

DISSERTATION

BREEDING WATERFOWL PRODUCTIVITY IN A FLOOD-IRRIGATED AGRICULTURAL  
LANDSCAPE

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## ABSTRACT

### BREEDING WATERFOWL PRODUCTIVITY IN A FLOOD-IRRIGATED AGRICULTURAL LANDSCAPE

Similar to agricultural production, the sustainable management of waterfowl populations across the western United States inherently depends on limited water availability. Both endeavors are increasingly challenged by municipal demands for water, drought, and changes in the seasonality of precipitation. Healthy wetlands for wildlife can be sustained in conjunction with the needs of agricultural producers on working lands, but the multifaceted importance of water management is rarely quantified. Information pertaining to the multiple benefits of water management practices might bring to light the larger societal importance of sound water management. This may allow natural resource managers to allocate resources more efficiently and effectively by directing them towards the practices with demonstrated advantages for both wildlife and agricultural producers. The North Platte Basin in north-central Colorado (hereafter North Park) is a model system to evaluate benefits and trade-offs of hydrological manipulations that benefit both agricultural producers and fish and wildlife. Not only are waterfowl and water management already being conducted by federal and state agencies and NGOs like Ducks Unlimited, but North Park is also representative of many working lands throughout the Intermountain West. Agricultural producers in North Park flood irrigate rather than using center-pivot irrigation, which strongly affects on hydrological regimes, water tables, wetlands, and stream flows. Flood irrigation more closely resembles natural stream and river flood regimes and is thought to be more beneficial for wildlife, water table recharge, and evaporative cooling of

return flow water. As water resources become diverted for urban municipal uses and the increasing frequency of drought reduces water availability in the semi-arid West, it is believed that the North Platte Basin may begin to play a significant role in the production of waterfowl on a statewide or even a flyway scale. As private land becomes an increasingly important component of waterfowl habitat and water resources become limiting, a strong foundational knowledge regarding how flood-irrigated systems impact wetland-dependent species will therefore be imperative to properly manage waterfowl populations in coordination with agricultural production.

We first sought to evaluate the efficacy of flood-irrigated agricultural lands as nesting habitat for breeding waterfowl in the context of land-use intensity. The debate over the best agricultural practices for biological conservation typically focuses on land sharing and land sparing production strategies. One end of the spectrum posits that high-intensity agriculture and the smaller footprint associated with it allows for other land parcels to be spared for biodiversity and therefore provides more suitable habitat, whereas others argue that agricultural lands should be cultivated at a low intensity and interspersed with wildlife habitat, therefore sharing the land with wildlife. We evaluated the demographic consequences of land-sharing and land-sparing practices on breeding bird nest site selection and nest survival, focusing specifically on waterfowl in a flood-irrigated hay agricultural system. We specifically assessed the habitat features related to both shared and spared lands driving nest site selection at two scales and how those same features scaled up to impact nest survival. Nests were located disproportionately closer to uncut irrigated meadows and farther from harvested hay meadows relative to available points, but closer to irrigation ditches. Nests closer to irrigation ditches, uncut irrigated meadows, and open water also experienced higher nest survival. This system is representative of

many agricultural systems around the globe and illustrates the ways agricultural practices can shape habitat selection have reproductive consequences for wildlife.

After evaluating the importance of wetlands associated with flood irrigation for nesting, we focused our efforts on elucidating their contributions as foraging habitat. Food availability varies considerably over space and time in wetland systems, and consumers must be able to track those changes during energetically-expensive events like breeding. Resource tracking has been studied frequently among herbivores, but rarely receives attention among consumers of macroinvertebrates. We evaluated the change in resource energy density across habitat types and time, and the ability of waterfowl to track macroinvertebrate resources across wetland types and over the course of the breeding season in a high-elevation, flood-irrigated system. We also assessed whether the density of energy resulting from macroinvertebrates explained more of the variation in waterfowl abundance across habitats, or whether the consistency (i.e., temporal evenness) of the resource played a larger role using a pseudo- $R^2$  metric. Energy density varied widely across wetland types, but was highest in basin wetlands (i.e., ponds) and was higher in wetlands with higher temperatures, specific conductivity, and lower dissolved oxygen. Both breeding pair abundance and duckling abundance were positively associated with energy density and resource consistency ( $R^2 = 0.06$  for pair abundance and  $0.31$  for duckling abundance), but energy density explained more of the variation in both waterfowl responses ( $R^2 = 0.77$  for pair abundance and  $0.58$  for duckling abundance). These results have the potential to not only elucidate mechanisms of habitat selection among waterfowl, but also indicate where and when water resources should be allocated as climate conditions become increasingly arid.

The technological tools we used initially to evaluate waterfowl use of flood-irrigated habitats (i.e., Global Positioning System [GPS] tags) have become a common tool in ecological

studies of animal behavior and demography despite previous research indicating negative impacts on vital rates across a variety of taxa. We therefore focused next on evaluating the impacts of GPS tags on our focal waterfowl species and others across the life-history spectrum. Researchers face tradeoffs when deciding whether they are an appropriate tool because GPS tags may impact vital rates, but they provide detailed data on movements and behavior that often cannot be obtained in other ways. Using band recovery data from hunter harvests, we evaluated the strength of effects induced by GPS tags on annual mortality of adult females across 13 waterfowl species, and whether species with a slower life-history strategy might be more resilient to GPS tag effects than their fast-lived counterparts. Hazard ratios, indicating the risk of death for individuals wearing GPS tags compared to those wearing only metal bands, ranged from 0.92 - 4.38 and the mean difference in survival between marker types across species was 0.31, but these results are averaged across the study period. The magnitude of tag effects remained constant across life-history tempo, indicating that slower-lived species were not able to buffer the effect of wearing GPS tags. When scaling effect sizes up to a currency of fitness, slower-lived species exhibited a similar handicap of wearing GPS tags compared to species with a faster life-history strategy, and the effects were notable. Our results highlight that even small impacts to important vital rates can affect inference pertaining to survival and mortality as well as fitness from birds affixed with GPS tags. The results of this study revealed considerable survival effects across species, although time trends illustrated decreasing effect sizes for most species over time. Results emphasize the importance of testing for such effects in future research as technology advances.

Finally, we used components of each previous chapter to characterize the population of breeding ducks in this system and the demographic consequences of environmental conditions.

Waterfowl populations in the Intermountain West rely upon water availability and are not as frequently studied as populations within North American core breeding areas like the Prairie Pothole Region. Different species experience different environmental conditions during peak nest initiation depending on their breeding phenology, especially in variable environments like those associated with high-elevation systems. We fit species-specific integrated population models to evaluate the demographic drivers of mallard and gadwall populations breeding in a high-elevation intermountain basin in Colorado representative of many Intermountain West habitats from 2018-2022. Each species initiated nests at opposite ends of the phenological spectrum, allowing us to assess the effects of environmental conditions on demography. Both mallard and gadwall annual after-hatch-year (AHY) female survival probabilities were comparable to estimates from other regions (hatch-year [HY] mallards = 0.48 [SD = 0.09] to 0.53 [SD = 0.07], AHY mallards = 0.53 [SD = 0.07] to 0.57 [SD = 0.05], HY gadwall = 0.44 [SD = 0.13] to 0.52 [SD = 0.14], AHY gadwall = 0.56 [SD = 0.11] to 0.66 [SD = 0.12]). Annual recruitment, a metric of the number of females produced per breeding pair, was similar among gadwall (0.62 [SD = 0.80] to 1.04 [SD = 1.04]) and mallards (0.40 [SD = 0.48] to 1.59 [SD = 0.95]), but realized population growth rate ( $\lambda$ ) did not vary as much for gadwall (0.93 [SD = 0.56] to 1.21 [SD = 0.59]) as it did for mallards (0.76 [SD = 0.24] to 1.55 [SD = 0.24]). Recruitment of both species exhibited quadratic relationships with spring growing degree days, indicating recruitment was higher during springs with intermediate temperatures, and spring snow-water equivalent metrics in the surrounding mountains positively impacted HY and AHY mallard survival in addition to HY gadwall survival. The results of this study emphasize the need for continued monitoring of waterfowl outside of traditional survey areas and provide insight into water management strategies to target important vital rates as climate and land use change.

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## TABLE OF CONTENTS

ABSTRACT .....	ii
ACKNOWLEDGMENTS .....	vii
CHAPTER 1 – CONSEQUENCES OF LAND-SHARING AND SPARING PRACTICES ON AVIAN REPRODUCTIVE SUCCESS .....	1
INTRODUCTION .....	1
METHODS .....	7
Study System .....	7
Data Collection .....	8
Nest Site Selection .....	10
Nest Survival .....	11
RESULTS .....	12
Nest Site Selection .....	12
Nest Survival .....	13
DISCUSSION .....	13
LITERATURE CITED .....	24
CHAPTER 2 – RIDING THE WETLAND WAVE: DO WATERFOWL TRACK MACROINVERTEBRATE RESOURCES ACROSS THE BREEDING SEASON?.....	38
INTRODUCTION .....	38
METHODS .....	42
Study Area .....	42
Macroinvertebrate Data Collection.....	42
Waterfowl Data Collection.....	43
Macroinvertebrate Analyses .....	44
Waterfowl Analyses .....	46
RESULTS .....	47
Drivers of Energy Density .....	47
Waterfowl Resource Tracking.....	48
Temporal Resource Stability .....	48
Comparing Resource Tracking Mechanisms.....	48
DISCUSSION .....	49
LITERATURE CITED .....	64

CHAPTER 3 – CAN WATERFOWL BUFFER THE DEMOGRAPHIC HANDICAP INDUCED BY GPS TAGS? A CAUTIONARY TALE FOR APPLIED INFERENCE ACROSS LIFE HISTORIES.....	74
INTRODUCTION.....	74
METHODS .....	78
Data Organization .....	78
Estimation of GPS Tag Effects on Annual Survival and Mortality.....	81
Life-History Patterns in GPS Tag Effects on Annual Mortality.....	83
Life-History Patterns in Effects of GPS Tags on Fitness.....	86
RESULTS .....	87
GPS Tag Effects on Annual Survival and Mortality .....	87
Life-History Patterns in GPS Tag Effects on Annual Mortality.....	88
Life-History Patterns in Projected Effects of GPS Tags on Fitness .....	88
DISCUSSION .....	89
LITERATURE CITED.....	101
CHAPTER 4 – CHARACTERIZING THE POPULATION DYNAMICS OF BREEDING WATERFOWL IN THE INTERMOUNTAIN WEST.....	111
INTRODUCTION.....	111
METHODS .....	114
Study System.....	114
Demographic Data Collection .....	115
Climate Data Collection .....	116
Integrated Population Model .....	117
State-Space Model .....	118
Survival Model .....	119
Recruitment Model .....	120
Model Fitting .....	122
Transient Life Table Response Experiment .....	122
RESULTS .....	124
Demographic Parameters .....	124
Environmental Effects.....	125
Transient Life Table Response Experiment .....	126
DISCUSSION .....	127
LITERATURE CITED.....	140
APPENDIX S1 .....	148

APPENDIX S1.2.....155  
APPENDIX S2.....156  
APPENDIX S3.....157

## CHAPTER 1 – CONSEQUENCES OF LAND-SHARING AND SPARING PRACTICES ON AVIAN REPRODUCTIVE SUCCESS

### INTRODUCTION

The land-sparing vs. land-sharing debate has permeated the field of conservation biology over the last several decades (Green et al. 2005, Fischer et al. 2008, Kremen 2015). A key goal is to discern how to allocate land in ways that both sustain biodiversity and meet global demands for food (Fischer et al. 2014). Protected areas are no longer sufficient to maintain species diversity and ecological functions, so the conversation has shifted to the areas of land in between (Jules and Shahani 2003, Foley et al. 2005, Hakkila et al. 2017). As agriculture is intensified to increase yield on smaller parcels of land, theoretically the land that is idle should be available or “spared” for conservation purposes (Green et al. 2005). Spared lands can support species that are more sensitive to human disturbance (Phalan et al. 2011, Driscoll et al. 2013), reduce human-wildlife conflict (Crespin and Simonetti 2019), and protect biodiversity (Cannon et al. 2019). Conversely, some conservationists emphasize the need to intersperse wildlife habitat within the boundaries of agricultural production, thereby “sharing” the land and reducing the impacts of agriculture on native species (Phalan et al. 2011). These so-called “wildlife-friendly farming practices” have been shown to reduce habitat fragmentation (Lamb et al. 2016), increase ecosystem resilience in the face of environmental change (Tittonell 2020), and create more opportunities for biodiversity-mediated services like pest control, thus potentially reducing the need for chemical inputs (Senapathi et al. 2015).

Many studies have evaluated the trade-offs between the two ends of the agriculture-nature spectrum, both conceptually and empirically, but these studies have mostly focused on

metrics of biodiversity at the community level (Green et al. 2005, Egan Franklin and Mortensen 2012, Dotta et al. 2016, Cannon et al. 2019). A large number of studies have also examined the comparative benefits of land sparing and land sharing to pollinators and to crops that require pollination (Kovacs-Hostyanszki et al. 2017, Henriquez-Piskulich et al. 2021). Relatively few studies have evaluated direct demographic consequences of the two strategies, nor critically assessed possible habitat preferences within areas of land-sharing or “environmentally-friendly farming” (Sidemo-Holm et al. 2021).

There are pros and cons to both land-sharing and sparing, and many have argued for a nuanced rather than a binary approach to conservation and agricultural production (Kremen 2015). For example, land that is shared has been shown to be less valuable the further it is from intact tracts of spared habitats, suggesting each strategy is less useful in isolation (Cannon et al. 2019). Additionally, in some cases land that is spared from agricultural production may not be of the same habitat quality as the land that is cultivated, and socio-political influences may make protecting or restoring uncultivated land difficult (Balmford et al. 2019). On the land-sharing end of the agricultural continuum, both the pros and cons can be best illustrated by common cattle ranching practices. Cattle are some of the biggest contributors of greenhouse gases and soil conservation problems globally, but ranches also support wildlife habitat and provide ecosystem services (Maestas et al. 2003). The habitat cattle ranches provide has been linked to the preservation of native vegetation (Pannell et al. 2021) and relatively high metrics of biodiversity (Drouilly and O’Riain 2019), but also to increased disease transmission among wildlife (Rulli et al. 2021) and decreased presence of charismatic megafauna (Drouilly and O’Riain 2019). Perhaps ranchlands would be more beneficial to biodiversity conservation if they were strictly protected (e.g., rewilding; Pettorelli, Durant, and Du Toit 2019), but sustainable grazing practices

have the potential to conserve or restore structural vegetation heterogeneity (Rischette et al. 2023), and ranching generally produces fewer detrimental ecological effects than exurban development or high-intensity production practices like cattle feedlots and cultivated crops (Maestas et al. 2003, Knight 2007).

Although high-intensity agricultural practices may preclude animals from using those habitats in favor of the spared habitats, lower-intensity practices may still reduce habitat quality in unexpected or indirect ways. For example, ecological traps can occur in environments altered by humans when the proximate cues a habitat provides do not align with the ultimate quality of the habitat (Dwernychuk and Boag 1972, Gates and Gysel 1978, Schlaepfer et al. 2002, Hale et al. 2015, Devries et al. 2018, Buderman et al. 2020, 2023). Human intervention has been shown to nullify the cues animals use to select breeding habitat (Shiple et al. 2013, Demeyrier et al. 2016) and foraging areas (Sherley et al. 2017), and to introduce novel resources that resemble those animals have evolved to use (Schlaepfer et al. 2005). The potential for land that integrates both agricultural and ecological functions (e.g., haylands) to lead to ecological traps is high because these lands may resemble native ecosystems (e.g., grasslands). Alternatively, shared lands may provide refuge from human disturbance and food subsidies, incurring gains in vital rates that even carry over to subsequent seasons and years (Abraham et al. 2005, Alisauskas et al. 2011, Fowler et al. 2020). They may also provide more consistent or reliable resources because those resources follow agricultural schedules that remain predictable from year to year. Accounting for the ways in which anthropogenic land-use could affect animal fitness is therefore imperative from a conservation biology perspective (i.e., to invest in the most appropriate habitats in the face of global change) and from a basic ecological perspective (i.e., to better understand the mechanisms driving habitat selection).

Birds are a particularly useful taxon for evaluating the effects of land use on fitness globally. Breeding birds must select nest sites that maximize fitness using landscape cues available to them early in the breeding season, often before vegetation greenup. A chosen nest location can determine whether the nest is successful (Setash et al. 2020), whether offspring have access to foraging areas (Dyson et al. 2018), and whether the female survives the breeding season (Boyer et al. 2018). These selective pressures should therefore be realized by a propensity to optimally time nest initiation and to select nest sites associated with a high probability of successful reproduction (Clark and Shutler 1999, Gibson et al. 2016, Messmer et al. 2021). In semiarid landscapes where water can be a limiting factor, wetland-dependent species may be forced to use wetlands created for purposes other than wildlife habitat. Globally, some of the more common wetland types available to breeding birds are those associated with flood-irrigated agriculture (Galbraith et al. 2005, Fleming et al. 2014, Katayama et al. 2015). Waterbirds have been observed using flood-irrigated wetlands for foraging (Burke 2020, Lovvorn and Crozier 2022, Moulton et al. 2022), nesting (Hartman and Oring 2009, Lopez-Pomares et al. 2015, this study), and brood-rearing (Lovvorn and Crozier 2022) during the breeding season, but assessments of the demographic consequences of this habitat use are rare. In one evaluation, Buderman et al. (2020) found a preference for agricultural cropland among breeding northern pintails (*Anas acuta*) in the Prairie Pothole Region of North America, which resulted in reduced demographic performance, presumably due to nest failures associated with agricultural practices.

Hay meadows and their associated irrigation ditches may appear to breeding waterbirds as high-quality nesting areas at different points during the breeding season. They consist of vast expanses of grass or perennial legume cover (e.g. alfalfa) with high levels of connectivity among flooded patches of potential habitat, and they are also flooded earlier and more consistently than

natural wetlands (Peck and Lovvorn 2001, van Rees et al. 2018). The vegetation adjacent to irrigation ditches cannot be cut by tractors during harvest, leaving corridors of lush graminoids, forbs, and low shrubs that could be attractive to ground-nesting birds, but might also create abrupt edges that have been shown to act as corridors for nest predators (Ratti and Reese 1988, Frey and Conover 2010, Pierluissi 2010, Suvorov et al. 2014). Conversely, hay meadows are often cut during the same time period that some bird species are undergoing the final stages of nesting, making the nests susceptible to mechanical destruction (Hoekman et al. 2006). Though the specific mechanisms may differ, hay meadows and irrigation ditches could therefore both affect reproductive success as consistent breeding refugia or as ecological traps. An understanding of how breeding birds are impacted by flood-irrigation practices in agricultural settings is thus necessary to effectively manage limited water resources in regions where an increasing proportion of wetlands are privately-owned and declines in precipitation are possible, if not likely.

As an empirical example of the impacts of land sharing and sparing conservation practices on avian reproductive success, we focused on a working lands study system in which ranches produced hay and cattle but also provided habitat for breeding waterfowl. Long-term drought has limited the availability of natural wetlands in this study system and increased the importance of artificial wetlands associated with agriculture for wetland-dependent species (Donnelly et al. 2019, Donnelly et al. 2022). However, aging irrigation infrastructure and large-scale pressures to increase water-use efficiency have simultaneously limited agricultural practitioners' ability to flood irrigate (Perera et al. 2021). Conservation organizations have historically focused limited conservation funding on improving irrigation infrastructure to allow private landowners to irrigate more effectively and efficiently, with the goal of benefitting the

wildlife that use seasonal wetlands created via irrigation. The effects of these wetlands on the species that use them have rarely been tested, however. Additionally, there are public conservation lands that exist alongside private ranches that use irrigation practices similar to those used on private lands, but focus habitat management specifically on wetland-dependent species and therefore do not harvest the irrigated vegetation. These conservation lands are lightly grazed (via grazing leases) to mitigate encroachment of woody plants, but are much closer to the spared end of the land-use spectrum than shared working ranchlands with hay cultivation, the latter of which are best described as low-intensity agricultural lands (i.e., shared lands). This study system thus provided an ideal natural experiment, allowing for the evaluation of the demographic consequences of land-sharing vs. land-sparing practices in the context of avian reproductive success.

Our goal was to evaluate the fitness consequences of breeding habitat-selection decisions based on environmental cues associated with various habitats. Specifically, we evaluated breeding waterfowl habitat selection decisions across a matrix of upland habitats and those surrounding natural and created wetlands associated with flood irrigation. Our primary objective was to determine whether habitats selected preferentially as nest sites within low-intensity agricultural lands were in turn beneficial or detrimental to the success of the nests, compared to spared parcels of habitat. We predicted that shared lands, more so than spared, would exhibit signs of ecological traps given their potentially attractive cues early in the nesting season contrasted against their potential for increased rates of predation and mechanical destruction of nests (Schlichting et al. 2019, Gehring et al. 2021). The single harvest of hay meadows near the end of the growing season generally results in sparse residual vegetation present the following year. We therefore predicted this could alternatively render hay meadows unattractive to early-

nesting ducks, presenting reliable cues for nesting ducks to avoid being trapped, but also failing to provide nesting habitat.

## METHODS

### *Study System*

We used an exemplar system in north-central Colorado, USA, to study avian reproductive impacts across land-sharing and land-sparing agricultural strategies within a common landscape (Figure 1.1). The North Platte Basin (hereafter North Park) is a high-elevation (2500 m on average) intermountain basin characterized by sagebrush (*Artemisia* spp.) steppe and riparian corridors used as sources of water to flood irrigate hay meadows (by diverting water into irrigation ditches). Land-sharing practices typically take the form of large cattle ranches that also actively produce high-quality, flood-irrigated hay that is cut each year. Harvested meadows consist primarily of Timothy hay (*Phleum pretense*), and are flooded in May, dried anywhere from July to August, and then harvested from July-September. Because of the short growing season, a single cut of hay is typical. The system also has public land parcels that are spared from harvested agricultural practices, primarily Arapaho National Wildlife Refuge (NWR). This NWR was created to benefit migratory and breeding waterfowl as mitigation for the conversion of high-quality waterfowl breeding wetlands in the Prairie Pothole Region of North America to high-intensity agriculture production in the 1960s and 1970s. The NWR flood-irrigates wet meadows that are not cut, and typically exhibit more diverse vegetation communities than hay meadows, including forbs, sedges, rushes, and grasses interspersed by small areas of greasewood shrubs (*Sarcobatus vermiculatus*) and sagebrush. In addition to the NWR, there are also state wildlife areas (SWAs) on which managers flood irrigate to create wetland habitat, as well as

waterfowl management areas (WMAs) managed by the Bureau of Land Management (BLM) specifically for breeding waterfowl. Wetland habitats on the parcels of public land included in the study are comprised of large water storage reservoirs with variable amounts of submerged aquatic vegetation, basin wetlands with rings of emergent vegetation, and irrigated meadows consisting of graminoids and occasionally robust emergent vegetation (e.g., cattails [*Typha* spp.] and bulrush [*Scirpus* spp.]).

### *Data Collection*

We searched systematically for upland-nesting duck nests across the study area from 2018-2022. Study sites included five private ranches on which agricultural production was consistent with land-sharing practices, in addition to Arapaho NWR, Lake John SWA, and Hebron WMA, which are multi-use parcels of public land spared from agricultural production with the exception of light cattle grazing. We searched randomly-selected nest plots across land-use types in addition to searching opportunistically between plots. We randomly selected 16 8-ha square plots within uncut irrigated meadows on spared land to sample portions of the large expanses of irrigated meadow, whereas plots on shared lands followed natural boundaries of hay meadows, which were often smaller and more easily definable. Access to ranches varied across seasons, which subsequently altered the number of plots searched each year. The number of plots we searched therefore varied from five during a pilot year to 131 and plots ranged from 0.14-35.83 ha, averaging 6.44 ha. Additionally, we randomly selected 500-m length sections of riparian areas and irrigation ditches across land-use types, searching within a 200 m buffer of the edges, and systematically searched the perimeter of all basin wetlands out to a radius of 200 m. We searched plots 1-3 times per year, most commonly searching each plot twice to evaluate detection probability of nests (Péron et al. 2014). We used a combination of rope drags (Higgins

et al. 1969) and systematic foot searches to flush incubating hens off of the nests and marked the location. We identified the species incubating each nest as the hen flushed and used the size and color of the eggs to verify the identification. We candled several eggs in each nest to calculate the date at which the nest was initiated, backdating from the date the nest was located based on the embryonic stage of development and the number of eggs in the nest (Klett et al. 1986). As incubating hens typically cover their eggs with down feathers upon leaving the nest, we also covered eggs after each nest visit and placed two pieces of grass across the top of the nest in an “x” shape to determine whether the hen returned to the nest or abandoned after disturbance. We monitored each nest approximately every five to seven days, making note of its incubation status, the hen’s presence, and ultimately the fate of the nest.

Regardless of whether a nest failed (i.e., eggs were eaten by a predator or abandoned by the hen) or was successful, we conducted vegetation surveys on the estimated hatch date. We calculated hatch date based on the stage of embryonic development of the eggs during each nest visit and the average incubation time for each species. In the case of successful nests, we conducted surveys the day after ducklings left the nest. Vegetation surveys occurred at the nest bowl and at four randomly-selected points within a 200-m radius of the nest bowl. Surveys included visual estimation of percent cover within a 1-m Daubenmire frame (Daubenmire 1959). We estimated percent cover of bare ground, litter, water, grasses, forbs, shrubs, sedges, and rushes, and we allowed total percent cover to sum to more than 100% because vegetation was often layered vertically. We also measured average visual obstruction rating using a 1-m Robel pole from each cardinal direction (Robel et al. 1970).

We measured broad-scale habitat characteristics using a geographic information system (Esri ArcGIS Pro 2.8.0) to evaluate the drivers of nest site selection within a potential home

range. We created ~10000 random points across the study area in all habitats we consistently searched for nests, and calculated the distance of each random point and nest site from the nearest irrigation ditch, river, open water (i.e., ponds, marshes, or reservoirs), road, harvested hay meadow, and uncut irrigated meadow using a 2011 National Land Cover Database (NLCD) layer (Northrup et al. 2013). Hay meadows differed from uncut irrigated meadows in that they were harvested annually whereas uncut irrigated meadows were not, leading to substantial differences in the vegetation community within these habitats. We assigned each random point generated using the GIS to a duck species wherein the number of points assigned to each category was proportional to the number of nests comprised of each species so we could include species as a random effect in the resource selection models (Gillies et al. 2006). We could not include year as a random effect because the GIS layer was not year-specific.

### *Nest Site Selection*

We constructed two resource selection functions (RSF) to evaluate nest site selection of breeding waterfowl across habitats and uses of land. We included all upland-nesting dabbling duck species (American green-winged teal [*Anas carolinensis*], blue-winged teal [*Spatula discors*], cinnamon teal [*Spatula cyanoptera*], northern shoveler [*Spatula clypeata*], gadwall [*Mareca strepera*], American wigeon [*Mareca americana*], mallard [*Anas platyrhynchos*], and northern pintail [*Anas acuta*] in our analysis, which comprised the vast majority of monitored nests. In one RSF analysis we evaluated fine-scale (i.e., third-order) selection of nest sites where the randomly-selected points at which we measured vegetation metrics were conditional on the nest site (Manly et al. 2002, Johnson et al. 1980). We included nest as a random effect to account for the fact that randomly-selected points were not independent of the nest site in addition to random effects for species and year. In the second RSF we evaluated patch-level metrics of

habitat that dabbling ducks might use to select a nest site. We included distance to river, open water (e.g., ponds, marshes, etc.), irrigation ditch, road, harvested hay meadow, and uncut irrigated meadow as standardized covariates in addition to a random effect for species. Other than the random effects, we fit univariate fixed-effect models for both scales of nest-site selection to mitigate effects of multicollinearity that arose when multiple predictors were included in the same model.

### *Nest Survival*

We evaluated nest survival for all upland-nesting duck species using a Bayesian nest survival model (Schmidt et al. 2010). To allow for comparison with nest-site selection results, we also fit a fine-scale model and patch-scale model using the same covariates to evaluate the effects of habitat conditions on nest survival. We included random effects for species and year, and also fit univariate effects of each predictor to avoid multicollinearity as stated above.

All analyses were conducted in a Bayesian framework using the rjags package in Program R. We used vague priors on the logit scale for all intercepts and slope coefficients in the RSFs and nest survival models (Northrup and Gerber 2018). We present posterior means and standard deviations for each parameter and the proportion of each posterior greater than zero ( $f$ ) as a metric of support. We fit three chains for 10000 iterations with a 1000 iteration burn-in period, and checked for convergence via visual examination of trace plots and Gelman-Rubin statistics, ensuring all were  $\leq 1.1$ .

## RESULTS

We located 145 nests of all dabbling ducks over the course of the five-year study. We sampled a total of 125 of those nests for vegetation metrics to be used in the nest site selection analysis. We removed nests from the nest survival analysis at which the hen abandoned as a direct result of investigator activity ( $n=19$ ) and any that abandoned immediately after the nest was located ( $n=9$ , which may have also been due to investigator activity), resulting in 117 nests used to evaluate nest survival. Nests failed for a variety of reasons, including egg depredation ( $n=62$ ), abandonment unrelated to investigator activity ( $n=9$ ), flooding ( $n=2$ ), direct depredation of the hen ( $n=2$ ), livestock trampling ( $n=5$ ), or for unknown reasons ( $n=3$ ).

Both spared and shared habitats varied considerably in their vegetation communities and habitat features (Figure 1.2). Spared lands exhibited lower percent cover of forbs and lower visual obstruction rating, but higher litter percent cover than shared on average. Spared lands were also further from harvested hay meadows and ditches, roads, and rivers, but closer to uncut irrigated meadows and open water on average.

### *Nest Site Selection*

At the finer spatial scale measured, the average dabbling duck selected nest sites that were associated with high visual obstruction ( $\beta_{\text{VOR}} = 0.56$ ,  $\sigma_{\text{VOR}} = 0.08$  [standard deviation of the posterior],  $f = 1$ ), high percent cover of shrubs ( $\beta_{\text{Shrubs}} = 0.27$ ,  $\sigma_{\text{Shrubs}} = 0.08$ ,  $f = 1$ ), sedges ( $\beta_{\text{Sedges}} = 0.16$ ,  $\sigma_{\text{Sedges}} = 0.08$ ,  $f = 0.97$ ), and grasses ( $\beta_{\text{Grasses}} = 0.10$ ,  $\sigma_{\text{Grasses}} = 0.09$ ,  $f = 0.88$ ), and low percent cover of litter ( $\beta_{\text{Litter}} = -0.24$ ,  $\sigma_{\text{Litter}} = 0.10$ ,  $f = 0$ ), rushes ( $\beta_{\text{Rushes}} = -0.17$ ,  $\sigma_{\text{Rushes}} = 0.11$ ,  $f = 0.05$ ), and forbs ( $\beta_{\text{Forbs}} = -0.22$ ,  $\sigma_{\text{Forbs}} = 0.12$ ,  $f = 0.03$ ; Figure 1.3). At the patch scale, selected nest sites were commonly located far from rivers ( $\beta_{\text{Rivers}} = 0.56$ ,  $\sigma_{\text{Rivers}} = 0.05$ ,  $f = 1$ ) and hay meadows ( $\beta_{\text{Hay}} = 0.71$ ,  $\sigma_{\text{Hay}} = 0.05$ ,  $f = 1$ ), and closer to uncut irrigated meadows ( $\beta_{\text{Meadows}} = -1.63$ ,  $\sigma_{\text{Meadows}} =$

0.20,  $f = 0$ ), roads ( $\beta_{\text{Roads}} = -0.36$ ,  $\sigma_{\text{Roads}} = 0.10$ ,  $f = 0$ ), open water ( $\beta_{\text{OW}} = -0.81$ ,  $\sigma_{\text{OW}} = 0.14$ ,  $f = 0$ ), and irrigation ditches ( $\beta_{\text{Ditches}} = -0.73$ ,  $\sigma_{\text{Ditches}} = 0.12$ ,  $f = 0$ ; Figure 1.4). All species and year random effects indicated very little variation among species and years, and the estimates are presented in Appendix S1.

