2014

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Recommended Citation
Hansen, Warren Kevin, "Causes of annual reproductive variation and anthropogenic disturbance in harlequin ducks breeding in glacier national park, montana" (2014). *Theses, Dissertations, Professional Papers.* Paper 4290.

CAUSES OF ANNUAL REPRODUCTIVE VARIATION AND ANTHROPOGENIC DISTURBANCE IN HARLEQUIN DUCKS BREEDING IN GLACIER NATIONAL PARK, MONTANA

By

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Thesis

Presented in partial fulfillment of the requirements for the degree of

Master of Science
In Wildlife Biology

The University of Montana

Missoula, MT

May 2014

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Hansen, Warren, M.S. Draft, May 2014

Sources of annual reproductive variation and anthropogenic disturbance in harlequin ducks breeding in Glacier National Park, Montana

Advisor: Dr. Creagh Breuner

ABSTRACT

Annual reproductive variation is the central focus of many ecological studies. Variation in reproductive success is an important vital rate to study because it can lead to inferences about population health, extinction risk, human disturbance and habitat quality. The identification of the causes of reproductive variability can help guide conservation and management efforts of a species. In Glacier National Park, Montana I studied causes of annual reproductive variation and behavioral responses to human disturbance in a breeding population of harlequin ducks (*Histrionicus histrionicus*). Harlequins are rare sea ducks with a Holarctic distribution and winter along rocky coast lines of North America. Females reach reproductive maturity at age 3. At this time they bond with a male that they will breed with for life. Recent band re-sighting has revealed that these ducks can live up to at least 21 years. In spring pairs migrate inland to the female's natal montane stream to breed. My study focused on the breeding season from April – September on Upper McDonald Creek, Glacier National Park, Montana. My objective was to study 3 potential indirect and direct sources of reproductive variation in Harlequin ducks on this breeding stream; 1) stream flow effects on annual reproductive success, 2) human presence and effects on stream patch occupancy and resource selection, and 3) carry-over effects of physiological measures of body condition, baseline corticosterone levels (primary stress hormone in birds), and integrated measures of corticosterone deposition in feathers. For my first objective I identified 4 different parameters of stream flow that accounted for 32% of the annual variation in reproductive success. I conclude that these parameters will be very sensitive to climate change, making reproduction challenging for harlequins into the future. For my second objective I found greater probability of occupancy of ducks in high human use sites and in stream patches closer to roads. I also found greater occupancy in pool habitat; surprisingly, this pool habitat also had a greater distribution close to road. I conclude from this analysis that there were no strong negative effects of human disturbance on harlequin duck occupy and resource selection, but recommend that harlequin habitat near to human use areas be monitored closely. For my third objective I found that concentrations of corticosterone deposited in feathers grown just prior to reproduction predict reproductive success for that year. I did not find any predictive value of body condition or baseline corticosterone levels. The carry-over effects that I documented in the feathers grown during the prenuptial molt indicate that is an import period that reflects reproductive decision (may be 2 month separation from feather growth to egg lay). These 3 lines of inquiry identified important sources of annual reproductive variation and will help guide management and conservation efforts. We recommend further study to better understand important resources that harlequins select for on the breeding stream and intensive study of harlequin wintering habitat, especially prenuptial molt areas.

ACKNOWLEDGEMENTS

Many thanks to all the organizations that provided financial support that made this project possible. This work was supported by The Federal Highway Administration grant to LJB, a Rocky Mountain-Cooperative Ecosystem Studies Unit grant to LJB and CWB, Glacier National Park Conservancy grant to LJB, Jerry O'Neal National Park Fellowship grant to WKH, Mission Mountain Audubon Society grant to WKH, National Science Foundation (PSI-0747361) grant to CWB, Glacier National Park, and the University of Montana Wildlife Biology Program.

First I need to thank my Advisor Creagh Breuner. She has provided me with opportunities that I never would have dreamed possible. She has opened my eyes to the field of conservation physiology which I believe will be the key to the future of wildlife conservation. I am very grateful for her sticking with me and guiding me through this research.

This work was made possible by numerous park service employees that contributed to all aspects of this research. Lisa Bate initially received the first grant to initiate a harlequin duck research project. She had faith in my enthusiasm to learn and she recommended me for the project. She has been an incredible field biology mentor and an awesome resource at acquiring funding for the project. I have John Waller to thank for recommending to Lisa that she hire a graduate student to assist her on the harlequin project. John has been an excellent resource that has helped to guide the project. Mark Biel has been integral at providing administrative support in difficult times and field support. Courtney Raukar, Alaina Strehlow, Mary Ann Donovan and Clay Miller were phenomenal wildlife technicians that enabled consistent data collection and sacrificed their bodies on slippery rocks, hawthorn and devils club to ensure the safety of the ducks during trapping. They were also excellent company in the field and great friends to have during this project.

I am forever indebted to all of the volunteers that donated thousands of hours of their time and expertise surveying streams, trapping, tracking with telemetry and veterinary services: DVM Dan Savage, John Ashley, Cyndi Smith, Barbara Summer, Jim Rogers, Barry Hansen, McKay Breuner, Heather Jameson, Lindy Key, Peter Brumn, Dustin Allen, Tim Fawell, Gerard Byrd, Laura Holmquist, Gary Moses and Becca Marshall, Julian Cunningham, Marika Cunningham. Each person here was able to contribute an invaluable skill and was a critical link to the project that ensured its success. The veterinary support, years of harlequin knowledge in behavior and trapping, ecological knowledge of the system, photography, dedication, enthusiasm and friendship that all of the volunteers provided made this a very special project. I will always remember and hold these people in the highest regards.

Additionally I need to thank the Chizé Center for Biological Studies, Olivier Chastel, Fred Angelier, Stéphanie Dano, Charline Parenteau and Colette Trouvé. This group taught me the protocol, techniques, and assay for corticosterone extraction from feathers. They were very kind and helpful. Mostly they were very patient with my complete inadequacy of the French language.

Thank you to the University of Montana faculty for all of your support with idea development, proof reading, statistical knowledge and guidance: Art Woods, Paul Lukacs, Mark Hebblewhite and Jeanne Franz.

Finally I need to thank my family: my parents Barry and Anita for teaching me the value of the natural world, my brother Robin, sisters Buffy, Karen and Annie and my partner Heather for providing unwavering support throughout the duration of this project.

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CHAPTER 1: INTRODUCTION

The harlequin duck (*Histrionicus histrionicus*) is a small sea duck that winters along the coastal waters of North America and migrates inland to breed along montane streams. Harlequin duck breeding habitat is restricted to relatively undisturbed mountain streams, thus they are considered good indicators of stream ecosystem health (Montana Fish Wildlife and Parks 2012). Females do not reach reproductive maturity until age 3 and males at age 2. Pairs bond in the spring on the wintering grounds before migration to the breeding grounds. Pair bonds are strong and last for life (Smith et al. 2000). Due to their older breeding age and relatively low reproductive output, harlequin ducks are slow to recover from perturbations such as timber harvest, oil spills, and hunting (Wiggins 2005, Iverson and Esler 2010). As a result of this vulnerability, harlequin ducks are listed as a species of special concern in Montana (Montana-F.W.P. 2012) and across the rest of their range in the Pacific Northwest including Canada. Harlequin ducks in Montana are rare with a statewide population estimate of 150-200 pairs (Reichel 1996a). The highest density of breeding harlequin ducks in Montana exists on Upper McDonald creek in Glacier National Park. Twenty five percent of known harlequin duck broods are produced along a 16 km reach of Upper McDonald creek (Reichel 1996a). Park staff began studying Harlequin behavior and ecology in 1974 (Kuchel 1977a), but did not rigorously monitor breeding pairs until 1990. In 2010 no chicks were observed during standard surveys, suggesting complete reproductive failure of this breeding population (Bate 2010). Many studies report large annual variation in brood production, but have not conclusively identified the causes. There are likely multiple factors influencing potential declines in harlequin brood success in Upper McDonald Creek. Here I examine the importance of 3 potential factors: 1) Human disturbance, 2) Stream flow, 3) Stress physiology. The principle goal of my research is to better inform managers of the impacts of these 3 factors and how they contribute to annual reproductive variation.

Human presence in harlequin duck breeding territories in Glacier National Park may influence the behavior of resource selection and occupancy of breeding harlequin ducks. Roughly 2 million visitors come to Glacier National Park annually (IRMA data system 2014). Human disturbance has been considered a disturbance to breeding harlequin ducks, thus such activities as recreational boating have been banned on many breeding streams (Hume 1976b). Here I identify changes in behavior around human infrastructure and high human use areas by evaluating foraging activities and changes in occupancy and resource selection over time (Andersen 1990) as human presence increases as a function of traffic volume. Changes in distributions of heavily used areas by ducks and movements subjected to disturbance can elucidate how animals respond to changes in their environment (Dyke 1996).

Humans are additionally altering environments by impacting climate. Climate change in the Pacific North West is having profound effects on vital ecosystem processes (Stewart et al. 2005, Mote and Salathe Jr 2010, Goode et al. 2013). Harlequin ducks are at particular risk from changes in stream flow as a result of the changing climate. Harlequin duck reproductive phenology is closely tied with stream flow phenology. Harlequins lay their eggs close to the stream edge and are at risk of flooding during variable spring runoff years. Increasing spring temperatures are causing snow packs to melt earlier resulting in phenological mismatch with harlequin duck breeding ecology. In this study I measure how stream flow variability correlates with annual reproductive success. These results inform predictions about how trends in stream flow variability will be influencing harlequin reproduction in the future.

Causes of reproductive variability are not confined to events on the breeding grounds. Although, understanding how the environment outside of the breeding season influences reproductive variation is logistically difficult. The field of conservation physiology uses physiological metrics to understand the health and reproductive success of an individual. The suite of different physiological metrics can inform investigators of how an animal perceives it environment (Huey 1991). For example heart rate monitors can be used to understand perceived risk of predators and human disturbance (MacArthur et al. 1979), energy requirements can be directly measured during different life history phases using doubly labeled water (Westerterp and Bryant 1984) and previous reproductive success in some birds can be predicted by measuring concentrations of stress hormones in feathers (Bortolotti et al. 2008, Crossin et al. 2013). Physiological measures can offer investigators direct measures of individual quality and provide links to environmental stressors such as human disturbance, pollution, adverse weather, habitat fragmentation, food scarcity and predation (Wingfield et al. 1997, Ellis 2012). In this study we analyzed the concentrations of the primary stress hormone corticosterone deposited in feathers to predict carry-over effects during feather growth on reproduction.

Natural History

The Harlequin Duck (*Histrionicus histrionicus*) is an attractive and charismatic bird with an unusual life-history strategy. Harlequins spend the winter foraging along rocky shore lines in the surf zone from northern California to Alaska and breed inland on fast moving streams (Robertson 1999). Females reach reproductive maturity at age 3 and are monogamous (Smith et al. 2000; Bellrose 1980). Pair bonds are formed on the wintering grounds and then pairs migrate from the coast to the female's natal stream to breed (Robertson 1998b). Females make their nest close to the stream and have an average clutch size of 4.5 – 5.5 eggs depending on region (Bengtson 1966, Smith 2000, W. Hansen, personal observation) In North America, harlequins are segregated into two distinct populations. There is an eastern population whose coastal wintering area ranges from Maryland to Greenland (Vickery 1988, Scott 1996). A much larger population exists on North America's west coast from

Northern California to Alaska (Isleib 1973, Hare 1995). This population has experienced significant historical declines, but today the western population is believed to be stable with rough estimates ranging from 150,000 to 250,000 birds (Robertson 2004). Despite the apparent stability, many Canadian and American agencies identify these populations to be of special management concern because of their low breeding densities (Wiggins 2005). Very little scientific research was dedicated to the harlequin duck until the mid-1990s, when they were listed as an endangered species in Canadian provinces. In the decade following their listing, most research focused on identifying harlequin breeding streams, staging areas, and distribution and recovery of the species. These contributions ultimately led to the delisting of the species in 2001. However, significant gaps in our knowledge of the breeding ecology of Harlequin ducks exist, primarily due to the mountainous breeding habitats that are difficult or impractical to survey, the low pair density at most breeding sites, and the intensely cryptic nature of their nests. Many of the research objectives proposed in the mid-1990s remain unaddressed, including identifying specific factors that may limit productivity (Reichel 1996b, Esler 2007), the impact of human disturbance on nest success (Reichel 1996b, Jean-Pierre L. Savard 2008), correlates of spring runoff (Robertson 1999), and standardized methods for surveying breeding streams.

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CHAPTER 2: STREAM FLOW AND REPRODUCTIVE SUCCESS IN THE HARLEQUIN DUCK (HISTRIONICUS HISTRIONICUS): USING HISTORICAL PATTERNS TO PREDICT EFFECTS OF CLIMATE CHANGE

ABSTRACT

Climate change is having significant impacts on the timing of ecosystem processes (e.g. earlier insect emergence, plant blossom and stream flow). Many migratory animals depend on the predictability of this phenology to maximize reproductive success. When phenology at the breeding grounds significantly changes or becomes unpredictable, reproductive success usually declines. I measured how different aspects of stream flow influence the reproductive success of Harlequin ducks to explore how climate change may impact this species in the future. Harlequin ducks are a rare species of special concern and threatened or considered for listing throughout portions of their range. I used a 24-year data set of harlequin surveys taken on upper McDonald Creek in Glacier National Park, Montana to assess how annual variation in brood abundance relates to stream flow. Four stream flow parameters were captured by a single principal component that explained 32% of variation in harlequin reproductive success. All four parameters loaded positively on PC1, so that higher and less predictable flows predict reduced reproductive success. Additionally, all four parameters are predicted to become more extreme with climate change based on previous studies of stream flow and climate change. Based on this result I conclude that this population of breeding harlequin ducks will face significant challenges in future years. We recommend that harlequin populations and habitat be maintained and restored where necessary to allow for dispersal and adaptation into the future.

INTRODUCTION

Seasonal animals depend on environmental rhythms for timing of reproduction. Many migratory animals use photoperiod to time arrival at the breeding grounds. Migratory behavior has evolved to use environmental cues such as photoperiod to time arrival on breeding grounds when it is best for reproductive success. Global climate change is altering the phenology of these environmental pulses (insect emergence, plant phenology) on the breeding grounds causing a mistiming of arrival for many migratory species, which can lead to decreased reproductive performance and ultimately population declines (Both et al. 2006, Post and Forchhammer 2008, Saino et al. 2011).

Mistimed arrival at the breeding grounds can alter reproductive success through reduced nutrient acquisition, nest site availability and juvenile survival. Many species are robust to temporal changes in phenology, but if variation continues to increase through time these populations can assume greater extinction probabilities (Gilpin and Soulé 1986). Climate change is expected to increase variation in the phenology at the breeding grounds. In the Pacific Northwest these changes will include increased mean temperatures, earlier insect emergence, earlier plant blossom and cessation, earlier peak stream runoff, greater extremes of high and low stream flows and decreased snowpack (Stewart et al. 2005, Bernstein et al. 2007, Mote and Salathe Jr 2010, Goode et al. 2013). These changes will likely have strong effects on the reproductive rates of many migratory species.

Harlequin ducks (*Histrionicus histrionicus*) are longitudinal migrants that have been listed by the state of Montana as most sensitive to climate change. They breed on alpine streams where they build their nest on the ground usually < 1 m from the stream edge. Food resources (benthic invertebrates) that are required for egg production comes from these low productivity montane breeding streams (Bond et al. 2007). Breeding pairs arrive at the stream early in spring when the stream is near base flow; initiation of incubation occurs on or near peak stream flow ~ 4-5 weeks after arrival (Figure 2-

2). These life history traits put harlequins at risk of reduced reproduction with climate change because earlier and more unpredictable spring temperatures may limit foraging ability after arrival and may wash out nests (Gangemi 1991, Robertson and Goudie 1999, Wiggins 2005).

Here I evaluated the relationship between stream discharge and reproductive success from a long-term study of harlequin ducks in Glacier National Park, Montana. Over the past 24 years Glacier National Park staff has documented a large degree of variation in annual reproductive success in the breeding population. I hypothesized that stream flow phenology is a major component driving breeding variation in this population. I predicted that greater extremes in stream flow during egg lay and incubation correlate with decreased reproductive success through nest failure. This interaction is important to understand for the management of this species into the future, as climate alters phenology at the breeding site.

