2009 increased reproductive output and contributed to positive population growth for approximately one year following creation. Despite construction of sandbar habitat, plovers were at or near carrying capacity throughout the pre-flood portion of this study (Catlin et al. 2015). In comparison, the 2011 flood increased the amount of suitable habitat 10-fold from pre-flood levels, resulting in lower densities and sustained, and high population growth. Although habitat decreased between 2013 and 2014, reproductive output remained high, indicating that the population remained below carrying capacity.

Given the increased demographic rates observed in this study, we hypothesized that plover condition would increase following the flood. Contrary to our expectations, condition appeared unchanged (adult mass, egg mass, chick growth rates) following the flood, and although egg mass and chick growth rates increased in the year following the flood (2012), there was also evidence for a decreasing trend for both as the post-flood habitat aged. In a variety of avian species, chick condition is positively related to habitat quality and prey abundance (Kersten and Brenninkmeijer 1995, Loegering and Fraser 1995, Park et al. 2001, Schekkerman et al. 2002, 2008, Pearce-Higgins and Yalden 2004, Kentie et al. 2013). For the 3 years of our study, we found a similar trend for plovers on the Missouri River as we were able to infer that clutch mass, and chick growth rates followed a similar trend to invertebrate prey abundance. Although we detected a decreasing trend in condition as the post-flood habitat aged, it is also possible that with just 3 years of data following the flood, we were unable to parse out environmental variation from this trend.

While condition can have short-term effects on demography (Kentie et al. 2013, Catlin et al. 2014), plover reproductive output in this system appeared to be driven by density-dependent predation (Catlin et al. 2015). Owing to density-dependent predation pressure, reproductive output was lower from 2005–2009 than from 2012–2014, even including the reality that predator management was in place prior to, but not after, the flood (Catlin et al. 2015). Predator communities living on sandbars or the floodplain may have experienced increased mortality through displacement (Yeager and Anderson 1944) or increased mortality of their prey (Blair 1939, Andersen et al. 2000, Chamberlain et al. 2003) during the floods. It also possible that the flood-created sandbar habitat was an unknown environment for predators, and low nesting densities following the flood may have made nests and pre-fledged chicks harder to locate (Burger 1984, Catlin et al. 2015), suggesting that predation may be density-dependent.

To combat predation, managers have used nest exclosures (Johnson and Oring 2002, Neuman et al. 2004, Niehaus et al. 2004, Boettcher et al. 2007, Isaksson et al. 2007) and predator removal (USFWS 1985, USFWS 2009; Cohen et al. 2009, Catlin et al. 2011a) to increase reproductive output. On the Missouri River, predator exclosures were used on 39–56% of the piping plover nests from 2005–2009, and numerous great horned owls (*Bubo virginianus*) were trapped and removed off of engineered sandbars from 2007–2010 (Catlin et al. 2015). The use of exclosures on the Missouri River increased nest success prior to the flood, and great horned owl removal increased chick survival in one of two years (2008; Catlin et al. 2011a, Catlin et al. 2015). In contrast, following the flood, predator management wasn't necessary and reproductive output remained higher than the pre-flood value, suggesting that increased habitat (assuming decreased densities) can relieve predation pressure better than control measures.

More broadly, the results from this work highlight the importance of natural ecosystem processes. Traditionally, due to financial or other constraints, management or restoration of riparian ecosystems has focused on smaller scales (e.g., single reaches, species, or habitats), such that restoration has sought to recreate an environment thought to be favored by a particular species, or focuses a particular habitat type (Clarke et al. 2003). Such approaches may ignore underlying geomorphic riverine processes, and consequently they depend on additional management input (Clarke et al. 2003), such as habitat construction and predator management on the Missouri River. Management on the Missouri River has often been species-, taxa-, or habitat-specific and the construction of sandbar habitat for plovers and terns on the Gavins Point Reach from 2004–2009 provides an example. Although Catlin et al. (2015) provided Missouri River managers with recommendations regarding the location and timing of future sandbar construction, they concluded that piping plovers will not reach a stage where management actions are no longer necessary unless we dramatically alter the way we manage their habitat.

The return of a more natural flood process in 2011 resulted in benefits (albeit varying) for a number of flood-dependent Missouri River species. For piping plovers, the amount of suitable sandbar habitat available after the flood will continue to decrease due to erosion and vegetation succession, likely resulting in decreased plover numbers without intensive management, such as habitat construction, or another flood event. High flows in 2011 were related to increases in pallid sturgeon migration below the Fort Peck dam and the first documented successful spawning in the upper Missouri River (DeLonay et al. 2014, Delonay et al. 2016). On the lower Missouri, high flows came too late to cue migration and spawning, but pallid sturgeon were found utilizing the inundated floodplain (DeLonay et al. 2014), which appeared to improve the fish's condition (Delonay et al. 2016). The partial inundation of the floodplain created the first aquatic floodplain habitats since the mainstem dams were closed, and, at least in the short term, native fish species appeared to benefit (Steffensen et al. 2014). However, for plains cottonwoods, another flood-dependent taxon, increased inundation during the dispersal season (Dixon et al. 2015) and the lack of lateral movement following the flood (Johnson et al. 2015), leading to decreased cottonwood recruitment.

Where possible, rather than restoration or management focused on single taxa or a specific habitat type, river managers should aim to restore a dynamic system characterized by spatial and temporal variations in channel geometry and biotic abundance and composition that reflect those in the natural system (Palmer et al. 2005, Wohl et al. 2015). A number of restoration projects have demonstrated that reintroducing key aspects of the natural flow regime may result in the successful restoration of riparian ecosystems (Jansson et al. 2007). However, restoration can be challenging when information on the pre-alteration system is incomplete. Attempts to recreate a self-sustaining natural system require understanding of underlying processes and what flow regimes are required to drive these processes (Clarke et al. 2003), as well as an understanding of conditions prior to anthropogenic alterations (Nilsson and Berggren 2000). Fortunately, gages have been in place since the late 1800's on the Missouri River, providing knowledge of the hydrograph prior to and after dam construction (Hesse and Mestl 1993), and a baseline flow regime to mimic.

Although riparian ecosystem restoration is in vogue, it is unlikely that in many locations, including the Missouri River, we will be able to completely restore natural ecosystem processes. Intense management of the system did maintain plover populations in the absence of natural processes (Catlin et al. 2015), but those populations depended on continued management (Catlin et al. 2016). In order to create long term, sustainable management practices for multiple species and the habitats they rely on, an ecosystem management approach may be the only choice. This will likely require changes in operations meant for flood control, navigation, hydropower, water supply, water quality, irrigation, and recreation (USACE 2006).

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