### *Nest Survival*

Average dabbling duck nest survival responded to habitat features at both measured spatial scales associated with land sharing and sparing practices. At the fine scale measured, higher percent cover of rushes was associated with lower nest survival ( $\beta_{\text{Rushes}} = -0.14$ ,  $\sigma_{\text{Rushes}} = 0.12$ ,  $f = 0.07$ ), as was a higher proportion of litter ( $\beta_{\text{Litter}} = -0.28$ ,  $\sigma_{\text{Litter}} = 0.14$ ,  $f = 0.03$ ), whereas a higher proportion of shrubs ( $\beta_{\text{Shrubs}} = 0.17$ ,  $\sigma_{\text{Shrubs}} = 0.15$ ,  $f = 0.87$ ) and sedges were associated with increased nest survival ( $\beta_{\text{Sedges}} = 0.38$ ,  $\sigma_{\text{Sedges}} = 0.17$ ,  $f = 0.99$ ; Figure 1.3). At the patch scale, nests that were located closer to roads ( $\beta_{\text{Roads}} = -0.14$ ,  $\sigma_{\text{Roads}} = 0.12$ ,  $f = 0.12$ ), open water ( $\beta_{\text{OW}} = -0.19$ ,  $\sigma_{\text{OW}} = 0.13$ ,  $f = 0.07$ ), and irrigation ditches ( $\beta_{\text{Ditches}} = -0.16$ ,  $\sigma_{\text{Ditches}} = 0.13$ ,  $f = 0.10$ ) exhibited higher nest survival than those situated far from these habitat patches (a negative coefficient implied that increasing distance from a patch led to lower nest survival). Whereas nests far from rivers survived better than those close to rivers ( $\beta_{\text{Rivers}} = 0.11$ ,  $\sigma_{\text{Rivers}} = 0.14$ ,  $f = 0.80$ ; Figure 1.4). Daily survival rate estimates were consistently 0.95 (SD = 0.02) across fine- and patch-scale models (Appendix S1.2). All species and year random effects indicated very little variation among species and years (Appendix S1).

## DISCUSSION

A case for the most effective conservation strategy for agricultural landscapes is only as strong as the empirical evidence backing it up (Kremen 2015). The results of our study provide

evidence for several of the benefits of both land-sharing and sparing practices, especially when used in conjunction with one another. While most nesting habitat types spanned both spared and shared land designations, harvested hay meadows were solely associated with shared lands while uncut irrigated meadows were only on spared lands. Contrary to our predictions, irrigation ditches associated with agricultural production did not induce ecological traps for breeding waterfowl, and were, in fact, preferentially selected as nesting habitat and beneficial to the nest survival of dabbling ducks (Figure 1.4). While ducks in other systems have been found nesting in harvested hay meadows (Earl 1950, Greenwood et al. 1995, Lovvorn and Crozier 2022), we found that harvested hay meadows were strongly avoided as nesting habitat, although we did not detect a strong influence of hay meadows on survival of the few nests located within or near these patches of habitat. In contrast, nesting ducks strongly preferred uncut irrigated meadows compared to hay meadows despite relatively neutral effects on nest survival. However, our sample size of located nests was likely too small to detect potentially important differences among species and years. It may have also been insufficient to detect possible underlying differences in nest survival across habitats. The coexisting matrix of both shared and spared lands may therefore be important in flood-irrigated systems to ensure productive habitat for breeding birds.

The nesting habitats associated with shared lands were unexpectedly benign in terms of waterfowl nest survival. We expected nest predators to use corridors created by irrigation ditches, thereby decreasing nest survival, but nests closer to irrigation ditches actually exhibited higher survival. In systems where nest density is low, predators may not be as successful at searching for nests along irrigation ditches and may switch to other prey items, habitat, or behavioral cues to locate nests and other prey (Lariviere and Messier 1998, Ackerman 2003, Bety et al. 2003,

Ellis et al. 2020). Working ranches may also actively manage populations of mesopredators or conduct operations that unintentionally haze predators away from their properties (Minnie et al. 2018). Anecdotally, land sharing practices often had the highest benefits to wildlife when the landscape features that were created to benefit agricultural operations also resembled naturally-occurring habitat. For example, water storage (AKA stock) ponds provided brood habitat and produced consistent macroinvertebrate resources for waterfowl foraging (Setash Chapter 2), and nests on ranches were often located closer to wetlands with open water like ponds, riparian corridors, or irrigation ditches that resembled riparian corridors. Hay meadows, on the other hand, exhibited lower vegetation density and diversity in addition to lower macroinvertebrate density and diversity compared to uncut irrigated meadows, and less topographical structure to provide dry nesting areas for ground-nesting birds (Setash Chapter 2).

While the diverse habitats associated with spared lands provided extensive nesting cover, they also presented threats to nests that, on the surface, appeared to have nothing to do with agricultural production. For example, nests closer to rivers often exhibited lower nest survival, potentially as a result of the frequency with which riverbanks, and thus nests, flooded (Simpkins et al. 2015, Thompson et al. 2023). However, spared lands were more likely to harbor wetland complexes, providing a diversity of wetland sizes and hydrologies that might meet the many needs of waterbirds throughout the breeding season, especially given our results revealing the importance of fringe habitats near open water, such as ponds, for nest site selection and nest survival. These same wetlands support excellent macroinvertebrate food resources to nesting hens, and to ducklings during the subsequent phase of the life cycle (Setash Chapter 2).

Most studies evaluating nesting preferences of waterfowl across an agricultural gradient have occurred in the Prairie Pothole Region of North America. Many species of dabbling ducks

have been shown to preferentially select nesting habitats in large swaths of grassland, which have been restored at broad scales within individual farms and ranches via programs like the Conservation Reserve Program (CRP; Reynolds et al. 2001, Stephens et al. 2005). Ducks use both broad-scale habitat cues to select nest sites as well as fine-scale cues like litter cover and vegetation species composition (Ringelman et al. 2018, Dyson et al. 2019). Consequently, ducks may not have selected hay meadows in our system due to the lack of residual litter and therefore available nest sites during the selection period. Both fine-scale nest-site selection metrics and daily nest survival rates were comparable to those in more heavily-studied regions, and daily nest survival rates of approximately 0.95 would translate to a 31-day nest survival rate of 0.20, indicating a stable or increasing population of breeding birds (Cowardin et al. 1985). Year and species effects went undetected given limited sample size, but may have been significant in the boom and bust, high elevation system. Nest survival has been shown to vary considerably across years and by species within a year in much of the waterfowl literature and has also been shown to contribute more than other vital rates to changes in population growth rate (Hoekman et al. 2002).

Though nest survival generally improves with amount of grassland cover in the landscape, research has also detected low nest survival at intermediate levels of grassland edge (Stephens et al. 2005). In our study system, ranches produced grass hay as a crop in suitable meadows, thereby interspersing other wetland types with grassland edge and fragmenting what would have historically been larger meadows. Shared lands, whether landowners attempt to mimic natural habitats or not, have been shown to introduce habitat edges onto the landscape in a variety of ways (Gilroy et al. 2014, Lamb et al. 2016). Linear features such as irrigation ditches, fencerows, and abrupt field edges associated with land-sharing practices may fragment habitats,

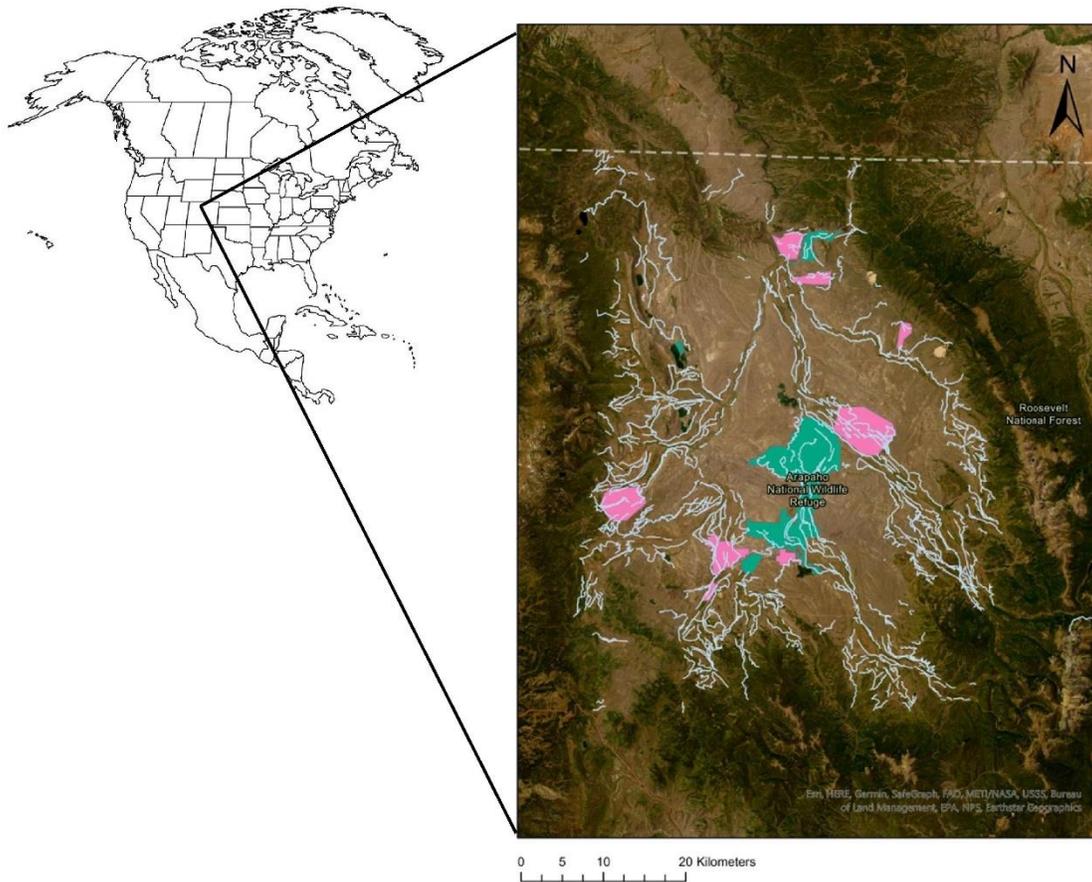
altering nest predator-prey interactions by increasing nest visibility along edges and funneling predators or livestock down corridors associated with edges (Cutting et al. 2019, Jokimaki et al. 2020). We therefore expected irrigation ditches to introduce detrimental edge habitat into the shared landscapes common in our study system. As habitat fragmentation can often be the ultimate cause of nest failure among birds, we expected to observe lower nest survival associated with the fragmenting habitat features (Stephens et al. 2004). Why, then, were irrigation ditches not too “edgy” for nesting waterfowl in this system, and what can be gleaned about them when creating or updating irrigation infrastructure in other regions? The predator assemblage may be responsible given that avian predators were the most common in our study system, which may be more successful in open habitats rather than along densely vegetated ditches. Additionally, ditches often had relatively wide margins, providing cover, and sloped sides that may have prevented livestock from traversing them frequently. Irrigation ditches have been shown to act as “keystone habitats” for waterbirds on drained agricultural lands, especially those with wide, grassy margins (reviewed by Herzon and Helenius 2008), and may be a source of habitat connectivity for swimming species rather than a dividing, fragmenting feature in some landscapes (Earl 1950, Jones and Hungerford 1972).

Having protected land interspersed with “shared” land was likely essential to maintaining a stable nesting population of waterfowl, given their strong preference against hay meadows as nesting habitat. Hay meadows comprise the largest proportion of flood-irrigated land in the semiarid agricultural lands of western North America and globally (Donnelly et al. 2019). Despite the lack of strong demographic consequences of nesting in hay meadows, the very fact that so much of the available habitat was comprised of these meadows suggests that they may limit the utility of land-sharing practices when nesting birds so strongly avoid them. If hay

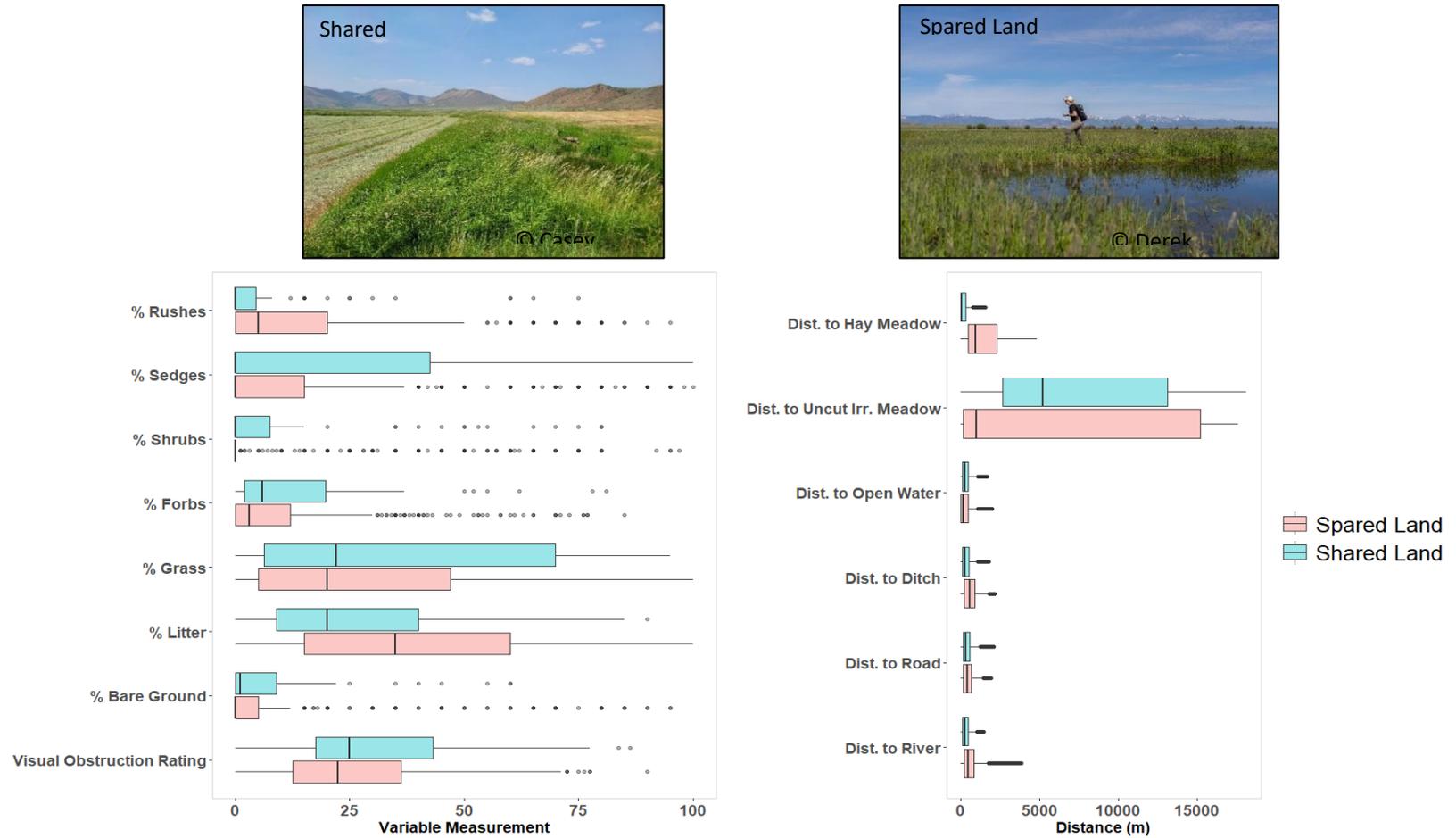
meadows had been the only nesting habitat available, rather than being augmented by “spared” refugia, the shared lands may have acted as a population sink for breeding birds. Spared lands provided a higher proportion of favorable habitat for breeding waterfowl relative to shared habitat given that uncut irrigated meadows went mostly undisturbed and birds preferentially selected them. The spared land in our study system was also centrally located within the matrix of agricultural lands, and large enough to provide wetland habitats for a diversity of waterfowl (Cannon et al. 2019). The existence of these refugia likely allowed breeding birds to take advantage of shared agricultural habitats when resources were available while still being able to rely on consistent, reliable habitats associated with spared lands. Agricultural producers and policymakers may consider ways in which lands in production might better mimic natural habitats without compromising yields (Samways et al. 2020, Williams et al. 2021). This could take a variety of forms, including the addition of small storage water complexes (Tomscha et al. 2020), wider uncut margins around irrigation ditches, or incentive programs to persuade producers to leave portions of hay meadows uncut or to reflood them after harvest to regrow a portion of the vegetation as a means to provide better nesting cover for early nesting ducks in subsequent years (Pernollet et al. 2015). Further research is needed to evaluate these details, and to gain better insight into possible differences among species within the dabbling duck community and other guilds.

Overall, the complementary habitats associated with both shared and spared lands resulted in relatively benign demographic consequences and maintained a stable nesting population of waterfowl. Even with relatively abundant avoided habitats propelling our study region towards a possible population sink status, literature on source-sink dynamics posits that the existence of sinks can support greater overall population abundance across the landscape than

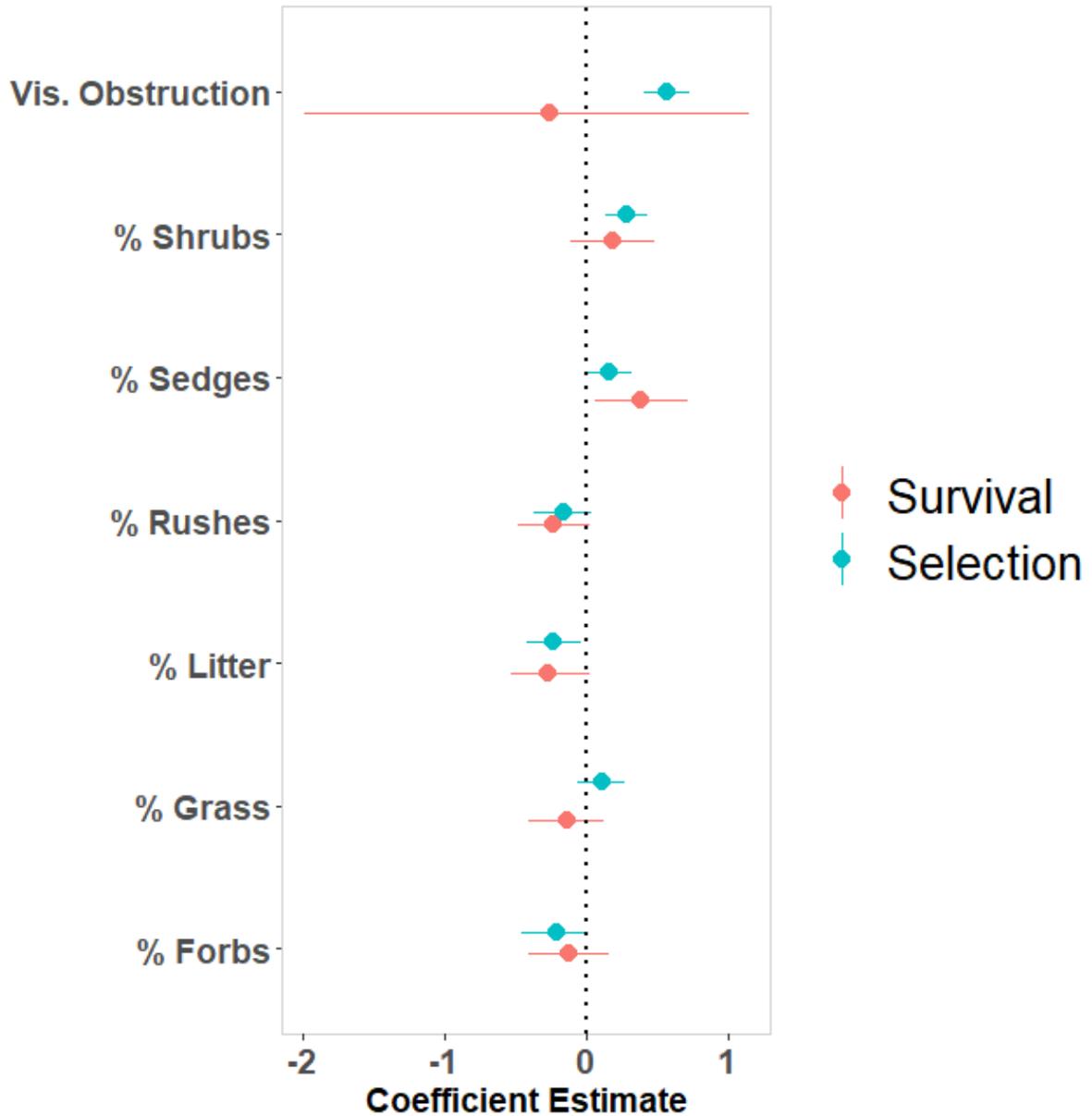
if the sink habitats did not exist, but that removing or altering the source habitats or populations may lead to the collapse of the overall population (Pulliam 1988, Howe et al. 1991). It is therefore imperative to understand the mechanisms maintaining stable populations in the more fringe habitats within a species' range. Our study suggests that when those fringe habitats are comprised of shared agricultural lands, removing the spared component of the system may result in more negative consequences for breeding birds. The results of this study not only have widespread implications for waterbird conservation and population persistence across arid landscapes on working lands as hydrology becomes increasingly modified by humans, but also provide an empirical example of the indirect effects of land-sharing practices in an ever more cultivated world (Tilman 1999).



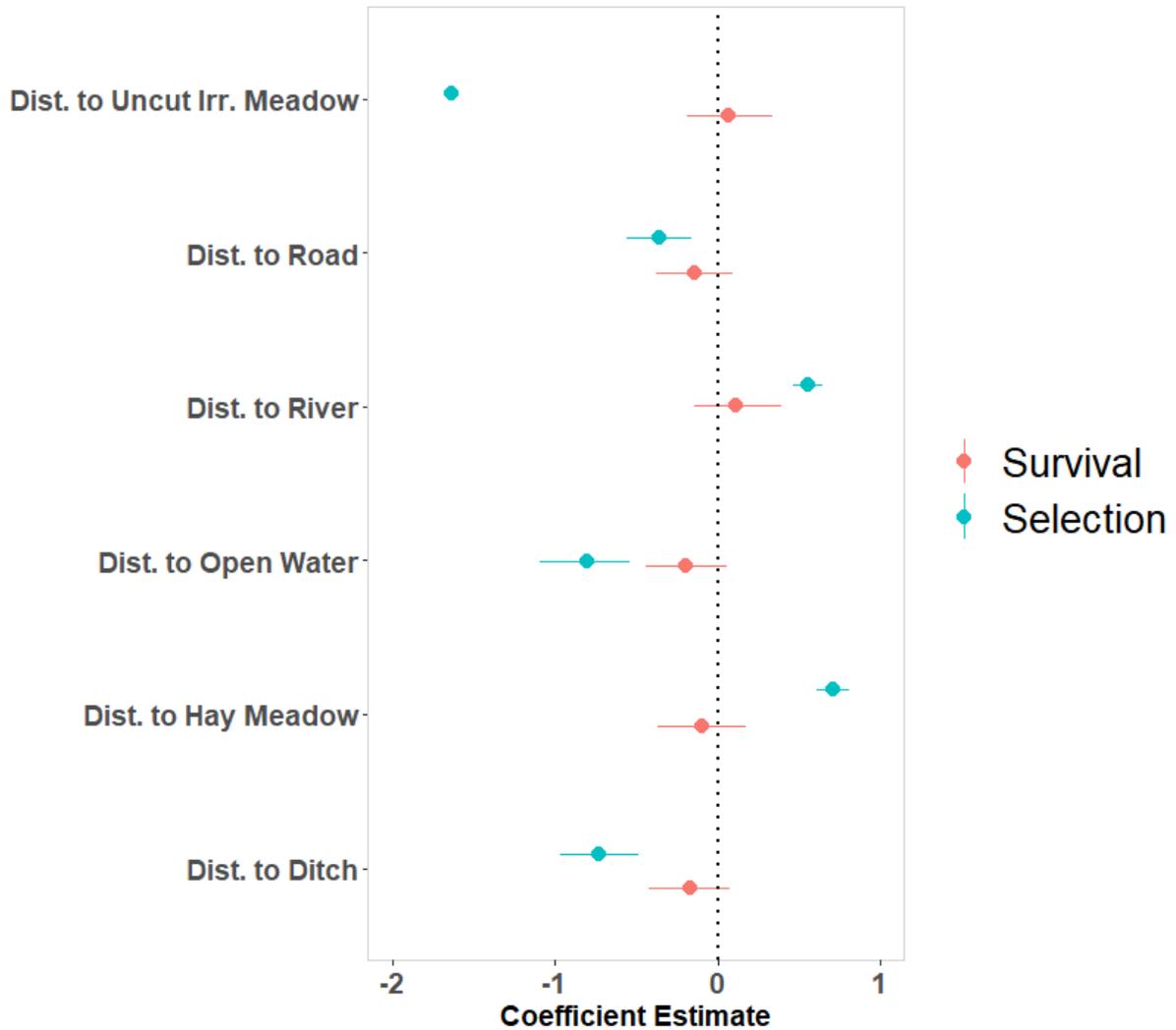
**Figure 1.1:** Study site for evaluating the effects of land sparing and land sharing on nesting ducks in North Park, Colorado. Shared lands are shaded in pink and spared lands are shaded in teal. The dashed line designates the Colorado-Wyoming state line and the light blue lines designate streams stemming from the tributaries of the North Platte River.



**Figure 1.2:** Summary box and whisker plots illustrating measured fine-scale (third order) and patch-scale habitat characteristics across shared and spared lands.



**Figure 1.3:** Comparison of results from a Bayesian resource selection function and a Bayesian nest survival model illustrating the relative probabilities of selecting nest sites associated with fine-scale habitat features (third order) by upland-nesting dabbling duck species in North Park, Colorado, USA and the effects of the same nest site characteristics on probabilities of daily nest survival. Dots represent posterior means and error bars represent 95% credible intervals. Nest data were collected during the breeding seasons of 2018-2022.



**Figure 1.4:** Comparison of results from a Bayesian resource selection function and a Bayesian nest survival model illustrating the relative selection probabilities of patch-scale habitat metrics by upland-nesting dabbling duck species in North Park, Colorado, USA and the effects of the same patch-scale habitat metrics on daily nest survival. Dots represent posterior means and error bars represent 95% credible intervals. Nest data were collected during the breeding seasons of 2018-2022.

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## CHAPTER 2 – RIDING THE WETLAND WAVE: DO WATERFOWL TRACK MACROINVERTEBRATE RESOURCES ACROSS THE BREEDING SEASON?

### INTRODUCTION

The amount and availability of food resources is a fundamental component of ecology and dictates many decisions an animal makes. Consumers must find available resources during the correct timeframe and at sufficient quantities for consumers to survive and reproduce, with availability being a function of both phenology and the ability of the consumer to track that phenology (Abrahms et al. 2021). Consumers are impacted by multiple dimensions of resources, including the spatial variability across the landscape and limitations that inhibit the consumer from being ideal and free to track spatio-temporal variability in resource availability (e.g., defending a breeding territory, maintaining vigilance against predators, or rearing offspring; Fretwell and Lucas 1970, Behney et al. 2018, Fraser and Catlin 2019, Baert et al. 2021). The study of how consumers locate and consume resources spans several sub-fields of ecology from behavioral ecology to landscape ecology, depending on the spatial and temporal scales under evaluation (Abrahms et al. 2021). Resource tracking over time lies somewhere in the middle of that spectrum, and refers to the ability of individual animals to locate ephemeral resources across the landscape as they emerge.

Many species take advantage of pulses in resources throughout their annual cycles, often tracking these pulses through space and time (Armstrong et al. 2016). Some even track resources during seasonal migrations (Evans and Bearhop 2022). This concept has been popularized by the idea of a “green wave” among migratory herbivores, which closely track spring green-up patterns as they proceed toward the breeding grounds (van der Graaf et al. 2006, Merkle et al.

2016). The ability of some animals to track ephemeral resources has considerable fitness consequences, including both direct and indirect effects on survival and reproduction (Middleton et al. 2018, Evans and Bearhop 2022). The synchrony of phenological events is especially important in systems where both the consumer demand and resource availability distributions are narrow, as is often the case in extremely seasonal habitats like those at high latitudes or elevation (Both et al. 2010, Linden 2018). Additionally, phenological mismatches are becoming increasingly common as climate change alters temporal resource distributions, migratory pathways and timing, and habitat conditions across the globe (Visser et al. 2012, Visser and Gienapp 2019, Lawrence et al. 2022). Consumers that exploit transient pulses in resources during times of brief, but extreme energetic demand are often at the highest risk of fitness consequences (Simmonds et al. 2020, Clark and Hobson 2022, Kubelka et al. 2022). For example, insectivorous great tits (*Parus major*) rely on pulses of winter moth (*Operophtera brumata*) caterpillar abundance during the breeding season to successfully reproduce and have been shown to exhibit thresholds in the plasticity of nest initiation with direct fitness consequences (Simmonds et al. 2020). Plasticity in foraging behavior and specificity can thus be adaptive in terms of which resources can be exploited and which habitats can be used in the face of global change.

The extent to which consumers must expend energy tracking resources is influenced by the temporal variability in resource availability (i.e., the spread of the distribution of resource abundance over time and how much overlap there is with the distribution of consumer requirements). Habitats harboring consistent, abundant resources across the consumer's period of need likely have the highest probability of providing enough energy while limiting additional movements among habitats (Pöysä et al. 2000, Gurney et al. 2017). The exploitation of

temporally stable resources may therefore provide an alternative mechanism explaining the patterns of observed consumer habitat use. When both resource pulses and temporally stable resources exist within a single system, preferences of consumers can be evaluated and inferences can be drawn about the dominant mechanisms driving foraging behaviors and habitat needs.

Breeding waterfowl, especially those toward the income end of the capital-income spectrum of energetic investment in breeding (Ankney and Alisauskas 1991, Alisauskas and Ankney 1992), commonly take advantage of pulses in invertebrate resources during the energetically-expensive breeding season as those resources emerge and become available across variable habitats (Gammonley and Laubhan 2002, Anteau 2012, Stafford et al. 2016). Breeding waterfowl must be able to either select habitats where there is temporal stability in the resource or must be able to track resource pulses over space and time to ensure that their life-history events overlap with the life stages at which resources are available (i.e., ride the resource wave; Armstrong et al. 2016, Deacy et al. 2018). Dabbling duck females must acquire protein-rich invertebrates to produce eggs and maintain their body condition throughout nest incubation (or at least minimize losses), and females with broods must maximize energy acquisition (predominately invertebrates) for offspring growth and survival as well as recovering their own energy reserves lost during incubation (Sedinger 1992, Cooper and Anderson 1996). Whether waterfowl have the capacity to follow and exploit resource pulses within a season has yet to be evaluated empirically (but see Gammonley and Laubhan 2002), but has the potential to elucidate mechanisms driving habitat selection, movement patterns, and fitness components.