METHODS

Study site

I studied harlequin ducks on Upper McDonald Creek in Glacier National Park, Montana (Figure 2-1). This stream comprises 25% of known harlequin duck broods produced in Montana, and has the highest density of breeding harlequins in the lower 48 states (Montana Natural Heritage Program 2014). Upper McDonald Creek is a relatively pristine fourth-order watershed tributary to the Middle Fork of the Flathead River. Its headwaters originate along the west slope of the Continental Divide at elevations of up to 1859 (m). Upper McDonald Creek has a large cobble substratum and waters that are generally low in dissolved ions, nutrients, and suspended particulates (Lowe and Hauer 1999). The study site has an open canopy of mixed conifer/deciduous trees that have remained unchanged for nearly 80 years since the construction of the Going-to-the-Sun-Road in 1933 (with the exception of wildfire in the upper 3 (km) reach in 2003).

Metrics of Reproductive Success

In avian reproductive studies many metrics are used for reproductive success (reviewed in Kosciuch et al. 2001). Here I define reproductive success as the ratio of number of females on the breeding stream to the number of broods. This metric accounted for annual variation in the number of females present, which alters the likelihood of brood production independently of stream flow. Hence I have evaluated the probability that a female will produce a brood, not the absolute number of broods produced. This annual ratio will be referred to as annual reproductive success (Figure 2-4c).

Glacier National Park has surveyed Upper McDonald Creek between Lake McDonald and Logan Creek on a regular basis since 1991. The park's objectives were to document the number of individual ducks, pairs, and juveniles occurring on Upper McDonald Creek to monitor the creek's seasonal harlequin population. Multiple surveys were conducted during the pair season (mid April – May when pairs arrive to the park) and during the brood season (mid July – early September when chicks hatch and emerge on the stream). Abundance estimates of pairs and broods for each year were determined by the highest count from an individual survey within a single season. This eliminated variation in survey effort because every year the park conducted at least 1 full survey. To explore how annual variation in survey date influenced peak abundance counts I performed an analysis of variance (ANOVA) in high counts of pairs and broods across all years of survey data. Pair surveys showed no significant difference in peak abundance across 4 weeks of the early season (Figure 2-2a), and all years had at least 1 survey from that peak period. There was no peak in brood abundance over the brood surveys (Figure 2-2b), therefore I did not consider what week the annual brood high count was conducted.

Hydrography

Historical gauge data (hourly or daily flow statistics) do not exist for Upper McDonald Creek. I did collect daily gauge data during the breeding season (April 15-September 1) during years 2011-2013. I compared these flow statistics to 8 gauged streams in Northwest Montana. I found the strongest correlation ($R^2 = 0.84$) with Swiftcurrent Creek which neighbors Upper McDonald Creek to the east (Swiftcurrent Creek; gauge station: 48°47'55.80"N, 113°39'24.23"W; http://waterdata.usgs.gov/usa/nwis/rt) (Figure 2-1).

I used Swiftcurrent creek flow data corrected for the larger watershed area of McDonald Creek watershed. I made the correction by calculating the unit area flow of Upper McDonald creek by multiplying daily Swiftcurrent Creek flow statistics by the watershed area of Swiftcurrent creek and dividing that quantity by the area of the Upper McDonald Creek watershed.

I developed 4 metrics that characterize different aspects of stream flow likely to have the most impact on harlequin duck reproductive success. These 4 metrics were developed *a priori* to reflect the most challenging stream conditions that breeding harlequins face. There have been anecdotal suggestions in the harlequin literature that 1) high stream flow will delay egg lay and reduce foraging efficiency over the season (reviewed in LeBourdais 2006); and 2) spikes in stream flow after egg lay can wash out nests (Wiggins 2005). My first metric was average stream flow prior to peak incubation (May 5 to June 10). This should best reflect nest site availability and forage ability prior to incubation. Harlequins have been observed nesting in the same place year after year (Chubbs et al. 2000, W. Hansen, personal observation, Smith 2000) usually within 1 m of the stream's edge. Hence, high flow years should delay egg lay as the females wait for nest sites to emerge. High stream flow early in the season also makes foraging more difficult (Gangemi 1991, Robertson and Goudie 1999, Wiggins 2005); since harlequins fund egg production on primarily on energy intake, and not internal energy stores (Bond et al. 2007), this increase in flow could possibly delay egg lay or reduce the number of eggs laid. The second metric was the cumulative number of hydrographic spikes that occurred over the duration of the breeding season (April 1 – September 15). Spikes were determined by a sudden increase and decrease in flow that had amplitude of > 50 cubic feet/second. These values provide an index of predictability of stream flow. The third metric was the cubic feet/second value of the greatest single hydrographic peak post average peak flow. Harlequins incubate through the declining arm of the hydrograph, and spikes during this time can wash out nests. The fourth metric was the average flow that occurred from the beginning to the end of the incubation period (June 15 – July 20). This metric best reflects the conditions that the female would be foraging in during incubation. See Appendix 1 for a more detailed description of stream flow metrics. I refer to the sum of these 4 metrics as the spectrum of high and low stream flow severity.

Visual comparisons of hydrographs were made by average, most extreme and least extreme water flow years. Extreme years were grouped by averaging the upper and lower quartiles of the principal component analysis ranked stream flow severity years (described below in statistical analysis).

Statistical Analysis

All analyses were completed using Program R (R Core Team 2013). The 4 stream flow metrics were combined using Principal Component Analysis (PCA). Reproductive success (ratio broods to pairs) had a right skewed distribution so I log transformed the data for normalization. The relationship between reproductive success (response variable) and principal component 1 (PC1) (predictor variable) was evaluated using simple linear regression. Principal component analysis is commonly used in regression analysis to reduce the number of covariates when there are many collinear covariates involved. This is often done to maintain important information from each covariate vs. removal of covariates when screening for collinearity in multivariate regression (Jolliffe 2005). The collinearity between my 4 stream flow metrics ranged from 0.05—0.81 (Table 2-1). I chose to use PCA to maintain all potentially biologically relevant stream flow metrics.

RESULTS

Stream flow

Principal component analysis identified a primary component with all four variables loading positively (Figure 2-3 and Table 2-2), in that a greater component score represents an increase in severity in stream flow conditions for that year (e.g., higher stream flow, greater number of peaks and elevated highest peak). Principal component 1 explained 54% of the variation in the dataset. Subsequent components did not extend explanatory power for the stream flow variation, and so were not considered further. Hydrograph comparison of the upper and lower quartiles illustrate the differences in high (red line) vs low (blue line) extreme flow. Phases of the breeding season have been overlaid on the figure for reference (Figure 2-2).

Abundance Data

Abundance of breeding pairs on UMC peaked from weeks 17-20 (May 1 – May 21), (Figure 2-4a), with no significant difference (α=0.05) among those weeks (ANOVA, df= 1, F=0.15, p=0.701), and decreases thereafter (mean abundance during week 17-20 = 6.9 ± 1.3 and week 21-23 = 2.1 ± 1.25, Welch Two Sample t-test, t=7.2, df =69.7, p= <0.001). There was no significant variation in brood abundance over time (Figure 2-4b) (ANOVA, df=10, F=1.29, p=0.259).

Abundance by stream flow

Annual reproductive success decreased with increasing stream flow severity (Figure 2-4; Logistic Regression, R^2 = 0.32, p=0.004, F=10.51). The blue line in figure 2-5 represents the 95th quantile fitted to the harlequin ~ stream flow analysis. These data were best described as a triangular relationship, with greater variation in reproductive success across low severity stream flow years.

DISCUSSION

These results reveal a strong negative relationship between annual reproductive success of harlequin ducks and higher stream flow severity. The negative relationship between these two has long been hypothesized by biologists in this system (Reichel 1996a, Robertson and Goudie 1999, Wiggins 2005) but reports have all been anecdotal. Stream flow is clearly an important abiotic influence on harlequin duck reproduction. This study does not identify the specific mechanism (e.g. limiting forage, limiting available nest sites or washing out nests), but suggests a range of hypotheses to be tested to better understand the interaction between stream flow and reproduction. For example, foraging behavior and clutch size could be good indicators that variable stream flow is limiting nutrient uptake and decreasing reproduction in more extreme years. Individual age and experience could also play a role in nest site selection. Older birds may pick better nest sites or may be better competitors than younger birds for optimal nest sites. Long term banding data could identify population demographics that could lend insight to this theory.

The unexpected result of this analysis is the triangular shape of the plot when the 95th quantile is fit. This biological implication suggests that severe stream flow limits nest success in a more predictable way (possibly through limits on nest initiation or early nest persistence), while other, more variable mechanisms are at work when stream flow is less severe, and a greater number of nests can persist past the early stages. Predation may be a factor inducing variation in less severe years. During incubation females and their nests are highly susceptible to predation (Bond et al. 2009). I documented pine marten, mink, red squirrel and wolf preying on the eggs of harlequin nests. This triangular pattern has been observed in a variety of other systems, particularly in the in the mesopredator release literature (Johnson and VanDerWal 2009, Letnic et al. 2011). Mesopredator release dynamics are described as the removal of an apex predator from a system causing an increase in population in the smaller predators resulting in greater predation pressure on prey foods.

Variation in spring discharge is a natural phenomenon dictated by winter and spring weather patterns. Numerous factors contribute to the severity of spring runoff. In the central Rocky Mountains, snow pack, rate of spring warming and spring precipitation are the primary drivers of spring runoff severity (Stewart et al. 2004). Harlequin ducks appear to time important phases in their reproductive life history around stream flow patterns (Gigure 2-2).

Climate change will likely enhance the prevalence of the severe stream flow factors that limit harlequin reproductive success. These changes are expected to have significant impacts on stream flow across the west based on current models in the next 50 to 75 years (Goode et al. 2013). My first stream flow severity metric (average discharge from May 5-June 10) will likely increase substantially given that peak runoff is expected to occur earlier in the spring. By pushing peak runoff earlier into the spring, there will be an overall increase in flow, thus increasing average flow during this time frame. Increases in early discharge will reduce foraging efficiency in females preparing to lay, and delay egg lay until historical nest sites become available. The second metric (number of spikes during the breeding season) is more difficult to predict. Stream flow has been modeled to become more unpredictable with greater variation, but it is difficult to predict when this variability will occur on the hydrograph. If the timing of spikes occurs after peak flow, greater number of nests could be washed out once incubation has started and after males have left. If more variation occurs prior to peak flow, harlequins may select poor nest sites with greater probability of flooding. The third metric (height of peak stream flow) is expected to increase through time as the effects of climate change become more pronounced. Substantial increases in peak flow over time pose the greatest risk to flooding nests. Harlequins likely select nest sites as close to the stream edge as possible based on previous experience. Dramatic and unpredictable changes in peak flow will render previous experience useless. My fourth metric (average discharge between peak incubation and peak hatching) is expected to decrease. There are a variety of predicted effects that this might have on harlequin reproduction. Decreased flow at this period may increase the foraging ability for incubating females to an extent. However, many females incubate eggs off of the main stream on smaller tributaries, these streams may become dry or have insufficient flow for chicks to navigate or avoid predators. Back water habitat has also been shown to be an important feature during brood rearing during the first 3 weeks of life (Kuchel 1977b). These backwaters may be dried up by August if flows become significantly decreased in the future. In summary, three of the four metrics in this analysis are expected to increase in severity with climate change. These predictions indicate a high likelihood of increasing challenge to harlequins breeding in GNP in the future.

The Glacier National Park harlequin population is the densest breeding population in the lower 48 United States. The 15 km stretch on Upper McDonald Creek produces 25% of harlequin young in Montana (Montana Natural Heritage Program 2014). Although dispersal is thought to be very low (Cooke et al. 2000), this population could serve as source to repopulate locally extinct populations. Given the predictions of current climate models, we may see a greater frequency and severity of the red hydrograph from figure 1. An increase in the frequency of flow severity is shown here to have significant negative impacts on breeding harlequin ducks in GNP. Breeding success of harlequins is generally thought of as boom/bust, an increase in stream flow severity may reduce the number of boom years in the future. Average reproductive success of harlequin ducks breeding in the central Rocky Mountains may reflect what we see furthest to the right in figure 2-4 in the next 50 to 75 years. We think that an important next step in the conservation of harlequin ducks is to collect robust vital rates at all life stages to model population growth rates along a continuum of stream flow severity.

CONCLUSION

Reproductive success is an important component to understand vital rates of a population. The source and extent of this variation is an important variable because it can lead to inference about the evolution and life-history of a species (Murray 1991), extinction probability (Gilpin and Soulé 1986) population forecasts, and sources of environmental or anthropogenic disturbance to reproduction (Wingfield 1988, French et al. 2011). Our study demonstrates that variation in stream flow metrics explain 32% of variation in annual reproductive success in harlequin ducks breeding on Upper McDonald Creek.

Based on the results of this study, climate change forecasts and its effects on stream flow, harlequin ducks are going to face major challenges in the next 50-75 years. To make these populations robust to change we need to ensure that the ecosystems used during each life history stage are fully intact and functional. Breeding populations of harlequin ducks need to reach full potential to allow for adaptation and evolution into a changing future.

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FIGURES AND TABLES

Figure 2-1. Study area in Glacier National Park, Montana. The large shaded area encompasses the entire Upper McDonald Creek watershed with Upper McDonald Creek running through the center. The smaller shaded area is neighboring Swiftcurrent Creek watershed.

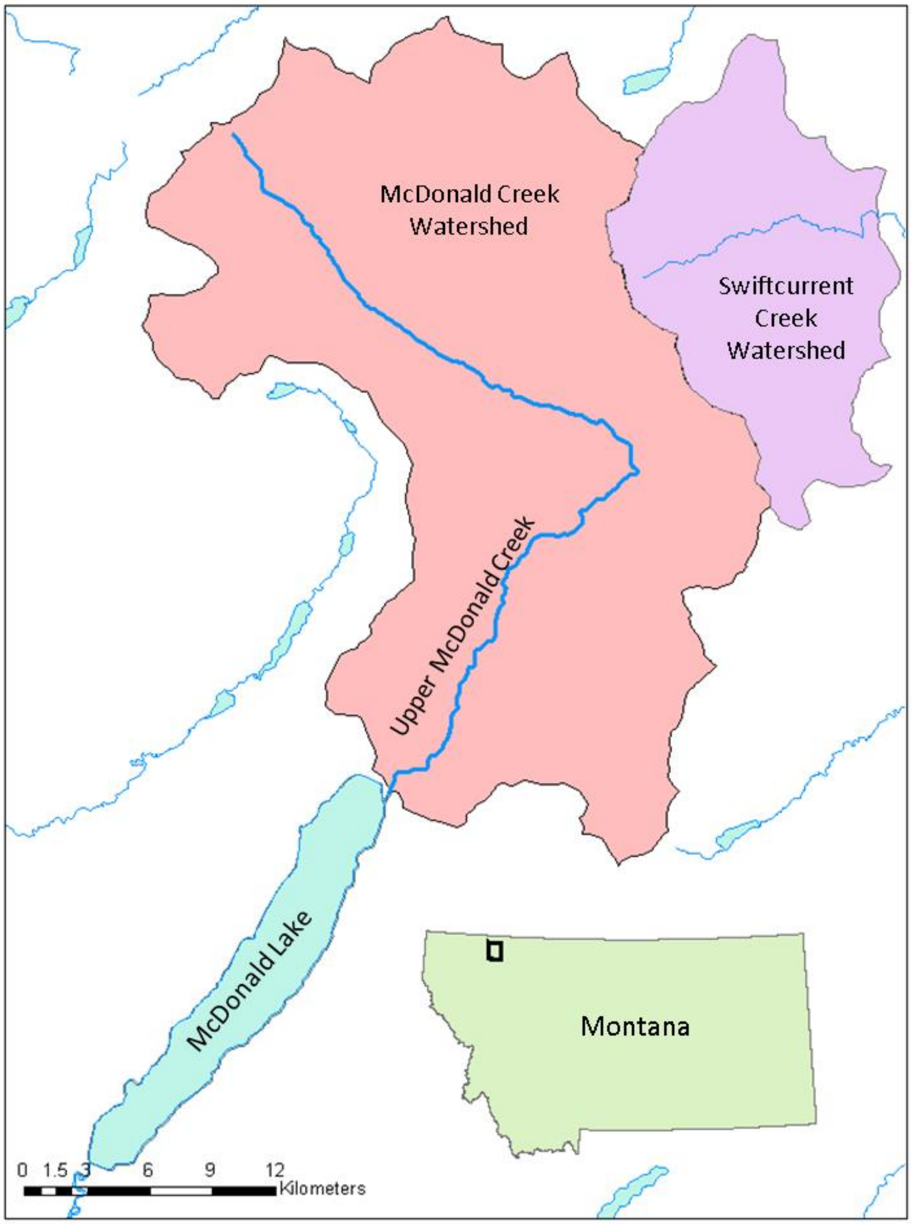


Figure 2-2. Graph represents hydrographs of historical average (backline) taken from previous 24 years of stream flow data, average high severity (green line) taken from the upper quartile of high severity years from the PCA, and average low severity (red line) taken from the lower quartiles of the PCA. The boxes reflect 4 different phases of reproduction; arrival, laying, incubation, and hatching.

