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Influence of Streamflow on Reproductive Success in a Harlequin Duck (*Histrionicus histrionicus*) Population in the Rocky Mountains

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Abstract.—Aspects of streamflow and reproductive success of Harlequin Ducks (*Histrionicus histrionicus*) were measured to explore how variation in streamflow impacts reproduction, and to consider how climate change might influence these parameters in the future. A 24-year data set (1990-2013) of Harlequin Duck breeding season surveys conducted on Upper McDonald Creek in Glacier National Park (GNP), Montana, USA was used to assess how annual variation in the proportion of broods to pairs (reproductive success) relates to streamflow. Between 1990 and 2013, GNP staff and volunteers conducted 102 spring surveys and 112 brood surveys counting 896 total ducks, 212 pairs, 56 broods, and 278 ducklings. Four streamflow metrics (pre-incubation streamflow - corresponding with nutrient acquisition and nest site selection, hydrographic peaks – corresponding with nest site selection and availability, value of the greatest single hydrographic peak post average peak flow - corresponding with risk of a nest washing out, and average streamflow during incubation - corresponding with foraging condition for an incubating female) were all negatively related to reproductive success. The first three of these metrics are predicted to become more extreme with climate change, with potential negative effects on breeding Harlequin Ducks. *Received 2 January 2019, accepted 12 June 2019.*

Key words.—Glacier National Park, Harlequin Duck, reproductive success, streamflow

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Animals depend on environmental rhythms for timing of reproduction. Many migratory animals use photoperiod to time departure for the breeding grounds. This behavior has evolved to match environmental rhythms to maximize reproductive success (Gwinner 2003; Bradshaw and Holzapfel 2007). Global climate change is altering the phenology of these environmental pulses (e.g., insect emergence and plant phenology) on many breeding grounds, causing a mistiming of arrival for many migratory species (e.g., Post and Forchhammer 2007) This timing mismatch can lead to decreased reproductive performance and ultimately population declines (Both *et al.* 2006; Post and Forchhammer 2007; Saino *et al.* 2010).

An ecological mismatch upon arrival at the breeding grounds can alter reproductive success through reduced nutrient acquisition, nest site availability and juvenile survival (Visser *et al.* 2004). 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 1986). Climate change is expected to increase variation in phenology at the breeding grounds (Walther *et al.* 2002). In the Pacific Northwest of the United States, these changes are forecast to include increased mean temperatures, earlier insect emergence, earlier plant blossom and cessation, earlier peak stream runoff, greater extremes of high and low streamflow, and decreased snowpack (Stewart *et al.* 2004; Mote and Salathé 2010; Goode *et al.* 2013; Pachauri *et al.* 2014). These changes will likely have strong effects on the reproductive success of many migratory riverine species (Royan *et al.* 2014).

Harlequin Ducks (*Histrionicus histrionicus*) are longitudinal migrants that have been listed by several states and provinces as most sensitive to climate change (Hammond 2010; Goudie 2013; Whitman *et al.* 2013). They breed on alpine streams where they build their nest on the ground, usually < 1 m from the stream edge (Robertson and Goudie 1999), although variation in this distance exists (Reichel 1996; Smith 1996). Food resources (benthic invertebrates) required for egg production come from these low productivity, montane breeding streams (Bond *et al.* 2007). Breeding pairs arrive at the stream early in spring (April) when the stream is near the annual mean low flow. Egg laying begins shortly thereafter (May), and initiation of incubation occurs on or near peak streamflow (early June) after all eggs are laid, approximately 4-5 weeks after arrival (Kuchel 1977). These life history traits put Harlequin Ducks at risk of reduced reproduction with climate change, because earlier and more unpredictable spring temperatures may cause streamflows that wash away nests (Gangemi 1991; Robertson and Goudie 1999; Wiggins 2005) and may limit foraging opportunities after arrival due to increased turbidity in the stream limiting their ability to visually detect prey (Martin *et al.* 2007). Since Harlequin Duck males depart for coastal areas shortly after the female begins incubation, there is no opportunity for re-nesting if the nest is destroyed. While climate indicators point towards increased difficulty in harlequin reproduction, there are no quantitative data describing how changes in streamflow affect reproductive output in this species. Understanding the link between streamflow and breeding success in Harlequin Ducks might also be informative for management of a broad range of ground-nesting riverine waterbirds.