The macroinvertebrate resources waterfowl exploit often remain in their various life stages ephemerally, and have evolved developmental phenologies via top-down (e.g., phenology of competitors and predators; Moore and Schindler 2010) and bottom-up (e.g., temporal shifts in

water chemistry, temperature, and primary productivity; Whiles and Goldowitz 2001) selective forces. Developmental phenology of macroinvertebrates can vary by species or habitat type (Anderson et al. 2017) and even within species depending on environmental conditions (Murillo-Rincon et al. 2016). Wetland habitats that are altered by humans, such as those in agricultural landscapes, may impact phenological drivers further, resulting in resource pulses that differ in magnitude and/or timing from naturally-occurring wetlands. Ducks breeding in a matrix of natural and artificial wetlands therefore face especially significant trade-offs in habitat selection decisions, and their selection preferences or tracking abilities may imply advantages to restoring particular wetland types (Davis and Bidwell 2008, Wrubleski and Ross 2011, Harrison et al. 2017). Alternatively, a diverse matrix of both agricultural and naturally-occurring wetlands in close vicinity to one another may present more opportunities to waterfowl by creating habitat for a diverse community of macroinvertebrates that emerge chronologically, thus providing consistent resources over time.

We evaluated the drivers of spatio-temporal variation in macroinvertebrate energy density and the extent to which breeding waterfowl tracked energy density across the various natural and created wetlands associated with flood-irrigated agriculture. We predicted that waterfowl would exploit brief pulses in invertebrate resources, indicated by a positive correlation between waterfowl and energy density across habitat types during the early nesting period (i.e., egg development period). Waterfowl are more mobile prior to nesting compared to when they are rearing broods, however, so we predicted brood densities would be more strongly related to temporal resource stability than to the phenology of absolute resource density. The results of this study have the potential to inform wetland restoration practices across arid landscapes in addition to the mechanisms driving habitat selection decisions of breeding waterfowl and other birds.

## METHODS

### *Study Area*

Our study occurred throughout the North Platte Basin in Jackson County, Colorado (North Park) along the North Platte River and its tributaries from 2020-2021. North Park is a rural mosaic of natural and artificial wetlands resulting from flood-irrigated hay agriculture. This high elevation (2600 m) basin is dominated by salt desert shrubs and sagebrush steppe interspersed by lakes, ponds, irrigation ditches, irrigated hay fields, and the tributaries of the North Platte River. Land ownership is approximately 73% public, with the US Forest Service owning the largest parcels of public land (32%) that border the valley (Lemly and Gilligan 2012). Arapaho National Wildlife Refuge (NWR), several State Wildlife Areas, Bureau of Land Management properties, and privately irrigated fields encompass many of the wetlands available to breeding and migrating waterfowl in the region and especially in the state of Colorado. Hay meadows primarily consist of Timothy grass (*Phleum pratense*) interspersed with sedges (Cyperaceae) and rushes (Juncaceae). They are often bordered by willows (*Salix* spp.) and other riparian plants that grow along the tributaries from which meadows are flooded.

### *Macroinvertebrate Data Collection*

We collected nektonic invertebrate samples using 2-L activity traps in 2020 and 2021. Traps had a 15 cm opening at the widest part of the funnel and a 2 cm opening at the narrowest part of the funnel. We placed traps at randomly-selected points within 40 wetland sites that encompassed five different wetland types, including reservoirs, basin wetlands (i.e., ponds), irrigation ditches, flooded hay meadows, and streams. Trap sites spanned three properties, including two private ranches, Arapaho NWR, and two public reservoirs (Hebron Slough Waterfowl Management Area and Cowdrey Reservoir). We selected three trap points in each

wetland and three wetlands from each habitat category on each property, with the exception of reservoirs. We randomly selected two 200 m sections of shoreline on each of the three sampled reservoirs and placed three traps at random intervals along each section, resulting in 126 traps total during each sampling occasion. Traps remained in the wetlands for 48 hours every fourteen days, resulting in six sampling occasions each year over the course of the breeding season (13 May through 22 July). No traps were placed if the wetland was dry on a given sampling occasion. Occasionally traps became dislodged and either went missing or floated to the surface, in which case we replaced traps and allowed them to remain in the wetland for the subsequent 48 hours. We used a YSI Pro 2030 Dissolved Oxygen and Conductivity Meter to sample water temperature (°C), dissolved oxygen (%), and specific conductivity ( $\mu\text{S}/\text{cm}$ ) at each site upon collection of each trap in 2021.

Upon collection, traps were emptied into a mesh sieve-bottom bucket. All individual invertebrates from the sample were placed into plastic storage cups and stored in 70% ethanol until processing could occur. We emptied samples into 0.355 mm gauge mesh sieves in a wet lab and moved all individuals to a Petri dish for identification and counting. We placed samples under a dissecting microscope (AmScope SM-1BSY-64S Stereo Zoom Microscope) and identified individuals to taxonomic Family. Any sample containing more than 1000 individuals of a given Family was subsampled using a 6 x 6 square gridded Petri dish. We counted individuals in six of the 36 cells and multiplied by six to estimate the total number of individuals of that Family in the sample.

#### *Waterfowl Data Collection*

We conducted breeding pair counts of waterfowl on the same wetland sites being sampled for macroinvertebrates (n=40) using a dependent double-observer methodology during the

breeding seasons of 2020 and 2021 (Nichols et al. 2000). Pair count survey timing coincided with the first three macroinvertebrate sampling occasions. A primary observer counted every individual dabbling and diving duck observed and reported the number to a secondary observer, who recorded data while also recording any observations missed by the primary observer. Counts were separated by social status (i.e., lone drake vs. drake-hen pair) to estimate the number of indicated breeding pairs (Dzubin et al. 1969). Reservoirs often held large congregations of waterfowl that were too numerous to count using this methodology. They were instead counted by both observers to obtain a single total estimate of each species regardless of social status.

Brood count surveys also occurred on the same sites sampled for macroinvertebrates, but followed an independent double-observer methodology during 2020-2021. The smaller number of ducklings commonly observed at one time relative to pairs allowed for accurate count comparisons between observers (Pagano and Arnold 2009). The timing of counts coincided with the latter three macroinvertebrate sampling occasions. Observers counted all ducklings within a given brood and identified their age class according to Gollop and Marshall (1954). Observers spent a minimum of ten minutes at each wetland site and conducted surveys using window- or tripod-mounted spotting scopes and binoculars.

### *Macroinvertebrate Analyses*

We used a subset of the dataset to evaluate only the densities of macroinvertebrates commonly known to be eaten by waterfowl. We searched the literature to find evidence indicating whether each observed Family could be considered a common waterfowl food item and the average energy density associated with a given individual of each selected family (kcal/g; Nudds and Bowlby 1984). We multiplied the energy density of each Family by the mean mass of an individual associated with that family in grams, resulting in the average

kcal/individual (Table 2.1). These energy densities multiplied by the number of individuals of each Family observed in a given sample resulted in an estimate of kcal/sample, which we converted to kcal/cm<sup>3</sup> of water sampled and then joules (J) per cm<sup>3</sup>.

Temporal resource stability has been evaluated using a myriad of methodologies. We chose to use a common approach in the community ecology literature, the Species Rank Abundance Curve (MacArthur 1957, Whittaker 1965), and applied it to the energy density distribution across sampling occasions to evaluate the “evenness” of energy over time. We ranked each sampling occasion by the average energy density (kcal/cm<sup>3</sup>) across sampled sites associated with a given type of wetland habitat, creating an energy rank abundance curve for each habitat type and year. From these curves, we calculated a metric of evenness,  $E_Q$ , which is a measure of the slope of the curves over time and thus how quickly energy density drops off across occasions (Avolio et al. 2019). A higher  $E_Q$  indicates a more even/stable energetic resource for the consumer within a given habitat type and year.

Energy data were strictly positive with true structural zeros occurring in dry wetlands. We therefore fit a lognormal hurdle model to energy density over the sampling period to evaluate drivers of temporal shifts in energy density within each habitat, and across wetland habitat types. Fixed effects included habitat, sampling occasion, water temperature, dissolved oxygen, specific conductivity, wetland size (ha), and an interaction term of habitat x sampling occasion. We included a habitat effect on the Bernoulli process determining whether a given site had a non-zero energy density. We imputed missing covariate values and provided vague priors for all parameters. The predicted energy density for each habitat-occasion combination was derived to visualize the phenological shifts of energy density in the system and make inference on the drivers of those shifts. We also fit a second model including site, sampling occasion, and year as

fixed effects, and an interaction term between the three. This allowed us to derive a predicted energy density at each site-occasion-year combination to use as a predictor of waterfowl density in subsequent models.

### *Waterfowl Analyses*

We processed data to obtain a count of total waterfowl abundance at each site-occasion-year combination ( $\# \text{ lone drakes} + (2 \times \# \text{ pairs})$ ), and applied a concurrent, previously-estimated detection probability to the counts to obtain unbiased abundance estimates (Behney et al. 2022). We fit a zero-inflated Poisson model to the abundance data, with fixed effects for site-, occasion-, and year-specific model-predicted nektonic invertebrate energy density, and wetland size. We also included a partial interaction term between sampling occasion and energy density to evaluate whether the relationship between duck abundance and macroinvertebrates changed throughout the early breeding season. We used vague priors on the intercepts and slopes for each sampling occasion. We repeated these analyses using duckling abundance as a response variable to evaluate resource tracking across the full breeding cycle (where the latter three invertebrate sampling occasions were used to inform the energy explanatory variable). To evaluate our alternative hypothesis that waterfowl abundance would be more positively correlated with the stability of the resource they were exploiting, we also fit Poisson regression models, using both pair and brood counts aggregated by habitat type and year as response variables, and habitat- and year-specific temporal evenness ( $E_Q$ ) as a predictor. We also calculated a pseudo- $R^2$  value to evaluate the amount of variation in pair/brood abundance that was explained by each energetic mechanism (i.e., energy density vs. resource stability) using Equation 6 in Grosbois et al. (2008).

We conducted all analyses in a Bayesian framework using the jagsUI package in Program R. We ran three chains for 40000 iterations, a burn-in period of 5000 iterations, and kept every

third iteration to thin the chains. We checked for convergence visually using trace plots and evaluated Rubin-Gelman statistics, ensuring all were  $\leq 1.1$ . We provide posterior means and standard deviations, as well as the proportion of the posterior that was on the same side of 0 as the mean for each parameter, denoted as  $f$ . We present 95% highest posterior density intervals (HPDI) in all applicable figures.

## RESULTS

We collected 778 site- and occasion-specific invertebrate samples across 40 wetland sites in 2020 and 668 samples across the same 40 sites in 2021. Of the total samples, 171 and 147 were from wetlands that were dry on a given sampling occasion in 2020 or 2021, respectively. We identified a total of 125 unique invertebrate taxa at the lowest level of identification possible (mostly Families, but some Orders and Classes) and used a subset of 28 Families that are commonly known to be eaten by waterfowl in our analyses (Table 2.1).

### *Drivers of Energy Density*

Macroinvertebrate energy density varied considerably by habitat and over the course of the breeding season (Figure 2.1, Table S2.1). Basin wetlands and reservoirs had the highest, most consistent energy resources of any wetland type, with energy in basins peaking earlier and more strongly than in reservoirs and subsiding later in the season, whereas energy in reservoirs remained relatively high throughout the season. Energy density in other wetland types did not vary considerably over time, instead remaining consistently low. Flood-irrigated hay meadows pulsed higher in energy density than reservoirs on two sampling occasions, but otherwise contained relatively low energy density (Figure 2.1). Higher water temperature and conductivity,

and lower dissolved oxygen were associated with higher energy density, whereas wetland size did not exhibit a relationship with energy density (Figure 2.2).

### *Waterfowl Resource Tracking*

Breeding waterfowl exhibited a positive relationship with energy density that varied by sampling occasion. Early in the breeding season (mid-May), ducks responded strongly to energy density in sampled wetlands ( $\beta_{\text{energy}1} = 1.34$ ,  $\sigma_{\text{energy}1} = 0.07$ ,  $f = 1$ ; Figure 2.3), whereas the strength of the relationship decreased in the second ( $\beta_{\text{energy}2} = 0.16$ ,  $\sigma_{\text{energy}2} = 0.04$ ,  $f = 1$ ; Figure 2.3) and third ( $\beta_{\text{energy}3} = 0.75$ ,  $\sigma_{\text{energy}3} = 0.07$ ,  $f = 1$ ; Figure 2.3) sampling occasions. Ducklings also exhibited a positive relationship with energy density across all sampling occasions ( $\beta_{\text{energy} - \text{ducklings}} = 0.17$ ,  $\sigma_{\text{energy} - \text{ducklings}} = 0.08$ ,  $f = 0.99$ ; Figure 2.4).

### *Temporal Resource Stability*

The evenness metric we computed,  $E_Q$ , varied from 0.08 in hay meadows (2021) to 0.36 in irrigation ditches (2020; Figure 2.5). The average duck density per survey across habitats and years varied from 0.18 ducks/ha in hay meadows (2021) to 9.49 ducks/ha in basin wetlands (2021). Duckling density also varied by habitat type, ranging from 0 in both hay meadows and ditches (2020 and 2021) to 0.90 ducklings/ha in riparian wetlands (2020). Both duck density during the early breeding season ( $\beta_{E_Q - \text{Pairs}} = 0.28$ ,  $\sigma_{E_Q - \text{Pairs}} = 0.19$ ,  $f = 0.93$ ) and duckling density ( $\beta_{E_Q - \text{Ducklings}} = 1.40$ ,  $\sigma_{E_Q - \text{Ducklings}} = 0.89$ ,  $f = 0.96$ ) were positively related to the temporal evenness of energy density (Figure 2.6).

### *Comparing Resource Tracking Mechanisms*

The predicted number of ducks or ducklings observed at a given site in a given habitat type varied based on the modeled mechanism of resource use (e.g., tracking energy density pulses vs. exploiting habitats that provide temporally consistent/even resources; Figures 2.7 and

2.8). In separate analyses conducted at different scales amenable to the predictor variables, we found that both invertebrate energy density and temporal evenness of energy were related to duck abundances across spatial habitats and over chronological time. Given the respective spatial and temporal scales of each analysis, however, invertebrate energy density appeared to be superior at explaining spatio-temporal variation in duck abundance during the early breeding season (pseudo- $R^2 = 0.77$ ; Grosbois et al. 2008) compared to the temporal stability of invertebrate resources across different habitats (i.e.,  $E_Q$ ; pseudo- $R^2 = 0.06$ ). This pattern continued into the brood-rearing period, with energy density explaining variation in duckling density better (pseudo- $R^2 = 0.58$ ) than resource stability (pseudo- $R^2 = 0.31$ ), though the relationship of ducklings with resource stability was stronger (steeper slope of relationship and higher pseudo- $R^2$ ) compared to that for duck abundance during the early breeding season.

## DISCUSSION

The mechanisms driving breeding habitat selection and resource tracking are complex and vary across species and ecosystems. In an ecosystem characterized by highly variable water availability and a short growing season, we found differences in nektonic invertebrate energy density across wetland types and a positive relationship between waterfowl abundance and energy density, contrary to previous studies conducted in similar landscapes (Gammonley and Laubhan 2002). Our results suggest that waterfowl are tracking macroinvertebrate resources during times of most essential energetic need and that they are capable of locating consistent, abundant resources across the landscape. Other studies have detected similar matches between resources and consumers, particularly those examining the relationship between avian frugivores and their preferred fruits (Guitian and Munilla 2008). Fruit abundance has been shown to dictate

not only the distribution of frugivores, but also the abundance across time and space, as well as the species richness in birds exploiting that resource (Mulwa et al. 2012), suggesting that birds can readily cue in on resource abundance. Among waterfowl, most research of breeding habitat selection has occurred in the prairies of North America, and has rarely evaluated food as a driving factor. O'Neil et al. (2014) found that behavior drives pre-breeding habitat selection more so than habitat attributes like food availability, but, there is some evidence that mallards can forecast wetland conditions to a future time during which broods will need high-quality foraging sites (Poysa et al. 2000). In our study, wetland types that harbored the most consistent macroinvertebrate resources over time typically also held the highest energy densities, indicating that both ephemeral pulses in resources and diversity in resource phenology may be important for foraging waterfowl during the breeding season (Ernest and Brown 2001). While energy density explained more variation in waterfowl abundance than resource stability, further experimental research could provide deeper insight into the community compositional shifts of aquatic macroinvertebrates and the role that plays in resource stability, energy density, and subsequent waterfowl use (e.g., Benoy et al. 2002).

Wetlands associated with flood-irrigated agriculture exhibited both lower macroinvertebrate energy density and fewer observed waterfowl. Additionally, variation in water across wetland types was associated with energy density, indicating that both the physical and chemical properties of a wetland might further impact patterns of invertebrate distribution (Kantrud 1986, Swanson et al. 1988, Longcore et al. 2006). Irrigation ditches hold flowing water that has been recently redirected from rivers, and hay meadows are typically engineered to have inflows and outflows so water is continuously moving through the system (Tate et al. 2005). These attributes result in higher dissolved oxygen and lower water temperatures, which were

associated with lower energy density. In addition, hay meadows are typically a monoculture of Timothy grass (*Phleum pretense*), which is short in stature early in the growing season (because it is cut near the end of the previous growing season) and does not provide a diverse substrate on which macroinvertebrates might feed and develop (Fredrickson 1988, Harrison et al. 2017). Waterfowl have been shown to avoid hay meadows when selecting a nesting site (Setash Chapter 1), and may be cueing in on the lack of available macroinvertebrate resources as one of their selection criteria. Hay meadows occasionally harbored energy densities comparable to those in more semi-permanent wetland types, but the rapidly-changing water levels may have resulted in more ephemeral energy availability that ducks found more difficult to exploit. Semi-permanent basin wetlands and reservoirs, on the other hand, have hydrologies that encourage the growth of submerged aquatic vegetation (SAV), which provide growth and reproduction substrates for macroinvertebrates (Fredrickson 1988).

The amount of food in a given wetland is not always directly proportional to the observed abundance of waterfowl using that wetland, and many components of the habitat may preclude waterfowl from freely distributing themselves according to food availability (Brasher et al. 2007, Hagy and Kaminski 2015). In this system, agricultural wetlands were flooded and dried according to production needs, often resulting in dry, mowed fields during the peak of brood-rearing (Duebbert and Frank 1984, McVey 2011). In contrast, reservoirs and basin wetlands consistently held water towards the end of the breeding season when broods congregated to forage. Semi-permanent wetlands also typically had more open water, which may have allowed birds to use observable SAV as an indication that a given wetland may provide food for their ducklings and find refuge in large water bodies away from edges and dense cover (Fredrickson 1988, Behney et al. 2018). Birds may therefore be cueing in on water availability in addition to

invertebrate availability, conspecific habitat use (Poysa et al. 1998), or unmeasured cover characteristics, which may all vary over the course of the breeding season. Some of these wetland traits may have been interacting with birds' energetic demands early in the breeding season to result in the variable relationships observed between waterfowl abundance and energy density across sampling occasions. Birds likely needed more protein soon after arriving on the breeding grounds, and may have found that protein in early-thawing semi-permanent wetlands (Murkin and Kadlec 1986, Tidwell et al. 2013, Schepker et al. 2019). After initiating nests, however, birds may have prioritized foraging in wetlands closer to their nest sites, wetlands with more cover for subsequently rearing broods, or relied on body reserves more so than taking frequent foraging trips. The different foraging preferences exhibited by nesting hens over the course of laying and nest initiation are primed for further research and may elucidate mechanisms driving reproductive success.

As weather and precipitation patterns become more variable and water becomes increasingly limiting, having an understanding about which habitats provide food for wetland-dependent species will become ever more important (Skagen et al. 2016, Zhao et al. 2019). The results of our study suggest that providing consistent resources promotes wetland use by breeding waterfowl, and that these resources may be especially important during the very early breeding season, when pre-nesting birds are courting and preparing to nest, and the late breeding season, when broods are faced with a high protein demand and low water availability. The patterns of observed energy density within basin wetlands and reservoirs suggest that having the infrastructure to move water between habitat types, and to prioritize these types of wetlands during dry years, may prove essential to maintaining stable breeding populations of waterfowl across the semiarid West (Downard and Endter-Wada 2013, Sueltenfuss et al. 2013, Downard et

al. 2014). Still, periodic drying of wetlands within this system maintains long-term productivity and emphasizes the importance of diverse wetland types and hydrologies (Fredrickson 1991). Breeding waterfowl take advantage of ephemeral resources across their annual cycle and they appear to be adept at tracking those ephemeral resources. Still, ensuring that wetlands exist that provide the most diverse, stable resource possible during each component piece of that cycle may limit the energy they must expend tracking resources and benefit all wetland-dependent species.

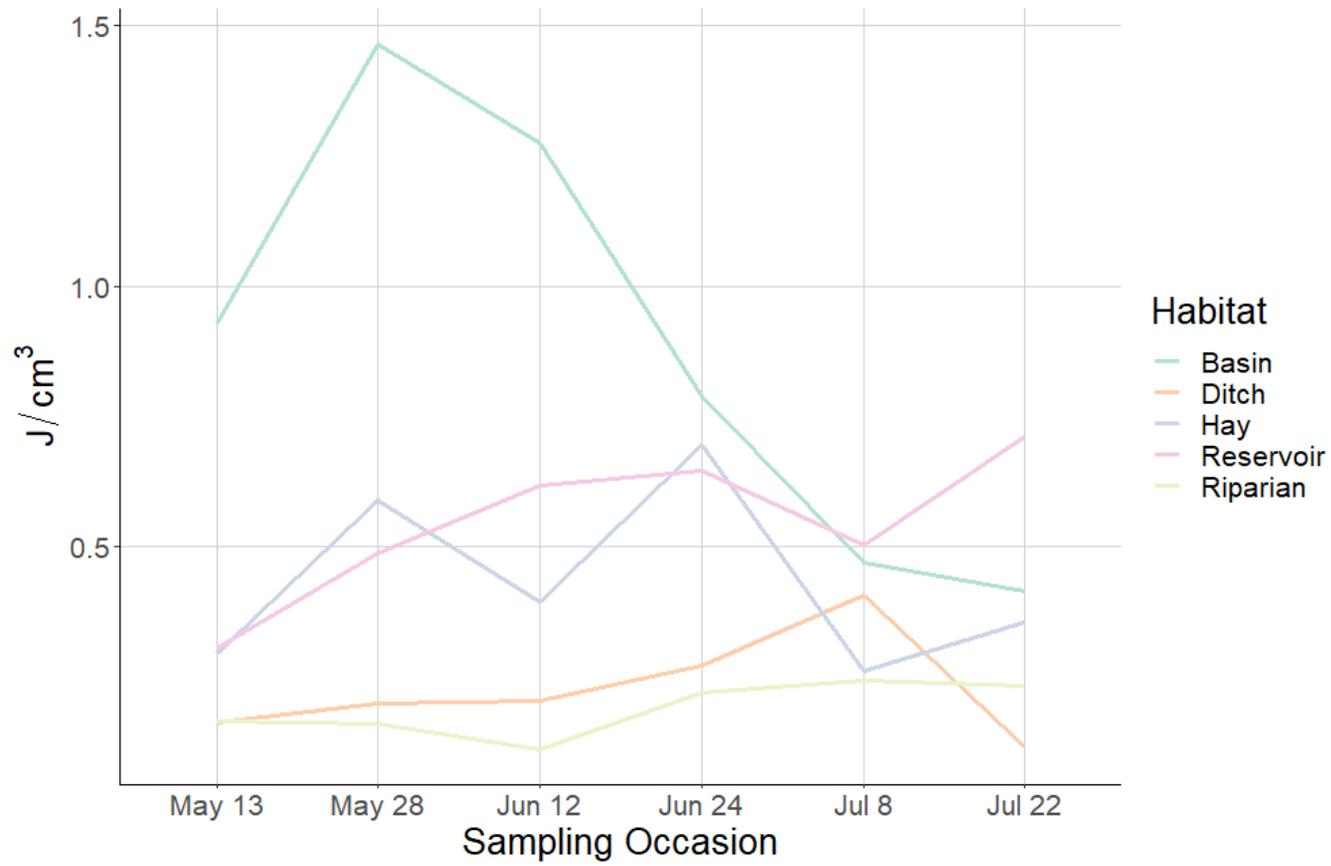
**Table 2.1:** Macroinvertebrate families observed in wetland samples taken from 2020-2021 in North Park, Colorado that were considered important food items for breeding waterfowl.

<b>Order</b>	<b>Family</b>	<b>Common Name</b>	<b>Mean Mass (g)</b>	<b>Mass Citation</b>	<b>kcal/g (Nudds and Bowlby 1984)</b>	<b>Important Waterfowl Food?</b>	<b>Food Citation</b>
Amphipoda	Gammaridae	Scuds	0.0105	Driver et al. 1974	2.32	Yes	Eldridge 1990
Anostraca	Chirocephalidae	Fairy Shrimp	0.00037	Hildrew 1985	5	Yes	Eldridge 1990
Calanoida	Diaptomidae	Copepods	3.30E-12	Stead et al. 2003		Yes	de Szalay and Resh 1997
Cladocera	Daphniidae	Water Fleas	0.00493	Dumont and Dumont 1975	4.8	Yes	Eldridge 1990

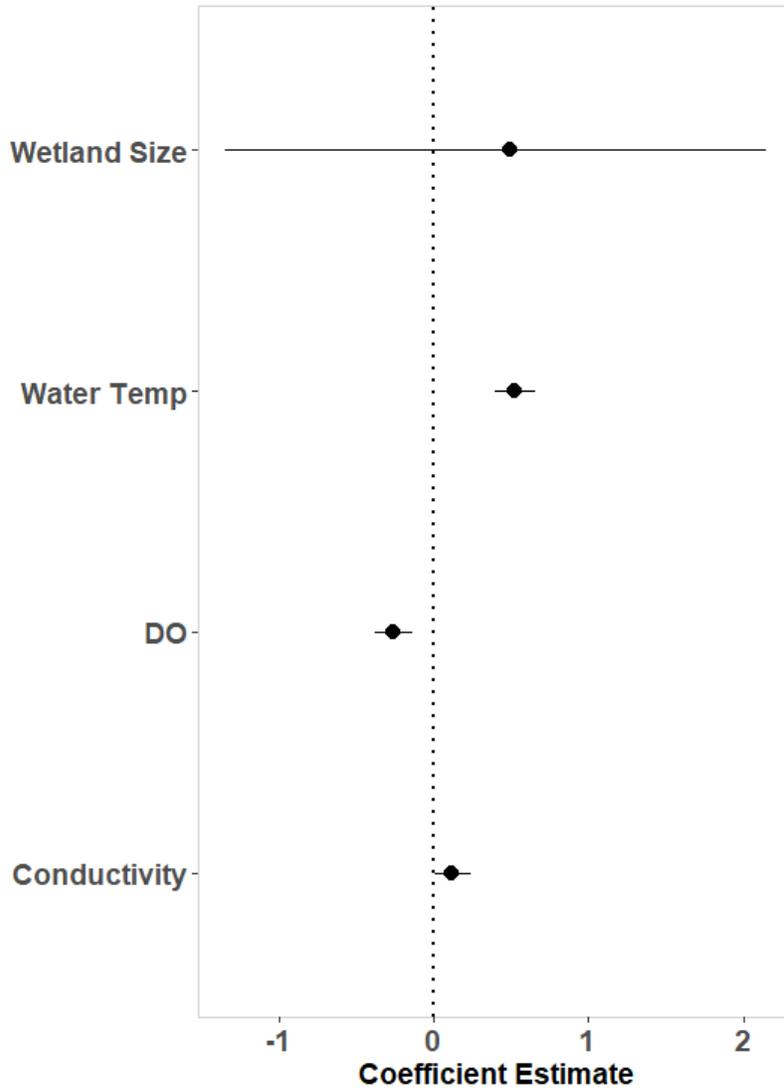
Coleoptera	Dytiscidae	Predaceous Diving Beetles	0.013167	Driver et al. 1974	5.3	Yes	de Szalay et al. 2003
Coleoptera	Hydrophilidae	Water Scavenger Beetles	0.013167	Driver et al. 1974	5.6	Yes	de Szalay et al. 2003
Diptera	Ceratopogonidae	Biting Midges	0.0045	Driver et al. 1974	5.2	Yes	Eldridge 1990
Diptera	Chironomidae	Non-Biting Midges	0.0045	Driver et al. 1974	5.5	Yes	Eldridge 1990
Diptera	Culicidae	Mosquitoes	0.0058	Driver et al. 1974	5.2	Yes	Eldridge 1990
Diptera	Simuliidae	Black Flies	0.0045	Driver et al. 1974	5.2	Yes	Eldridge 1990
Gastropoda	Ancylidae	Limpets	0.0367	Driver et al. 1974	1	Yes	Eldridge 1990
Gastropoda	Lymnaeidae	Pond Snails	0.0367	Driver et al. 1974	1	Yes	Eldridge 1990

Gastropoda	Physidae	Pouch Snails	0.0367	Driver et al. 1974	1	Yes	Eldridge 1990
Gastropoda	Planorbidae	Orb Snails	0.0367	Driver et al. 1974	1	Yes	Eldridge 1990
Hemiptera	Corixidae	Water Boatmen	0.0033	Driver et al. 1974	5.5	Yes	de Szalay and Resh 1997
Ostracoda	Ostracoda	Seed Shrimp	0.000282	Stead et al. 2003	5	Yes	Eldridge 1990
Plecoptera	Chloroperlidae	Green Stoneflies	0.034833	Allan 1982	5.5	Yes	McCutchen and Ydenberg 2005
Plecoptera	Perlodidae	Stripetail Stoneflies	0.034833	Allan 1982	5.5	Yes	McCutchen and Ydenberg 2005
Plecoptera	Plecoptera	Unknown Stoneflies	0.034833	Allan 1982	5.5	Yes	McCutchen and Ydenberg 2005
Trichoptera	Brachycentridae	Humpless Casemaker Caddisflies	0.011618	Driver et al. 1974	5.4	Yes	Eldridge 1990