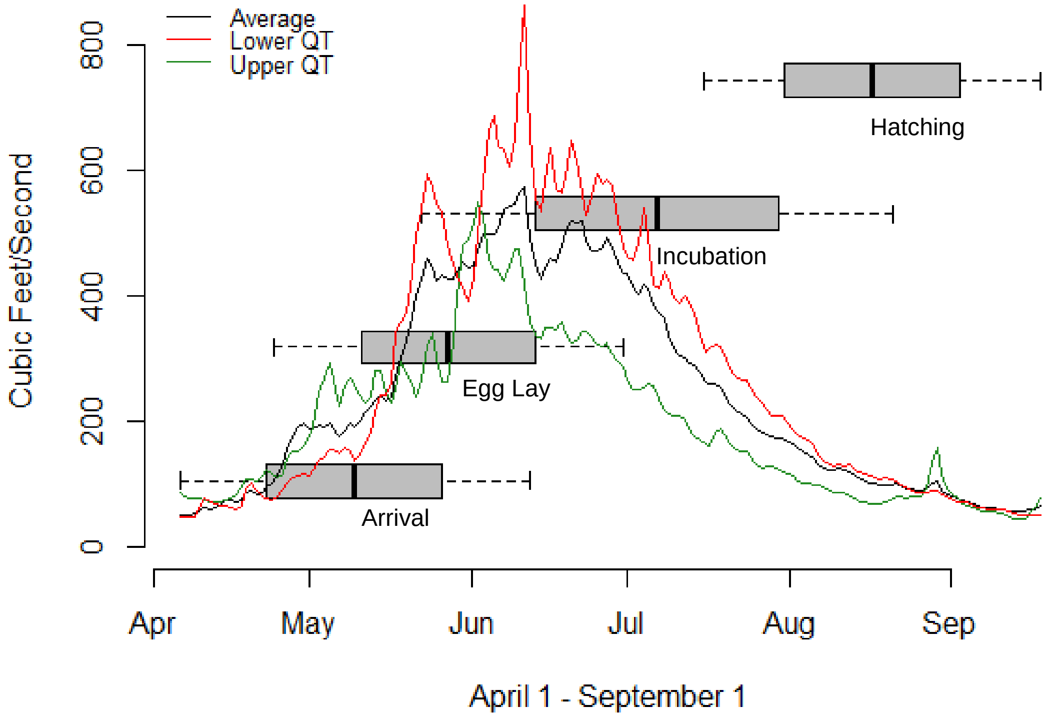


Figure 2-3: Biplot of the 4 metrics used in the principal component analysis. The arrows indicate the direction and the component that each metric loading on. Metric 1 is the average CFS from peak arrival to peak incubation, metric 2 is the number of spikes throughout the breeding season, metric 3 is the largest spike post historical peak flow and metric 4 the average flow from peak incubation to peak hatching.

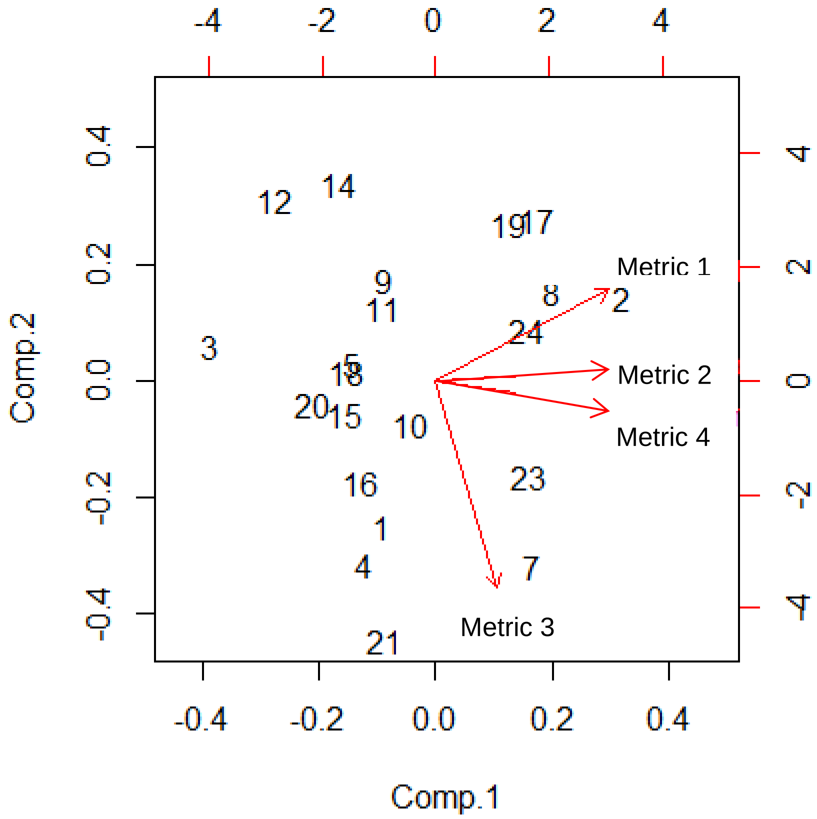
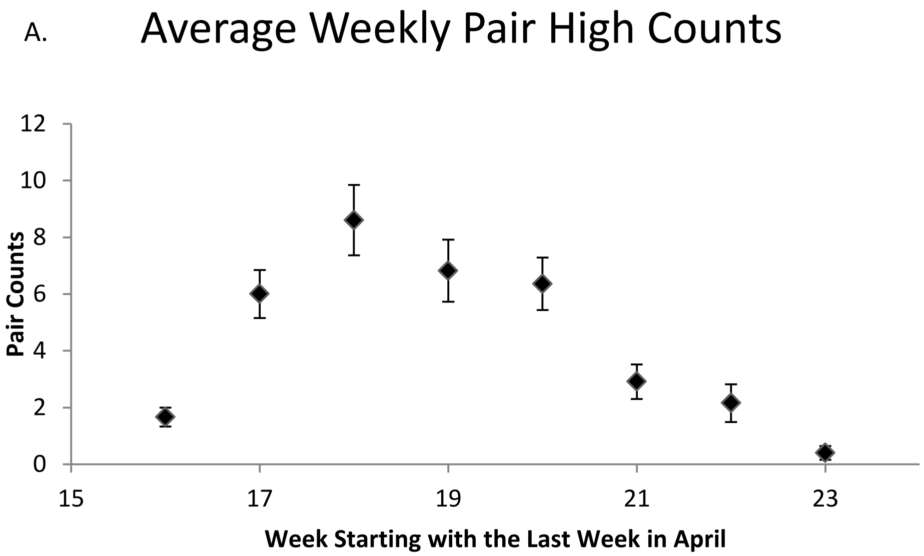
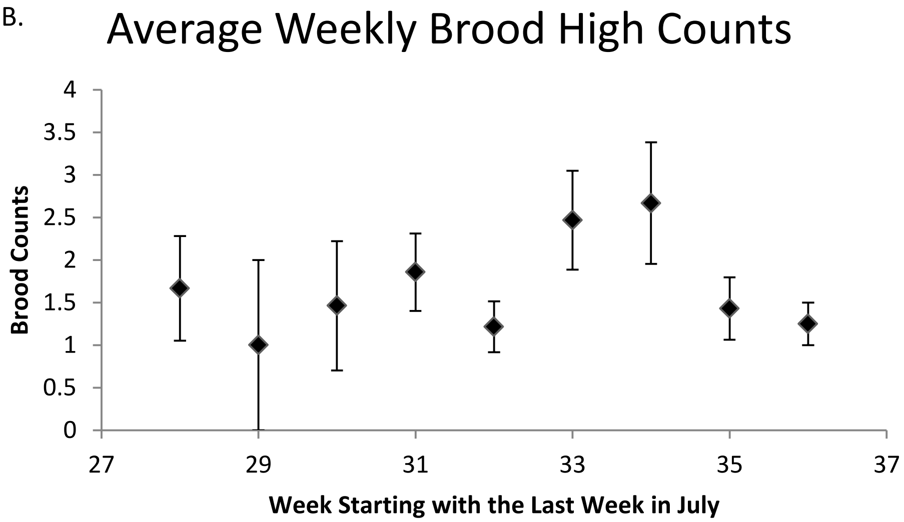


Figure 2-4. Weekly high counts averaged across the previous 13 years of survey data with standard deviation bars around each point. Graph A, no significant difference between weeks 17-20. Graph B, no significant difference between all weeks surveyed. α=0.05. Graph C, ratio of pair high count to brood high counts for years 1990-2013 with the exception of 1992 where a pair survey was not conducted in weeks 17-20.

A.



B.



C.

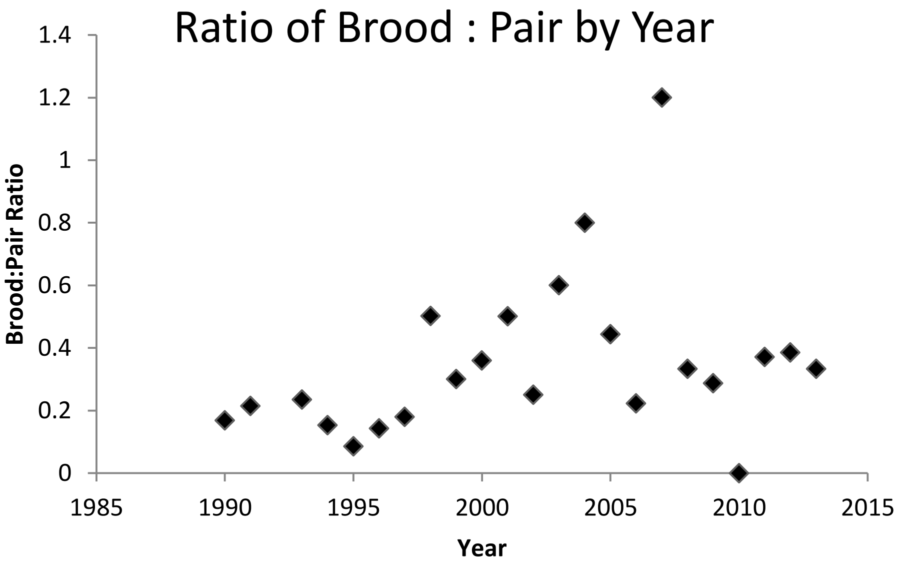

Ratio of Brood : Pair by Year
Brood:Pair Ratio
1.4
1.2
1
0.8
0.6
0.4
0.2
0
1985
1990
1995
2000
2005
2010
2015
Year

Figure 2-5. Graph of brood:pair ratio ~ PCA of stream flow severity. Lower stream flow severity at negative values and increased severity at positive values. Red dotted line represent the best fit line of the data with $R^2 = 0.32$, p=0.004. Blue Solid line represents the 95th quantile of the data.

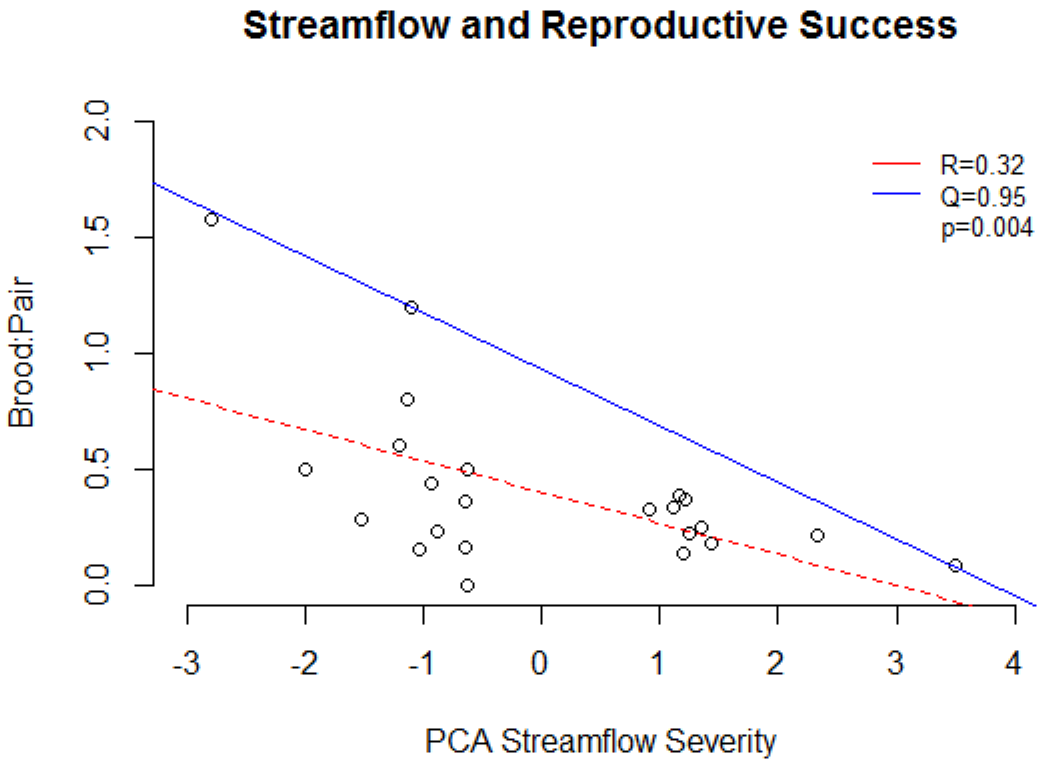


Table 2-1: Correlation table of the 4 stream flow metrics used in principal component analysis. Metric 1 is the average CFS from peak arrival to peak incubation, metric 2 is the number of spikes throughout the breeding season, metric 3 is the largest spike post historical peak flow and metric 4 the average flow from peak incubation to peak hatching.

	1	2	3	4
1	1.000	0.814	0.017	0.003
2	-0.051	1.000	0.233	0.432
3	0.481	0.253	1.000	0.001
4	0.580	0.168	0.615	1.000

Table 2-2: Description of stream flow metrics and associated eigen values from principal component analysis.

Stream Flow Metrics		**Eigen Value**
1	Average CFS from peak arrival to peak incubation	0.53
2	Spike number throughout breeding season	0.19
3	Largest spike post historical peak flow	0.60
4	Average flow from peak incubation to peak hatching	0.58

See appendix 1 for full descriptions of the how each metric was determined and extracted from the database.
Each value was calculated per year for the PCA analysis.
CFS: cubic feet per second

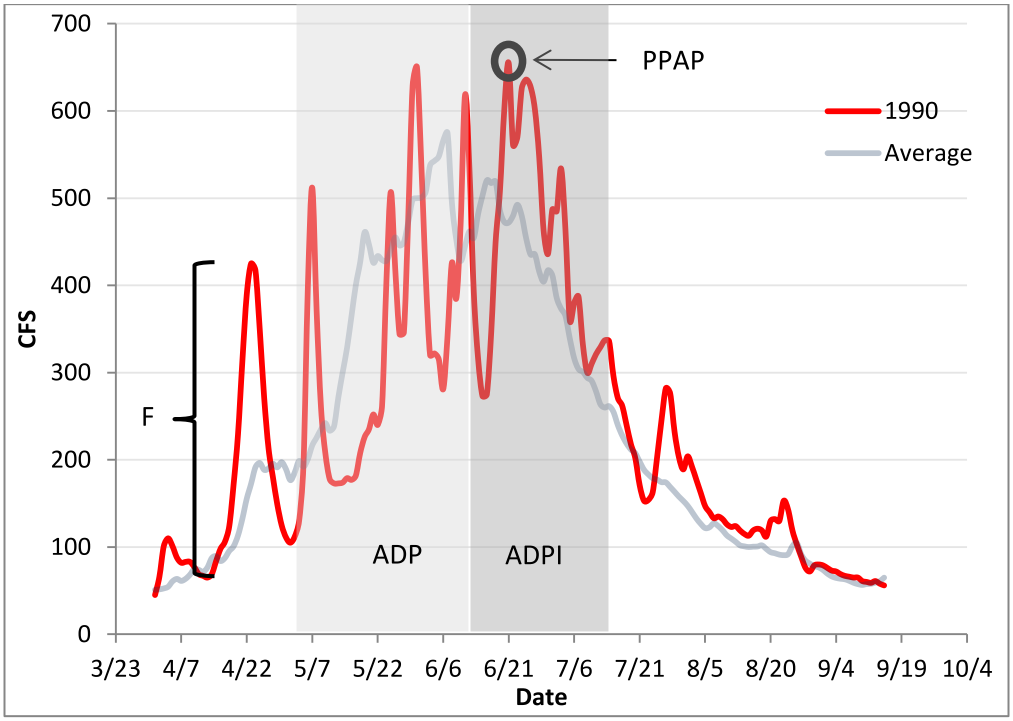
APPENDIX 2-1

Variable Definition:

5. Average discharge from peak arrival to the beginning of incubation (May 5 to June 10) (Figure 1: ADP).
6. How flashy is the stream (F)
    a. Add together the total number of all of peaks from trough to peak that are > 50cfs from April 1 to September 15.
7. Height of largest peak post average peak (PPAP)
    a. These are cubic feet/second values. They are the peak discharge value for the largest spike post the historical average spike.
8. Average discharge overlapping with the incubation period (June 10 to July 15) (ADPI)

Dates for breeding chronology were adapted from (Kuchel 1977b) and refined using our telemetry data from 2011 to 2013. Hourly discharge values were obtained from http://waterdata.usgs.gov/usa/nwis/rt. I averaged the hourly data into 24 hour bins to get daily discharge values from April 1 to September 15 (full extent of the harlequin breeding season). The hydrograph for each year (1990-2013) was plotted in excel. Steam variables defined above were manually extracted following the example below. These variables were used to construct the Principal Component Analysis.