We evaluated the relationship between stream discharge and reproductive success from a long-term study of Harlequin Ducks in Glacier National Park (GNP), Montana. Between 1990 and 2013, GNP Staff have documented a large degree of variation in annual reproductive success in the breeding population (CCRLC 2017). We hypothesized that variation in streamflow is a major component driving variation in breeding success in this population. We predicted that greater extremes in streamflow (high and low) during egg-laying and incubation periods correlated with decreased reproductive success through nest failure. This interaction is important to understand for the management of this species into the future, as climate change alters phenology on the breeding stream.

METHODS

Study Area

We studied Harlequin Ducks on Upper McDonald Creek (UMC) in Glacier National Park, Montana, USA (Fig. 1). This stream produces approximately 25% of known Harlequin Duck broods annually in Montana and has the highest density of breeding harlequins in the lower 48 states (Harlequin Duck 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 substrate and waters that are generally low in dissolved ions, nutrients, and suspended particulates (Lowe and Hauer 1999). The study area has an open canopy of mixed conifer/deciduous trees that have remained mostly unchanged for nearly 80 years since the construction of the Going-to-the-Sun Road (GTSR) in 1933 (with the exception of wildfire in the upper 3 km reach in 2003).

Field Surveys for Harlequin Ducks

Glacier National Park staff and volunteers have surveyed UMC between Lake McDonald and Logan Creek on an annual basis since 1990 and intermittently since the 1970's. The survey objectives were to document the number of individual adult ducks, pairs, and ducklings occurring on UMC to monitor the seasonal Harlequin Duck population. This system is an open population that is receiving migrants to the breeding stream until mid-May, and pairs begin to disappear from the stream in early June as females begin incubation of eggs and males depart for the coast. Multiple surveys were conducted during the pair season (late-April to early-June, when pairs arrive on UMC) and during the brood rearing season (mid-July to early September, when ducklings hatch and appear on the stream). The same stretch of stream was surveyed every year from the mouth of McDonald Creek at Lake McDonald to the confluence with Logan Creek located 16 km upstream (Fig. 1). This survey section we refer to as a full survey. A full survey consists of two survey sections (upper and lower) roughly 8 km each. These sections were surveyed at the same time on the same day by two separate groups made up of two person teams. A typical survey would take 4-6 hours depending on the season. A survey team would begin walking upstream together scanning the stream with binoculars looking for Harlequin Duck pairs (pair season) or broods (broods season). Harlequin Duck pairs are easy to spot due to their active foraging, hauling out on rocks in the stream and mate guarding behavior. If at any time the stream became too difficult to walk up, the survey group would start "leap frogging" up stream. One surveyor would remain at the