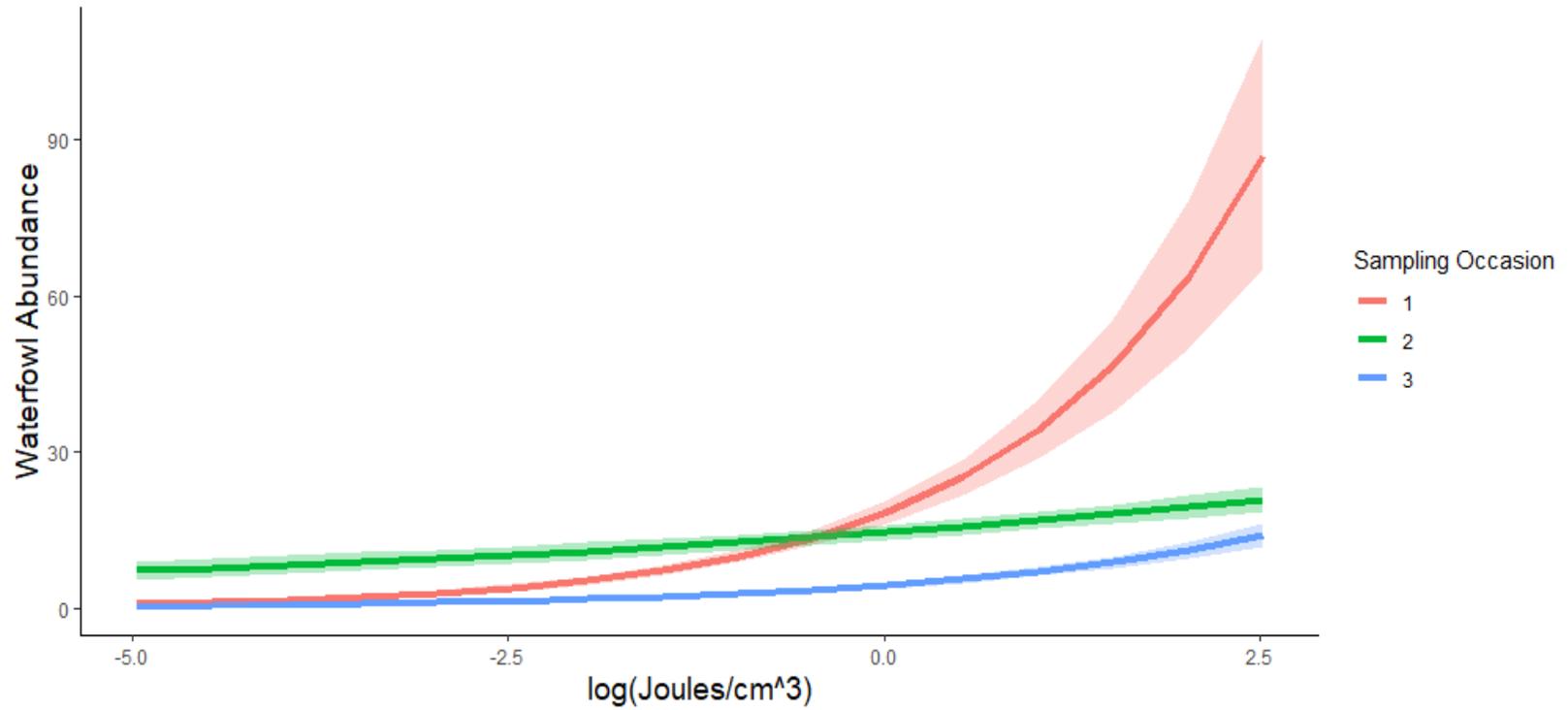
Trichoptera	Lepidostomatidae	Scaly-Mouth Caddisflies	0.011618	Driver et al. 1974	5.4	Yes	Eldridge 1990
Trichoptera	Leptoceridae	Long-Horned Caddisflies	0.011618	Driver et al. 1974	5.4	Yes	Eldridge 1990
Trichoptera	Limnephilidae	Northern Caddisflies	0.011618	Driver et al. 1974	5.4	Yes	Eldridge 1990
Trichoptera	Odontoceridae	Mortarjoint Casemaker Caddisflies	0.011618	Driver et al. 1974	5.4	Yes	Eldridge 1990
Trichoptera	Phryganeidae	Giant Casemaker Caddisflies	0.011618	Driver et al. 1974	5.4	Yes	Eldridge 1990
Trichoptera	Polycentropodidae	Tube-Making Caddisflies	0.011618	Driver et al. 1974	5.4	Yes	Eldridge 1990
Trichoptera	Trichoptera	Unknown Caddisflies	0.011618	Driver et al. 1974	5.4	Yes	Eldridge 1990
Trombidiformes	Hydrachnidia	Water Mites	0.0148	Driver et al. 1974	5.6	Yes	Bartonek and Murdy 1970



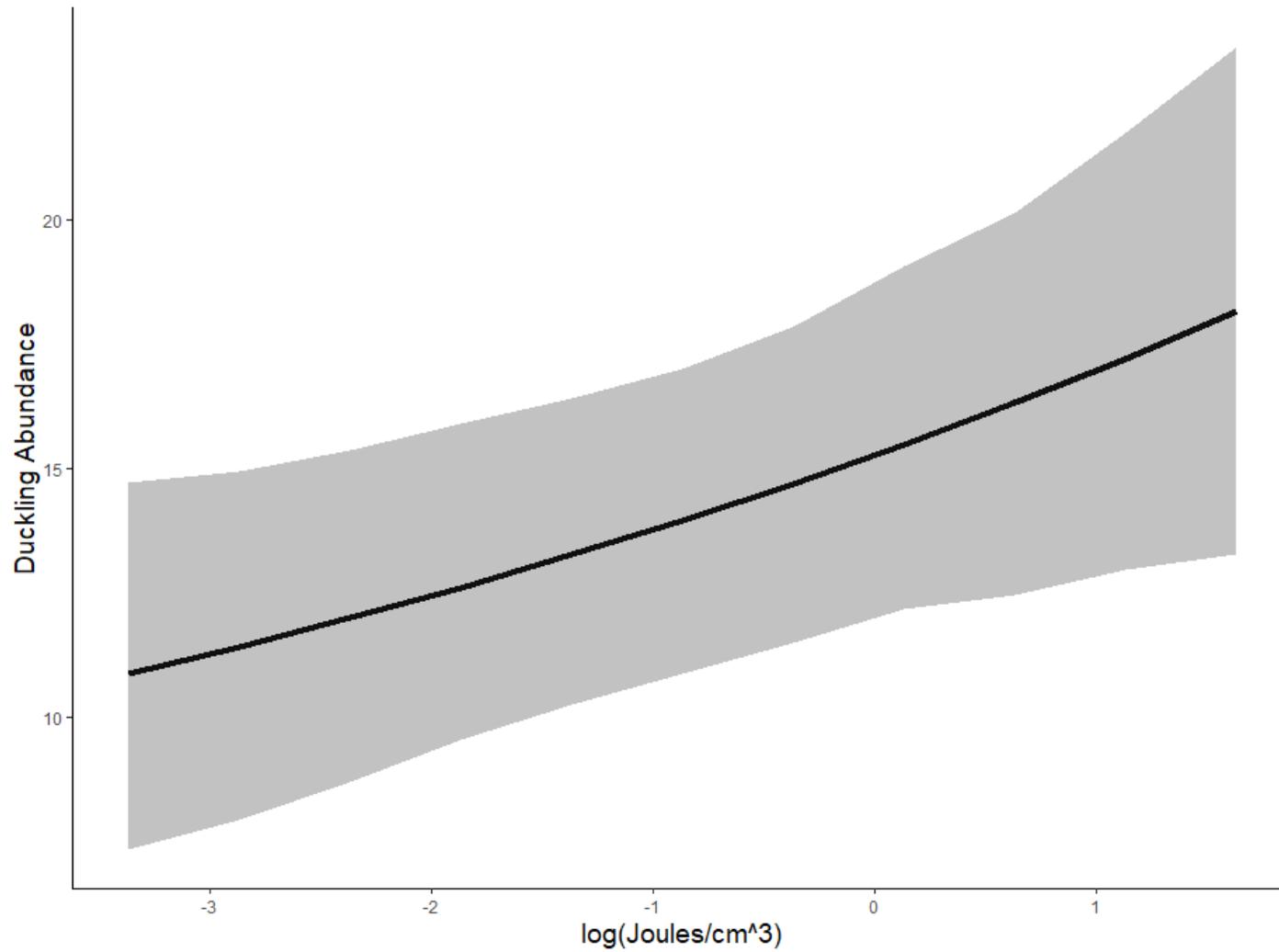
**Figure 2.1:** Model-predicted estimates of energy density ( $J/cm^3$ ) across wetland habitats throughout the breeding season (May-July) in North Park, CO, 2020-2021.



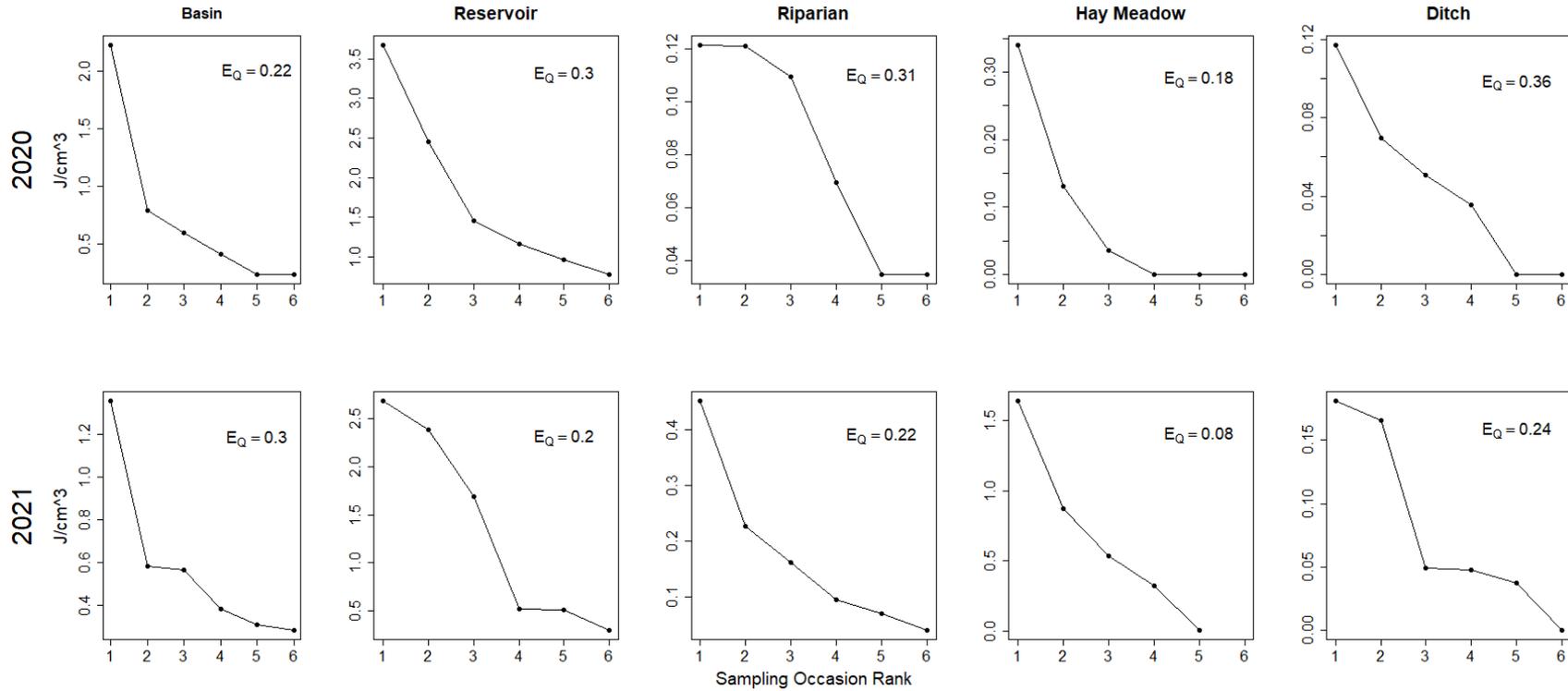
**Figure 2.2:** Coefficient estimates and 95% highest posterior density intervals for wetland covariates included in a lognormal hurdle model to evaluate energy density ( $J/cm^3$ ) differences across wetland types and time in North Park, CO from 2020-2021.



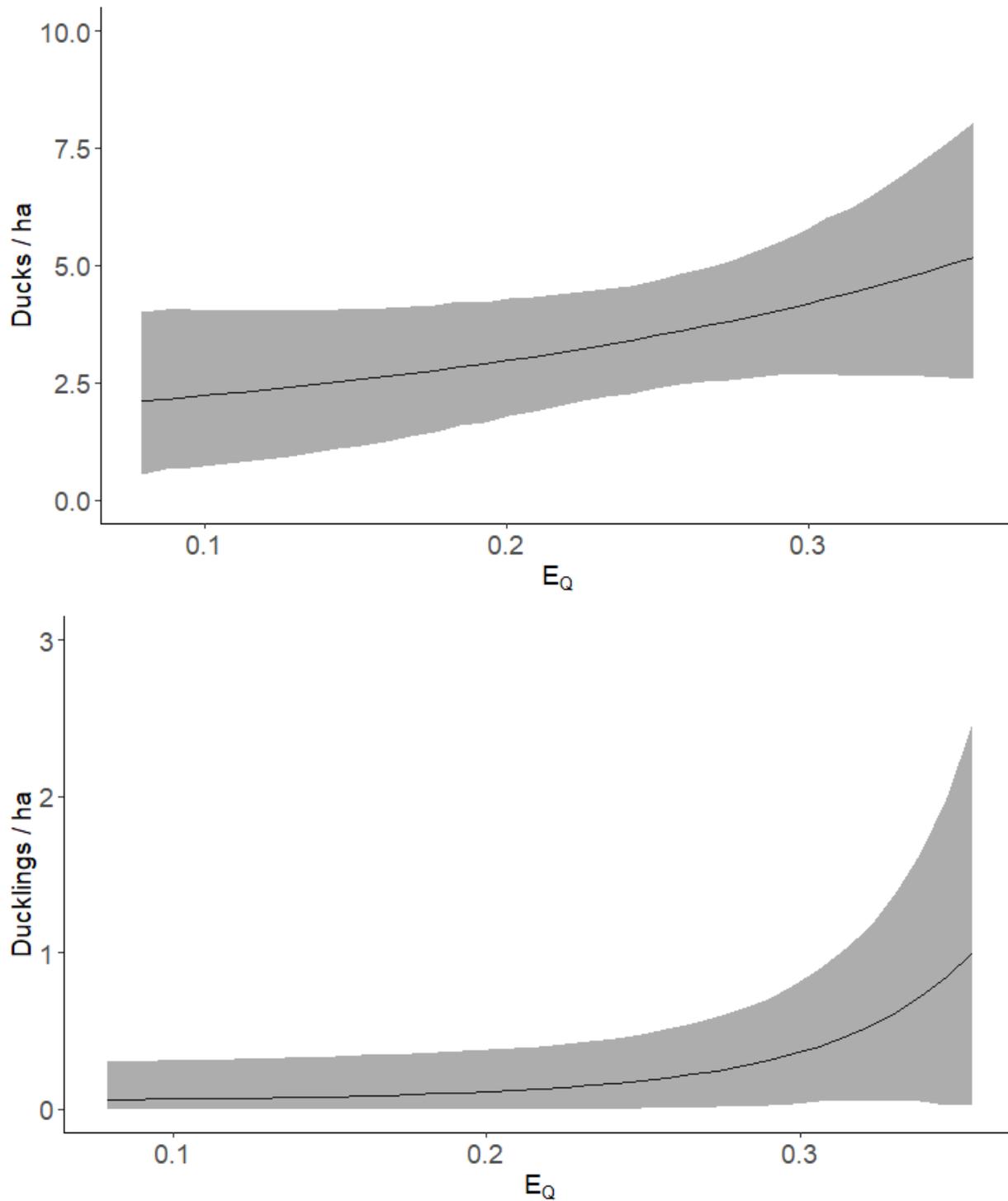
**Figure 2.3:** Relationship between waterfowl abundance and the log of energy density ( $\log(\text{J}/\text{cm}^3)$ ) across wetlands in North Park, CO from 2020-2021.



**Figure 2.4:** Relationship between duckling abundance and the log of energy density ( $\log(\text{J}/\text{cm}^3)$ ) across wetlands in North Park, CO from 2020-2021.



**Figure 2.5:** Temporal rank abundance curves created by ranking the energy density ( $J/cm^3$ ) of a given wetland type across six sampling occasions in 2020 and 2021.  $E_Q$  was calculated using the Codyn package in Program R and provides a metric of the evenness of a resource as measured by the slope of a rank abundance curve.



**Figure 2.6:** Relationship between duck (top panel) or duckling (bottom panel) density and the temporal evenness of macroinvertebrate resources in North Park, CO from 2020-2021, as measured by  $E_Q$ .

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## CHAPTER 3 – CAN WATERFOWL BUFFER THE DEMOGRAPHIC HANDICAP INDUCED BY GPS TAGS? A CAUTIONARY TALE FOR APPLIED INFERENCE ACROSS LIFE HISTORIES

### INTRODUCTION

Bio-logging devices such as global positioning system (GPS) tags have become ubiquitous in ecological studies of animal behaviour, movement, and demography, and have largely replaced very high frequency (VHF) radio tags across many taxa. Various models of GPS tags can send location, acceleration, and other data points remotely through satellites or mobile phone networks, thus greatly reducing personnel time and effort that would have traditionally been spent tracking and triangulating telemetered individuals (Kays et al. 2015, Wilmers et al. 2015). They can also provide data at much finer spatial and temporal resolutions than VHF radio tags. When deploying GPS tags (hereafter tags) for the purpose of estimating demographic parameters, researchers aim to uphold a key assumption of any mark-recapture study that markers do not affect the demographic parameters of interest. When this assumption is violated, marked animals are not representative of the larger unmarked population, resulting in biased estimates of focal parameters and in some cases affecting the inference that can be made from tagged individuals (Lindberg and Rexstad 2002). While empirical tests have been conducted on the effect of tag weight on survival, reproduction, and activity of some birds (Naef-Daenzer et al. 2001, Gomez et al. 2013, Lislevand and Hahn 2013, Scandolara et al. 2014), data have been lacking on many groups of birds, especially pertaining to the magnitude of tag effects. Unlike collars used for mammals, GPS tags are typically attached to the backs of birds via harnesses of varying materials and attachment styles (McDuie et al. 2019), around the individual's legs resting on their rump (Thaxter et al. 2014), or occasionally as neck collars on larger-bodied birds

like geese and swans (Kolzsch et al. 2016). As technology advances, tag impacts on the biology of any species of interest must continue to be evaluated and transparently reported. Additionally, researchers should continue to test the assumption that markers do not impact an animal's ability to survive so that demographic information attained from tagging studies can continue to effectively guide conservation actions.

Multiple studies over the past several decades have evaluated the effects tags can have on the birds they adorn. While results have been mixed based on the length of time birds are monitored and the specific behaviours or vital rates of interest, researchers have observed negative impacts on everything from migration return rates (Lameris et al. 2018; odds ratio of returning compared to control group = 0.32) to body mass among harvested gamebirds associated with tag attachment (Fleskes 2003; tagged birds weighed 133 g less than unmarked females, SE=25 g). Bodey et al. (2018) provide a comprehensive review of the effects of bio-logging devices on birds in which they found standardized effect sizes of harness and tail-mount tags on survival ranging from -0.08 to -0.2, and of collar-style tags on reproduction of -0.23 across taxa. Geen et al. (2019) found that the reporting of tag effects on birds declined over time and increased with device mass, indicating that with increased ubiquity of devices comes the possible acceptance of devices by the ecological community despite possible biases that may remain unreported (Lameris and Kleyheeg 2017). In terms of effects on survival and mortality, no studies to date have directly compared species' abilities to cope with tag effects across life-history strategies, but there is some evidence that larger species with slower life-history strategies might not experience the same magnitude of tag effects as faster-lived counterparts. For example, Constantini and Moller (2013) and Brlik et al. (2020) both found stronger negative effects of geolocators on smaller bird species and those with shorter migration distances (i.e.,

fast-lived), with survival effect sizes (Hedges'  $g$ ) ranging from -0.2 to -0.1. In contrast, slow-lived Manx shearwaters (*Puffinus puffinus*) attached with GPS tags considerably altered their foraging behaviour during the breeding season to maintain the same level of breeding success as their unmarked counterparts (Gillies et al. 2020). The arena of avian bio-logging is thus perfectly primed for an evaluation of tag effect size across the life-history spectrum.

Among birds, waterfowl are a particularly apt taxon for comparing tag effects across a range of life-history strategies. Their population dynamics are well-studied, thousands of individuals are outfitted with leg bands (A.K.A. rings) each year, and the sample of recovered birds with GPS tags has reached a level that allows for the assessment of device impacts on survival using traditional band-recovery methods (A.K.A., tag-recovery and ring-recovery). Though waterfowl are relatively large-bodied birds that one might *a priori* believe to be resistant to tag effects, Lameris and Kleyheeg (2017) observed major negative impacts in 17% of waterfowl studies (and 40% of studies reporting potential effects) where tag effects were reported and called for greater reporting of effects among researchers. Additionally, waterfowl cover the entire spectrum of life-history strategies, from short-lived cinnamon teal (*Spatula cyanoptera*) that attempt to reproduce during the first breeding season following hatch, to black brant (*Branta bernicla nigricans*) that have high adult survival, delayed age at first reproduction, and skip reproduction attempts thereafter if conditions are unfavorable (Koons et al. 2014). We can therefore test whether effect sizes of GPS tags on mortality vary across life-history strategies and how these effects scale up to affect a currency of evolutionary fitness.

Though any effects of tags should be of concern, species should not be expected to exhibit uniform responses (i.e., effect sizes) to wearing GPS tags because they vary widely in their life-history strategies. Fitness of long-lived species with slow life histories is highly

sensitive to proportional changes in adult survival, whereas fast-lived species are typically more sensitive to proportional changes in reproductive rates (Heppell et al. 2000, Sæther & Bakke 2000). The demographic buffering hypothesis predicts that species should possess traits that allow them to buffer the vital rates having the greatest impact on fitness against environmental change (Figure 1; Gillespie 1977, Pfister 1998, Gaillard et al. 2000). If they did not, such changes would have the most deleterious impacts on fitness in time-varying environments. Outfitting an individual with a tag presents a potential alteration of their environment, and therefore we might predict less considerable effects of tags on adult survival in species with slow life histories because they should plastically adjust activities to maintain their chances of surviving (e.g., skipped breeding, higher vigilance rates, etc.; Behney et al. 2019). We might also expect greater effects of GPS tags on adult survival and mortality in fast-lived species because of their greater investment in reproduction at the cost of allowing survival to be more greatly affected by environmental factors (i.e., handicaps imposed by tags; see Figure 1). If tag effect sizes are similar across the life-history spectrum, we might conclude that, barring statistical noise, effects on species with slow life histories are so great that the handicap of wearing GPS tags overrides their evolved life history strategy of investment in longevity (Figure 1). Such effects would be of concern in studies using GPS-marked individuals to inform demography and population dynamics. Changes in annual survival and mortality attributed to GPS tags might also act as an indicator of sublethal marker effects on traits associated with survival, which would warrant further investigation into plausible effects until technological advances eliminate them altogether.

Using waterfowl band-recovery data, we compared annual survival and mortality between North American waterfowl fitted with GPS tags to those affixed with only a United

States Geological Survey (USGS) metal leg band, predicting that GPS tags would 1) negatively impact annual survival (and positively impact annual mortality) across waterfowl species, and 2) the severity of adverse effects of tagging would depend on life-history tempo and should be less pronounced in slower-lived compared to faster-lived species due to greater ability of demographic buffering in the former group (see Figure 1). However, 3) even if effect sizes are smaller among species with a slow life-history strategy, the effect on fitness could still be similar to those for fast-lived species because fitness is more greatly affected by changes in survival among long-lived species with slow life-history tempos. Our primary goals were to evaluate the impacts of GPS tags on annual survival and mortality across the spectrum of waterfowl life-history strategies, to motivate stakeholders to consider whether they provide appropriate inference for guiding conservation decisions associated with population dynamics, and to further encourage researchers to measure and account for their effects in future studies as technology advances.

## METHODS

### *Data Organization*

We downloaded banding release and recovery records from the GameBirds Database (Bird Banding Lab, USGS Patuxent Wildlife Research Center). We subset the data to species of ducks and geese that breed in North America marked with GPS tags from 1990-2021, which are also required to be marked with a metal leg band. We restricted data to birds released alive in the same 10-minute geographical block in which they were banded and birds banded in the United States or Canada. We also restricted our analysis to birds banded as after-hatch-year (AHY) females, given that 62.8% of our total transmitter sample was comprised of AHY females and

most studies deploying GPS tags affix them to this age-sex class. We next restricted band-only data to the geographic flyways and years during which GPS tags had been deployed for each species to ensure the geographic areas and time periods for which survival was evaluated were comparable between GPS-tagged and ‘band-only’ samples (years listed in Table 3.1). We removed any record in the band-only data for which the bander included an “Additional Information” code that indicated any other type of auxiliary marker was affixed to the bird. This included nasal discs, wing tags, plastic neck collars, and any type of VHF transmitter, including code 89 (Transmitter – Obsolete).

We identified birds with GPS tags either by subsetting records with the Additional Information code 80 (Satellite/Cell/GPS Transmitter) or by searching through comments made on records associated with other Additional Information codes (e.g., 19: Blood sample taken plus an additional auxiliary marker, 89: Transmitter – Obsolete, 85: Miscellaneous). In some cases, we searched the literature to locate studies and reports that could verify specific birds were fitted with GPS tags if comments were inconclusive in the original banding data. Given that GPS tags are an increasingly used technology, often by multiple investigators studying the same species simultaneously, we removed release data (and associated recoveries) from 2018-2022 contributed by investigators involved in ongoing studies who did not wish for their data to be included (see also the Data Statement).

Some species of waterfowl are more commonly fitted with GPS tags during the non-breeding or breeding seasons rather than during typical pre-hunting-season banding operations, so for such species we split the dataset by release date to fit a seasonal band-recovery survival model rather than excluding a large portion of the tagged sample. The number of seasons of release varied from one to three for each species depending on what the data could support. For

species with year-round releases, we considered birds banded from January-April as winter releases, May-July as summer releases, and August-September as part of the pre-hunting-season sample (hereafter: pre-season). Species with three seasons of release included greater white-fronted geese (GWFG; *Anser albifrons*), Canada geese (CANG; *Branta canadensis*), cinnamon teal (CITE), gadwall (GADW; *Mareca strepera*), mallard (MALL; *Anas platyrhynchos*), and lesser scaup (LESC; *Aythya affinis*). For species with band releases occurring during two distinct time periods, we assigned releases from May-September as summer releases and those occurring from January-April as winter. Species with two seasons of release included lesser snow geese (LSGO; *Anser caerulescens caerulescens*), greater snow geese (GSGO; *Anser caerulescens atlanticus*), American wigeon (AMWI; *Mareca americana*), American black ducks (ABDU; *Anas rubripes*), and northern pintail (NOPI; *Anas acuta*). For yet other species, including black brant (BLBR) and wood ducks (WODU; *Aix sponsa*), we restricted releases to those from May-September. We restricted the recoveries to consider only birds harvested during the North American hunting seasons, which included August-January for all species except snow geese, which included August-May to allow for recoveries from the spring light goose conservation order, which allows for harvest of snow geese past the end of the traditional waterfowl hunting season into the spring (Reed and Calvert 2007, Leafloor et al. 2012). We retained species in our analysis for which there were >3 hunter recoveries of individuals outfitted with GPS tags, which included the 13 species listed above. Though other species were frequently fitted with GPS tags, there were too few hunter recoveries (or none) of these individuals for the species to be included in our analyses. We compiled band-recovery data into m-arrays, which are compact versions of a capture history indicating how many individuals of a cohort marked in a given year are

recovered in the same or subsequent years in matrix form (Burnham et al. 1987, Kéry and Schaub 2011).

### *Estimation of GPS Tag Effects on Annual Survival and Mortality*

We did not use any location or other data collected by GPS tags specifically, only band releases and hunter recoveries of banded and tagged birds in order to facilitate comparable evaluations of survival and mortality between birds marked with only a band and those marked with both a band and a GPS tag. Using these data we fit a Bayesian band-recovery model to estimate annual survival of AHY females for each species with and without GPS tags (Brownie et al. 1985, Williams et al. 2002, Schaub and Kéry 2022). We included either one (pre-season banding operations), two (pre-season banding operations and winter banding operations), or three (pre-season, winter, and summer banding operation) seasons depending on the data to account for differences in exposure time to mortality events. We calculated annual survival as a derived multiplication of monthly survival, which we kept constant across seasons of release because of sample size restrictions (i.e., we did not estimate seasonal differences in survival and mortality; Hearn et al. 1998, Devers et al. 2021).

We fit a band-recovery model for each species separately, whereby mortality was modeled on the log-hazard scale and Seber recovery probabilities were modeled on the logit scale using  $\text{link}(A) = \boldsymbol{\beta}\mathbf{X} + \varepsilon_t$ . Here,  $A$  denotes either a mortality hazard or recovery probability,  $\boldsymbol{\beta}$  denotes a vector of estimated coefficients,  $\mathbf{X}$  denotes a matrix of linear predictors, and for some  $A$ ,  $\varepsilon_t$  denotes a random effect for temporal variation among years. For mortality hazards, we first evaluated effects of geographic area of release. This involved a determination of which geographic Flyways (as designated by the US Fish and Wildlife Service; Atlantic, Mississippi, Central, and Pacific) had both band-only and GPS tag releases for a given species,

and then we modeled differences in mortality hazards across pertinent Flyways using an intercept offset evaluated relative to a reference Flyway, which was set to the Flyway with the largest number of band releases for a given species. Analyses at smaller spatial scales were not possible because of limited sample size for several species. If the proportion of the posterior  $> 0$  or  $< 0$  (labeled  $f$ ) for each Flyway's intercept offset was  $< 0.15$  or  $> 0.85$ , we retained the geographic variation among those Flyways, whereas if  $f$  was between  $0.15$  and  $0.85$ , we removed the intercept offset for such Flyways and they were subsequently treated as equivalent to the reference Flyway (Buderman et al. 2023). Therefore, each model could include variation in mortality by all Flyways, some Flyways, or no geographic variation. Once we had determined the level of geographic variation supported by the data for each species, we repeated these steps to evaluate linear time trends on mortality hazards of GPS-tagged birds (i.e., using a standardized year covariate in the  $X$  matrix). Using the same thresholds described above for  $f$ , we evaluated estimated posterior distributions to determine whether the data supported each linear time trend. This allowed us to evaluate whether the effects of GPS tags on mortality may have changed over time. To account for temporal variation in mortality for band-only birds associated with robust sample sizes, we always included a random time effect  $\varepsilon_t$  that followed a normal distribution with mean 0 and standard deviation  $\sigma_t$ . These models for temporal variation allowed us to account for important process-based heterogeneity in the data and assess possible convergence between mortality of band-only and GPS-tagged birds over time, presumably in response to improvements in GPS tag technology or styles of attachment (which could not be explicitly examined because attachment style was not always reported for each tagged individual). For Seber recovery rates, we included an intercept and an offset for direct recoveries (i.e., birds recovered during the hunting season immediately following release) specific to each season of

release supported for a given species, where indirect recoveries were the reference level. Additionally, we included an offset for GPS tagged individuals to compare recovery rates among the two groups.

We specified normal priors for all tag-related coefficients on the logit scale for Seber recovery probabilities (Northrup and Gerber 2018) and the log-hazard scale for mortality (D. Gibson, personal communication) that yielded vague priors on the real parameter scale. We sampled posterior distributions of each parameter using a Markov chain Monte Carlo algorithm (MCMC; Gelfand and Smith 1990) in JAGS 4.3.0 (Plummer 2012), using the jagsUI package in Program R (Kellner 2016). We present the final structure of each species-specific model supported by the data and the derived annual survival probabilities at the level of variation supported (Figures 2 & 3). We sampled the posterior distributions of the parameters using three chains that each included 50,000 MCMC iterations with a burn-in of 25,000 and thinned each chain to keep every 25<sup>th</sup> value. We examined Gelman and Rubin (1992) statistics for all parameters to ensure  $\hat{R} \leq 1.1$  and visually inspected trace plots to check for convergence (Hooten and Hobbs 2015). We report means of posterior distributions and 90% Bayesian credible intervals where appropriate, in addition to the metric that indicates the proportion of the posterior on the same side of 0 as the mean (labeled  $f$ ).

#### *Life-History Patterns in GPS Tag Effects on Annual Mortality*

To investigate patterns in the effect size of tags on adult female mortality across waterfowl life histories, we conducted a two-stage analysis. Specifically, we used Bayesian posterior distribution results for effect sizes from the band-recovery analysis (level 1), and then examined their relationship with the pace of species' life histories (fast to slow; level 2). We quantified effect sizes for each species using the hazard ratio, which indicates the risk of death

for individuals wearing GPS tags compared to those wearing only metal bands and used these as the response variable in the second stage of the two-stage analysis. Unlike issues of scale that can complicate comparisons of probabilities that are bounded between 0 and 1, hazards ( $h_j = -\log(S_j)$ ) alleviate these issues by transformation to a much broader scale (0 to  $\infty$ ; Ergon et al. 2018). In order to consolidate results for each species, we used hazard rates calculated from a log-linear model that accounted for random time effects or linear time trends to compute the hazard ratios used in this second stage of the analysis (i.e., prediction based on an intercept or an intercept and a GPS tag effect). For species supporting geographic variation in hazard rates, we computed hazard ratios using the hazard rate estimates from the Flyway producing estimates with the highest precision.