Figure 1: Example of manually extracted hydrograph characteristics.



CHAPTER 3: HUMAN DISTURBANCE, RESOURCE SELECTION AND STREAM OCCUPANCY OF HARLEQUIN DUCKS BREEDING IN GLACIER NATIONAL PARK, MONTANA

ABSTRACT

Human disturbances to wildlife have been studied for decades to understand the impacts to behavior, population health and population projection. Here I measured the impacts of disturbance in Glacier National Park on a breeding population of Harlequin Ducks (*Histrionicus histrionicus*). I measured the influence of high human use areas, traffic volume and physical features of a major tourism road in Glacier National Park (the Going to the Sun Road) on harlequin occupancy and resource selection using three complementary approaches. I first used automated receiver units in 2 years to measure the presence/absence of radio-collared female harlequin ducks in high human use (disturbed sites) and low human use (undisturbed sites). I then used 24 years of stream survey data to measure occupancy in 100 m stream patches given variables distance to road, distance to backwater, road visibility and stream habitat features pool, riffle, rapid and run during pair season and brood season. In my third approach, I used radiotelemetry data from 45 radiocollared adult ducks over 3 years. I estimated resource selection by ducks for spatial resources including human infrastructure using radiotelemetry data (used) and randomly chosen (available) locations. I found greater probability of occupancy of ducks in high human use sites and in stream patches closer to the road. I also found greater occupancy in pool habitat which was also disproportionately closer to the road. My resource selection model revealed that ducks are selecting steam patches close to road later in the day with negative selection for rapid and riffle steam features. I concluded that the Going to the Sun Road and high human use areas are not contributing to negative selection or occupancy for these features at present. Strong selection for resources in roadside pool habitat may override any potential negative impacts caused by human use along the Going to the Sun Road. Habitat features such as pools close to road and staging areas close to road should be monitored and regulated closely to minimize any impacts to reproduction. Documenting duck behavioral response to human activity would increase our understanding of the impact of the Going to the Sun Road and different levels of human use.

INTRODUCTION

Anthropogenic disturbances have been well documented to have negative impacts on wildlife populations (Knight and Cole 1995). These impacts can range from displacement, habitat loss, fragmentation, isolation and eventually population declines (Hume 1976a, Klein et al. 1995, Gill et al. 1996). It is important to understand these impacts as human population continues to grow, especially for rare and sensitive species. National Parks are in a unique situation where they are committed to preserving natural landscapes and the animals that depend on them, along with supporting human visitation. Glacier National Park (GNP), Montana has been seeing a steady increase in human visitation since the formation of the park in 1910 (IRMA data system 2014). In recent years the park has consistently exceeded 2 million visitors annually. Many park managers have become concerned with how this level of visitation may be impacting wildlife populations. The area of greatest use in the park is the Going-to-the-Sun Road (GTSR). The road cuts through glacially carved McDonald valley, over Logan Pass and out on to the prairie of the Rocky Mountain front. Diverse compositions of rare and sensitive species exist along this route, one of them being the harlequin duck (*Histrionicus histrionicus*).

Harlequin ducks breed on Upper McDonald Creek (May—August) which parallels the GTSR for 15 km. Harlequin ducks are listed as a species of special concern in Montana (Montana Natural Heritage Program 2014) and other states and provinces throughout their range. They are long lived (> 20 years) and late to mature (3 years) with a low annual reproductive output making them rare across their range. Only 150-200 pairs breed in Montana (Montana Natural Heritage Program 2014). They are a small sea duck in the subfamily *Merginae* that winter along the coastal waters of North America and migrate inland to breed along fast moving montane streams where they place their nests on the ground usually < 1 m from the stream edge. Here harlequins forage on benthic invertebrates, primarily plecoptera, ephemeroptera and trichoptera. The first four to five weeks upon arrival is critical for nutrient acquisition for egg development (Bond et al. 2007). Any disturbance during this time may take away or limit resources required for successful reproduction. For this study I have analyzed the relationship between where breeding female harlequins are found on the stream in relation to specific resources and potential sources of human disturbance (high human use sites and traffic volume) along the GTSR.

To better understand where harlequin ducks are found on the landscape and how traffic volume influenced occupancy and use, I developed three questions and three different methods of data collection and analysis to answer these questions. My first three questions were descriptive questions asking: 1) What is the probability of a duck occupying a segment of stream overlapping a high human use area vs. the probability of a duck occupying a segment of stream that does not overlap a high human use segment of stream, 2) Does the GTSR displace harlequin ducks from occupying stream patches that are close to the GTSR or have full visibility of the GTSR? For these two questions I exclusively looked at presence/absence of ducks at specific resource units (high human and low human use stream patches). This first approach was limited temporally to 2 seasons and to only monitored sites. To complement this focused first approach, next, I used broader spatial scale radiotelemetry over 2 years, and finally, broad spatio-temporal occupancy modeling over 23 years. To understand how a broad suite of resources influence duck responses to human activity as a function of traffic volume, I asked, 3) what is the probability of a duck selecting resources that are available within my study area and how does the GTSR influence this selection? To answer these questions I measured the influence of the GTSR and high and low human use sites on the occupancy and resource selection of harlequin ducks on Upper McDonald Creek using three different, but complementary methods at different spatio-temporal scales. First I estimated the probability of occupancy at disturbed and undisturbed sites using automated receiver units (ARU) during years 2012-2013 (Part I). Second I estimated the probability of occupancy (MacKenzie et al.

2005) of breeding pairs and brooding females along different segments of Upper McDonald Creek using survey data that is considered a census of the breeding stream from years 1991-2013 (Part II). For the third method I used resource selection function (RSF) analyses based on VHF telemetry locations and a random sampling of availability on the stream to measure selection based on used and available stream patches (Part III).

METHODS/ ANALYSES

Study Site

My study site was located on Upper McDonald Creek in Glacier National Park, Montana (Figure 3-1). This site is considered an important breeding stream comprising 25% of known harlequin duck broods produced in Montana, and has the highest density of breeding harlequins in the lower 48 states (Reichel 1996a, Montana Natural Heritage Program 2014). Upper McDonald Creek is a relatively pristine fourth-order watershed and tributary to the Middle Fork of the Flathead River. Its headwaters originate along the west slope of the Continental Divide at elevations of up to 1859 (m). Upper McDonald Creek has a large cobble substratum and waters that are generally low in dissolved ions, nutrients, and suspended particulates (Lowe and Hauer 1999). The study site has an open canopy of mixed conifer/deciduous trees that have remained virtually unchanged for nearly 80 years since the construction of the Going-to-the-Sun-Road in 1933 (with the exception of wildfire in the upper 3 (km) reach in 2003.

Data collection

I captured harlequins using 3 × 18 (m) mist nets anchored across Upper McDonald Creek (Smith 1996) from 2011 – 2013. From these captures I equipped 45 female harlequin ducks with prong and suture Very High Frequency (VHF) transmitters (Model #A4420, Advanced Telemetry Systems) of likely reproductive age (age determined following Mather and Esler 1999). Transmitters were attached by the project veterinarian (DRS) following IACUC guidelines. All protocols were approved by The University of Montana Institutional Animal Care and Use Committee (IACUC; 011-11CBDBS-041311), and Glacier National Park (GLAC-2011-SCI-0165). Females were tracked and monitored daily with ~ 3 locations per individual/week.

Evaluating human disturbance using automated receiver units (ARU)

This section seeks to address the probability of a duck occupying a segment of stream overlapping a high human use area vs. the probability of a duck occupying a segment of stream that does not overlap a high human use segment of stream. I used software developed by Sparrow Systems LLC (Cochran 2014) to record presence/absence for each radio-collared individual every 1 minute, 24 hours/day on dispersed disturbed and undisturbed sites using ARUs I placed directional antennas for the ARUs > 3m from the stream edge and perpendicular to the stream. The ARU antennas were place perpendicular to the stream to reduce the detection of individuals that were near to the antenna, but not in front of the antennae. A duck's radio frequency could still be detected up to 100m to either side of the antenna, but the recorded frequency intensity would be much lower than frequency intensity of the duck's transmitter if it was very near to or in front of the antenna. I visually derived a frequency intensity cutoff of > 12,000 to classify a duck as present at a particular location (Cochran 2014). I binned the presence of ducks into 1 hour categories within a 24 hour cycle. To avoid false positive detections a duck needed to be present for at least 10 minutes within 1 hour to be recorded as present for that particular hour. Further justification for binning duck presence into hours was to facilitate comparison against traffic volume, which was recorded as total traffic counts/hour from April – September (time from radio-collar attachment to departure). The Department of the Interior (DOI) collects Integrated Resource Management Applications (IRMA) including traffic volume at all entrance points in Glacier National Park (IRMA data system 2014).

I categorized high human use areas as pullouts along the GTSR where visitors could park and access the stream by foot. These sites were developed by the park as scenic vistas, picnicking areas and fishing access. There are many pullouts along the GTSR, but only 5 pullouts have trail access down to the creek. I selected all 5 of these pullouts along GTSR to represent high human use sites along Upper McDonald Creek (Figure 3-1). Undisturbed sites were selected at 500 m intervals along Upper McDonald Creek starting at Lake McDonald and ending at the confluence with Mineral Creek. I chose 500 m intervals to ensure that a radio-collared duck could not be detected at more than one ARU at a single point in time. Three ARUs were used simultaneously to monitor occupancy by radio-collared HADU on the creek. The ARUs were randomly moved each week with one unit alternating between disturbed and undisturbed sites. For example on week one, two disturbed sites and one undisturbed site were randomly selected to monitor. Then the following week, two undisturbed sites and one disturbed site were randomly selected for monitoring. After each week I downloaded data from the ARUs and I moved that ARU to a new site.

Detection probabilities by ARUs were assumed to be 1 because all birds used in this analysis were marked with radio transmitters and all presences were recorded using ARUs. The proportion of occupied high human use and low human use sites was developed by taking the ratio of the number of sampling units occupied (hours) divided by unoccupied units. I estimated the general probability of occupancy using logistic regression (Lemeshow and Hosmer 2000) with a random intercept for each individual duck to account for autocorrelation within individuals(Gillies et al. 2006). Covariates of occupancy included human or low human use (categorical variable), date, hour and hourly traffic counts for the entire study period. I centered all of the covariates on their median value to increase interpretability and decrease scaling issues with covariates that are much larger than zero (Harrell 2001). I performed univariate analysis to remove correlated ($r < 0.5$) and uninformative variables. General Linear Models using the binomial family and the logit link function were used to identify covariates that best predicted ARU occupancy using Equation 1:

$$logit(p_{ij}) = \beta_{0\,Presence} + \beta_1 x_{Date} * \beta_2 x_{Hour} * \beta_3 x_{Traffic\,Vol.} + \beta_5 x_{Site} + \gamma_6 x_{Duck\,ID}$$

where β_0 is the intercept, $\beta_1 - \beta_5$ are the coefficients on the variables Date, Hour, Traffic Volume and Site, (*i* designates the number of observations (30,325) while *j* designates the number of individuals (1…38) The gamma (γ_0) is the random intercept term for each individual radio-collared duck. I used Akaike Information Criterion (AIC) and selected the top-ranked models with < 2 ΔAICc (Burnham and Anderson 2002). I used Receiver Operating Characteristic (ROC curve) to determine how well the top models fit the data (Fielding and Bell 1997). All analyses were conducted using Program R 3.0.3 (R Development Core Team 2013).

Occupancy Modeling

In addition to the telemetry data I used harlequin duck survey observations obtained by park biologists over that past 24 years to understand if the GTSR displaces harlequin ducks from occupying stream patches that are close to the GTSR or have full visibility of the GTSR. The area surveyed by the park was a 15 km stretch of stream from Lake McDonald to Logan Creek (Figure 3-1). Two periods of surveys were conducted each year to obtain estimates of pair abundance and brood abundance. Pair surveys were conducted each week in the spring starting in mid-April and ended in mid-June. Brood surveys were also conducted each week starting in August and ended in mid-September. A survey consisted of 2 people walking up the stream together, occasionally leapfrogging 100-200 m to get around stream obstacles. At least one person was always on the stream to be sure to observe any birds that flushed and/or were flying up or down stream. Each duck's location was recorded with a hand-held Global Positioning System (GPS) unit along with sex, behavior, age, social status (pair or single) and breeding status (brooding or single female). Pairs and broods have very different behavior and are likely occupying very different habitats during these different reproductive periods. For this reason I analyzed these data separately.

I divided the Upper McDonald Creek study site into 100 m patches to assess the probability of occupancy in a stream patch given the covariates distance to road, green barrier, and surface. I included year as a random effects to take into account annual variation in sightability such as weather and observers (Gillies et al. 2006). Date was not a variable that was included in the survey analysis because pair and brood survey occurred in short 4-5 week windows in spring and late summer. I pooled the survey data from all surveys within a year because harlequin pair and brood observations were so rare. For the pair surveys, I assigned each patch with a harlequin pair as present as (1) or absent (0) (single males and single females were excluded). For the brood survey data I assigned each stream patch with a female that had least one chick as present (1) or absent (0). During the last three years that stream survey were conducted (2011 – 2013), I also had radio-collared ducks on the stream. To estimate detection probability of radiocollared ducks on the stream, I simultaneously monitored radiocollared ducks using an omni-directional antennae along the surveyed section of stream. In 3 years we conducted 18 pair surveys with 90 successful detections out of 101 radiocollard ducks that were known to be in survey area. The probability of detection is 89%. Absences in this case are considered true absences because each survey was a near census of the stream.

I analyzed occupancy of stream patch of pairs and broods using logistic regression using Equation 2:

$$logit(p_{ij}) = \beta_{0\,Presence} + \beta_1 x_{Distance\ to\ GTSR} + \beta_2 x_{Road\ Visibility} + \beta_3 x_{Surface} + \gamma_4 x_{Year}$$

where β_0 is the intercept (presence/absence of ducks during surveys separated by pair and brood surveys), $\beta_1 \ldots \beta_3$ are the coefficients on the variables Distance to road, Road Visibility and Surface (*i* designates the number of occupied and unoccupied observations (pair =3205 with 922 occupied units, brood = 2,997 with 219 occupied units) while *j* designates the number of stream patches (1…175). I then predicted the probability of occupancy from β_0 and β_x (Manly et al. 1993). I centered all of the covariates on their median value and performed univariate analysis to remove correlated ($r < 0.5$) and uninformative variables. I first built a global model and used backward elimination to build a set of candidate models (Tables 2a (brood surveys) and 2c (pair surveys)). I then used AIC to select top models (Tables 2b and 2d). Hosmer and Lemeshow goodness of fit were used to test how the model fit the data (Lemeshow and Hosmer 1982, Hosmer et al. 1997) using the Hmisc package in R (Kohl 2013).