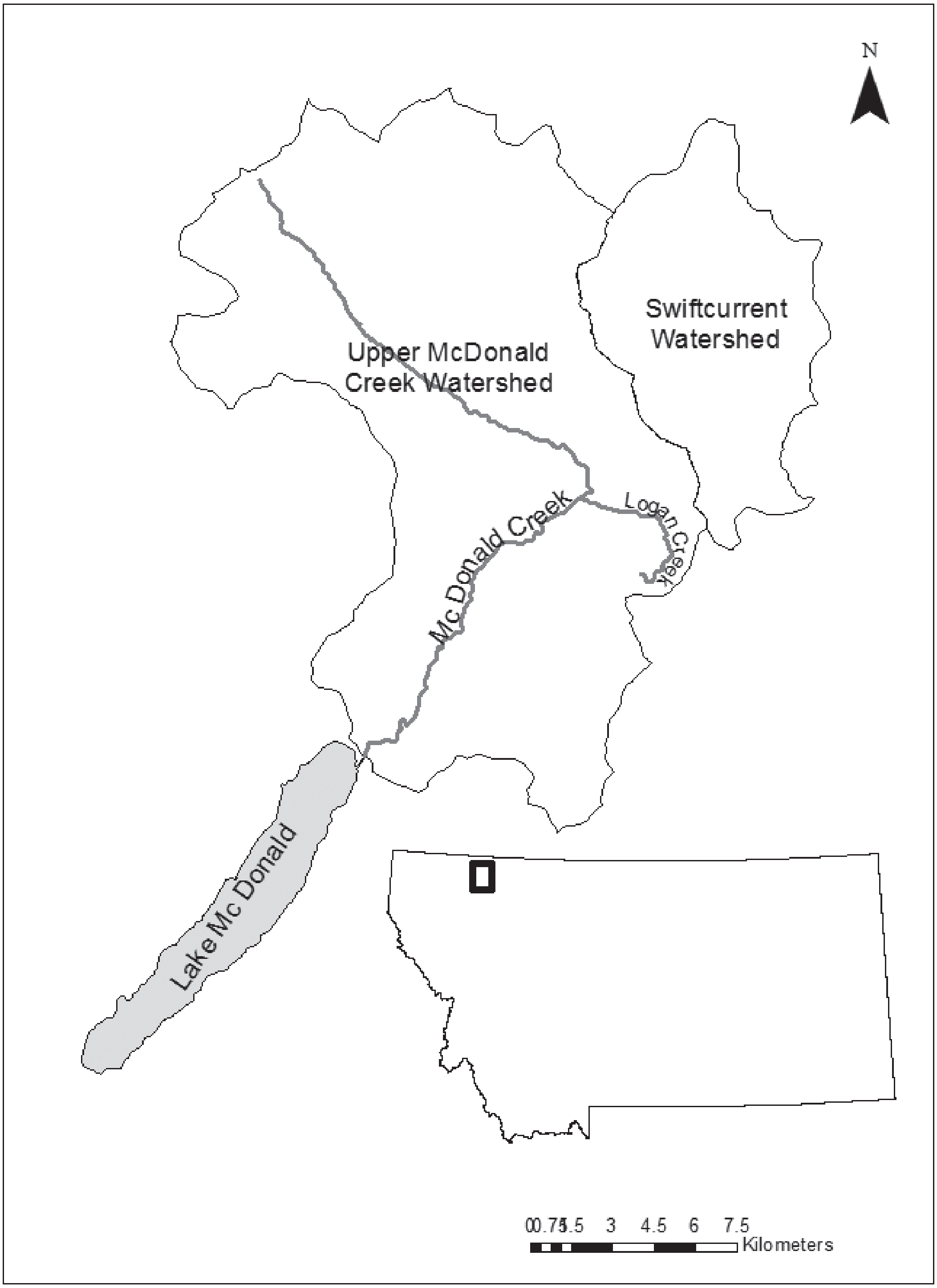

Figure 1. Study area in Glacier National Park, Montana, USA. The large outlined area encompasses the entire Upper McDonald Creek watershed with Upper McDonald Creek running through the center where surveys for breeding Harlequin Ducks (*Histrionicus histrionicus*) occurred annually 1990-2013 (from McDonald Lake to Logan Creek). The smaller outlined area is neighboring Swiftcurrent Creek watershed.

stream bank monitoring the stream, while the other surveyor would bushwhack upstream along the bank for approximately 100 m or the distance of stream visible to the downstream surveyor. When the upstream surveyor reached the stream bank, they would inform the lower surveyor that they were in place, and the downstream surveyor would then “leap frog” upstream in the same manner. If a Harlequin Duck was observed flying upstream past the survey group, that duck would not be counted, assuming that it was already accounted for, unless no Harlequin Duck had yet to be counted. After the next Harlequin Duck was encountered on the stream, it again would not be counted assuming it was the individual or pair that had previously flown up stream. All Harlequin Ducks flying downstream were counted. At the end of the survey, the surveyors would compare their observations and any ducks that were observed flying up or down stream. Based on the timing and location of observations the surveyors could usually identify birds that may have otherwise been double counted.