We quantified the pace of each species' life history using species-specific elasticities of population growth rate to changes in adult female survival, for which high elasticities are associated with slow life histories of long-lived species, and lower elasticities are associated with fast life histories of short-lived species (Sæther and Bakke 2000). To compute the elasticities, we created a simple matrix population model for each species, including the number of age classes appropriate for each species based on published literature and the annual survival estimates from stage one of our analysis for individuals wearing only metal bands. Rather than using published estimates of fecundity from studies conducted at small geographic scales, we scaled fecundity in each species' projection matrix such that the dominant eigenvalue ( $\lambda$ ) = 1 using numerical optimization in the R software (R Core Team 2019), which standardizes comparisons of elasticity across life-history strategies (see Stott et al. 2011, Koons et al. 2021). To ensure fecundities varied appropriately among age classes for a given species, we used published estimates of age-specific fecundity to calculate the proportional change in fecundity from one

age class to the next (i.e., we applied appropriate multipliers to our optimized constant to calculate fecundity for each age class while maintaining  $\lambda = 1$ ). Using mallards as an example to illustrate the process, we created a 2x2 matrix with fecundities on the top row and our estimated adult survival probability for band-only birds, averaged across study years, on the second row. Using the fecundity values of mallards presented in Hoekman et al. (2002) of 0.204 for second-year birds and 0.259 for after-second-year birds, we calculated a fecundity age “multiplier” of  $0.259/0.204=1.27$ . We therefore temporarily filled the top row of our projection matrix with  $F_1 = 1.00$  and  $F_1*1.27$ . We then used an optimization function in R to calculate the fecundity of second-year birds ( $F_1$ ) yielding  $\lambda = 1$ . Once the optimization procedure was complete for each matrix projection model, we calculated the elasticity of  $\lambda$  to each element of the matrix, summing the elasticities for the elements representing adult survival to attain the total elasticity of  $\lambda$  to adult survival. We repeated this process for every MCMC iteration of the posterior distribution for annual survival to derive posterior distributions for the elasticities, which allowed us to properly propagate uncertainty for the derived parameters (Zimmerman et al. 2010).

We fit the following log-linear model in a Bayesian framework to evaluate the relationship between each species’ (subscript  $i$ ) adult survival elasticity and the hazard ratio quantifying the risk of death for individuals wearing GPS tags compared to those wearing only metal bands:

(1)

$$\log(h'_i) \sim \text{normal}(\mu_{h,i}, \sigma_{h,i})$$

$$\mu_{h,i} = \gamma_0 + \gamma_1 e'_i + \varepsilon$$

$$e'_i \sim \text{normal}(\mu_{e,i}, \sigma_{e,i})$$

$$\gamma_0 \sim \text{normal}(0, 1000)$$

$$\gamma_1 \sim \text{normal}(0, 1000)$$

$$\varepsilon \sim \text{normal}(0, \sigma_\varepsilon^2)$$

$$\sigma_\varepsilon \sim \text{uniform}(0, 32)$$

where  $h'_i$  are posterior draws from the species-specific hazard ratio (i.e., strictly positive values),  $e'_i$  are posterior draws from the species-specific adult survival elasticity, the  $\mu$  and  $\sigma$  are the respective means and standard deviations of the estimated parameters, the specified priors on  $\gamma_0$  and  $\gamma_1$  indicate the mean and the variance, and  $\varepsilon$  is the residual variance, for which we used a uniform prior ( $\sigma_\varepsilon$ ). The model therefore propagates uncertainty from stage one of the analysis through stage two (Behney 2020, Buderman et al. 2023).

### *Life-History Patterns in Effects of GPS Tags on Fitness*

Heppell (1998) was one of the first to demonstrate how to calculate the effect on asymptotic population growth rate of a specified percentage change in a vital rate, which is tempered by the elasticity associated with the vital rate being changed or affected:

$$(2) \quad \text{Proportional change in } \lambda \approx \text{Proportional change in survival} \times \text{Elasticity}$$

We used this equation to further evaluate the projected effect of a proportional change in survival resulting from GPS tags on population growth rate, using it as a currency of fitness for a particular phenotype or ecotype (band-only or alteration by GPS tag) (Caswell 1980). Because of differences in the elasticity of population growth rate to changes in adult survival across life histories, equivalent impacts of GPS tags on adult mortality and survival are not expected to

yield equivalent impacts on fitness (see Eq. 2 above). Using the effect size on the projected currency of fitness as another response variable (i.e., the proportional change in  $\lambda$  [Eq. 2]) in this second stage of the analysis, we fit a hierarchical model with the same structure described in Eq. 1 (i.e., elasticity as a predictor) to evaluate patterns in the effect size across waterfowl life histories. We again used effect sizes averaged across years to assess these patterns.

## RESULTS

### *GPS Tag Effects on Annual Survival and Mortality*

We used records from 658652 total banded waterfowl and 61090 total encounters (hunter recoveries). Of these, 2182 bandings and 236 encounters were from individuals marked with both GPS tags and leg bands, and the remaining individuals were marked with leg bands only. Across species, the number of GPS tagged birds that were recovered ranged from five to 83, compared with a range of 42 - 30914 birds fitted only with metal bands (Table 3.1). Tags reduced annual survival (and increased mortality) of AHY females for all species at some point over the species-specific duration of use, but almost all (11 out of 13) linear time trends on GPS tag survival were positive, indicating an increase in survival of birds with GPS tags since their initial use (Table 3.1, Figures 2 & 3). Hazard ratios computed using the time-averaged hazard rates for both band-only and GPS tagged birds ranged from 0.92 for gadwall (indicating higher survival of GPS tagged birds at time-averaged values) to 4.38 for greater snow geese but were also quite high for lesser snow geese (3.23), American black ducks (3.12), and American wigeon (2.35). In addition to gadwall, hazard ratios were lowest for greater white-fronted geese (1.51) and black brant (1.76; Table 3.1). Interestingly, time trends for hazard rates of GPS-tagged birds were positive (i.e., increased mortality) for Canada geese (mean = 0.98, SD = 0.58,  $f = 0.70$ ) and

lesser snow geese (mean = 0.23, SD = 0.58,  $f = 0.67$ ) although imprecise, indicating tag effects may have worsened since the technology began being used. Estimates of band-only survival and recovery were comparable to other estimates found throughout the literature (Figure 2 and Table S1).

#### *Life-History Patterns in GPS Tag Effects on Annual Mortality*

Using the time-averaged estimates of GPS tag effects on annual survival and mortality, the inter-specific relationship between the elasticity of  $\lambda$  to adult female survival (which serves as an index of the pace of a life history) and hazard ratios exhibited a nearly flat relationship ( $\gamma_1 = 0.33$ ,  $\sigma_{\gamma_1} = 0.69$ ,  $f = 0.70$  Figure 4) despite precise results for the vast majority of species (Tables 3.1 & 3.2).

#### *Life-History Patterns in Projected Effects of GPS Tags on Fitness*

Proportional changes in  $\lambda$  resulting from equivalent proportional changes in adult survival (i.e., the elasticity) ranged from 0.39 for cinnamon teal to 0.93 for lesser snow geese (Table 3.2). When multiplying these elasticities by the estimated effect size of GPS tags on adult female survival, the projected net impact on  $\lambda$  ranged from -0.09 for gadwall (because annual survival of GPS tagged birds was higher than that of band-only birds at time-averaged values; Figure 2) to 0.39 for greater snow geese, and all effects were estimated precisely (Table 3.2). When examined across the pace of life histories for the 13 species, the effects of tags on  $\lambda$  for species with slow life-history strategies were notable, but similar to the effects on species with fast life-history strategies (Figure 5;  $\gamma_1 = 1.29$ ,  $\sigma_{\gamma_1} = 1.97$ ,  $f = 0.78$ )

## DISCUSSION

Our study provides insight into the magnitude of negative effects on annual survival (positive effects on annual mortality) for adult females wearing GPS tags across a spectrum of waterfowl species and life-history strategies. The evolved life-history and large body size of long-lived geese should make them more robust to the direct effect of GPS tags on adult survival probability, allowing them to somewhat buffer the effects of wearing tags. However, our results did not support this prediction and instead suggest that effects of GPS tags are consistent across life-history strategies, and that even small effects are important at the level of net fitness. This highlights an important reminder: it is essential to scale changes in vital rates up to the currency that natural selection operates on (i.e., net fitness), which is the same currency that is most important for guiding population-level conservation and management decisions (Baillie and Schaub 2009, Koons et al. 2016). While it is unrealistic to expect an entire population would be marked with GPS tags, the effects scaled up to  $\lambda$  emphasize the magnitude at which assumptions are violated when the marked sample experiences different demographic rates than the unmarked (or band-only) population (Lindberg and Rexstad 2002, Buderman et al. 2014, Cooch et al. 2021), and when comparing across species with different vital-rate elasticities.

There remains a tradeoff between the valuable information GPS tags can potentially provide (e.g., detailed individual movement, space use, and other behaviours) and the deleterious effects they can have on survival. We present estimates of tag effects averaged over the period of use specific to a given species to illustrate an intermediate effect rather than a best- or worst-case scenario. Optimistically, tag effects on mallard survival, which have been marked with tags more than any other species of waterfowl, have decreased drastically since their initial use (Figure 2), which likely represents improvements in GPS tag technology (i.e., smaller tags) and attachment

methods. However, Seber recovery rates ( $r$ ; Table S1; Seber 1972) were significantly higher among tagged birds than band-only birds, indicating that tags either make waterfowl more susceptible to harvest, or that hunters report these birds at a higher rate to the USGS Bird Banding Laboratory (i.e., a trophy effect; Arnold et al. 2020). The ability to visualize changes in the magnitude of GPS tag effect size over time is one benefit of incorporating temporal heterogeneity into evaluations of tag effects, and the time variation in band-only survival allows for a more realistic comparison of the two survival rates and whether they have converged over time. The incorporation of temporal variation also yields more precise time-averaged estimates of survival and mortality than if ignored. As sample sizes increase, it would eventually be beneficial to model more complex temporal variation for the sample with GPS tags (e.g., mixed models). The methods we used could easily be applied to non-game species that are recaptured or recovered as a simple way to evaluate tag effects across more taxa.

The mechanisms responsible for reductions in survival may be relatively similar across species, regardless of the magnitude of the effect size. Given that annual survival is an umbrella vital rate that represents the chance of surviving all possible causes of mortality and is intricately linked to other demographic parameters via life history trade-offs, it is worth considering how tags might affect other demographic parameters and traits associated with them (Ward and Flint 1995, Morris et al. 2008, Koons et al. 2014, Le Coeur et al. 2022). The sub-lethal effects of GPS tags may be difficult to account for, and information remains unavailable about the magnitude of these effects across a broad range of species (but see Barron et al. 2010). Behavioural changes have been noted in many species affixed with GPS tags, from increased preening and vigilance behaviours to impaired locomotion (Hupp et al. 2015, Gillies et al. 2020) and avoidance of conventional habitat preferences, which may reduce body condition due to limited food access

(Fleskes 2003, Kesler et al. 2014). Depending on the attachment style used, feather and skin abrasions may result from rubbing of the tag or the associated harness, potentially resulting in infection (Lameris and Kleyheeg 2017). Among game species, auxiliary markers may make birds more visible and more easily targeted by hunters (Sedinger et al. 2022) or predators (Severson et al. 2019), may impair birds by collecting ice on the device (Fox et al. 2014), or impaired body condition may induce them to more readily decoy and be harvested (Ackerman et al. 2006). Research into the specific mechanisms driving tag-related reductions in survival is warranted and may aid in mitigating specific impacts resulting from attachment style, tag design, or tag weight. In particular, further research into specific attachment methodology used on lesser snow geese and Canada geese should take priority, given signals that they may have experienced increasing tag effects over time (Figure 2).

This study synthesizes multiple species, geographic regions, life-history strategies, and band-recovery data to result in a cohesive message of caution to wildlife researchers and managers. Future studies focusing results on birds fitted with GPS tags should consider whether or not those birds are representative for objectives pertaining to demography and population dynamics, ensure they are transparent regarding any negative effects related to the tags (Constantini and Moller 2013, Bodey et al. 2018, Geen et al. 2019), and attain sample sizes that are robust enough to test for such effects (Lindberg and Walker 2007). Given that they are potentially such useful and widely-used tools, we do not expect the use of GPS tags to diminish in the coming years, but it is essential that future experimental design allows for the evaluations of impacts so they can be accounted for when interpreting results. Arranging study control groups for comparison with individuals fitted with tags will allow for the evaluation of effects, and being mindful that the

censoring of individuals should be random with respect to the outcome of interest will result in less biased estimates of tag effects on survival going forward (Sergio et al. 2019).

Replication of our study is warranted as additional harvests of tagged birds occur and as more GPS tags are deployed to verify the magnitude of marker effects across species as technology leads to less intrusive devices. While we indicated the primary attachment style for each species, we lacked the ability to investigate any relationships between attachment style and effect size because of limited reporting of such details. However, we were able to evaluate changes in the survival of birds fitted with GPS tags over time and most species experienced a decrease in tag effects (Figure 2). Some research has shown decreased impacts from implanted tags in dabbling ducks compared to other styles (Paquette et al. 1997, Arnold and Howerter 2012, Sheppard et al. 2017), although such tags still appear to cause a handicap in diving ducks, albeit lower in magnitude than other attachment styles (Latty et al. 2010). Future research into attachment styles and specific inquiry into possible effects of collar-based tags is warranted (LeTourneux et al. 2022), and new attachment styles might be considered as technology advances and device size decreases. Future studies might also benefit from assessing lagged tag effects in long-lived species to see whether tag effects are delayed and may result in premature senescence (Hupp et al. 2010). With respect to important vital rates such as survival and mortality, GPS tags are not yet entirely benign, despite apparent improvement since the inception of the technology. Efforts should therefore be made to mitigate, report, and interpret effects accordingly moving forward. Managers are therefore warranted in remaining cautious about using inference from GPS tag studies for informing conservation and management actions pertaining to population dynamics.

**Table 3.1:** Results from the Bayesian band recovery model for 13 species of waterfowl fitted with only a metal band or also with a GPS tag. Hazard ratios were calculated as the ratio of the hazard of dying for individuals wearing a GPS tag to the hazard for individuals wearing only a metal band. Species included lesser snow goose (LSGO), greater snow goose (GSGO), greater white-fronted goose (GWFG), black brant (BLBR), Canada goose (CANG), wood duck (WODU), cinnamon teal (CITE), gadwall (GADW), American wigeon (AMWI), mallard (MALL), American black duck (ABDU), northern pintail (NOPI), and lesser scaup (LESC). We used time-averaged hazard rates calculated from a log-linear model that accounted for random time effects or linear time trends to compute the hazard ratios and survival probabilities. All numbers are rounded to the second decimal place.

Species	S <sub>band</sub> (SD)	S <sub>tag</sub> (SD)	HR <sub>avg</sub> (SD)	Years	No. bands recovered (No. released)	No. tags recovered (No. released)
LSGO <sup>b</sup>	0.92 (0.01)	0.76 (0.09)	3.23 (1.36)	2012-2021	2338 (40948)	14 (122)
GSGO <sup>a</sup>	0.83 (0.05)	0.46 (0.09)	4.38 (1.39)	2006-2021	749 (4570)	24 (152)
GWFG <sup>b</sup>	0.77 (0.10)	0.71 (0.13)	1.51 (0.87)	2011-2021	1103 (9153)	12 (104)
BLBR <sup>a</sup>	0.88 (0.04)	0.81 (0.08)	1.76 (0.88)	2006-2021	292 (25288)	10 (111)
CANG <sup>b</sup>	0.77 (0.03)	0.54 (0.08)	2.34 (0.61)	2008-2021	30914 (293724)	28 (205)
WODU <sup>a</sup>	0.50 (0.03)	0.29 (0.21)	2.27 (1.37)	2006-2021	8281 (94916)	5 (33)
CITE <sup>a</sup>	0.39 (0.16)	0.18 (0.12)	2.08 (1.00)	2015-2021	58 (2065)	15 (119)
GADW <sup>a</sup>	0.47 (0.19)	0.56 (0.16)	0.92 (0.58)	2015-2021	42 (743)	13 (105)

AMWI <sup>a</sup>	0.56 (0.06)	0.30 (0.15)	2.35 (1.03)	2005-2021	112 (1516)	6 (75)
MALL <sup>a</sup>	0.53 (0.02)	0.31 (0.07)	1.89 (0.36)	2005-2021	15551 (156676)	83 (701)
ABDU <sup>a</sup>	0.62 (0.03)	0.27 (0.16)	3.12 (1.42)	2005-2021	1423 (22457)	6 (140)
NOPI <sup>a</sup>	0.50 (0.11)	0.28 (0.13)	2.11 (0.91)	2015-2021	82 (5556)	23 (218)
LESC <sup>c</sup>	0.58 (0.12)	0.37 (0.16)	2.02 (0.76)	2005-2021	145 (1040)	10 (97)

HR = Hazard ratio

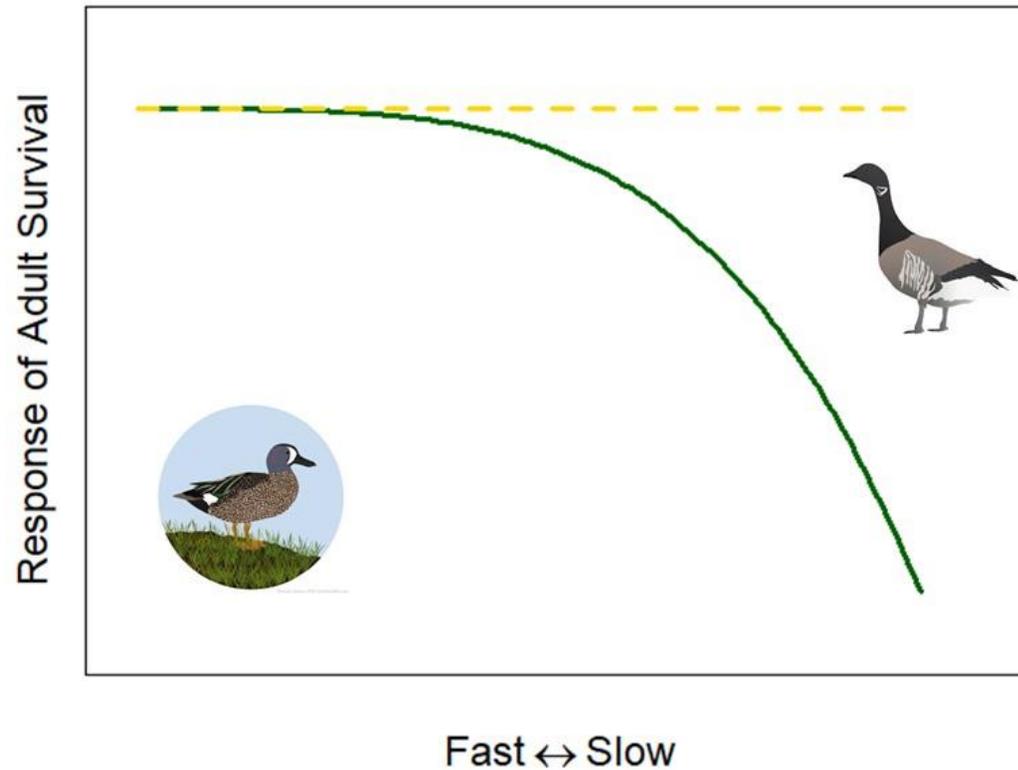
<sup>a</sup> - backpack attachment style comprised majority of sample

<sup>b</sup> - neck collar attachment style comprised majority of sample

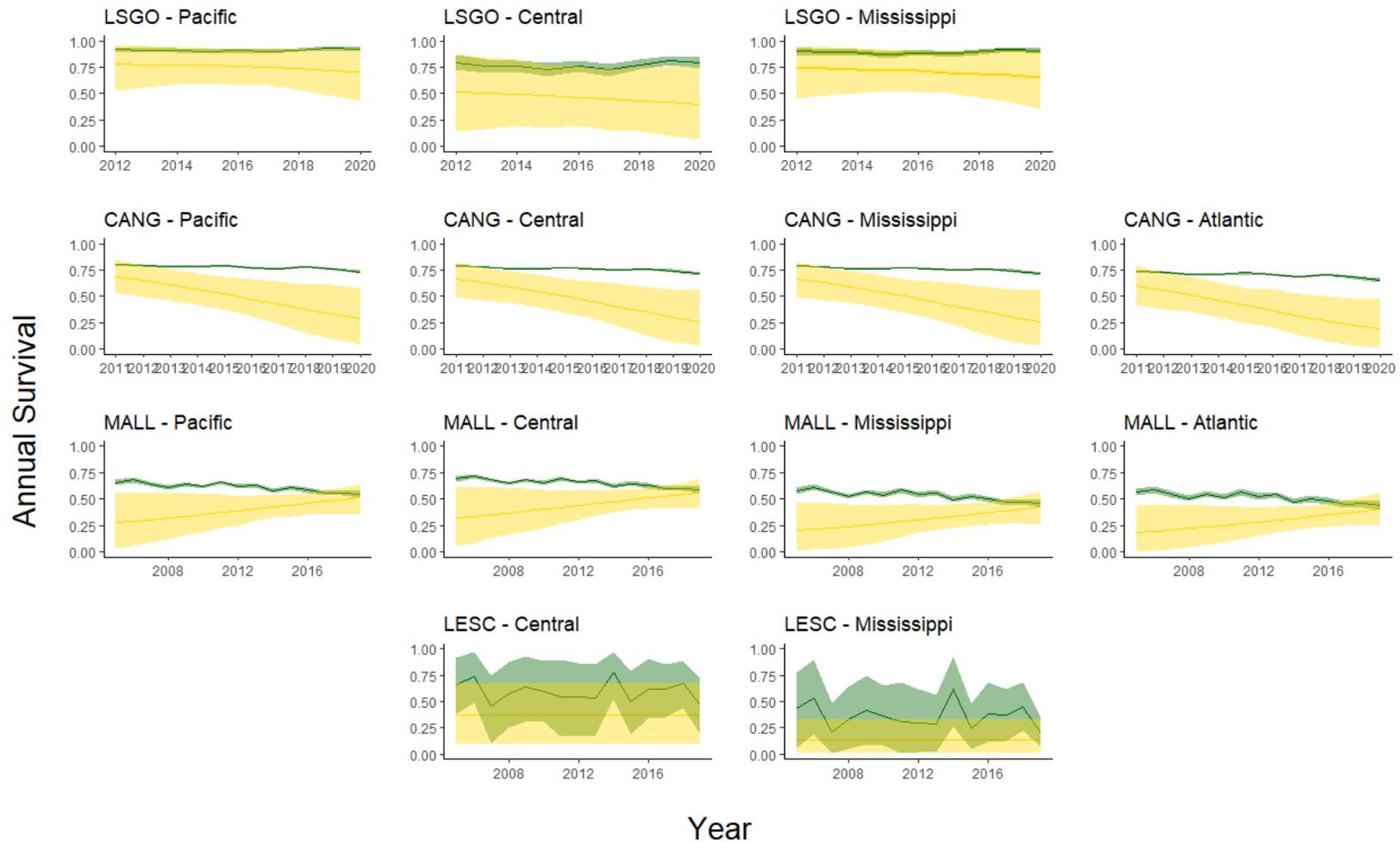
<sup>c</sup> - implant attachment style comprised majority of sample

**Table 3.2:** Calculated elasticities of population growth rate ( $\lambda$ ) to change in annual survival of adult females for 13 waterfowl species, and projected net impact on population growth rate of wearing a GPS tag. The latter were calculated using Equation 2 and indicate the proportional change in population growth rate associated with the proportional difference in annual female survival for individuals wearing GPS tags compared to those wearing only metal bands, tempered by the elasticity. Species evaluated included lesser snow goose (LSGO), greater snow goose (GSGO), greater white-fronted goose (GWFG), black brant (BLBR), Canada goose (CANG), wood duck (WODU), cinnamon teal (CITE), gadwall (GADW), American wigeon (AMWI), mallard (MALL), American black duck (ABDU), northern pintail (NOPI), and lesser scaup (LESC). All numbers are rounded to the second decimal place.

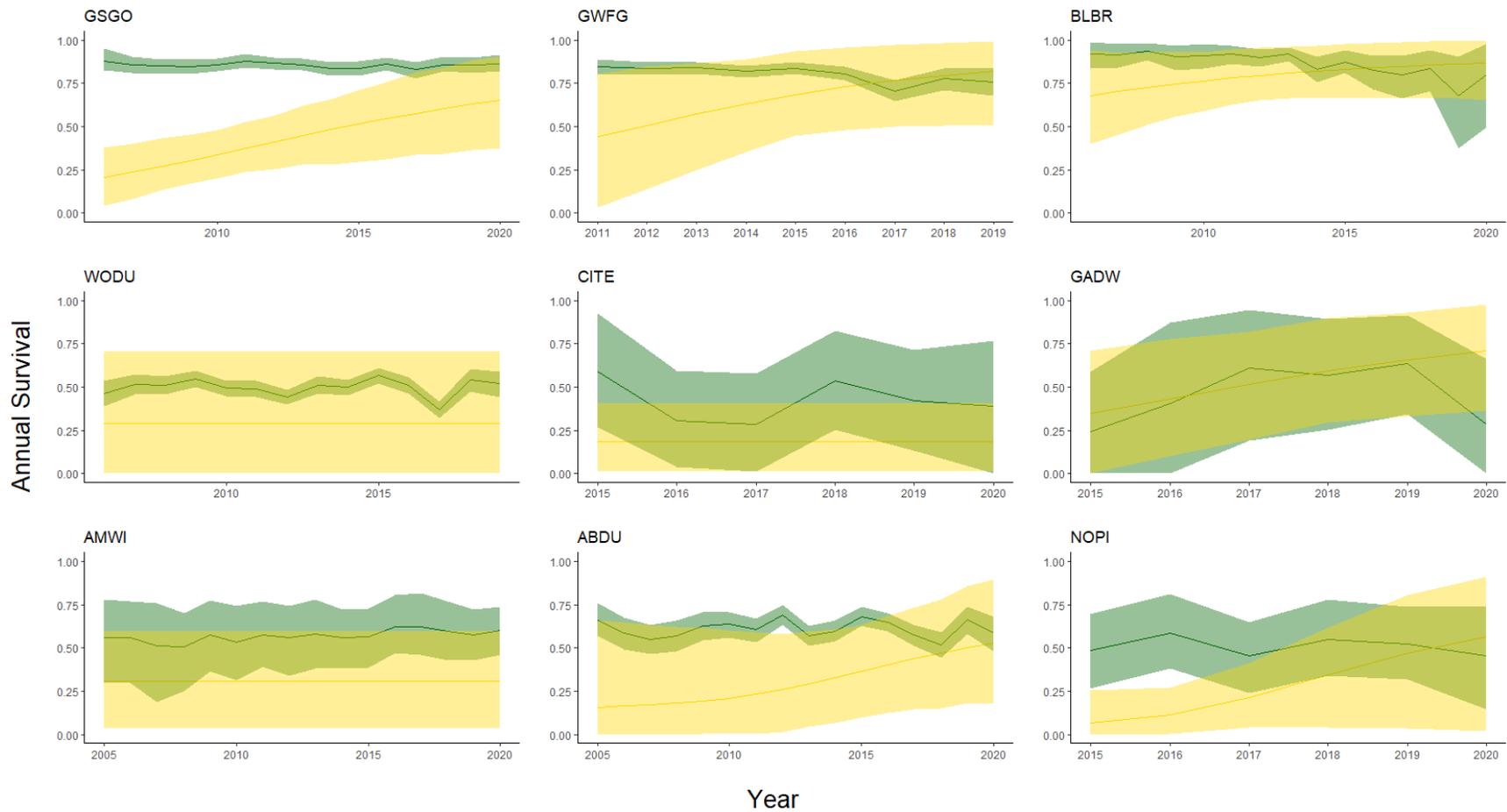
Species	Elasticity (SD)	Tag effects on $\lambda$ (SD) <sup>a</sup>
LSGO	0.93 (0.01)	0.16 (0.00)
GSGO	0.87 (0.03)	0.39 (0.01)
GWFG	0.84 (0.05)	0.07 (0.00)
BLBR	0.90 (0.03)	0.07 (0.00)
CANG	0.86 (0.01)	0.25 (0.01)
WODU	0.52 (0.03)	0.22 (0.01)
CITE	0.39 (0.16)	0.20 (0.09)
GADW	0.50 (0.19)	-0.09 (0.04)
AMWI	0.59 (0.06)	0.27 (0.03)
MALL	0.56 (0.02)	0.23 (0.01)
ABDU	0.64 (0.02)	0.36 (0.01)
NOPI	0.50 (0.11)	0.22 (0.05)
LESC	0.63 (0.10)	0.37 (0.04)



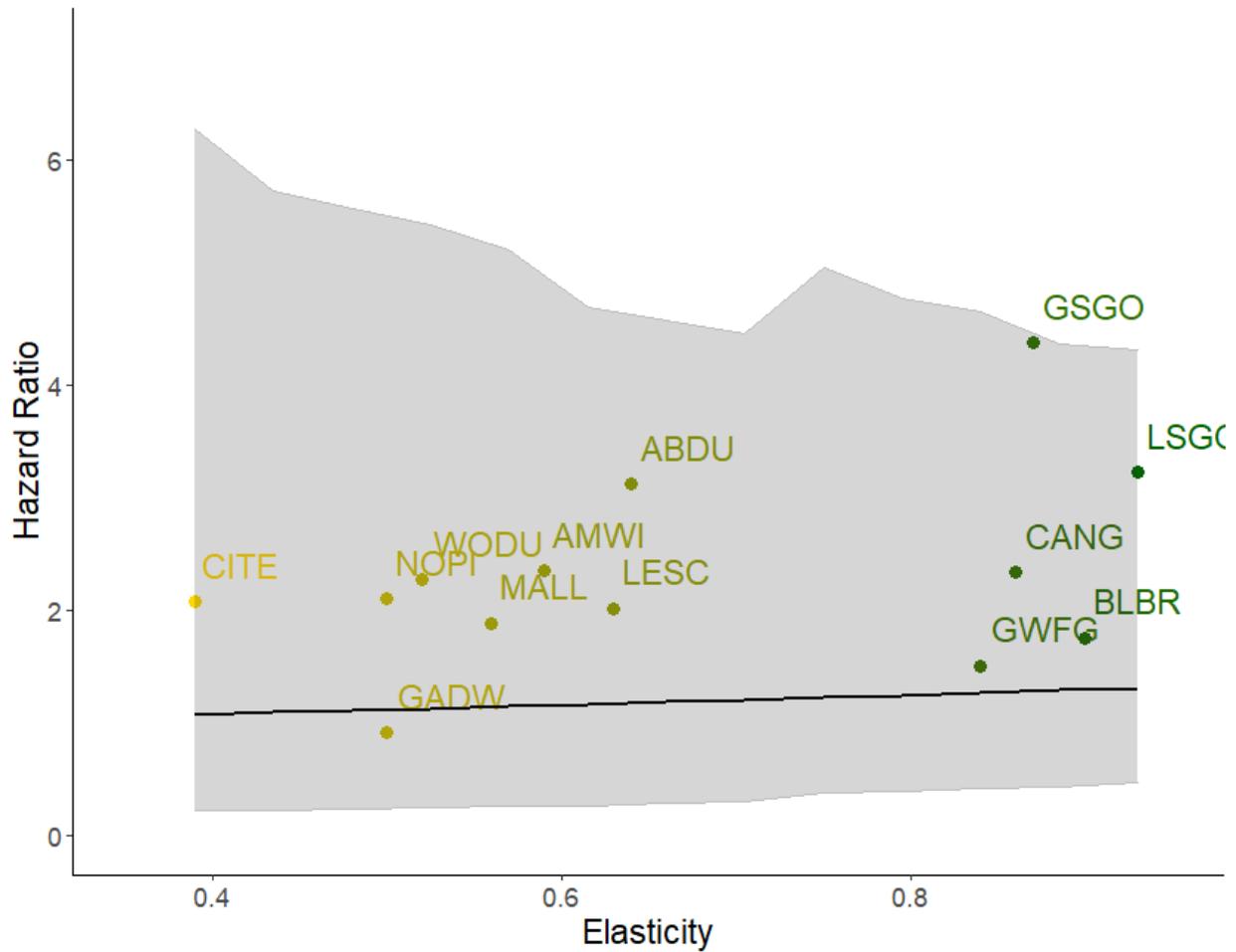
**Figure 3.1:** Conceptual schematic illustrating the demographic buffering hypothesis (solid line), inspired by Morris and Doak (2004) and Morris et al. (2008), whereby the response of adult survival to environmental fluctuations or changes is adaptively reduced in long-lived species with slow life histories because larger responses would most adversely affect fitness in species with these life histories (Pfister 1998). Conversely, a flat relationship would indicate a lack of demographic buffering and possibly maladaptive responses of slow life histories to environmental fluctuations or changes (dashed line).