Resource Selection Functions

Here, I used individually marked VHF radiocollared harlequin ducks to address whether the GTSR influence resources selection of harlequin ducks. I obtained 3 locations/week for most females (range 5 – 66) throughout the breeding season. Every week during the breeding season I randomly chose females for localization. After every female was found I would start the random selection over again. The same variables that were used in the ARU survey analysis were used in the telemetry analysis with the addition of date Equation 4:

$$logit(p_{ij}) = \beta_{0\,Presence} + \beta_1 x_{Date} * \ \beta_2 x_{Time} * \ \beta_3 x_{Distance\ to\ GTSR} * \beta_5 x_{Road\ Visibility} \\ + \ \gamma_6 x_{Duck\ ID}$$

where β_0 is the intercept, $\beta_{1\ldots}\beta_5$ are the coefficients on the variables Date, Time, Distance to road and road visibility, (*i* designates the number of observations (1,109) while *j* designates the number of individuals (1…38) The gamma (γ_6) is the random intercept term for each individual radio-collared duck. I included a random intercept for individual duck to take into account variation in selection between each duck and the variation in the number of localizations for each duck (Gillies et al. 2006). To increase the interpretability of the variables I centered all of the covariates on their median value (Harrell 2001). I also performed univariate analysis to remove correlated ($r < 0.5$) variables. Data were analyzed using logistic regression and ΔAIC was used to select top models (Equation 3) (Burnham and Anderson 2002). I used Receiver Operating Characteristic (ROC curve) to determine how well the top models fit the data (Fielding and Bell 1997). I used (Equation 4) to predict probabilities of resource selection(Manly et al. 1993)

Resource selection functions (RSF) are important tools for management and conservation, especially for rare and sensitive species similar to harlequin ducks. RSF's are generally applied to animal location data in 2 dimensional space (3 dimensions if you consider elevation). Harlequin ducks pose a unique challenge in that they occupy space in linear features (1 dimension) similar to other riverine species such as fish and Blakiston's fish owl (*Bubo blakistoni*) (Slaght et al. 2013). Harlequin ducks are almost never found off of the stream during the breeding season. When harlequins fly they keep close to the water surface (< 1 m) and follow the deepest part of the stream channel. Since harlequins were found at a constant rate throughout the study area, the entire stream in the study area was considered available to each radio-collared harlequin duck. Critical to RSF is the availability of resource units within the home range of the individual. I created used and available resource units along the liner riverine feature of Upper McDonald Creek by dividing the creek into 175 unique 100 m segments or patches. Each telemetry location was assigned the patch that it fell in and was categorized as used (1). Each used patch was paired with a random available patch (1-175), but could not be the patch that it was recorded in. Random available sites were chosen with replacement and coded as (0). I assessed model fit using ROC curves.

Habitat variables

For analysis parts II and III I developed a suite of functional habitat covariates based on both field and GIS measured covariates to explain where on the stream ducks were found and what features they were selecting for. These covariates represent discrete habitat units at relatively small geomorphological scale (Leopold et al. 2012) that align with the functional definition of habitat proposed by (Hutto 1985) and reviewed by (Gaillard et al. 2010). I divided the stream up into 100 m patches so that I could assign a score to each patch based on a specific covariate. Patches were created by generating points separated by 100 m in ArcGIS 10.1 along Upper McDonald Creek. Rectangular patches were then assigned to each point, with the point in the center of the rectangle.

These locations were transferred to handheld Garmin GPS 530HCx using DNRgarmin (MDNR 2008) so that these points could be visited in the field for measuring vegetation cover. The entire study area was comprised of 175 patches. The main covariates used to build predictive models of harlequin use and selection were distance to road, vegetation cover and stream surface. I calculated distance to road in ArcGIS 10.1 as the shortest straight line distance from GTSR to the center of each 100m patch. The vegetation cover was a measurement of vegetation masking the road from the stream, and was measured using a Robel pole 3 times during the growing season. This process required 2 people, 1 person stood on the highway with the Robel pole and the other person stood on the stream edge at the center of each patch and recorded the number of visible stripes on the Robel pole. The stream surface variable was categorical and consisted of pool, riffle, run and rapid and was coded 1-4 respectively. Each stream patch received a single surface category and was determined to be the dominant feature in that patch. Classification of the stream surface category was done using satellite (taken in July of 2013) imagery overlaid on the stream patches. Distance and visibility variables were centered on their median values. Univariate ($R = < 0.5$) and variance inflation (<2.0) analyses were done to identify correlated and uninformative variables. For all 3 data collection methods described above I used backward elimination to develop candidate models and compared competing models with all combinations of remaining variables using AIC and selected the top models with $\Delta AIC<2$.

RESULTS

Part I: Automated receiver data occupancy model

I recorded 2301 hours of presence out of 4322 hours of observation from disturbed sites and 1290 hours of presence out of 3630 hours of observation from undisturbed sites during the 2012-13 breeding seasons. The proportion of ducks found in disturbed sites vs undisturbed sites was significantly greater (mean disturbed = 0.53, mean undisturbed = 0.36, Welch Two Sample t-test, t=16.1, df =7811.9, p<0.0001) across the entire breeding season. The Ψ of a duck in a high human use stream patches did not change significantly over the season, however Ψ did significantly decrease over the season in low human use areas (Figure 3-2a). My top ranked ARU-occupancy model included a three-way interaction between date, hour and traffic volume (Table 3-1b). Duck Ψ decreased as the season progressed (date) in both high and low human use areas, the Ψ did not change with hour (time of day) in high human use sites, but did increase in low human use sites as hour increased. The Ψ also did not change as a function of traffic volume in high human use areas, but Ψ did decrease in low human use areas as traffic volume increased.

The proportion of occupancy changed each week in high human use and low human use locations. The proportion of occupancy was high in high human use sites early and late in the season with dramatic decline in occupancy from week 24-27 (second week of June – the first week in July). Undisturbed sites declined in occupancy throughout the season with a drop in occupancy on week 24 (Figure 3-2b). There was no significant difference in occupancy during the early season in high human use and low human use sites (Welch Two Sample t-test, t = -0.8235, df = 3815.662, p-value = 0.4103), but there was significant decreased proportion of occupancy in low human use sites in the late season (Welch Two Sample t-test, t = 12.0893, df = 1869.366, p-value < 2.2e-16).

Part II: Pair Survey

I recorded 3300 observations of presence/absence among 100m stream patches from 23 years of stream survey monitoring. From these observations 922 were recorded as presences. The top model included distance to road and surface (β=-0.003, SE=0.04, β•SE= -6.38, p=<0.001 and β=-0.82, SE=0.0077, β•SE=-10.64, p=<0.001) respectively, where a greater Ψ was observed closer to the road (Figure 3-3a) and the greatest Ψ in pools (Ψ in pools = 0.84) (Table 3-2a and b). This model differentiated between presence/absence well using goodness-of-fit test (Hosmer-Lemeshow C statistic = 0.21 and Hosmer-Lemeshow H statistic = 0.78).

Brood

For brood surveys, I recorded 3,000 presence/absence observations among 100 m patches from 24 years of stream survey monitoring. From these observations 222 were recorded are presences. The top model to describe Ψ included the variables distance to road and surface. The greatest Ψ is found close to road (Figure 3-3b and c) and greatest in riffles and rapids (β=0.78, SE=0.21, β•SE=3.62 p=<0.001 and β=1.35, SE=0.23, β•SE=5.95, p=<0.001), respectively. This model performed well using the Hosmer-Lemeshow C statistic, but not the Hosmer-Lemeshow H statistic (p= 0.31, p=0.0009, respectively).

Part III: Telemetry

The telemetry data set was comprised of 1,065 used and available observations taken from the breeding season (April – September) from 2011-2013. From these years I recorded GPS information from 35 individuals. Of these individuals, 11 had nested and only 3 of these managed to hatch chicks. One of the three did not nest in the study area and her chicks emerged very late in the season. One of the other females dropped her radiocollar before her chicks hatched. Therefore I only had GPS data on one female with chicks, thus I did not include this demographic into this analysis.

The global model was comprised of a four way interaction between Julian date, time, distance to road, road visibility and additive variables year and surface. The global model differentiated between used and available moderately (ROC = 0.63). The top model selected by AIC included an interaction between distance to road and time (β = 0.0009, SE = 0.0003, β•SE = 2.9, p = 0.004). Ducks selected stream patches closest to the road and later in the day. Ducks also had negative selection for stream patches dominated by rapids and riffles. The top model differentiated between used and available moderately (ROC = 0.62)

DISCUSSION

Part I: ARU

Overall, this study found radioed females occupying stream sites with higher human use over low human use, contrary to my *a-priori* expectation, where I expected birds to avoid high human use areas as traffic volume increased. Interesting patterns emerged when I looked at weekly occupancy probabilities. I found a sharp decline in occupancy at high human use sites during weeks 24-27 (second week in June—first week in July) and in week 24 in undisturbed sites. I predict 3 possible scenarios to explain this pattern: 1) as traffic volume increases along GTSR ducks react by avoiding disturbed sites, but gradually habituate and return to these sites. However, this prediction does not explain why I saw a drop in occupancy in undisturbed sites on week 24. 2) An alternative prediction is that week 24 coincides with the beginning of the incubation period. Many females at this time are spending the majority of their time incubating eggs and infrequently go on foraging bouts. When females are incubating eggs they are not present on the stream, thus unavailable for detection by ARUs. 3) Week 24 also coincide with average peak stream flow. During peak flow harlequins were regularly observed foraging on small tributary streams. Again similar to prediction 2 this behavior would make them undetectable by the ARUs. The probability of occupancy is reduced in week 24 in undisturbed sites similar to disturbed sites, but this pattern does not persist to week 27. There is no clear explanation for why occupancy would decrease in week 24 in undisturbed sites, but not persist like it does in disturbed sites to support hypothesis 2. These results are similar to the findings (Wallen and Groves 1989) that showed 60% of their harlequin observations were close to roads or trails. Harlequin ducks in their study were reported to appear to tolerate human activity. Although they do mention that where human activity was tolerated shrub density was high enough to shield from disturbance.

Part II: Survey

I found the highest Ψ of both pairs and broods close to the road. Pairs also had high Ψ in stream sections with pools and broods had higher Ψ in rapid and riffle stream sections. I did not expect to find greater occupancy of pairs closer to the road. I was however not surprised to see stream sections with pools having the greatest occupancy. A statistical test for collinearity suggested that these two variables (pools and distance to road) are not collinear (R^2 = -0.11), but a distribution of pools ~ distance to road clearly shows that more stream sections with pools exists close to the road (Figure 3-4). The difference in the predicted probabilities for patches with pools and patches close to road is 0.84 and 0.34 respectively, suggesting that ducks are selecting for stream patches with pools vs. patches close to close to road. Based on this difference of occupancy, the high occupancy probability close to road is likely an artifact of pool distribution. Additionally, I surmise that during the pair survey period (April – June) that that there is very little road disturbance given that the GTSR is closed to vehicles usually until mid-June (July 13, June 20 and June 21 in 2011, 2012 and 2013 respectively) when Logan Pass is cleared of snow, although the road is open at this time to hikers and bicyclists. The pair season for most waterfowl is a very active time for females to forage for nutrients required for egg production, mate guarding by males and territorial disputes by pairs. A combination of these intense behaviors, breeding hormones and little to no vehicle traffic on the GTSR likely make it a minimal disturbance to breeding pairs of harlequin ducks.

Broods had the greatest Ψ close to road and in all stream surface habitats. I did not expect to see greater occupancy of birds during brood surveys closer to the road because they are generally considered to be more sensitive to human activity (Kuchel 1977b, W. Hansen, personal observation). Over the past 24 years park biologists have observed a short segment of Upper

McDonald Creek where broods and females congregate at the end of the season. This behavior has been described as "clubbing" behavior seen in many migratory species known as staging areas. The majority of the parks brood survey observations come from this segment of stream (Figure 3-1). This segment is low in the watershed and close to the road. Many broods seem to congregate in this area from all over the watershed. Broods have been observed moving from a stream > 16 kilometers away to congregate in this area (Personal communication Ashley 2011). The frequency of observations coming from this area has likely masked the importance of other resources when the broods are at a younger life history stage. This stream section also has a large stream gradient buffer where the road and trail system is 10 m above the stream. These buffers have been identified as important for brooding harlequins to tolerated human activity (Wallen and Groves 1989).

The tolerance of harlequins to human activity has also been observed by (Wallen and Groves 1989). They report that when harlequin ducks arrive to the breeding stream in May, human activity is low the ducks and nest prior to increased human activity. Harlequin ducks must then tolerate human activity as it increases later in the spring and summer. The stress response of harlequin ducks measured by (Perfito et al. 2002) may also help explain this behavior. The stress response in harlequin ducks is decreased during the pair season (May—June) and then increases later in the brood season (August—September). (Breuner and Hahn 2003)have demonstrated that home-range increases after stress implant is administered in white crown sparrows (*Zonotrichia leucophrys*). Home-range size increases with the stress response because the individual becomes more eruptive to disturbance and has a greater drive to find food. The change in linear home-range size in harlequin ducks from pre-hatching to post-hatching measured by (Smith 2000) increased from 4 km to 18 km. This suggests a hormone mediated response for harlequins to tolerate human activity in the pair season and decrease tolerance in the brood rearing season.

Part III: Telemetry

Ducks selected stream patches closer to the road later in the day. Ducks also selected for rapids and runs. This is again not the *a-priori* result that I expected to see. Although the surface variable pools did not emerge in the top model, ducks were still occupying stream patches with pools, but not selecting for them. It is interesting that ducks are selecting stream patches close to road later in the day because traffic volume is at peak later in the afternoon (between 4 – 6 pm). It is apparent from this analysis that there is no clear evidence for avoidance of the GTSR. I think that if strong avoidance of the GTSR was occurring on the stream, it would have emerged in this analysis. Further research should explore human disturbance and focus on harlequin response to different human behaviors, as a function of traffic volume.

Challenges from this analysis were the stream habitat characteristics, which are difficult to identify as static features, as I have done here. Steam levels are constantly changing throughout the year in response to temperature and precipitation. Small changes in high gradient alpine steams are constantly creating and taking away resources that harlequins capitalize on for foraging. I tried to create static habitat variables from a very dynamic system by making coarse 100m habitat bins. At this scale I cannot make finer scale predictions for selection at finer scale habitat choices that harlequins may be making. Further challenges of this study were a lack of a control stream without any kind of human use or road nearby. Although McDonald Creek does meander far and close to the GTSR, the topography of the watershed constrained this variation and the majority of the stream is close to the road. Despite the potential disturbance of the GTSR to harlequins on Upper McDonald Creek, it still boasts the greatest breeding density in the lower 48 (Montana Natural Heritage Program 2014). It is important to note that there are numerous remote tributary streams in the Upper McDonald Creek watershed that I documented harlequin ducks using. There are a variety of reasons for why Upper McDonald Creek has such high density. For example, fish barriers exist low in the watershed that limit fish density and fish size which are thought to be the main competitors for food resources with harlequin ducks (Robert and Cloutier 2001, LeBourdais et al. 2009). Strong correlations have been shown between harlequin duck density and fishless streams (LeBourdais 2006). Most of the nesting sites that I identified were on pristine tributary streams of Upper McDonald Creek which Smith (2000) identified as important for nest success. Finally, recreational activities such as rafting and kayaking have been identified as strong disturbances to harlequins by (Reichel 1996a) and have been banned on Upper McDonald Creek since the early 1990's. For these reasons Upper McDonald Creek might be the best breeding stream in Glacier National Park and experiences higher densities to other comparable streams outside of the National Parks. Harlequin ducks in this system are likely tolerating the cost of human presence for the benefits of Upper McDonald Creek.

CONCLUSION

My main objective for this study was to explore the impacts of the GTSR on the occupancy and selection of harlequin ducks. The reoccurring theme from the three different analyses is that I do not see strong avoidance of high human use sites or the Going to the Sun Road. In fact I see high occupancy probabilities of pairs and broods close to the road and high selection of stream patches closer to the road. I suggest that this pattern during the pair season is a topographic constraint that the road and stream often have to be near each other, thus the distribution of pools is closer to the road. Regardless of the interpretation, harlequins are using stream segments close to road at a high rate. These areas need to be closely monitored and managed for minimum disturbance.

My resource selection model using the telemetry data also indicate that stream patches close to the GTSR are important resources that ducks are selecting for on Upper McDonald Creek. For more informative selection patterns with better model fit to emerge from this analysis I suggest finer scale measurements of habitat variables and increased sample sizes of use to obtain power to differentiate between different phases of reproduction. The telemetry data also did not include any females with broods, which are generally considered more sensitive to humans than single females or pairs (Kuchel 1977b, W. Hansen, personal observation). Harlequins are also highly mobile and are regularly observed swimming, floating or flying up and down stream. Transitions between different important habitat features were likely recorded. Future analysis should include a behavioral category associated with each GPS location.

Resource selection and occupancy is clearly complicated in a highly mobile animal in a very dynamic environment. Rapid changes in different life history phase's e.g. breeding, incubating, brood rearing and fledging likely require highly varied resources for harlequin ducks. Important habitats during these short and varied life stages are challenging to identify in a model. Rare animals like harlequins make it difficult to obtain adequate sample sizes at all of these different stages. Advances in technology and decreasing the weight and cost of satellite transmitters is on the horizon and is necessary to inform these kinds of models. More importantly, any future studies striving to understand impacts of human activity need to have an experimental design with multiple streams that experience a gradient of low human activity to high human activity. This design is imperative to disentangle duck tolerance (habituation) and responses to human activity.

Despite the limitation of experimental design in my study, I conclude that there is no current or past (23 year) strong signature of harlequin duck avoidance of human activity associated with the GTSR. This conclusion does not suggest that increased human activity will not adversely affect harlequin duck distribution on Upper McDonald Creek. Human activity is likely perceived by harlequin ducks, but is tolerated to certain level. Managers that are working to conserve harlequins should consider human activity, but should also consider all of the other important components to harlequin duck reproduction.

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TABLES AND FIGURES

Table 3-1a. Top ranking occupancy models with number of parameters and Akaike weights (ω) for occupancy of automated receiver unit data, 2012-2013, Glacier National Park. Top ranking models were models with ΔAIC scores <2.0.

Variable	K	ΔAICc	ω
Date:Hour:Traffic + site	**10**	**0.00**	**0.88**
Date:Hour + site	6	5.42	0.06
Date:Hour:Traffic	9	5.59	0.05
Date + Hour	4	12.77	0.00
Date:Hour	5	14.58	0.00
Hour + Traffic	4	46.64	0.00
Hour + site	4	54.34	0.00
Hour	3	54.78	0.00
Date:Traffic + site	6	70.56	0.00
Date:Traffic	5	73.99	0.00
Date + Traffic	4	91.04	0.00
Traffic + site	4	100.69	0.00
Traffic	3	102.51	0.00
Date + site	4	122.97	0.00
Date	3	132.71	0.00
site	3	170.46	0.00

Date = Julian day of the year, Hour = the hour out of a 24 hour period that a duck was detected in, Traffic = the total count of hourly traffic volume, site = binary variable of high human use or low human use sites.

Table 3-1b. HADU Occupancy model average coefficients, standard errors and p-values with * indicating significance for automated receiver unit data, 2012-2013, Glacier National Park, Montana.

Variable	B	SE	$B \cdot SE^{-1}$	p-value	
(Intercept)	-2.5709	0.1965	-13.0840	< 2e-16	***
Date	-0.3515	0.1691	-2.0780	0.0377	*
Hour	-0.0395	0.0091	-4.3240	0.0000	***
Traffic	-0.0908	0.2008	-0.4520	0.6512	
Site Un-disturbed	-0.1638	0.0597	-2.7440	0.0061	**
Date1:Hour	0.0112	0.0100	1.1120	0.2663	
Date1:Traffic	-0.2288	0.2217	-1.0320	0.3019	
Hour:Traffic	-0.0001	0.0116	-0.0120	0.9903	
Date1:Hour:Traffic	0.0217	0.0125	1.7320	0.0832	.

Table 3-2a. Top ranking models with number of parameters and Akaike weights (ω) for probability of occupancy of pair survey data, 1990-2013, Glacier National Park. Top ranking models were models with ΔAIC scores <2.0.

Model	K	ΔAICc	ω
Surface + Distance to Road	**6**	**0**	**0.35**
Distance to Road	3	0.64	0.25
Roble + Surface + Distant to Road	7	1.01	0.21
Distance to Road + Robel	4	1.29	0.18
Robel	3	31.2	0
Robel + Surface	6	33.5	0
Surface	5	40.79	0

Robel = road visibility index of stream patches, Distance to Road = shortest distance from the center of stream patch to the Going to the Sun Road, Surface = categorical variable of stream habitat type (pool, riffle, run or rapid).

Table 3-2b. Occupancy model average coefficients, standard errors and p-values with * indicating significance for probability of occupancy of pair survey data, 1990-2013, Glacier National Park.

Variable	B	SE	$B \cdot SE^{-1}$	p-value	
Pool	-0.89852	0.156792	-5.731	1.00E-08	***
Riffle	-0.03288	0.11855	-0.277	0.7815	
Run	-0.12387	0.10241	-1.21	0.2265	
Rapid	-0.36337	0.150413	-2.416	0.0157	*
Distance to Road	-0.00308	0.000495	-6.228	4.72E-10	***

Table 3-2c. Top ranking Harlequin duck occupancy models with number of parameters and Akaike weights (ω) for probability of occupancy of brood survey data, 1990-2013, Glacier National Park. Top ranking models were models with ΔAIC scores <2.0.

Variable	K	ΔAIC	ω
Surface + Distance to Road	**6**	**0**	**0.72**
Roble + Surface + Distant to Road	7	1.89	0.28
Surface	5	14.24	0
Robel + Surface	6	15.19	0
Distance to Road + Robel	4	45.04	0
Distance to Road	3	45.23	0
Robel	3	68.4	0

Table 3-2d. Model average coefficients, standard errors and p-values with * indicating significance for probability of occupancy of brood survey data, 1990-2013, Glacier National Park.

Variable	B	SE	$B\bullet SE^{-1}$	p-value	
Pool	-1.969	0.233	-8.451	<0.001	***
Riffle	-1.254	0.204	-6.142	<0.001	***
Run	-0.428	0.208	-2.058	0.040	*
Rapid	-1.283	0.234	-5.494	<0.001	***
Distance to Road	-0.004	0.001	-3.742	<0.001	***

Table 3-3a. Harlequin duck Resource Selection Function model averaged coefficients, standard errors and p-values with * indicating significance for duck radio telemetry locations, 2011-2013, Glacier National Park, Montana.

Variable	B	SE	B•SE-1	p-value	
Pool	0.176	0.343	0.513	0.608	
Distance to Road	-0.008	0.004	-1.989	0.047	*
Time	0.004	0.023	0.182	0.856	
Riffle	0.001	0.168	0.004	0.997	
Run	-0.473	0.154	-3.075	0.002	**
Rapid	-0.868	0.233	-3.732	<0.001	***
Distance to Road x Time	2.8E-3	0.000	0.949	0.343	

Date = Julian day of the year, Robel = road visibility index of stream patches, Distance to Road = shortest distance from the center of stream patch to the Going to the Sun Road, Pool, Riffle, Rapid and Run = stream habitat variables that dominated unique stream patches, Time = the exact minute in each day that a duck was detected.

Table 3-3b. Top ranking resource selection function models with number of parameters and Akaike weights (ω) for probability for Harlequin Duck radiotelemetry location, 2011-2013, Glacier National Park, Montana. Top ranking models were models with ΔAIC scores <2.0

Model	K	ΔAIC	ω
Distance X Time + Surface	**8**	**0**	**0.4**
Distance x Robel x Time + Surface	12	0.76	0.27
Distance x Time + Year + Surface	9	1.64	0.17
Distance x Robel x Time + Year + Surface	13	2.46	0.12
Date x Distance x Time + Surface	12	5.33	0.03
Date x Distance x Time + Year + Surface	13	6.96	0.01
Date x Robel x Distance x Time + Surface	20	10.72	0

Date = Julian day of the year, Robel = road visibility index of stream patches, Year = year data was collected from 2011-2013, Distance = shortest distance from the center of stream patch to the Going to the Sun Road, Surface = categorical variable of stream habitat type (pool, riffle, run or rapid).

Figure 3-1. **Study area on Upper McDonald Creek from McDonald Creek to Logan Creek. The five black dots represent locations of high human use areas (disturbed locations). The "hot-cold" areas on the map represent the highest densities of broods observed from 1992-2013 during the parks annual brood surveys.**

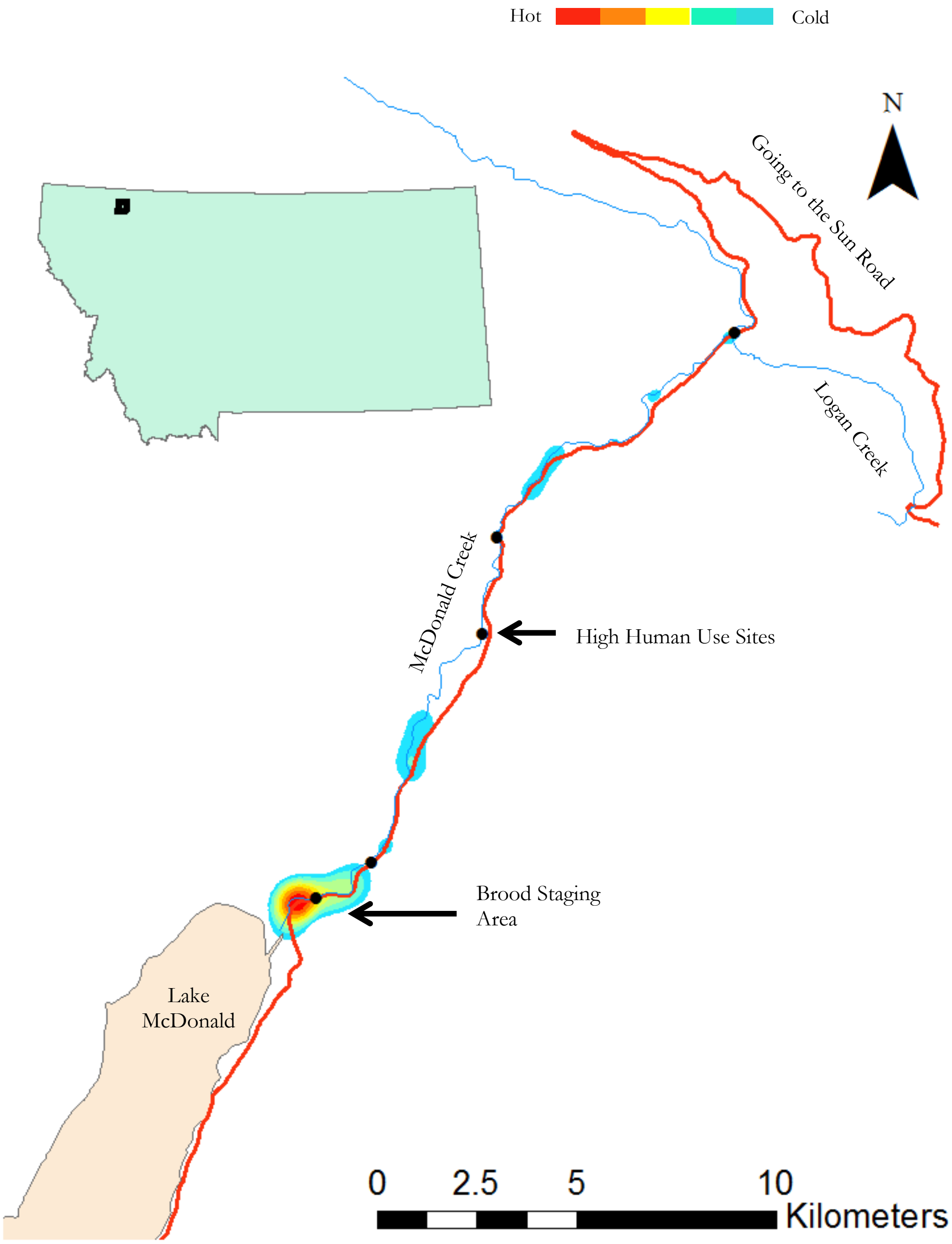


Figure 3-2a. **The Ψ for a radio-collared female harlequin duck in high human use patches and in low human use patches across the breeding season (April 15 – September 1) from years 2012 – 2013 (n = 18). Probabilities were estimated from the β's in table 3-1a.**

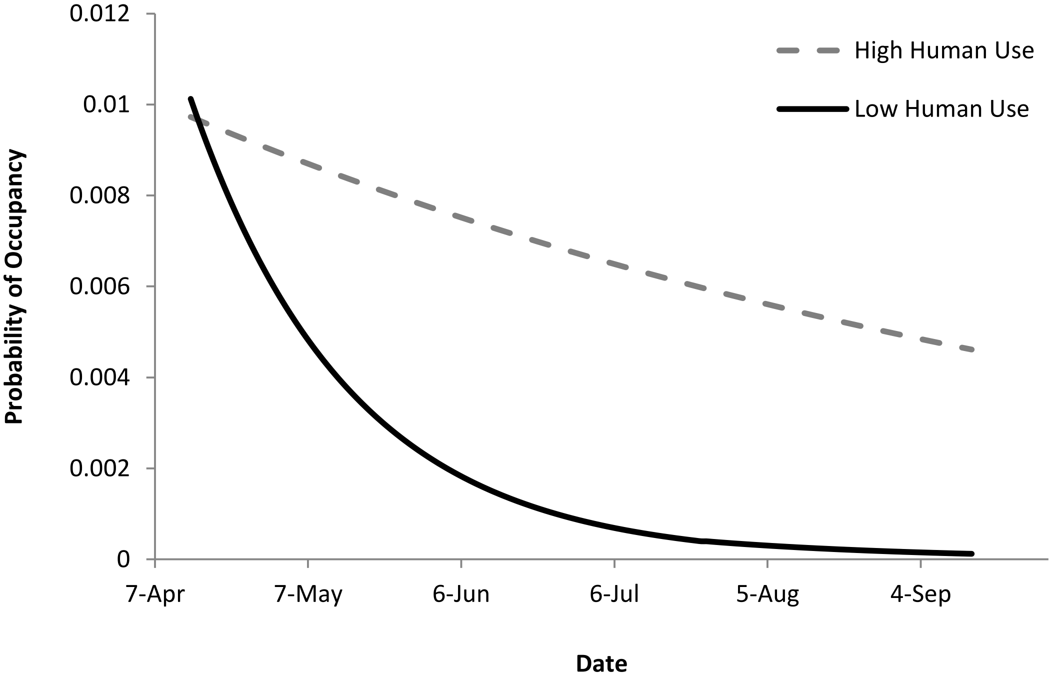


Figure 3-2b. The average occupancy probabilities for disturbed and undisturbed sites for season and by week. Weekly averaged traffic volume for 2013 and breeding chronology by week added for reference.

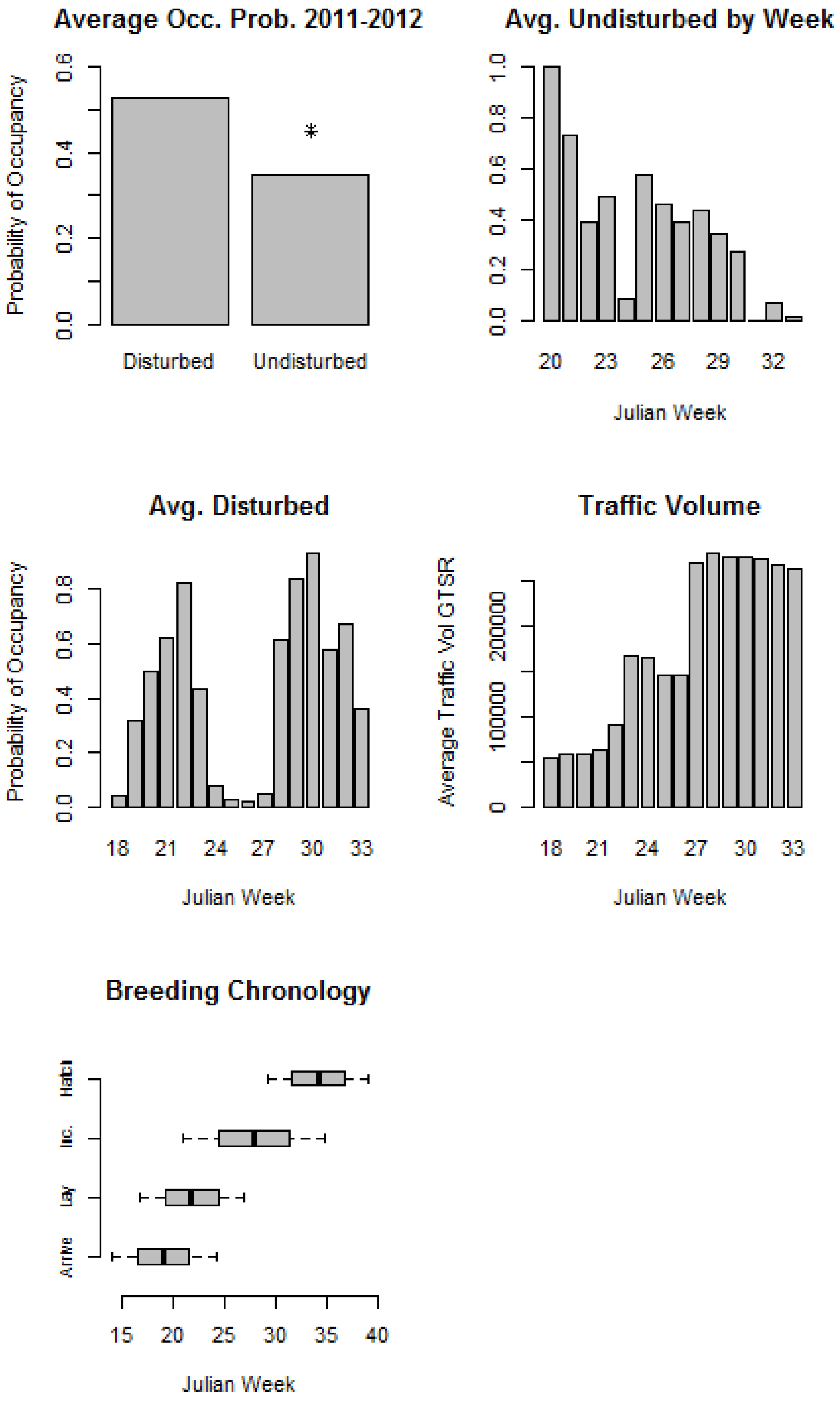


Figure 3-3. Relative occupancy probabilities of harlequin duck broods (solid line) and pairs (dashed line) in relationship to distance to the Going to the Sun Road calculated by equation $\frac{\exp(\beta_0+\beta_{1x1}+\cdots+\beta_{pxp})}{1+\exp(\beta_0+\beta_{1x1}+\cdots+\beta_{pxp})}$ from survey data collected in Glacier National Park on Upper McDonald Creek. Vertical tick marks indicate observed broods (light ticks) and observed pair (dark ticks) distances from the Going to the Sun Road.