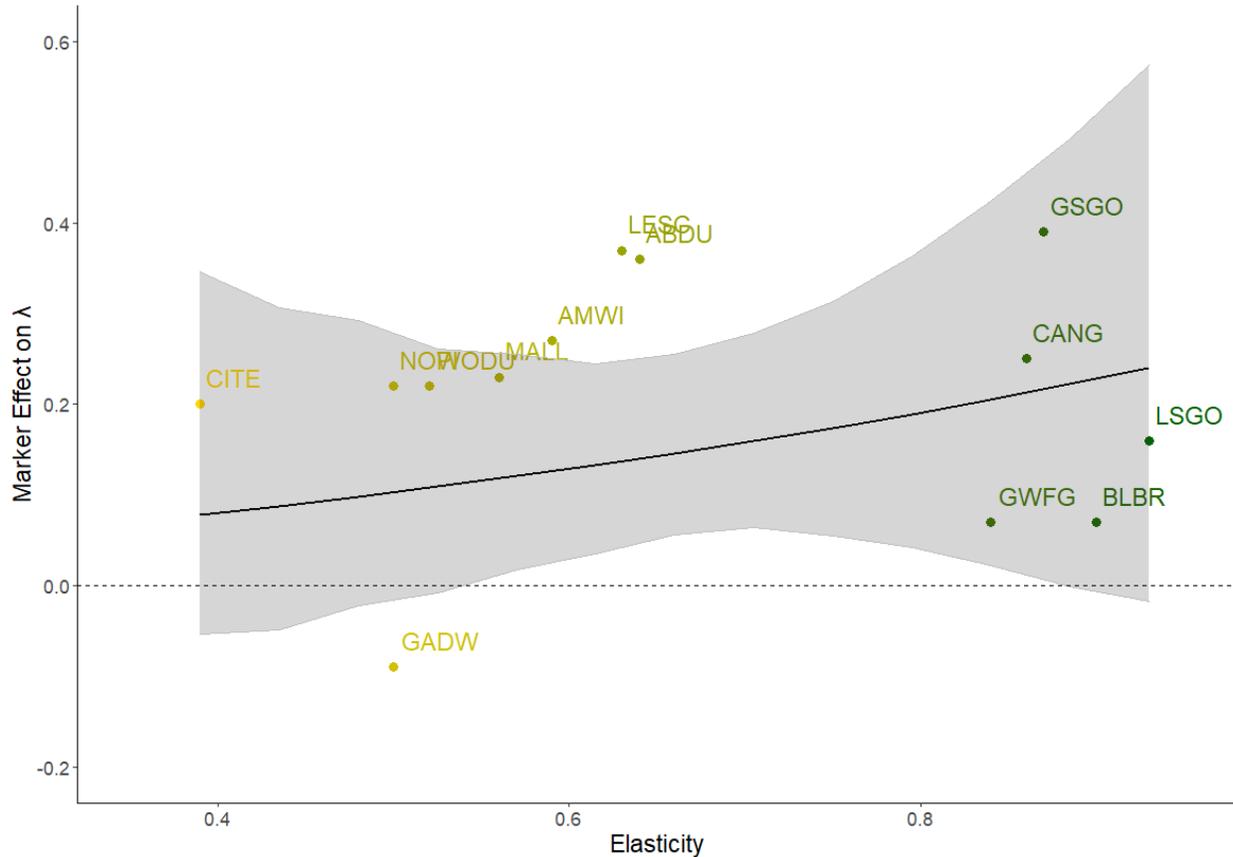
**Figure 3.2:** Time series of adult female annual survival of the four species of waterfowl for which survival varied by flyway of release. Annual survival of birds fitted with GPS tags is represented by gold and annual survival of birds fitted only with a metal leg band is represented by green. Each row within the panel represents a different species, with four-letter codes indicating species as follows: LSGO = lesser snow goose, CANG = Canada goose, MALL = mallard, and LESC = lesser scaup. Each column represents a unique Flyway as designated by the US Fish and Wildlife Service.



**Figure 3.3:** Time series of adult female annual survival of the nine species of waterfowl for which survival did not vary by flyway of release. Annual survival of birds fitted with GPS tags is represented by gold and annual survival of birds fitted only with a metal leg band is represented by green. GSGO = greater snow goose, GWFG = greater white-fronted goose, BLBR = black brant, WODU = wood duck, CITE = cinnamon teal, GADW = gadwall, AMWI = American wigeon, ABDU = American black duck, and NOPI = northern pintail.



**Figure 3.4:** Estimated relationship between species-specific hazard ratios (indicating the risk of death for individuals wearing GPS tags compared to those wearing only metal bands) and species-specific adult female survival elasticities across 13 species of waterfowl. For species with geographic variation in hazard rates, we used hazard rates from the Flyway with the most precise estimate of band-only hazard rates. Elasticity, used as an indicator of life-history tempo, is indicated by a color gradient from fast (gold) to slow (green). The bold line indicates the model-predicted mean effect and the grey shaded region indicates a 90% highest posterior density credible interval.



**Figure 3.5:** Estimated relationship between the projected impact on fitness ( $\lambda$ ) for individuals wearing GPS tags relative to those wearing only metal bands and species-specific adult female survival elasticities across 13 species of waterfowl. Effects were calculated using time-averaged hazard rates for both band-only and GPS tag rates. For species with geographic variation in hazard rates, we used hazard rates from the Flyway with the most precise estimate of band-only hazard rates to compute tag effects on  $\lambda$ . Elasticity, used as an indicator of life-history tempo, is indicated by a color gradient from fast (gold) to slow (green). The bold line indicates the model-predicted mean effect, grey shading indicates a 90% highest posterior density credible interval, and the dashed line denotes an effect of zero. Negative values represent scenarios wherein the hazard rate for band-only birds was higher (i.e., lower survival) than that of GPS tagged birds (i.e., higher survival).

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## CHAPTER 4 – CHARACTERIZING THE POPULATION DYNAMICS OF BREEDING WATERFOWL IN THE INTERMOUNTAIN WEST

### INTRODUCTION

Waterfowl are inherently tied to water availability and distribution throughout their annual cycle. It affects everything from food availability (e.g., aquatic invertebrates; see Ch 2) to roosting habitat (Varner et al. 2020) to nest safety (Jobin and Pickman 1997), and is the principal environmental predictor of breeding pair abundance throughout the Prairie Pothole Region (U.S. Fish and Wildlife Service 2022). In environments where water is intensively managed and access is restricted, small changes to the environment, whether through management actions or climatic variability, have the potential to drastically alter the amount of water on the landscape and therefore the species that rely upon it (Aagaard et al. 2019). Additionally, increased municipal and agricultural demand on water alongside climate-driven changes in precipitation are altering hydrologic regimes globally. The demographic consequences of shifts in water availability may vary spatially (Zhao et al. 2019), so it is imperative to determine how populations of wetland-dependent species respond to environmental conditions not only in their core geographic range, but in the environments along the edge of that range.

Within North America, much of the information we know about waterfowl demography and their responses to environmental conditions during the breeding season comes from the Prairie Pothole Region (Anderson 1975, Anderson and Burnham 1976). Far fewer studies have taken place along the fringes of the breeding range, and the extent to which species with significant portions of their breeding range outside of traditional survey areas contribute to the continental population is often unknown. The most heavily-used breeding areas may act as

sources to supply sink populations along range edges, which may in turn augment the overall population. Alternatively, range edges may act as sources when habitat in the core breeding area becomes heavily degraded (e.g., Buderman et al. 2020). Vital rates may also differ across the range of a given species depending on local annual climate and annual variation in habitat conditions (Ellis et al. 2022). Numerous studies have evaluated the population dynamics of mallards (*Anas platyrhynchos*), often focusing on the midcontinent population (Hoekman et al. 2002, Zhao et al. 2019), Great Lakes population (Coluccy et al. 2008), and eastern population (Hoekman et al. 2006, Roberts et al. 2023). While studies that have focused on western populations have not found drastic differences in demographic parameters compared to the rest of the continent (Dugger et al. 2016), populations are often isolated and low in density, making them more susceptible to regional climate patterns and environmental stochasticity. Mallards are among the earliest-nesting duck species, which makes them susceptible to variable spring conditions associated with short growing seasons (Sedinger et al. 2019), whereas gadwall are among the latest nesters, making them susceptible to wetland and environmental conditions during summer (Ross et al. 2015). Investigating the demographics of peripheral populations may therefore become increasingly important as land use, geographic ranges, and climate shift.

The intermountain west region of North America has received particularly little research attention with respect to waterfowl demography and is one of the more rapidly-changing landscapes on the continent (Ringelman 1992). Low precipitation is common and most systems are driven by snowpack, which has been declining for several decades due to drought and increasing spring temperatures (Brasher et al. 2019, Donnelly et al. 2019). Increasing variability in weather patterns has exacerbated the boom-and-bust nature of wetlands in the region, and drought has resulted in a landscape-level shift in wetland hydrology and function (Donnelly et al.

2022). Breeding waterfowl may be adept at exploiting the “boom” years along the edges of the breeding range, but little empirical evidence exists to support that hypothesis. The extent to which waterfowl populations breeding in these habitats differ in their demography from those in the core breeding area must first be evaluated before assessing their aptitude for exploiting them, however. Additionally, spatial variability in demography can impact different populations’ tolerance to harvest, thus having implications for harvest management (Sæther et al. 2008, Cooch et al. 2014). This may include how vital rates vary annually, the magnitude of each vital rate’s impact on population growth, and the response of each vital rate to environmental conditions (Harrison et al. 2017, Pöysä 2023), all of which have received little attention in the intermountain west. The contributions of environmental factors to demographic outcomes are often challenging to parse out because they act on multiple vital rates simultaneously and vital rates do not impact population growth independently (Iles et al. 2019). Studies that estimate the magnitude of environmental effects on each of multiple vital rates therefore have the greatest potential to integrate those estimates into an environmentally-explicit population model, which can then be used to explain and predict the effects of environmental change on population-level processes.

Our study aims to draw attention to the lack of empirical research evaluating population demography of waterfowl in the semiarid west and to parse out the mechanisms driving their populations. We use exemplar breeding populations of mallards and gadwall situated in an intermountain basin in northern Colorado, which is representative of the high climatic variability, short growing season, and snowpack-driven wetland systems common across the intermountain west. Mallards are the earliest-nesting species in this system, whereas gadwall are one of the latest, so a comparison of the two provides representation of the changing conditions and demographic outcomes across the breeding season. Our primary objectives were to identify the

vital rates most influential to population growth rate, whether the impacts of those vital rates were direct or indirect (i.e., via changes in population structure), and to evaluate the influence of climatic and environmental conditions on each vital rate as a case study of these types of systems. Decomposing the variation in realized population growth rates can elucidate the mechanisms selecting for certain ecological traits or life-history strategies as well as inform how to target vital rates via management actions and how those actions might affect population growth in the future (Zhao et al. 2016, Iles et al. 2019). We expected that, given the boom-and-bust nature of wetland habitats in intermountain systems, the growth rate of this breeding mallard population would be most influenced by recruitment, wherein late, cold springs would lower the nest survival of early nesters and reduce production. However, late-nesting gadwall should benefit from heavy snowpack early in the season and thus exhibit higher recruitment during those years. The results of this study have the potential to lay the groundwork for future research occurring within intermountain basins and emphasize the potential need for further demographic analyses of fringe populations as climatic and land-use changes shift waterfowl breeding ranges and population dynamics (Zhao et al. 2019).

## METHODS

### *Study System*

Our study occurred throughout the North Platte Basin in Jackson, County, Colorado (North Park). This high-elevation intermountain basin (~2500 m) is comprised primarily of sagebrush (*Artemisia* spp.) steppe and riparian corridors associated with the tributaries of the North Platte River. Wetlands are most commonly associated with the river corridors and with flood-irrigated hay meadows located on private ranches producing high-quality Timothy hay

(*Phleum pretense*), but also include small basins, streams and rivers, irrigation ditches, and large reservoirs from which municipal water reserves are drawn. Weather conditions are variable, and wetlands are fed via snowmelt from the surrounding mountain ranges. Rainfall rarely exceeds 38 cm in a year, but snow can persist on parts of the basin floor into June. Hay meadows are typically irrigated in April or May, dried in July or August, and harvested from mid-July until September, depending on the elevation.

### *Demographic Data Collection*

We monitored the waterfowl population in North Park, Colorado from 2018-2022. We conducted dependent double-observer pair counts each spring from April until July approximately weekly, wherein a primary observer detailed every pair or lone male observed of a given species to a secondary observer, who recorded the data and any additional birds missed by the primary observer (Pagano et al. 2009). We used counts from each sampled site on or closest to the date corresponding to average peak nest initiation date over the course of the study (30 May). This allowed us to avoid including spring migrants in the count of breeding ducks and to ensure breeding males had not begun grouping up during post-breeding molt (Dzubin 1969, Arnold et al. 2008). We also conducted banding operations from August-September each year using baited swim-in traps. We identified each bird, assigned it to an age and sex class using wing morphology and cloacal examination, and fit it with a United States Geological Survey (USGS) metal leg band. Age classes included local (L; i.e., unfledged ducklings that had hatched within the study area but were large enough to band), hatch-year (HY; fledged offspring of the year that could fly), and after-hatch-year (AHY; reproductively mature adults). We recorded any within- or across-season recaptures and downloaded harvested band recoveries from the USGS Bird banding Laboratory's GameBirds Database (Bird Banding Lab, USGS Patuxent Wildlife

Research Center). We also incorporated historic banding data from North Park to augment our sample size, using releases from 1971-1980 (for mallards; gadwall releases continued until 1985) and 2008-2010 in addition to our more recent sample. In order to evaluate recovery distributions and improve model fit, we computed the average age-specific distance between banding location and recovery location for birds that were recovered during the hunting season immediately following release (i.e., direct recoveries). We used the geosphere package in Program R (R Core Team 2020) to compute Haversine distances between release and harvest in kilometers for each individual and averaged distances for each age class for inclusion as a recovery covariate.

#### *Climate Data Collection*

Water in this system is primarily delivered via snowpack in the surrounding mountains, so we downloaded snowpack data from the United States Department of Agriculture's (USDA) interactive SNOwpack TELemetry Network (SNOTEL) map (USDA 2022) as an index of water conditions throughout the breeding season. We used snow-water equivalent (SWE) data from four stations surrounding the North Platte Basin, including Never Summer, Roach, Tower, and Zirkel, and recovered monthly averages from January 2018-December 2022. We averaged SWE across stations for each month and used data from May of each year of our study as a predictor variable. In addition to water conditions, we also assessed spring temperature and the resulting conditions in which vegetation could grow. Vegetation growth should be especially important for early-nesting mallards when seeking nesting habitat. We therefore calculated growing degree days (GDD) in April and May of each year using average daily temperature data from ten weather stations across North Park. We downloaded Global Historical Climate Network daily summaries (GHCN-Daily) from the National Oceanic and Atmospheric Administration's (NOAA) Climate Data Online database. We averaged the daily average temperature across

stations and computed  $GDD = T_{\text{Mean}} - T_{\text{Base}}$  for each day on which  $T_{\text{Mean}} \geq T_{\text{Base}}$  where  $T_{\text{Mean}}$  was the daily average temperature and  $T_{\text{Base}}$  was 4.4°C, the minimum of the tolerance range for Timothy grass (*Phleum pretense*), the dominant crop in this system. We assigned  $GDD = 0$  on days when  $T_{\text{Mean}} \leq T_{\text{Base}}$ , and note that GDD can also index the overall coolness (or warmth) of a given spring.

### *Integrated Population Model*

We constructed a female-only integrated population model (IPM) separately for mallards and gadwall, wherein each included three submodels to estimate an index of annual abundance, survival probabilities, and recruitment. Submodels interacted via a 2x2 stage-based matrix population model with a pre-breeding census where stages represented second-year (SY) and after-second-year (ASY) birds (Kéry and Schaub 2011, Schaub and Kéry 2022). Abundance surveys occurred in the spring and banding operations occurred in the late summer, creating a disconnect between the age classes that were counted versus banded. Banded birds were therefore classified as either local (L), hatch-year (HY), or after-hatch-year (AHY), whereas when those birds were counted the following spring, they would be classified as SY (L and HY birds that survived to the following spring) or ASY (AHY birds that survived to the following spring). We reconciled differences in survey timing using monthly survival rates exponentiated to the appropriate number of months a bird was in a given age class:

$$(1) \begin{bmatrix} N_{SY,t+1} \\ N_{ASY,t+1} \end{bmatrix} = \begin{bmatrix} F_t S_{HY,t}^9 & F_t S_{HY,t}^9 \\ S_{AHY,t-1}^3 S_{AHY,t}^9 & S_{AHY,t-1}^3 S_{AHY,t}^9 \end{bmatrix} \begin{bmatrix} N_{SY,t} \\ N_{ASY,t} \end{bmatrix}$$

where  $S$  is monthly survival (within a given year  $t$ ) of each age class,  $F_t$  is annual recruitment, and  $N_t$  is annual abundance of each age class.

### *State-Space Model*

We incorporated demographic stochasticity into the process model by sampling the abundance of a latent fledgling age class ( $N_{fl}$ ; representing fledged females at the end of the summer) from a Poisson distribution and the abundance of SY and ASY females from a binomial distribution. We then computed total abundance at time  $t$  as a derived quantity of the sum of  $N_{SY}$  and  $N_{ASY}$  at time  $t$ . Realized population growth rate ( $\lambda_t$ ) could then be computed as a derived quantity using abundance in sequential years:

$$(2) N_{fl,(t-1)} \sim \text{Poisson}((F_{t-1} * N_{SY,(t-1)}) + (F_{t-1} * N_{ASY,(t-1)}))$$

$$(3) N_{SY,t} \sim \text{binomial}(S_{HY,(t-1)}^9, N_{fl,(t-1)})$$

$$(4) N_{ASY,t} \sim \text{binomial}((S_{AHY,(t-2)}^3 * S_{AHY,(t-1)}^9), (N_{SY,(t-1)} + N_{ASY,(t-1)}))$$

$$(5) N_t = N_{SY,t} + N_{ASY,t}$$

$$(6) \lambda_t = N_{t+1}/N_t$$

Pair count data were specific to each wetland site within the study area, so we initially fit a zero-inflated Poisson model to pair count data separately from the IPM to obtain a single annual index of abundance to include in the observation model of the IPM. Mean pair abundance at each site was modeled as a function of a site-level intercept and a fixed year effect. We modeled each site-level intercept hierarchically as a function of wetland size (hectares) and habitat category, which included basin wetland, irrigation ditch, hay meadow, reservoir, and riparian areas. We calculated a derived quantity for the total surveyed abundance of mallards or gadwall in the sampling frame and scaled that value by the number of sites sampled each year to ensure estimates were comparable across years (Figure 1). Scaling involved dividing total abundance by the number of sites surveyed in a given year and multiplying the result by the median number of sites surveyed across the study period (Saunders et al. 2021). Once we had an

estimate of annual surveyed abundance and its variance, we included that in the IPM in an observation process to account for imperfect counting. We used a normal distribution with the variance from the posterior of scaled annual surveyed abundance  $y_t$  estimated from the zero-inflated Poisson model described above (Kéry & Schaub 2012, Schaub & Kéry 2022):

$$(7) y_t \sim \text{normal}(N_t, \sigma_y^2)$$

where  $\sigma_y^2$  is the posterior variance of each annual  $y_t$ . We specified priors for initial population size of SY and ASY birds from a normal distribution with a mean and variance based on the initial estimates of  $y_t$  from the zero-inflated Poisson model and apportioned according to a ratio of approximately 2:3 (SY:ASY).

### *Survival Model*

We used a band-recovery (i.e., Brownie) model to estimate survival and recovery rates (Brownie 1985). Data were compiled into m-arrays, which are banding recovery histories in matrix form that indicate the number of individuals within a release cohort that are recovered in the same or subsequent years (Burnham et al. 1987, Kéry and Schaub 2012). We separated the likelihood to estimate survival only during years in which banded birds were released and recovered, thus allowing recoveries to continue 5-10 years past the final year of release based on the data. To maintain computing efficiency and with approximately no impact on parameter estimation bias, we allowed recoveries to continue until there were zero recoveries for a given year for each species. For example, mallards were released from 1971-1980 and gadwall were released from 1971-1985, but birds from that cohort were recovered up until 1990. We therefore constrained the likelihood to match those years of release and recovery (Table 4.1). We incorporated covariates on survival and direct recovery using a logit-link function, and included a random time effect (shared between age classes) on both survival and recovery:

$$(8) \text{ logit}(S_{x,t}) = \alpha_x + \varepsilon_{S,t} + \beta_x * x_t$$

$$(9) \text{ logit}(r_t) = \gamma_x + \varepsilon_{r,t} + \zeta_x * x_{x,t}$$

Where the subscript x represents age class (HY or AHY), and  $\varepsilon_{S,t}$  and  $\varepsilon_{r,t}$  are temporal random effects on survival and recovery, respectively. We included an effect of May SWE on HY and AHY survival, and we also included distance between release and harvest locations as a covariate on direct recovery rate. Sample sizes of Local females released during banding were insufficient to explicitly estimate Local survival as an independent parameter, so we estimated Local survival using a correction factor (cf) multiplied by HY survival. We informed mean survival, mean recovery, and the cf parameters based on previous studies of mallard and gadwall vital rates. We constructed beta priors using moment-matching for all mallard survival and recovery rates with parameters equivalent to a mean of 0.54 for HY survival (SD = 0.079; Devers et al. 2021), 0.50 for AHY survival (SD = 0.05; Franklin et al. 2002), 0.20 for HY direct recoveries (SD = 0.10; Henny and Burnham 1976), 0.02 for AHY direct recoveries (SD = 0.02; Arnold and Howerter 2012), and 0.70 for cf (SD = 0.30; Hestbeck et al. 1992). There are fewer estimates of annual survival and recovery available in the literature for gadwall, so we used the same priors as mallards except for that of AHY survival, which we changed to a mean of 0.63 (SD = 0.10; Zhao 2020).

### *Recruitment Model*

Based on the assumption of a geographically closed population throughout the breeding season and including banding operations, recaptures of birds within a given banding season can be used to estimate recruitment using each age class's vulnerability to capture during banding and adjusting within-season age ratios at capture accordingly (Arnold 2018). This model takes

advantage of the age ratio of newly marked birds at banding, adjusted for the number of birds captured 1 versus 2 times (Chao 1989):

$$(10) \quad F_{Raw,t} = F_t * V_t$$

$$(11) \quad V_t = p_{juv}/p_{ad}$$

$$(12) \quad r_{juv,t} \sim \text{binomial}(p_{juv,t}, n_{juv,t})$$

$$(13) \quad r_{ad,t} \sim \text{binomial}(p_{ad,t}, n_{ad,t})$$

$$(14) \quad c_{juv,t} = F_{Raw,t}/(1 + F_{Raw,t})$$

$$(15) \quad n_{juv,t} \sim \text{binomial}(c_{juv,t}, n_{tot,t})$$

$$(16) \quad p_{juv,t} \sim \text{uniform}(0,1)$$

$$(17) \quad p_{ad,t} \sim \text{uniform}(0,1)$$

where  $F_{Raw,t}$  is a naïve estimate of annual fecundity (i.e., not adjusted for vulnerability to capture) and is used to connect adjusted fecundity ( $F_t$ ) to the remaining parameters,  $V_t$  is vulnerability to capture relative to each age class,  $r_{juv,t}$  and  $r_{ad,t}$  are the number of juvenile or adult individuals that were captured more than once within a year (i.e., within-season recaptured individuals),  $n_{juv,t}$  is the total number of juveniles captured each year,  $p_{juv,t}$  and  $p_{ad,t}$  are the capture probabilities for juvenile and adult females, and  $c_{juv,t}$  is the probability that an initial capture of any female will be a juvenile (Arnold 2018). We modeled annual GDD and a quadratic effect of GDD as covariates on  $F_t$  using a log link function:

$$(18) \quad \log(F_t) = \gamma_t + \zeta * GDD_t + \zeta' * GDD_t^2$$

We provided vague priors on the appropriate link scale (Northrup and Gerber 2018) for all parameters in the recruitment submodel.

### *Model Fitting*

We combined independent data likelihoods into a joint likelihood using Markov Chain Monte Carlo (MCMC) sampling methodology. Separate likelihoods informed shared parameters via the projection matrix in Eq. 1. We fit the IPM in a Bayesian framework (Kéry and Schaub 2012) using JAGS (Plummer 2003) via the jagsUI package in Program R (Kellner 2016). We ran three chains for 200000 iterations with a burn-in period of 20000 iterations and thinned chains by 50. We visually examined traceplots and Gelman-Rubin statistics ( $\hat{R}$ ) to assess convergence and report posterior means and 95% highest posterior density credible intervals (HPDI) where appropriate. We also report the proportion of the posterior distribution on the same side as the mean as an additional metric of support for each effect (labeled  $\gamma$ ; Riecke et al. 2022).

### *Transient Life Table Response Experiment*

We characterized the demographic mechanisms affecting the realized population dynamics of mallard and gadwall using a retrospective perturbation analysis. Specifically, the contribution of change in each demographic parameter (vital rates and stage structure) to change in the realized population growth rates was measured using a sequential transient life table response experiment (tLTRE; Koons et al. 2016 Eq. S 1.3 and S 1.4). We calculated the transient sensitivities of realized population growth rate to each parameter at the respective mean between successive time steps using Eq. 19-22 below.

$$(19) \quad \frac{\partial \lambda_t}{\partial F_t} = \frac{\left( S_{HY,t} * (\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t})) \right)}{(\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t}))}$$

$$(20) \quad \frac{\partial \lambda_t}{\partial S_{HY,t}} = \frac{\left( F_t * (\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t})) \right)}{(\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t}))}$$

$$(21) \quad \frac{\partial \lambda_t}{\partial S_{AHY,t}} = \frac{(\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t}))}{(\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t}))} = 1$$

$$(22) \quad \frac{\partial \lambda_t}{\partial n_{SY,t}} = \frac{((\widehat{n}_{SY,t} * \widehat{n}_{SY,t} * (1 - 1)) + (\widehat{n}_{SY,t} * (1 - 1)))}{(\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t})) - ((F_t * S_{HY,t}) * (\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t})) + (S_{AHY,t} * (\widehat{n}_{SY,t} + (1 - \widehat{n}_{SY,t})))) * (1 - 1) / (\widehat{n}_{SY,t} + (1 - (\widehat{n}_{SY,t})))^2} = 0$$

Next, we combined these sensitivities with respective changes in demographic parameters between sequential time steps to calculate the retrospective contribution of each demographic parameter to realized changes in population growth rates:

$$(23) \quad \Delta \lambda_{\text{realized}} = \sum_i (\theta_{i,t+1} - \theta_{i,t}) \frac{\partial \lambda_{\text{realized},t}}{\partial \theta_{i,t}} \Big|_{\bar{\theta}_i}$$

$$(24) \quad \chi_{\theta_i} = (\theta_{i,t+1} - \theta_{i,t}) \frac{\partial \lambda_{\text{realized},t}}{\partial \theta_{i,t}} \Big|_{\bar{\theta}_i}$$

where  $\widehat{n}_{SY,t}$  is the normalized proportion of the population comprised of SY individuals (and therefore the complement is the proportion of ASY individuals),  $\theta_{i,t}$  are the demographic parameters during each time step and  $\chi_{\theta_i}$  is the contribution of change in each  $\theta_i$  to  $\Delta \lambda_{\text{realized}}$ .

Taking advantage of having access to the entire posterior for each demographic parameter

(estimated from the IPM), we could fully propagate uncertainty to the temporal change in each realized population growth rate contributed by the temporal change in each demographic parameter.

## RESULTS

The number of female mallards and gadwall banded during each of the five years of the study varied from 134 and 12, respectively, in 2021 to 336 and 133 in 2020, but historic sample sizes were larger (Table 4.2). The number of sites on which pair counts were conducted varied from 72 to 133 with a median of 90.

### *Demographic Parameters*

Mallard survival of both age classes remained relatively stable over the course of the five-year study (Figure 2). Survival of HY birds ranged from 0.48 (SD = 0.09) in 2019 to 0.53 (SD = 0.07) in 2021, while survival of AHY birds ranged from 0.53 (SD = 0.07) in 2019 to 0.57 in 2021 (SD = 0.05; Figure 2). The penalty describing how much lower survival of local birds was relative to HY birds (cf) was 0.73 (SD = 0.19; therefore highly similar to the informative prior distribution), resulting in estimates of L survival ranging from 0.36 (SD = 0.11) in 2019 to 0.40 (SD = 0.12) in 2020. Direct recovery rates of HY birds were higher than those of AHY birds, ranging from 0.08 (SD = 0.02) in 2022 to 0.19 (SD = 0.04) in 2020, whereas for AHY birds they varied from 0.07 (SD = 0.01) in 2021 and 2022 (SD = 0.02) to 0.11 (SD = 0.03) in 2020. Distance between release and recovery positively impacted HY direct recovery probability ( $\beta_{Dist, HY} = 0.37$ , SD = 0.16,  $\gamma = 0.99$ ) but negatively impacted chances of AHY recovery ( $\beta_{Dist, AHY} = -0.12$ , SD = 0.13,  $\gamma = 0.83$ ). Recruitment varied from 0.40 females produced per pair

(SD = 0.48) in 2019 to 1.59 females (SD = 0.95) in 2020 (Figure 3). Realized population growth rates varied from 0.76 (SD = 0.24) in 2019 to 1.55 (SD = 0.58) in 2020 (Figure 4).

HY gadwall survival ranged from 0.44 (SD = 0.13) in 2022 to 0.52 (SD = 0.14) in 2018, but appears to have remained relatively stable since the 1970s (Figure 2). Survival of AHY gadwall was slightly higher than HY, varying from 0.56 (SD = 0.11) in 2020 to 0.66 (SD = 0.12) in 2018. The penalty describing how much lower survival of Local birds was relative to HY birds (cf) was 0.79 (SD = 0.16; also quite similar to the informative prior), resulting in estimates of L survival ranging from 0.35 (SD = 0.12) in 2022 to 0.41 (SD = 0.13) in 2018. Direct recovery rates of HY birds were higher than those of AHY birds, ranging from 0.10 (SD = 0.06) in 2018 to 0.23 (SD = 0.10) in 2019, whereas AHY direct recoveries ranged from 0.04 (SD = 0.03) in 2018 to 0.11 (SD = 0.06) in 2019. Distance between release and recovery did not impact recovery rates for HY birds ( $\beta_{Dist, HY} = 0.03$ , SD = 0.23,  $\gamma = 0.44$ ), but was negatively related to recovery of AHY birds ( $\beta_{Dist, AHY} = -0.30$ , SD = 0.25,  $\gamma = 0.88$ ). Average recruitment estimates were comparable to mallards but were imprecise, ranging from 0.62 in 2018 (SD = 0.80) to 1.04 in 2020 (SD = 1.04; Figure 3). Realized population growth rates varied from 0.93 (SD = 0.56) in 2019 (SD = 0.78) to 1.21 (SD = 0.59) in 2021 (Figure 4).