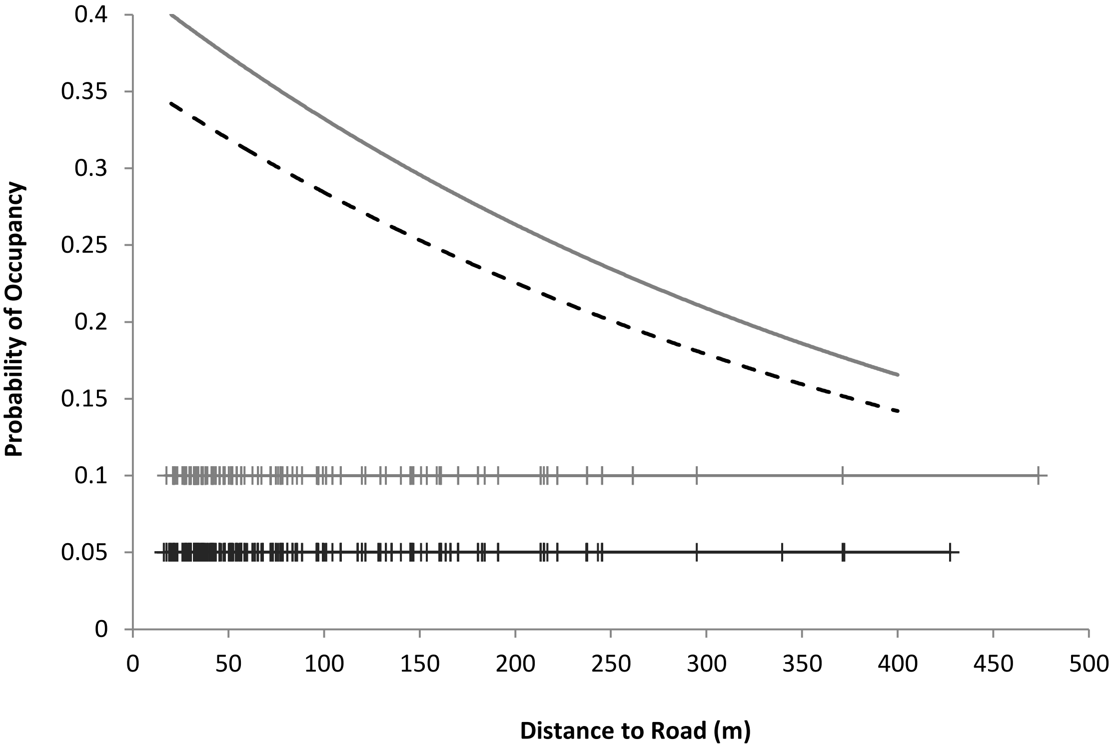
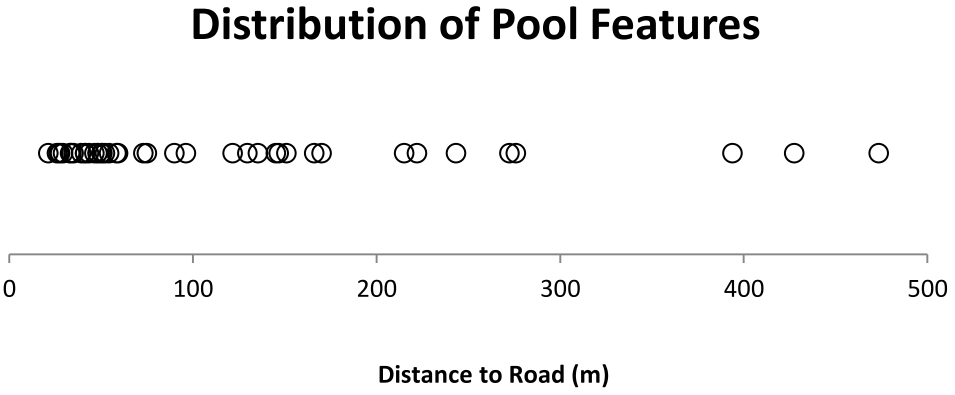


Figure 3-4. Distribution of pool habitat against the distance to the Going to the Sun Road. Increasing numbers on the x-axis correspond with increasing distance from road.



Appendix 3-1. **All resource selection function models with number of parameters and Akaike weights (ω) for probability for Harlequin Duck radiotelemetry location, 2011-2013, Glacier National Park, Montana. Top ranking models were models with ΔAIC scores <2.0**

Model	K	ΔAIC	ω
Distance X Time + Surface	**8**	**0**	**0.4**
Distance x Robel x Time + Surface	12	0.76	0.27
Distance x Time + Year + Surface	9	1.64	0.17
Distance x Robel x Time + Year + Surface	13	2.46	0.12
Date x Distance x Time + Surface	12	5.33	0.03
Date x Distance x Time + Year + Surface	13	6.96	0.01
Date x Robel x Distance x Time + Surface	20	10.72	0
Date x Robel x Distance x Time + Year + Surface	21	12.42	0
Distance x Robel x Time	9	16.04	0
Distance X Time	5	17.21	0
Distance x Robel x Time + Year	10	17.85	0
Distance X Time + Year	6	18.93	0
Date x Distance x Time	9	22.1	0
Date x Distance x Time + Year	10	23.82	0
Date x Robel x Distance x Time	17	25.37	0
Date x Robel x Distance x Time + Year	18	27.21	0
Time + Surface	6	35.34	0
Time + Year + Surface	7	37.35	0
Date x Robel x Time + Surface	12	39.29	0
Date x Time + Surface	8	39.37	0
Date x Robel x Time + Year + Surface	13	41.29	0
Date x Time + Year + Surface	9	41.39	0
Time	3	47.3	0
Time + Year	4	49.32	0
Date x Robel x Time	9	50.46	0
Date x Time	5	51.34	0
Date x Robel x Time + Year	10	52.49	0
Date x Time + Year	6	53.36	0
Distance + Surface	6	153.34	0
Distance x Robel + Surface	8	154.58	0
Distance + Year + Surface	7	154.91	0
Distance x Robel + Year + Surface	9	156.33	0
Date x Distance + Surface	8	156.76	0
Date x Distance + Year + Surface	9	158.28	0
Date x Distance x Robel + Surface	12	159.41	0
Date x Distance x Robel + Year + Surface	13	161.06	0
Distance x Robel	5	175.03	0
Distance	3	176.17	0

Distance x Robel + Year	6	176.91	0
Distance + Year	4	177.83	0
Date x Distance	5	179.84	0
Date x Distance x Robel	9	180.56	0
Date x Distance + Year	6	181.48	0
Date x Distance x Robel + Year	10	182.4	0
Surface	5	190.89	0
Date + Surface	6	192.9	0
Surface + Year	6	192.9	0
Robel + Surface	6	192.9	0
Date + Year + Surface	7	194.91	0
Robel + Year + Surface	7	194.91	0
Date x Robel + Surface	8	195.22	0
Date x Robel + Year + Surface	9	197.22	0
Robel	3	212	0
Date	3	212.27	0
Year	3	212.27	0
Robel + Year	4	214.01	0
Date + Year	4	214.28	0
Date x Robel	5	214.6	0
Date x Robel + Year	6	216.62	0

Date = Julian day of the year, Robel = road visibility index of stream patches, Year = year data was collected from 2011-2013, Distance = shortest distance from the center of stream patch to the Going to the Sun Road, Surface = categorical variable of stream habitat type (pool, riffle, run or rapid).

CHAPTER 4: FEATHER CORTICOSTERONE CONCENTRATIONS PREDICT FUTURE REPRODUCTIVE DECISION IN HARLEQUIN DUCKS (HISTRIONICUS HISTRIONICUS)

ABSTRACT

The sources of variation in annual reproductive success are important to understand to advance management, conservation, population ecology and life history theory. Most studies focus on current environmental events to understand sources of current year reproductive variation. However carry-over effects are likely mediators for future breeding success. These effects are difficult to study in migratory species such as birds. Here I measured corticosterone (CORT) in feathers to test how well they predict past and future reproductive success in harlequin ducks. I also examined how well feather CORT concentrations predict body condition and plasma CORT concentrations upon arrival to the breeding grounds. I found that back feather CORT (feathers grown just prior to the breeding season) predicted future breeding decision well, but did not predict body condition or plasma CORT levels. I was not able to test how well feathers grown just after the breeding season (tail feather grown during the basic molt) predicted past reproductive decision due to small sample size. These results highlight an important life history phase (pre-nuptial molt-just prior to the breeding season) that has an influence on future reproductive decision. This is an important management and conservation tool to for predicting future reproductive decisions and population health.

INTRODUCTION

Understanding the causes of reproductive variation can inform management and conservation decisions, population ecology and life history theory. Annual variation in predation, resource availability, weather or disturbance can drive population variation and reproduction (MacLulich 1957, Coulson et al. 2001, Visser et al. 2004). Furthermore, high variation in population demographics can lead to increased extinction risk in small populations (Boyce et al. 2006).

In birds, annual reproductive variation is a major contributor to population growth rate (Sæther and Bakke 2000). Highly variable annual reproductive rates are typically displayed in longer lived birds that experience high adult survival and late age of maturity. In these systems, adult survival is selected for over reproduction, where many adults make the decision to breed in good years when resources are plentiful and defer reproduction in bad years when resources are poor.

Most studies evaluate current environmental events that may limit reproductive success. However, carry-over effects (Stearns 1992, Webster et al. 2002, Norris 2005) are likely mediators for future breeding success(Inger et al. 2010, Harrison et al. 2011), and it is important to consider their role in reproductive decisions. In reproductive studies of migratory species it is logistically difficult to determine resource and environmental conditions on the wintering grounds that may influence reproduction. Different physiological metrics such as body condition (Angelier et al. 2011) and fat scores have been used to infer environmental conditions outside of the breeding period, but these metrics can change rapidly and may not be informative if subjects are not captured immediately upon arrival. Other more stable physiological records have been used to link large gaps in time to reproduction. For example stable isotopes have been used to identify individuals in the breeding season that had access to high quality forage during the previous winter (Marra et al. 1998). Individuals with a greater forage quality signature arrived earlier to the breeding grounds and had greater reproductive success.

Stress hormones or corticosteroids (CORT) have also been widely used to quantify individual quality and effects on fitness (Marra and Holberton 1998, Breuner et al. 2008, Bonier et al. 2009, Angelier et al. 2010). Corticosterone in the primary stress hormone released from the Hypothalamic-Pituitary-Adrenal (HPA) axis in birds in response to external perturbations. Activation of the HPA axis promotes survival, but chronic effects have deleterious effects on individual quality (Wingfield et al. 1998). Studies of baseline CORT have indicated that it plays an important role in mediating behavior, individual quality and reproductive decisions. For example, experimentally elevated baseline CORT in female kittiwakes during chick rearing initiated an earlier departure for the wintering grounds and these females stayed on the wintering grounds longer than control birds (Schultner et al. 2014). Higher baseline levels in breeding swallows has been shown to decrease the quality of offspring (Saino et al. 2005). Goutte et al. (2010) found that snow petrels with elevated baseline CORT during pre-egg lay were more likely to defer breeding. Although these studies do show evidence for CORT as mediators of important life history characteristics, but the time from sample to the next life history phase is relatively short. Recent studies of CORT concentrations in feathers have found similar results, but reflect a much longer time frame from the deposition of CORT into the feather to the behavior in the next life history phase. A study of red-legged partridges revealed that CORT deposited in feathers grown just after the breeding season reflects breeding success from that year (Bortolotti et al. 2008). In giant petrels, CORT deposited in feathers grown just after the breeding season has been demonstrated to predict reproductive success in the following year (Crossin et al. 2013). Hence, using feather glucocorticoid levels may allow for better incorporation of carry-over effects into determinants of reproductive decisions.

Here I measured CORT levels in plasma and feathers in harlequin ducks to explore how well this metric might predict future reproductive deferral. I predicted that high concentrations of corticosterone in feathers grown just prior to breeding would correlate with body condition, baseline CORT and reproductive deferral. My hypothesis was that a physiological link exists between CORT levels experienced during the prenuptial molt on the wintering grounds (feathers) to baseline CORT levels soon after arrival to the breeding grounds and current year reproductive decision.

MATERIALS AND METHODS

Study site and species

Data were collected in Glacier National Park (48°38'N, 113°52'W), Montana, during 2011—2013 on Upper McDonald creek, as described in chapter 2. Harlequin ducks are migratory sea birds with Holarctic distribution. They winter along northern latitude coastlines and migrate inland to alpine streams to breed. This study focused on the reproductive period from pair arrival on the breeding stream in May until the end of the breeding period in August.

Harlequin ducks are long lived and form life-long pair bonds (Smith et al. 2000), but only the females incubate and care for young (Bengtson 1972, Rohwer and Anderson 1988). Females are primarily income breeders: nutrients required for egg production are acquired from the breeding stream (Bond et al. 2007). Females lay 1-7 eggs in a ground nest close the stream edge (Kuchel 1977b). Males return to the wintering grounds soon after females initiate incubation, allowing for only 1 reproductive attempt per year. Chicks emerge on the stream in late July—August and remain on the stream until September when their mothers escort them to the wintering grounds. Upon arrival to the wintering grounds, (September-October) females undergo a pre-basic molt where all feathers are replaced. Just before the next breeding season (end of March—April) females undergo another molt, the pre-nuptial, and replace just body plumage (Figure 2) (Pyle 2008).

Sample Collection

The protocol was approved by IACUC (AUP 011-11), the NPS and USFWS. Pairs were captured on the breeding stream shortly after arrival using 3x10m mist nets. Blood samples were collected from the alar vein using a 30 gauge needle and heparinized micro hematocrit tubes. While collection of a baseline CORT sample in under three minutes is recommended (Perfito et al. 2002, Romero and Reed 2005), not all blood samples were collected in less than 3 min from time of hitting the net (Figure 3), and therefore time after capture was included as a cofactor in all plasma corticosterone analysis. Blood samples were kept on ice until later that same day when I returned to the lab, where plasma was separated using centrifugation and stored at -20°C. Birds were weighed to the nearest 5 g using a 1000 g Pesola spring scale, bill and tarsus measurements were made to the nearest 0.1 mm using a dial caliper. Each bird received a USFWS band and a plastic blue and white alpha-alpha leg band. Two mantel feathers and 1 outer-most right tail feather were collected and stored in labeled bags at -20°C until analysis. Females received an 8.5 g ATS VHF transmitter so that they could be tracked daily throughout the breeding season. When a female was found incubating eggs she was classified as having made the decision to reproduce.

Hormone Assays

I measured plasma CORT concentrations using enzyme-linked immunoassay (EIA) (Enzo Life Science cat # 901-097). I optimized the assay for harlequin ducks following Breuner et al. (2006). Plasma was assayed at a final dilution of 1:40 with 1% steroid displacement buffer.
Feather CORT extraction: I measured feather CORT at the Centre d'Études Biologiques de Chizé, France and in the Breuner Lab of Missoula, Montana. I used radioimmunoassay (RIA) following (Bortolotti et al. 2008), but modified this method for whole feather extraction. Briefly, I removed the calamus and measured the feathers to the nearest 1 mm. CORT was extracted from whole feathers with 5 mL of 99.99% pure methanol overnight in a 50°C water bath. Methanol was poured directly off the feather, and then evaporated off in a 50°C water bath under nitrogen. Extract residues were reconstituted in 300 ul phosphate-buffered saline with gelatin. If samples were not assayed the same day they were frozen at -20° until analysis. Extraction efficiencies were measured by adding recoveries (2000 CPM/50μL of ^{3}H-corticosterone) in the initial methanol incubation. Extraction efficiencies ranged from 100 to 58%, with a mean of 94%.

Radioimmunoassay: feather CORT extracts were measured using radioimmunoassay with a highly cross-reactive antibody from Sigma (C8784), appropriate when measuring corticosterone and its metabolites that end up in feathers (as per Lattin et al. 2011). Briefly, glucocorticoid metabolites were extracted from feathers in methanol overnight at 50°C. Methanol was poured off the feather; after methanol evaporation, metabolites were reconstituted in PBSG (pH = 7.0) for the RIA. Samples were incubated with 100 ul 1:100 Ab dilution and 100 ul 4000 cpm H^3-CORT. The standard curve ranged from 7.5 to 2000 pg/100 ul; external standards and blanks were run with each assay. Inter and intra-assay coefficients of variation were 2.8% and 19.8% respectively.

Data Analysis

All statistical analyses were performed with R 3.0.2 (R Core Team 2013) and GraphPad PRISM 6.0.4. To analyze breeding decision I used analysis of variance (ANOVA) to examine the mean differences between feather CORT and reproductive decision. I used a generalized linear modeling approach to explore the relationship between plasma CORT and reproductive decision with time from sample as a cofactor and the relationships between feather CORT, plasma CORT, body condition, and reproductive decision. Most of my blood samples could not be obtained in < 3 min. so I included time as an interaction with CORT concentration in my plasma models. To account for unequal sample sizes of successful and unsuccessful reproduction I used a bootstrapping procedure with k=1000.

RESULTS

I sampled 52 unique adult female harlequin ducks during spring trapping events from 2011-2013. During the course of this period I found 10 active nests. Females with confirmed nest sites had significantly lower concentrations of body feather CORT (ANOVA, F=5.5, p=0.02; Figure 4). This pattern was strengthened when I bootstrapped the data (Welch Two Sample t-test, t=90.1, p=<0.0001) (mean nest found = 10 pg/mm, N=10;mean no nest found = 20 pg/mm, N=42;). Tail feather CORT did not predict reproductive decision (ANOVA, F=0.22, p=0.64). Plasma CORT models with time since capture as a cofactor did not predict reproductive decision, body condition or body feather CORT concentrations (Generalized Linear Model, t=-0.768, p=0.44, t=-0.163, p= 0.87, t=0.246, p=0.81 respectively). Body feather CORT concentrations had no significant relationship to body condition and body condition did not predict reproductive decision (ANOVA, F=0.207, p=0.65, F=0.968, p= 0.33 respectively). See (Appendix 4-1) for all data used in the analysis.

DISCUSSION

Here I have demonstrated that concentrations of CORT deposited in feathers reflect reproductive decision, similar to studies by (Crossin et al. 2013) and (Bortolotti et al. 2008). However, the difference in my study is that I obtained CORT from feathers grown just prior to the current reproductive bout, rather than after reproduction. I cannot determine why unsuccessful reproductive individuals had higher CORT concentrations in their feathers vs successful individuals. Sources of stress during the prenuptial molt could range from adverse weather conditions, poor forage quality, con- and/or heterospecific social interactions, or human disturbances (reviewed in Wingfield et al. 1997). How this reflection of individual quality in feather CORT relates to reproductive success is also likely very complex. Periods of extreme stress or chronic stress can have many detrimental effects on reproduction (Wingfield and Sapolsky 2003). Although this review by Wingfield and Sapolsky points out that there are evolved mechanisms to overcome stress, long lived animals like harlequin ducks may simply choose not to reproduce when physiological conditions are not ideal, which would explain the connection I found between feather CORT and breeding decision. This observation has been made in many systems of long lived sea birds (reviewed in Erikstad et al. 1998, Goutte et al. 2010).

I did not find any relationship between tail feather CORT and future reproductive decision. Tail feathers are molted and grown in autumn when females returns to the wintering grounds (basic molt; Figure 2). Up to 8 months pass between tail feather growth and the next breeding season. This period of time may be too long for environmental conditions and CORT physiology to have an impact on future breeding decision. I would have liked to compare tail feather CORT concentrations to previous breeding decision, but I was unable to recapture enough females with known breeding decision from the previous year.

While I expected a relationship between body feather CORT and body condition, my results here were insignificant. These results are consistent with a similar study on eiders and snow geese (Legagneux et al. 2013) that found no connection between feather CORT and body condition. The authors note that this is surprising in eiders which are capital breeders and depend on fat reserves for successful reproduction. The lack of a connection between feather CORT and body condition in harlequin ducks may not be so surprising since harlequins are primarily income breeders and depend on nutrients acquired from the breeding grounds for egg development (Bond et al. 2007). Harlequins also do not fast during incubation and frequently come off of the nest to forage. Hence body condition may not be a good predictor of breeding propensity in this species because females are easily able to procure more resources during breeding. Additionally, I could not discern a link between plasma CORT and reproduction. I do not find this surprising given that I was unable to obtain baseline samples for the majority of individuals. I included minutes to sampling as a cofactor, but a line fit through that data (CORT by minutes to sample, figure 3) only explains 4% of the variation in CORT levels. Hence, my plasma CORT data are unlikely to give an adequate representation of endogenous stress levels. Additionally, single measures of plasma CORT may be insufficient for inference on physiological links between different life history phases (Bonier et al. 2009).

CONCLUSION

This study demonstrates the utility of feather CORT for predicting reproductive decision in migratory animals. Using these techniques I have identified that the prenuptial molt in harlequin ducks is an important life history phase that links to reproductive decision. Identifications of critical life history phases are paramount to efficient management of species. In this study I have shown a strong difference in the mean concentration of feather CORT between females that nested and females that did not nest, but there is a high degree of overlap in CORT concentration between these two categories of females (Figure 4). This suggests that CORT concentrations are not the only driver of reproductive variation within this population. Many other factors are likely influencing reproductive decision. I believe that fecal CORT measurements are a logical next step to quantify sources of environmental stress and their contribution to reproductive variation. Overall, while feather CORT has provided insight into Harlequin duck breeding biology, there are still factors that are unaccounted for and warrant further study.

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FIGURES

Figure 4-1. **Breeding pair of harlequin ducks stretching before next foraging bout on the breeding grounds on Upper McDonald Creek, Glacier National Park, Montana. Photo courtesy of John Ashley.**

Figure 4-2. **Molt chronology of female harlequin ducks. Month abbreviated with the first letter starting in September and ending in August.**

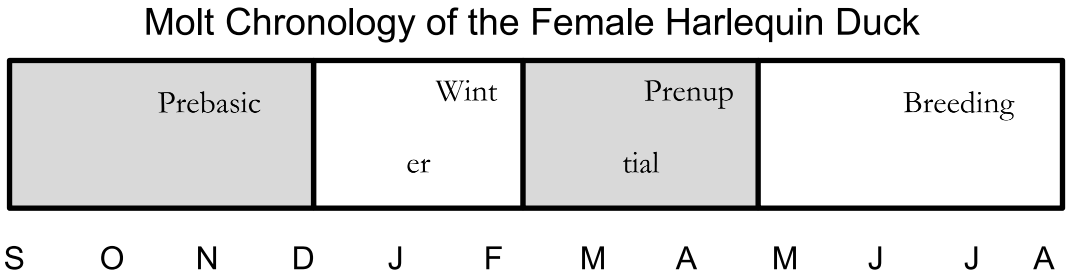


Figure 4-3. Distribution of plasma corticosterone concentrations (y-axis) since time of capture in minutes (x-axis). Green circles indicate bleed times < 3 minutes.

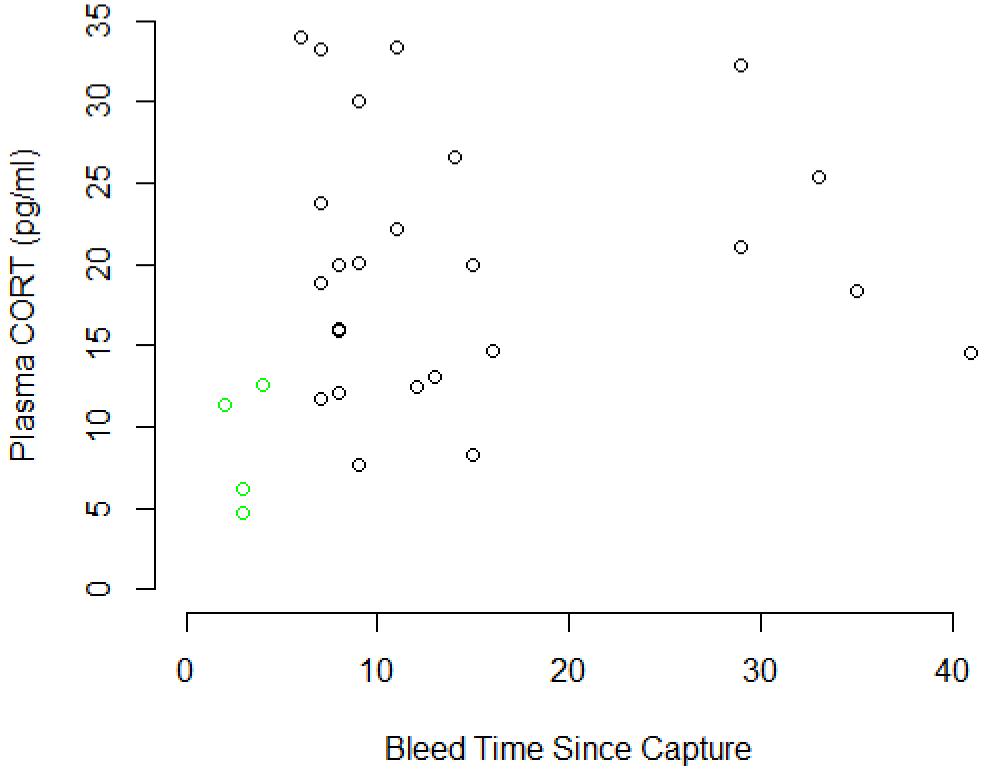
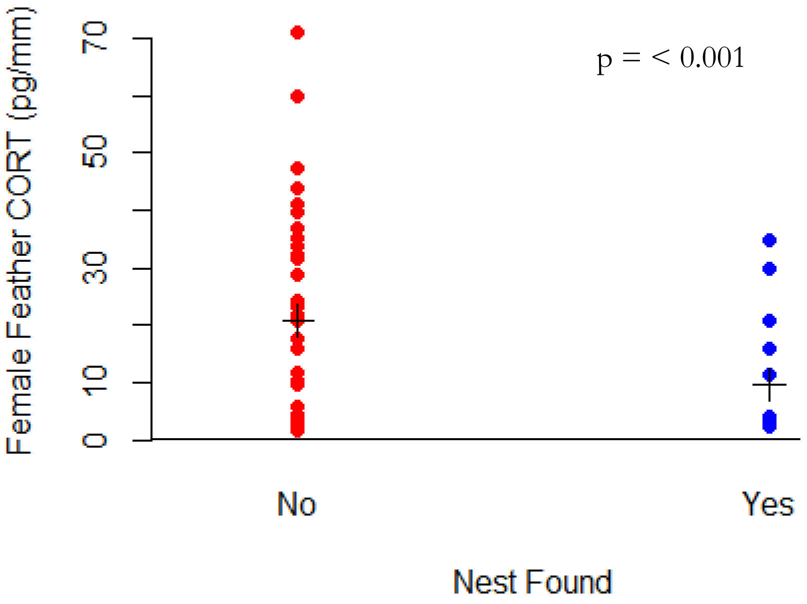


Figure 4-4. Distributions of female feather corticosterone concentrations (y-axis) and decision to reproduce (x-axis) (red = No, blue = Yes). The cross hairs on the data represent mean for each category (red =20 pg/mm, n=42, and blue= 10 pg/mm, N=10). The vertical lengths of the cross hairs represent the standard error means (SEM) (3.0, 2.8 respectively).



Appendix 4-1 Table of data used in this analysis, including the year the sample was collected (Year), individual identification (ID), Sex, reproductive status determined if a female was found incubating eggs (Reproduction), concentration of corticosterone/mm of back feather (Back Feather), concentration of corticosterone/mm of tail feather (Tail Feather), body condition index (g) (BCI) and plasma corticosterone concentration in pg/mm (Plasma). The standard error of the mean (SEM) for back feather, tail feather, BCI and Plasma were 2.5, 1.66, 8.7 and 1.15 respectively.

Year	ID	Sex	Reproduction	Back Feather	Tail Feather	BCI	Plasma
2011	AB	F	Yes	11.47	18.41	522.30	16.00
2013	AB	F	No	4.00	21.60	557.20	30.40
2012	AB	F	No	39.72	11.73	624.20	25.30
2011	AE	F	No	17.64	34.02	513.80	11.70
2011	AF	F	Yes	20.93	20.98	554.00	13.10
2013	AH	F	Yes	4.23	34.21	558.70	7.68
2012	AH	F	Yes	34.73	21.28	613.40	12.80
2011	AJ	F	No	59.90	10.78	576.80	14.60
2011	AN	F	Yes	30.06	8.24	565.10	18.40
2011	AT	F	No	43.80	22.94	622.90	NA
2012	AX	F	No	20.85	19.13	590.90	14.50
2013	AX	F	Yes	2.34	15.49	602.60	19.90
2011	AX	F	No	23.20	22.03	703.00	23.80
2012	AY	F	No	36.99	12.03	581.10	12.60
2011	AY	F	No	47.28	11.46	633.50	4.68
2011	AZ	F	No	33.71	34.02	606.20	34.00
2012	AZ	F	No	NA	NA	NA	20.00
2011	BD	F	No	5.84	12.81	585.40	20.10
2011	BD	F	No	31.81	37.62	585.40	13.50
2013	BF	F	No	3.97	13.90	494.40	6.19
2012	BF	F	Yes	15.94	25.76	495.50	18.30
2011	BF	F	No	41.01	26.61	554.00	28.00
2011	BJ	F	No	10.32	59.07	489.00	19.90
2011	BK	F	No	28.78	37.50	434.50	32.30
2011	BN	F	No	24.17	31.77	585.50	33.20
NA	BY	F	No	NA	NA	NA	15.90
2013	CU	F	Yes	3.30	15.04	498.40	7.43
2012	CU	F	No	71.08	13.98	522.40	11.40
2012	CV	F	No	32.40	23.06	586.50	NA
2013	HC	F	No	4.58	7.89	612.50	5.44

2013	HF	F	Yes	3.64	45.24	576.60	13.20
2012	IB	F	No	15.84	32.18	685.20	12.10
2013	IG	F	No	3.77	5.62	623.40	12.40
2012	IG	F	No	11.76	21.30	650.50	11.70
2012	IJ	F	No	15.92	30.46	627.70	18.80
NA	IJ	F	No	NA	NA	NA	9.07
2012	IL	F	No	35.04	25.41	476.90	22.20
2013	IM	F	Yes	3.39	20.93	555.00	21.00
2012	IM	F	No	44.03	17.78	604.40	32.50
2012	IR	F	No	21.80	21.74	557.90	8.30
2013	IT	F	No	2.40	22.21	523.10	16.80
NA	IT	F	No	NA	NA	NA	33.30
2013	JE	F	No	2.99	23.17	510.00	17.20
2013	JJ	F	Yes	2.38	26.02	587.30	16.00
2013	KC	F	No	9.53	53.88	607.40	9.37
2013	KF	F	No	3.13	11.18	460.40	24.00
2013	KG	F	No	2.69	20.09	490.50	33.90
2013	KI	F	No	9.67	9.71	598.70	16.00
2013	KK	F	No	2.91	10.62	568.20	10.20
2013	KM	F	No	1.74	12.18	642.00	22.10
2013	KN	F	No	2.77	22.65	705.20	13.80
2013	KR	F	No	3.46	31.01	578.90	12.40