### *Environmental Effects*

May SWE had a positive, but imprecise impact on both HY mallard survival ( $\beta_{SWE, HY} = 0.26$ , SD = 0.47,  $\gamma = 0.71$ ) and AHY survival ( $\beta_{SWE, AHY} = 0.11$ , SD = 0.12,  $\gamma = 0.82$ ; Figure 5). SWE also had a positive, but imprecise impact on HY gadwall survival ( $\beta_{SWE, HY} = 0.26$ , SD = 0.30,  $\gamma = 0.81$ ) but no discernable effect on AHY survival ( $\beta_{SWE, AHY} = -0.09$ , SD = 0.19,  $\gamma = 0.69$ ; Figure 5). Both mallard recruitment ( $\beta_{GDD} = 0.33$ , SD = 0.64,  $\gamma = 0.70$ ,  $\beta_{GDD^2} = -0.53$ ,

SD = 0.42,  $\gamma = 0.89$ ; Figure 6) and gadwall recruitment ( $\beta_{GDD} = 0.28$ , SD = 0.78,  $\gamma = 0.63$ ,  $\beta_{GDD^2} = -0.81$ , SD = 0.65,  $\gamma = 0.90$ ; Figure 6) were higher at intermediate GDD levels.

#### *Transient Life Table Response Experiment*

Annual recruitment made the largest contributions to changes in realized population growth rate of mallards over the course of the study (Figure 7). Recruitment contributed to a decrease in population growth rate from the 2018  $\lambda$  to the 2019  $\lambda$  ( $\mu_F = -0.05$ , SD = 0.08, whereby years refer to the leading year of change in abundance between years), a positive contribution to increased growth rate between the 2019  $\lambda$  and 2020  $\lambda$  ( $\mu_F = 0.09$ , SD = 0.09), and a negative contribution to decreased growth between the 2020  $\lambda$  and 2021  $\lambda$  ( $\mu_F = -0.06$ , SD = 0.16; Figure 7). AHY survival also contributed somewhat to a decrease in population growth rate from 2018 to 2019 ( $\mu_{SAHY} = -0.01$ , SD = 0.07), an increase from 2019 to 2020 ( $\mu_{SAHY} = 0.03$ , SD = 0.07), and another increase from 2020 to 2021 ( $\mu_{SAHY} = 0.01$ , SD = 0.6; Figure 7).

Vital rate contributions for gadwall were similar to mallards over the course of the study, despite population growth rate remaining relatively more stable. Recruitment and AHY survival contributed to a decrease in population growth rate from 2018 to 2019 ( $\mu_F = -0.06$ , SD = 0.79;  $\mu_{SAHY} = -0.02$ , SD = 0.12; Figure 7). Recruitment again contributed most to the changes in  $\lambda$  from 2019 to 2020 ( $\mu_F = 0.32$ , SD = 0.95; Figure 7) and very little from 2020 to 2021 ( $\mu_F = 0.01$ , SD = 0.88; Figure 7). Contributions from age structure were always zero because, given the data, the vital rates in the pre-breeding census model (Eq. 1) were not different between the SY and ASY age classes.

## DISCUSSION

The intricacies of population demography are at the forefront of waterfowl management in North America (Nichols et al. 1995, Johnson et al. 2015, Roberts et al. 2023). Evaluating and understanding differences in the drivers of demography across geographies, spatial scales, and species are fundamental to informing management and harvest plans, especially as climatic variation and land use change continue to shift waterfowl distributions and available resources (Zhao et al. 2016, Zhao et al. 2020). The results of this study highlight the need for continued or reinvigorated monitoring in habitats that have historically been underrepresented in survey efforts, but that might prove increasingly influential to waterfowl demography in coming years. Additionally, evaluating the sensitivity of specific populations' growth rates to different vital rates and the lability of each vital rate to environmental conditions and management actions is necessary to not only assess how that population might change in the future (Koons et al. 2014), but also to mitigate the effects of increasing aridity on wetland-dependent species (Donnelly et al. 2019). To our knowledge, this is the first perturbation analysis assessing gadwall population demography (but see Zhao 2020 for a gadwall IPM). Our results confirmed that recruitment to the fall flight played the largest role in changing population growth among both focal species and that spring weather patterns had considerable impact on this important vital rate. This is consistent with some of the seminal population perturbation analyses that focused on mallards in both the mid-continent and the Great Lakes regions, both of which have been used extensively to inform mallard management across the United States and Canada (Hoekman et al. 2002, Coluccy et al. 2008). These results provide evidence that waterfowl populations breeding in high-elevation basins of the West share demographic similarities to other regions, and that there are potential water application decisions that can mitigate the effects of suboptimal spring breeding

conditions at small scales. For example, maintaining heterogeneous wetland complexes and vegetation communities may ensure that habitats are available regardless of species-specific phenological tendencies. Additionally, our results highlight the importance of intermountain basins as breeding gadwall habitat and augment a relative paucity of gadwall population studies.

Retrospective perturbation analyses assess the contributions that changing vital rates made to observed or ‘realized’ population growth rates. It is worth noting that, in our study, survival did not vary considerably over the course of the study, whereas mean annual recruitment varied far more for both species. Contrastingly, mid-continent mallards have exhibited interannual variation in survival and recent declines among AHY females (Riecke et al. 2022). The relatively stable survival probabilities in our study system therefore could not have contributed as substantially to the changes in realized population growth rate as recruitment. This phenomenon is common among waterfowl, many of which have evolved to buffer the vital rates to which population growth is most sensitive against variability (Chapter 3, Pfister 1998, Morris and Doak 2004). Most waterfowl populations exhibit the highest elasticities to adult female survival except the species with the fastest life-history strategies (e.g., blue-winged teal [*Spatula discors*] and cinnamon teal [*Spatula cyanoptera*]). The North Park mallard population is similar to other waterfowl populations, however, in that the vital rates that realized population growth is most affected by (e.g., recruitment) are not always necessarily the most elastic, but are the most labile to environmental conditions and management actions.

Realized population growth rates in North Park closely tracked annual recruitment, both of which fell to relatively low levels during 2019 among mallards and gadwall. That year was characterized by an extremely cold, snowy spring, with heavy precipitation through June. Early-nesting mallards may have experienced reduced opportunity to nest either because snowy

conditions obfuscated nesting cover, cold prevented new vegetation growth, or icy conditions precluded settling by migrating mallards. Alternatively, snow could have caused failure of early nests and the growing season is too short to allow for intensive re-nesting opportunities compared to the prairie pothole region (Raquel et al. 2016). Realized population growth rate was concurrently estimated at 0.76 (SD = 0.24) for mallards and 0.93 (SD = 0.56) for gadwall from 2019-2020, indicating a precipitous drop in population size during that time. While low, this is not far outside the possible ranges estimated for other populations, including a  $\lambda$  of 0.82 at mean vital rate values estimated by Hoekman et al. (2002) in midcontinent mallards and 0.77 (95% confidence interval = 0.53-1.11) estimated by Amundson et al. (2013) in North Dakota. We had predicted that cold, snowy springs may produce high-quality nesting and brood-rearing habitat for gadwall, which nested nearly a month later than mallards, on average, despite impeding mallard nesting. Gadwall appeared to fare better than mallards during cold springs, but still experienced the cost of harsh conditions on reproduction. Further research into the differences in demography across species in these systems is therefore warranted given the high variability in nest initiation dates and the rapid changes in conditions within a given breeding season. Gadwall, while abundant in this system, were difficult to trap using baited swim-in traps and required specialized night-lighting capture efforts. Focused efforts in the future to increase banded sample sizes would improve the precision needed to detect biologically-relevant changes in recruitment across years.

The results of our study suggest that management strategies might prioritize improving habitat for waterfowl by focusing on habitats that benefit recruitment rather than on HY or AHY survival in the Intermountain West. Across most waterfowl populations, the primary predictor of population size, growth, and recruitment is typically water availability (e.g., pond count; Krapu

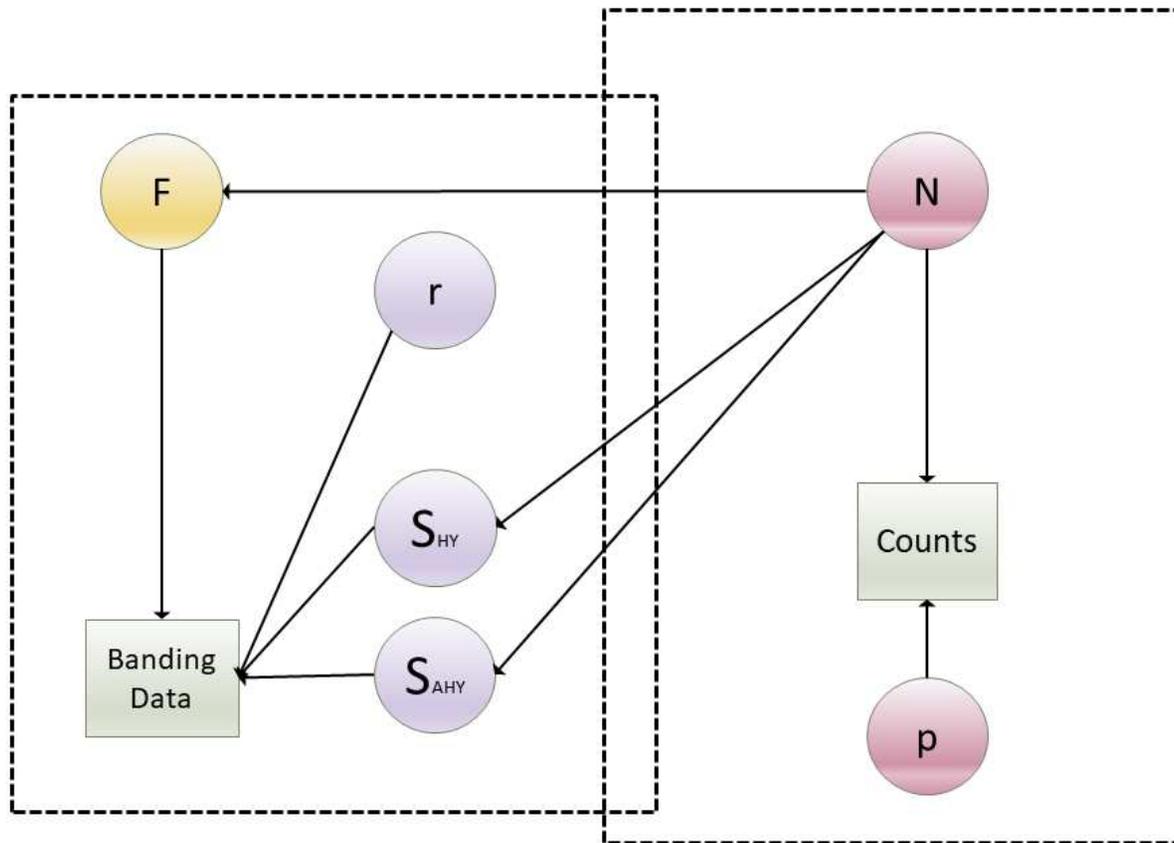
et al. 1983, Batt et al. 1989, Walker et al. 2013). In this system, snowpack predominantly drives hydrology and spring conditions disproportionately affect early nesters like mallards. Years with higher snow-water equivalent measurements in the mountains surrounding the study system were associated with higher AHY survival. Additionally, we found that recruitment exhibited a quadratic relationship with growing degree days, indicating that recruitment was highest when spring conditions were intermediate rather than extremely cold or extremely warm. This may suggest that mallards are not nesting when conditions are too snowy and cold (or not succeeding), reducing the cost-of-reproduction effects on survival, but limiting contributions to the population the following year. This might be a sign that habitats along the edge of the core waterfowl breeding area are acting as intermittent sinks for the source population within the midcontinent. In other words, they are allowing mallards to exploit them when conditions are just right and thus augmenting the overall population, but contributing less to the continental population when conditions deviate slightly from “average.” This concept warrants further exploration, as it would have considerable implications for the viability of fringe populations as climate and land-use change continue to alter the productivity of core breeding areas. Studies like ours lay the foundation for continued efforts to understand long-term dynamics of populations at key breeding locations and how those dynamics might vary spatially across heterogeneous landscapes and conditions.

**Table 4.1:** Years of release for mallards and gadwall banded in North Park, Colorado. Releases were included in a Brownie band-recovery model and constraints were placed on each likelihood to allow recoveries until the year noted in the table.

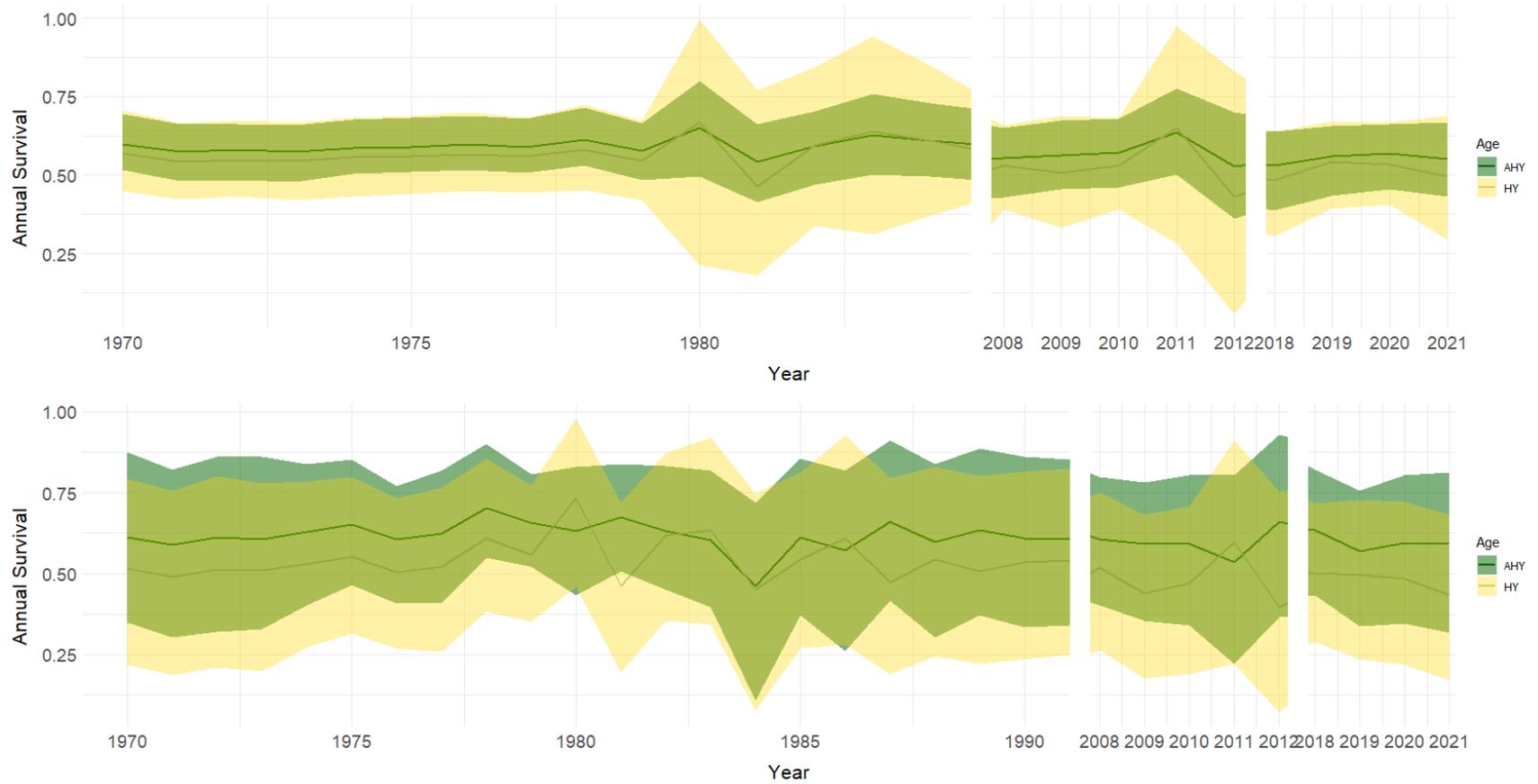
<b>Year Cohort</b>	<b>Recovered Until</b>
1971-1980 (mallards)	1990
1971-1975 (gadwall)	1990
2008-2010	2015
2018-2022	2023

**Table 4.2:** Sample sizes of banded mallards and gadwall during each year of release included in the Brownie band-recovery submodel of an integrated population model.

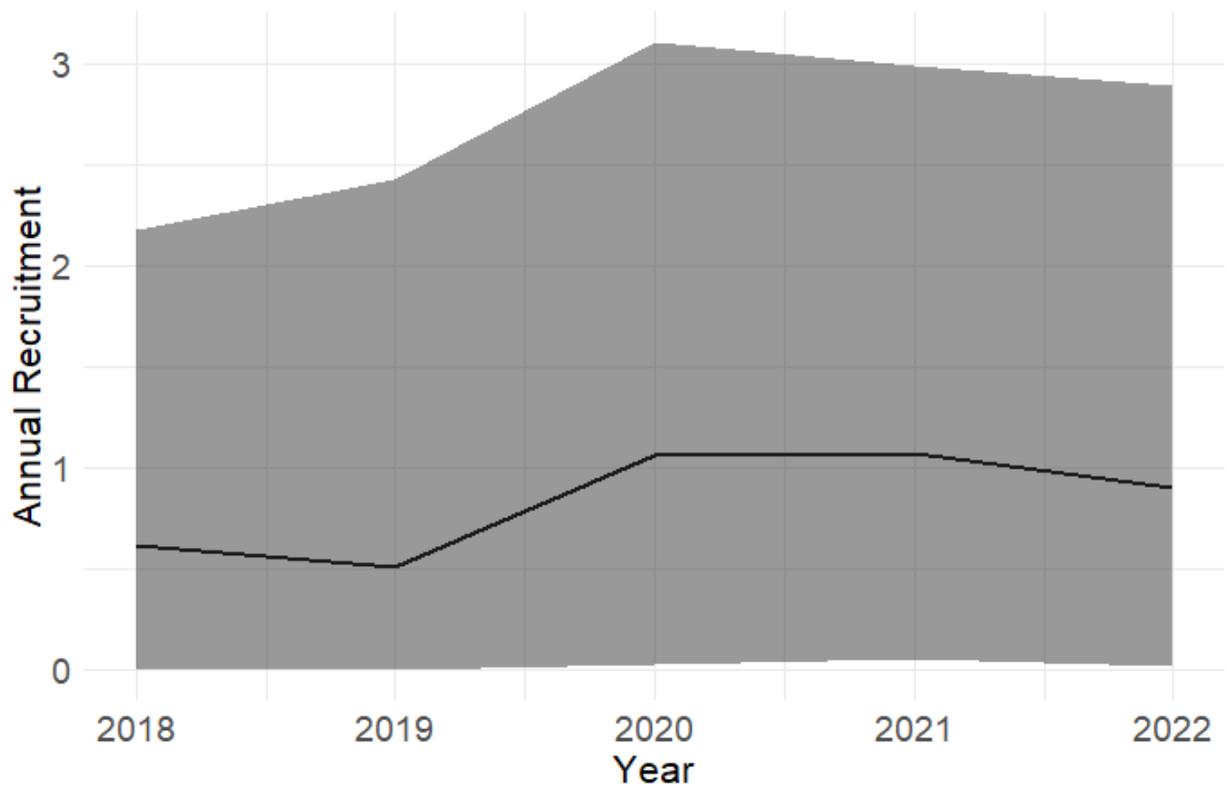
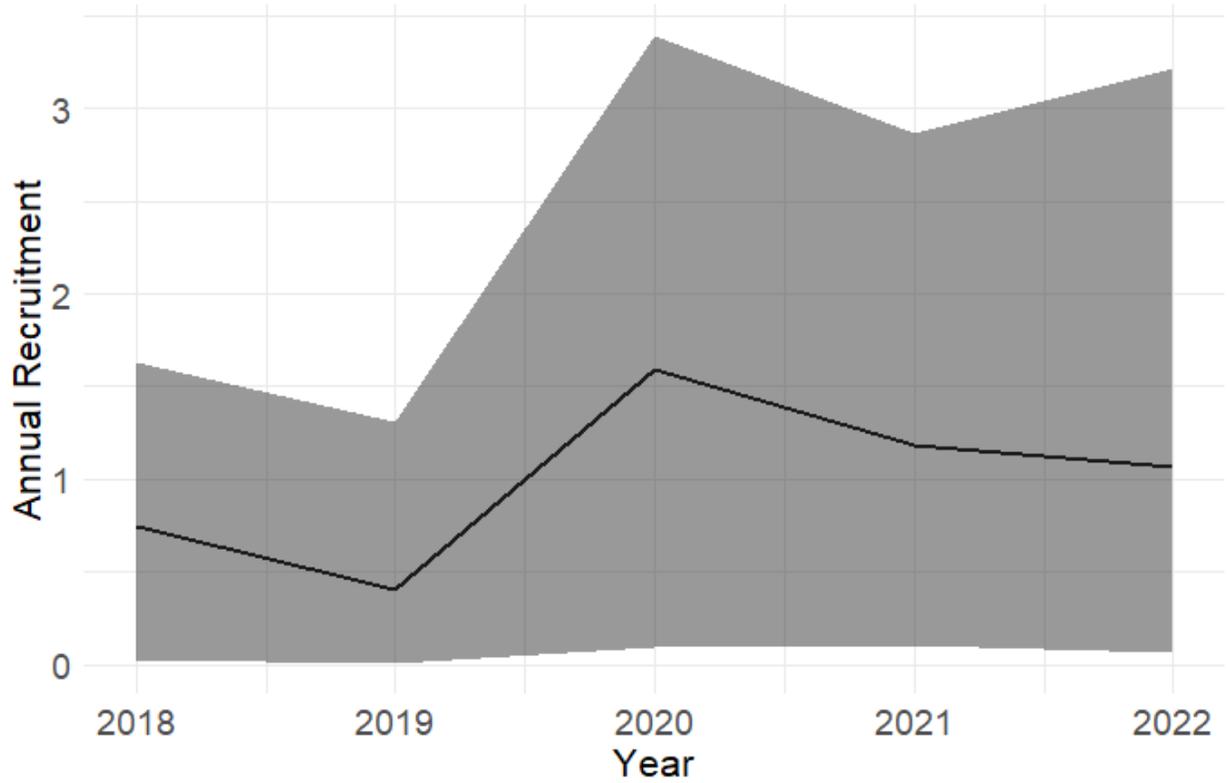
<b>Year</b>	<b>No. Mallards Released</b>	<b>No. Gadwall Released</b>
1971	555	1
1972	549	63
1973	523	12
1974	626	9
1975	521	88
1976	487	304
1977	490	331
1978	390	115
1979	666	380
1980	459	344
1981	0	269
1982	0	226
1983	0	296
1984	91	333
1985	19	292
2008	108	113
2009	201	72
2010	156	87
2018	214	12
2019	183	41
2020	336	133
2021	134	12
2022	169	89



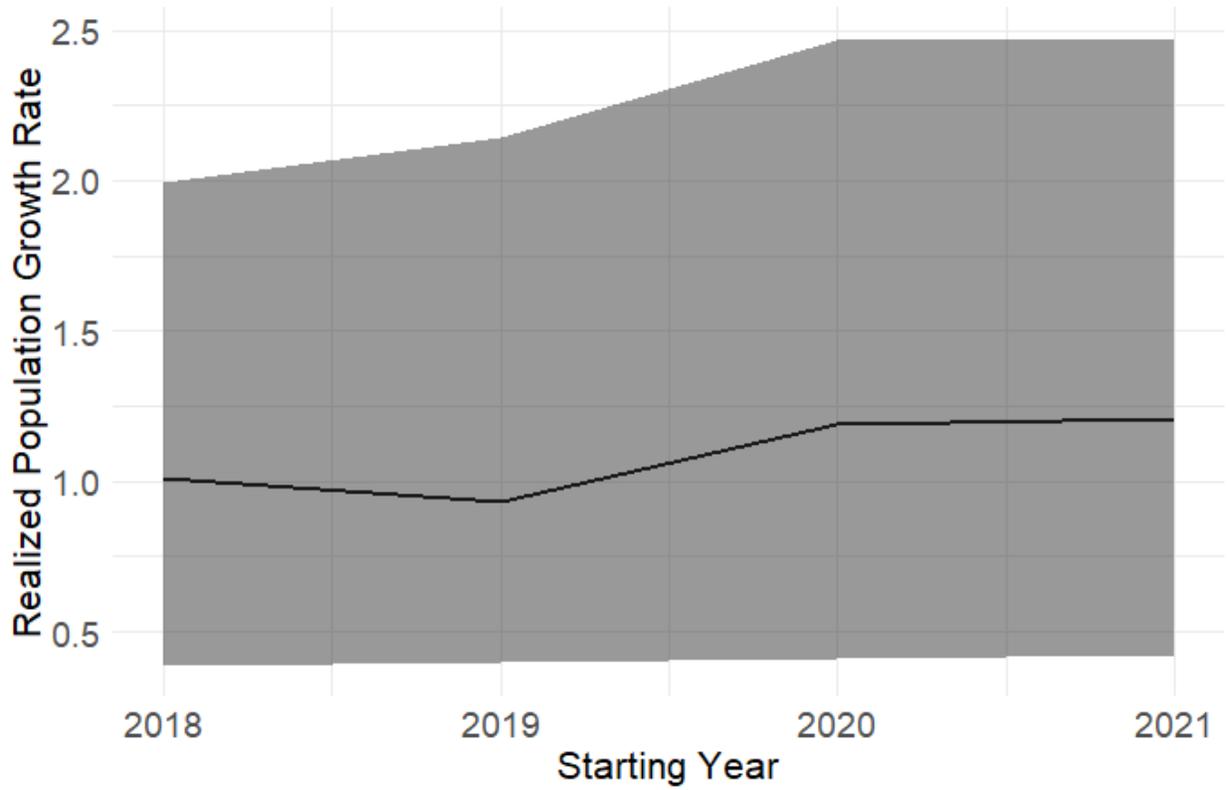
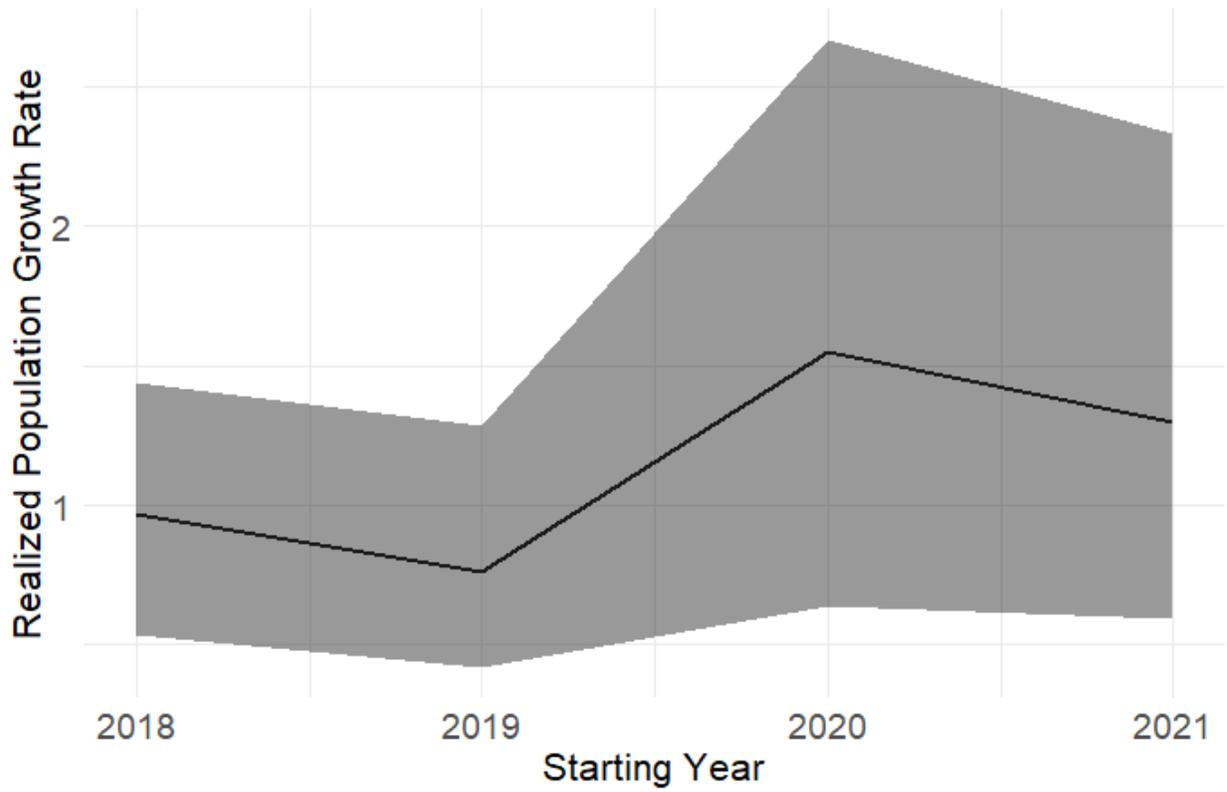
**Figure 4.1:** Heuristic diagram of an integrated population model combining multiple waterfowl datasets from the North Park study area. Demographic parameters are represented by circles and data are represented by squares. Arrows indicate dependencies between nodes, dashed boxes indicate which parameters share information, and abbreviations are described in the main text.



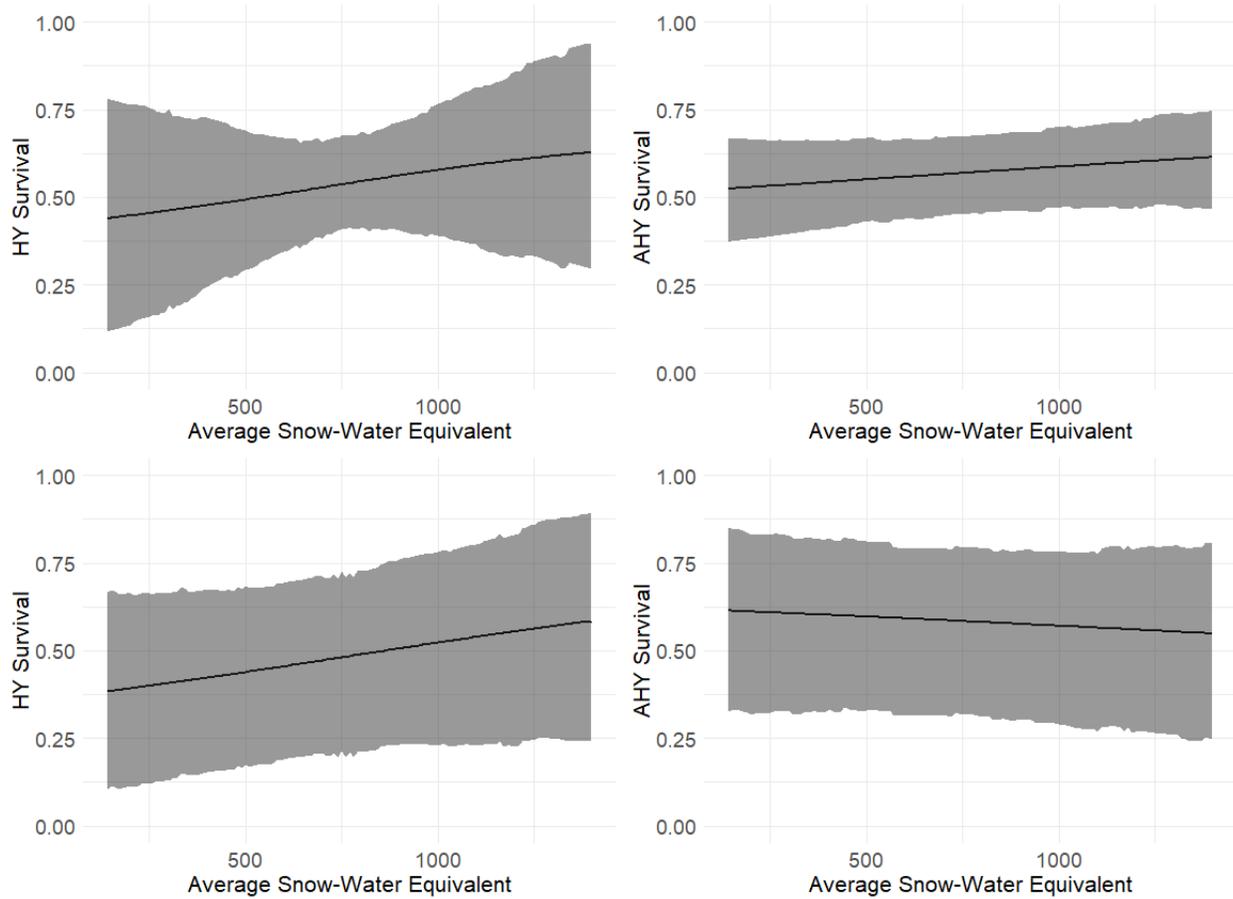
**Figure 4.2:** Survival probabilities of mallards (top) and gadwall (bottom) from 1970-2022 in North Park, Colorado.



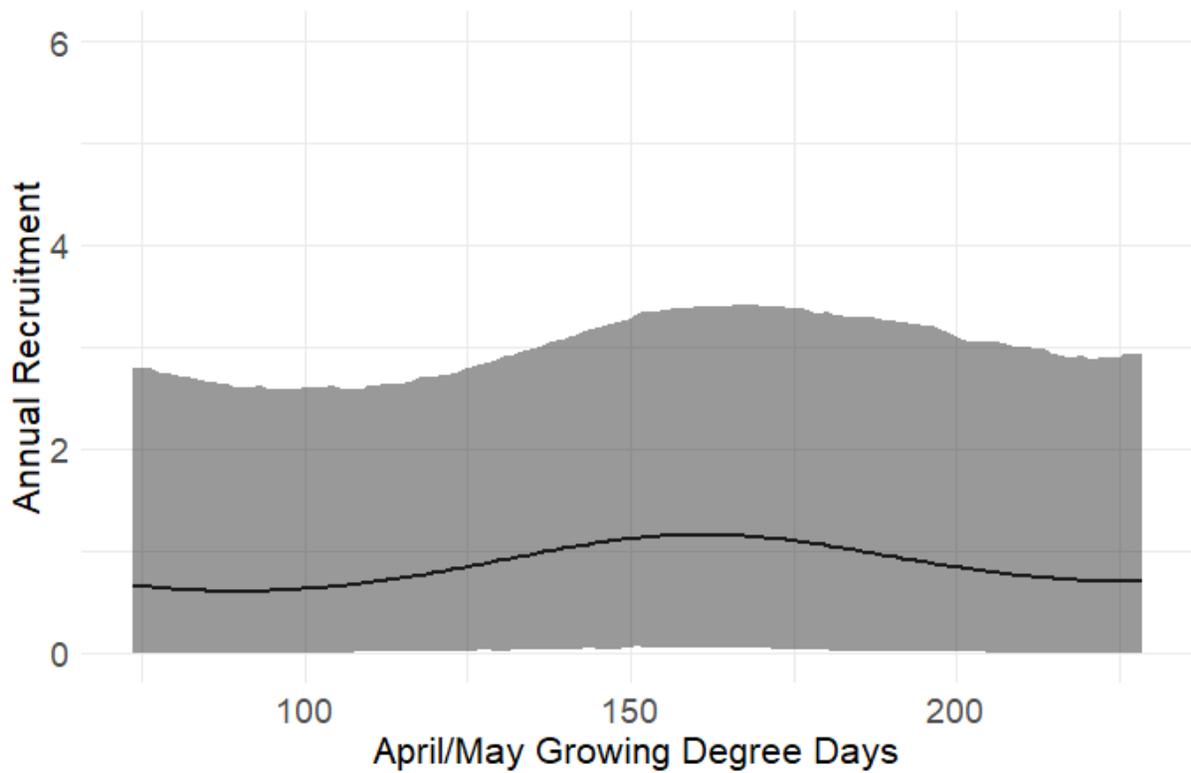
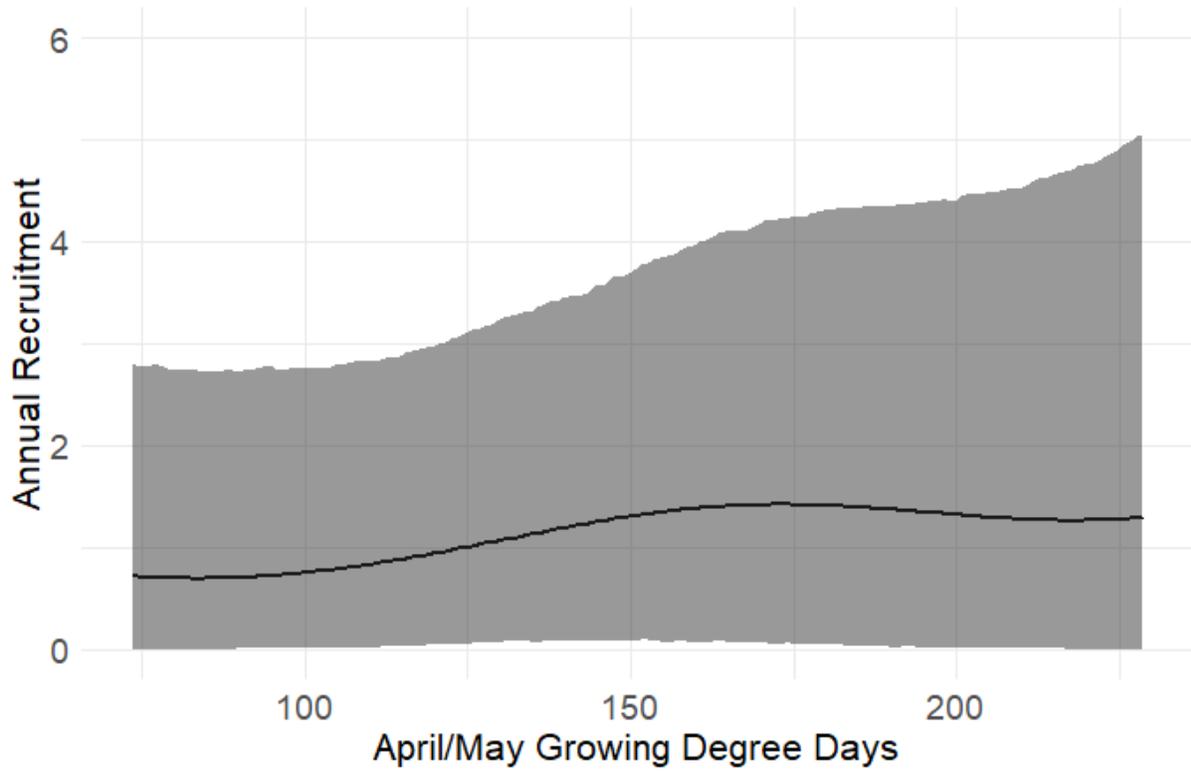
**Figure 4.3:** Recruitment estimates of mallards (top) and gadwall (bottom) in North Park, Colorado from 2018-2022.



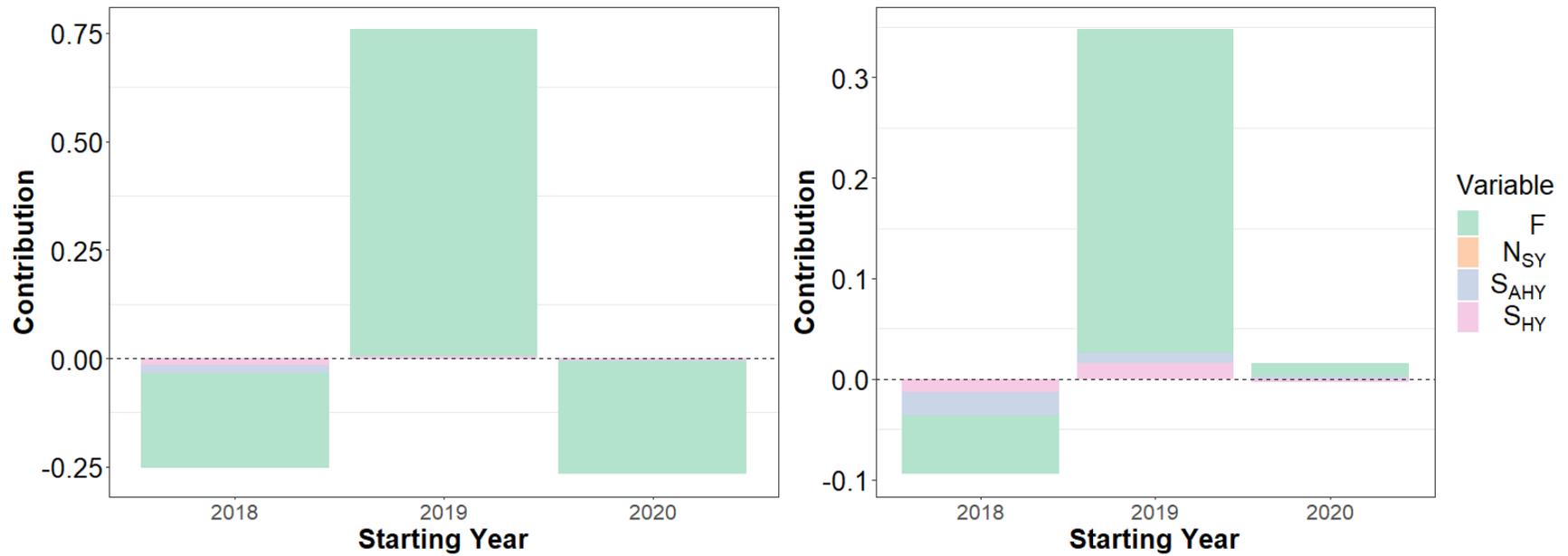
**Figure 4.4:** Realized population growth rate of mallards (top) and gadwall (bottom) in North Park, Colorado from 2018-2022.



**Figure 4.5:** Prediction plots showing the relationship between annual survival and May snow-water equivalent from 2018-2022 in North Park, Colorado. Mallards are represented by the top two panels and gadwall are represented by the bottom panels. Left panels are hatch-year (HY) survival and right panels are after-hatch-year (AHY) survival.



**Figure 4.6:** Relationship between growing degree days (GDD) and annual recruitment for mallards (top) and gadwall (bottom).



**Figure 4.7:** Plot showing the contribution of each demographic parameter to the change in realized population growth rate each year of the study. Years represent the starting year used to compute  $\Delta\lambda_t$ . Mallards are represented by the left panel and gadwall are on the right.

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APPENDIX S1

**Table S1:** Species and year random effect estimates resulting from fine-scale nest site selection and nest survival models including visual obstruction as a covariate.

Random Effect	Fine-Scale Nest Site Selection (SD)	Nest Survival (SD)
Species 1 - AGWT	-0.01 (0.19)	-0.19 (0.68)
Species 2 – AMWI	-0.02 (0.20)	0.34 (0.66)
Species 3 – BWTE	0.01 (0.20)	0.20 (0.59)
Species 4 – CITE	0.00 (0.14)	-0.10 (0.33)
Species 5 – GADW	0.01 (0.14)	0.01 (0.31)
Species 6 – MALL	-0.11 (0.17)	-0.06 (0.32)
Species 7 – NOPI	0.00 (0.18)	-0.05 (0.46)
Species 8 – NSHO	0.02 (0.15)	-0.21 (0.40)
Species 9 – Teal spp.	0.02 (0.19)	
Species 10 – Unknown	-0.01 (0.19)	
Year 1 – 2018	-3.44 (0.51)	0.46 (0.49)
Year 2 - 2019		0.30 (0.49)
Year 3 – 2020	-3.30 (0.51)	-0.12 (0.46)
Year 4 – 2021	-3.06 (0.50)	-0.32 (0.47)
Year 5 – 2022	-3.46 (0.51)	-0.27 (0.47)

**Table S2:** Species and year random effect estimates resulting from fine-scale nest site selection and nest survival models including percent cover of litter as a covariate.

Random Effect	Fine-Scale Nest Site Selection (SD)	Nest Survival (SD)
Species 1 - AGWT	-0.40 (1.02)	-0.11 (0.45)
Species 2 – AMWI	-0.36 (0.95)	0.24 (0.56)
Species 3 – BWTE	-0.35 (0.98)	0.14 (0.49)
Species 4 – CITE	-0.38 (0.94)	-0.06 (0.25)
Species 5 – GADW	-0.39 (0.94)	-0.01 (0.24)
Species 6 – MALL	-0.36 (0.93)	-0.01 (0.24)
Species 7 – NOPI	-0.37 (0.97)	-0.03 (0.38)
Species 8 – NSHO	-0.36 (0.93)	-0.11 (0.30)
Species 9 – Teal spp.	-0.34 (0.94)	
Species 10 – Unknown	-0.37 (0.99)	
Year 1 – 2018	-2.06 (0.90)	0.43 (0.46)
Year 2 – 2019		0.34 (0.47)
Year 3 – 2020	-2.10 (0.92)	-0.15 (0.44)
Year 4 – 2021	-2.11 (0.92)	-0.39 (0.44)
Year 5 – 2022	-2.06 (0.92)	-0.29 (0.45)

**Table S3:** Species and year random effect estimates resulting from fine-scale nest site selection and nest survival models including percent cover of grass as a covariate.

<b>Random Effect</b>	<b>Fine-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.02 (0.25)	-0.23 (0.71)
Species 2 – AMWI	-0.02 (0.25)	0.41 (0.72)
Species 3 – BWTE	-0.02 (0.28)	0.22 (0.65)
Species 4 – CITE	-0.03 (0.23)	-0.13 (0.33)
Species 5 – GADW	-0.03 (0.23)	0.02 (0.31)
Species 6 – MALL	-0.03 (0.23)	-0.04 (0.31)
Species 7 – NOPI	-0.03 (0.26)	-0.03 (0.47)
Species 8 – NSHO	-0.03 (0.24)	-0.24 (0.40)
Species 9 – Teal spp.	-0.02 (0.25)	
Species 10 – Unknown	-0.02 (0.25)	
Year 1 – 2018	-2.40 (1.31)	0.51 (0.50)
Year 2 – 2019		0.37 (0.50)
Year 3 – 2020	-2.35 (1.31)	-0.11 (0.45)
Year 4 – 2021	-2.37 (1.31)	-0.30 (0.44)
Year 5 – 2022	-2.37 (1.31)	-0.26 (0.46)

**Table S4:** Species and year random effect estimates resulting from fine-scale nest site selection and nest survival models including percent cover of forbs as a covariate.

<b>Random Effect</b>	<b>Fine-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.00 (0.16)	-0.20 (0.68)
Species 2 – AMWI	-0.00 (0.15)	0.38 (0.74)
Species 3 – BWTE	-0.00 (0.16)	0.25 (0.67)
Species 4 – CITE	-0.01 (0.13)	-0.09 (0.31)
Species 5 – GADW	-0.01 (0.12)	0.03 (0.30)
Species 6 – MALL	0.01 (0.12)	-0.09 (0.31)
Species 7 – NOPI	0.00 (0.16)	-0.04 (0.49)
Species 8 – NSHO	-0.00 (0.13)	-0.23 (0.39)
Species 9 – Teal spp.	-0.01 (0.16)	
Species 10 – Unknown	-0.01 (0.17)	
Year 1 – 2018	-2.52 (0.27)	0.43 (0.41)
Year 2 – 2019		0.26 (0.42)
Year 3 – 2020	-2.53 (0.28)	-0.14 (0.37)
Year 4 – 2021	-2.50 (0.27)	-0.30 (0.37)
Year 5 – 2022	-2.46 (0.28)	-0.23 (0.38)

**Table S5:** Species and year random effect estimates resulting from fine-scale nest site selection and nest survival models including percent cover of shrubs as a covariate.

<b>Random Effect</b>	<b>Fine-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.03 (0.19)	-0.34 (1.04)
Species 2 – AMWI	0.00 (0.19)	0.48 (1.03)
Species 3 – BWTE	0.00 (0.18)	0.41 (1.27)
Species 4 – CITE	0.01 (0.13)	-0.15 (0.38)
Species 5 – GADW	-0.03 (0.13)	-0.01 (0.35)
Species 6 – MALL	-0.04 (0.13)	-0.08 (0.36)
Species 7 – NOPI	0.01 (0.17)	-0.06 (0.53)
Species 8 – NSHO	0.02 (0.14)	-0.22 (0.45)
Species 9 – Teal spp.	0.01 (0.19)	
Species 10 – Unknown	0.01 (0.17)	
Year 1 – 2018	-2.36 (1.19)	0.48 (0.45)
Year 2 – 2019		0.34 (0.45)
Year 3 – 2020	-2.45 (1.20)	-0.11 (0.41)
Year 4 – 2021	-2.30 (1.18)	-0.24 (0.40)
Year 5 – 2022	-2.44 (1.20)	-0.27 (0.40)

**Table S6:** Species and year random effect estimates resulting from fine-scale nest site selection and nest survival models including percent cover of sedges as a covariate.

<b>Random Effect</b>	<b>Fine-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.00 (0.16)	-0.17 (0.62)
Species 2 – AMWI	-0.00 (0.15)	0.33 (0.65)
Species 3 – BWTE	-0.00 (0.16)	0.18 (0.61)
Species 4 – CITE	-0.00 (0.12)	-0.04 (0.29)
Species 5 – GADW	-0.01 (0.12)	0.04 (0.28)
Species 6 – MALL	-0.01 (0.12)	-0.07 (0.29)
Species 7 – NOPI	0.00 (0.15)	-0.03 (0.44)
Species 8 – NSHO	0.01 (0.13)	-0.22 (0.39)
Species 9 – Teal spp.	0.00 (0.15)	
Species 10 – Unknown	0.00 (0.15)	
Year 1 – 2018	-3.68 (0.89)	0.57 (0.54)
Year 2 – 2019		0.37 (0.55)
Year 3 – 2020	-3.62 (0.90)	-0.21 (0.51)
Year 4 – 2021	-3.65 (0.89)	-0.31 (0.49)
Year 5 – 2022	-3.66 (0.89)	-0.21 (0.50)

**Table S7:** Species and year random effect estimates resulting from fine-scale nest site selection and nest survival models including percent cover of rushes as a covariate.

<b>Random Effect</b>	<b>Fine-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	0.00 (0.14)	-0.29 (0.2)
Species 2 – AMWI	-0.01 (0.14)	0.60 (0.91)
Species 3 – BWTE	0.00 (0.14)	0.33 (0.86)
Species 4 – CITE	-0.01 (11)	-0.17 (0.40)
Species 5 – GADW	-0.00 (10)	0.05 (0.38)
Species 6 – MALL	-0.01 (0.10)	-0.05 (0.39)
Species 7 – NOPI	-0.00 (0.13)	-0.06 (0.60)
Species 8 – NSHO	-0.00 (0.12)	-0.41 (0.53)
Species 9 – Teal spp.	0.00 (0.14)	
Species 10 – Unknown	-0.01 (0.14)	
Year 1 – 2018	-3.12 (1.58)	0.49 (0.45)
Year 2 – 2019		0.31 (0.46)
Year 3 – 2020	-3.15 (1.59)	-0.16 (0.42)
Year 4 – 2021	-3.10 (1.57)	-0.34 (0.42)
Year 5 – 2022	-3.11 (1.58)	-0.26 (0.42)

**Table S8:** Species and year random effect estimates resulting from patch-scale nest site selection and nest survival models including distance to river as a covariate.

<b>Random Effect</b>	<b>Patch-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.72 (0.75)	-0.17 (0.60)
Species 2 – AMWI	-0.71 (0.76)	0.34 (0.68)
Species 3 – BWTE	-0.66 (0.88)	0.25 (0.68)
Species 4 – CITE	-0.08 (0.53)	-0.07 (0.29)
Species 5 – GADW	-0.61 (0.52)	0.03 (0.28)
Species 6 – MALL	-0.55 (0.52)	-0.01 (0.28)
Species 7 – NOPI	-0.55 (0.69)	-0.03 (0.44)
Species 8 – NSHO	0.00 (0.55)	-0.23 (0.38)
Year 1 – 2018		0.47 (0.42)
Year 2 – 2019		0.32 (0.43)
Year 3 – 2020		-0.13 (0.40)
Year 4 – 2021		-0.37 (0.39)
Year 5 – 2022		-0.25 (0.39)

**Table S9:** Species and year random effect estimates resulting from patch-scale nest site selection and nest survival models including distance to irrigation ditch as a covariate.

<b>Random Effect</b>	<b>Patch-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.76 (0.75)	-0.22 (0.76)
Species 2 – AMWI	-0.69 (0.76)	0.41 (0.88)
Species 3 – BWTE	-0.73 (0.85)	0.29 (0.85)
Species 4 – CITE	-0.07 (0.52)	-0.07 (0.34)
Species 5 – GADW	-0.56 (0.51)	0.05 (0.33)
Species 6 – MALL	-0.54 (0.51)	-0.05 (0.33)
Species 7 – NOPI	-0.62 (0.68)	-0.01 (0.50)
Species 8 – NSHO	0.10 (0.55)	-0.20 (0.40)
Year 1 – 2018		0.43 (0.41)
Year 2 – 2019		0.27 (0.41)
Year 3 – 2020		-0.13 (0.39)
Year 4 – 2021		-0.34 (0.38)
Year 5 – 2022		-0.22 (0.38)

**Table S10:** Species and year random effect estimates resulting from patch-scale nest site selection and nest survival models including distance to road as a covariate.

<b>Random Effect</b>	<b>Patch-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.72 (0.76)	-0.20 (0.68)
Species 2 – AMWI	-0.62 (0.75)	0.38 (0.70)
Species 3 – BWTE	-0.70 (0.84)	0.21 (0.66)
Species 4 – CITE	-0.05 (0.52)	-0.10 (0.33)
Species 5 – GADW	-0.56 (0.51)	0.02 (0.31)
Species 6 – MALL	-0.53 (0.52)	-0.08 (0.32)
Species 7 – NOPI	-0.66 (0.70)	-0.03 (0.46)
Species 8 – NSHO	0.11 (0.55)	-0.16 (0.38)
Year 1 – 2018		0.46 (0.45)
Year 2 – 2019		0.26 (0.46)
Year 3 – 2020		-0.20 (0.45)
Year 4 – 2021		-0.33 (0.43)
Year 5 – 2022		-0.27 (0.44)

**Table S11:** Species and year random effect estimates resulting from patch-scale nest site selection and nest survival models including distance to open water as a covariate.

<b>Random Effect</b>	<b>Patch-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.69 (0.75)	-0.14 (0.56)
Species 2 – AMWI	-0.62 (0.75)	0.31 (0.63)
Species 3 – BWTE	-0.72 (0.86)	0.20 (0.56)
Species 4 – CITE	-0.12 (0.53)	-0.09 (0.36)
Species 5 – GADW	-0.58 (0.51)	0.03 (0.35)
Species 6 – MALL	-0.57 (0.52)	-0.04 (0.36)
Species 7 – NOPI	-0.60 (0.68)	-0.04 (0.46)
Species 8 – NSHO	0.05 (0.55)	-0.20 (0.44)
Year 1 – 2018		0.51 (0.45)
Year 2 – 2019		0.33 (0.46)
Year 3 – 2020		-0.10 (0.43)
Year 4 – 2021		-0.37 (0.42)
Year 5 – 2022		-0.32 (0.43)

**Table S12:** Species and year random effect estimates resulting from patch-scale nest site selection and nest survival models including distance to harvested hay meadow as a covariate.

<b>Random Effect</b>	<b>Patch-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.79 (0.75)	-0.16 (0.61)
Species 2 – AMWI	-0.65 (0.73)	0.35 (0.65)
Species 3 – BWTE	-0.66 (0.87)	0.20 (0.60)
Species 4 – CITE	-0.11 (0.52)	-0.10 (0.31)
Species 5 – GADW	-0.62 (0.51)	0.02 (0.30)
Species 6 – MALL	-0.60 (0.51)	-0.10 (0.31)
Species 7 – NOPI	-0.65 (0.68)	-0.03 (0.46)
Species 8 – NSHO	0.08 (0.55)	-0.23 (0.39)
Year 1 – 2018		0.52 (0.49)
Year 2 – 2019		0.34 (0.50)
Year 3 – 2020		-0.10 (0.46)
Year 4 – 2021		-0.38 (0.45)
Year 5 – 2022		-0.27 (0.45)

**Table S13:** Species and year random effect estimates resulting from patch-scale nest site selection and nest survival models including distance to unharvested irrigated meadow as a covariate.

<b>Random Effect</b>	<b>Patch-Scale Nest Site Selection (SD)</b>	<b>Nest Survival (SD)</b>
Species 1 - AGWT	-0.81 (0.75)	-0.17 (0.66)
Species 2 – AMWI	-0.72 (0.74)	0.34 (0.73)
Species 3 – BWTE	-0.83 (0.87)	0.23 (0.68)
Species 4 – CITE	-0.16 (0.53)	-0.10 (0.37)
Species 5 – GADW	-0.70 (0.52)	0.02 (0.35)
Species 6 – MALL	-0.64 (0.52)	-0.08 (0.36)
Species 7 – NOPI	-0.54 (0.70)	-0.05 (0.46)
Species 8 – NSHO	0.05 (0.55)	-0.19 (0.42)
Year 1 – 2018		0.48 (0.44)
Year 2 – 2019		0.31 (0.45)
Year 3 – 2020		-0.13 (0.42)
Year 4 – 2021		-0.35 (0.42)
Year 5 – 2022		-0.29 (0.43)

APPENDIX S1.2

**Table S1.2:** Daily survival rate estimates and standard deviations from each nest survival model including fine-scale vegetation covariates.

<b>Model Structure</b>	<b>Daily Survival Rate Estimate (SD)</b>
Visual obstruction rating	0.95 (0.02)
% Litter	0.95 (0.02)
% Grass	0.95 (0.02)
% Forbs	0.95 (0.02)
% Shrubs	0.94 (0.04)
% Sedges	0.95 (0.03)
% Rushes	0.95 (0.03)

**Table S2.2:** Daily survival rate estimates and standard deviations from each nest survival model including patch-scale vegetation covariates.

<b>Model Structure</b>	<b>Daily Survival Rate Estimate (SD)</b>
Distance to river	0.95 (0.02)
Distance to irrigation ditch	0.95 (0.02)
Distance to road	0.94 (0.03)
Distance to open water	0.95 (0.02)
Distance to harvested hay meadow	0.94 (0.06)
Distance to uncut irrigated meadow	0.95 (0.02)

APPENDIX S2

**Table S2.1:** Coefficient estimates for habitat effects and habitat x sampling occasion interactions in a model of macroinvertebrate energy density (joules/cm<sup>3</sup>).

<b>Coefficient Description</b>	<b>Coefficient Value (SD)</b>
Habitat – Basin	0.00 (0.00)
Habitat – Ditch	-1.91 (0.27)
Habitat – Hay Meadow	-1.26 (0.63)
Habitat – Reservoir	-1.22 (0.66)
Habitat – Riparian	-1.89 (0.28)
Basin x Occasion 1	0.00 (0.00)
Basin x Occasion 2	0.00 (0.00)
Basin x Occasion 3	0.00 (0.00)
Basin x Occasion 4	0.00 (0.00)
Basin x Occasion 5	0.00 (0.00)
Basin x Occasion 6	0.00 (0.00)
Ditch x Occasion 1	0.00 (0.00)
Ditch x Occasion 2	-0.28 (0.41)
Ditch x Occasion 3	-0.10 (0.38)
Ditch x Occasion 4	0.74 (0.39)
Ditch x Occasion 5	1.75 (0.52)
Ditch x Occasion 6	0.51 (0.56)
Hay x Occasion 1	0.00 (0.00)
Hay x Occasion 2	0.26 (0.76)
Hay x Occasion 3	-0.03 (0.71)
Hay x Occasion 4	1.12 (0.70)
Hay x Occasion 5	0.62 (0.76)
Hay x Occasion 6	1.09 (0.95)
Reservoir x Occasion 1	0.00 (0.00)
Reservoir x Occasion 2	0.01 (0.44)
Reservoir x Occasion 3	0.42 (0.41)
Reservoir x Occasion 4	1.00 (0.41)
Reservoir x Occasion 5	1.29 (0.43)
Reservoir x Occasion 6	1.81 (0.40)
Riparian x Occasion 1	0.00 (0.00)
Riparian x Occasion 2	-0.52 (0.42)
Riparian x Occasion 3	-0.77 (0.39)
Riparian x Occasion 4	0.49 (0.39)
Riparian x Occasion 5	1.18 (0.42)
Riparian x Occasion 6	1.26 (0.39)

APPENDIX S3

**Table S3.1:** Seber recovery results from the Bayesian band recovery model for 13 species of waterfowl fitted with only a metal band or also with a GPS tag. Species included lesser snow goose (LSGO), greater snow goose (GSGO), greater white-fronted goose (GWFG), black brant (BLBR), Canada goose (CANG), wood duck (WODU), cinnamon teal (CITE), gadwall (GADW), American wigeon (AMWI), mallard (MALL), American black duck (ABDU), northern pintail (NOPI), and lesser scaup (LESC). All numbers are rounded to the second decimal place. All estimates represent recovery rates for birds released during the pre-hunting-season banding period, regardless of how many seasons of release were included in the model to allow for comparisons.

Species	$r_{\text{band}}$ (SD)	$r_{\text{tag}}$ (SD)	Years	No. bands recovered (No. released)	No. tags recovered (No. released)
LSGO <sup>b</sup>	0.12 (0.01)	0.12 (0.06)	2012-2021	2338 (40948)	14 (122)
GSGO <sup>a</sup>	0.07 (0.01)	0.24 (0.05)	2006-2021	749 (11925)	24 (152)
GWFG <sup>b</sup>	0.14 (0.09)	0.17 (0.13)	2011-2021	1103 (9153)	12 (104)
BLBR <sup>a</sup>	0.04 (0.01)	0.11 (0.05)	2006-2021	292 (25288)	10 (111)
CANG <sup>b</sup>	0.25 (0.01)	0.10 (0.02)	2008-2021	30914 (293724)	28 (205)
WODU <sup>a</sup>	0.12 (0.00)	0.17 (0.08)	2006-2021	8281 (94916)	5 (33)
CITE <sup>a</sup>	0.08 (0.03)	0.21 (0.06)	2015-2021	58 (2065)	15 (119)
GADW <sup>a</sup>	0.22 (0.12)	0.32 (0.16)	2015-2021	42 (743)	13 (105)
AMWI <sup>a</sup>	0.11 (0.09)	0.16 (0.13)	2005-2021	112 (1516)	6 (75)
MALL <sup>a</sup>	0.22 (0.00)	0.27 (0.03)	2005-2021	15551 (156676)	83 (701)

ABDU <sup>a</sup>	0.17 (0.01)	0.22 (0.10)	2005-2021	1423 (22457)	6 (140)
NOPI <sup>a</sup>	0.04 (0.01)	0.24 (0.06)	2015-2021	82 (5556)	23 (218)
LESC <sup>c</sup>	0.13 (0.06)	0.29 (0.13)	2005-2021	145 (1040)	10 (97)

<sup>a</sup> - backpack attachment style comprised majority of sample

<sup>b</sup> - neck collar attachment style comprised majority of sample

<sup>c</sup> - implant attachment style comprised majority of sample