Metrics of Reproductive Success

We defined reproductive success as the proportion of observed broods to paired females (assuming unpaired females did not lay eggs) on the breeding stream (Murray Jr. 2000; Kosciuch *et al.* 2001). We calculated this proportion by dividing the number of broods by the sum of females with broods and the maximum number of paired females detected during the spring surveys. A female with a brood, regardless of the number of chicks with her, was considered reproductively successful. This metric accounted for annual variation in the number of breeding females, brooding females and chicks present, which alters the likelihood of brood production independently of streamflow. Hence we have evaluated the probability that a breeding female will produce a brood, not the absolute number of chicks produced. This annual proportion will be referred to as annual reproductive success.

During years 2011-2013, we attached prong and suture radio transmitters to females starting in late April when pairs arrived to the breeding stream and ending in late May when streamflow levels became unsafe for researches to net in (see Smith *et al.* 2015 for capture methods). Over the course of the 3-year study we attached 45 transmitters. In addition, we attached stainless steel federal leg bands and alpha-alpha colored leg bands for individual field identification. After completion of each stream survey we would return to the starting point by driving along the GTSR that parallels the 16-km section of stream that was just surveyed (mean distance from road to stream = 107 m; range 16-474 m), using a handheld VHF receiver with a vehicle-mounted omni whip antennae to scan for radio-marked individuals. We validated the number of unique radio-marked individuals that we counted on the survey with the number that were detected using VHF on the drive back to the starting point to determine the maximum number of paired females for that survey.

We determined annual abundance estimates of pairs and broods from the highest count from an individual survey within a single season. In this analysis, all years contained at least one survey that was conducted during average annual peak abundance. To identify average peak abundance periods, we performed an analysis of variance (ANOVA) of average weekly counts of pairs and broods across all years of survey data.

Hydrography

Streamflow on UMC is typically characterized by a low flow period from October to April. Streamflow typically begins to rise in mid-April when snow begins to melt, and flow gradually increases through May and peaks after the first week of June. Peak flow is followed by a gradual decrease and returns to low flow by September. We collected stream height data during the breeding season (15 April-15 September) during all pair and brood surveys since 1990, and daily during 2011-2013 at a gauge under a bridge crossing UMC near its inflow into Lake McDonald (Fig. 1). We compared these daily gauge heights to eight other gauged streams in northwest Montana using Welches Two-Sample T-test. We found that Swiftcurrent Creek, which borders UMC to the east (Fig. 1), performed the best at describing variation in UMC streamflow (R^2 = 0.84), (Swiftcurrent Creek gauge station: 48° 47′ 55.80″ N, 113° 39′ 24.23″ W; http://waterdata.usgs.gov/usa/nwis/rt; Fig. 1). To assess hydrography of UMC over all survey years, we used Swiftcurrent Creek flow data corrected for the larger area of the McDonald Creek watershed (Yuan 2013). We made the correction by calculating the unit area flow of UMC by dividing daily Swiftcurrent Creek flow data by its watershed area (8,035 ha), then multiplying that quantity by the area of the UMC watershed (16,275 ha) (Toprak *et al.* 2009). We developed 4 metrics that characterize different aspects of streamflow 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 Harlequin Ducks face. We refer here to the phases of the breeding season from Kuchel (1977), but the dates of the phases were modified based on observation from our telemetry data, with slightly earlier shifts in all phases except for arrival (W. Hansen, unpubl. data).

Metric 1: Average Streamflow prior to Incubation. Harlequin Ducks have been observed nesting in the same place year after year (Chubbs *et al.* 2000; Smith 2000; W. Hansen, pers. obs.) usually within 1 m of the stream's edge. There have been anecdotal suggestions in the Harlequin Duck literature that high streamflow will delay egg laying and reduce foraging efficiency over the season (reviewed in LeBourdais 2006). Therefore, our first metric was average streamflow during the period (5 May-10 June) prior to peak incubation (Fig. 2). We determined peak incubation based on when our radio- marked individuals were discovered incubating eggs. This period also agrees with observations made by Kuchel (1977). This metric should best reflect nest site availability and foraging opportunities prior to incubation.

Metric 2: Hydrographic Peaks. High streamflow makes foraging more difficult (Gangemi 1991; Robertson and Goudie 1999; Wiggins 2005); since Harlequin Ducks fund egg production primarily on energy intake, and not internal energy stores (Bond *et al.* 2007), this increase in flow could wash away nests, delay egg laying, reduce the number of eggs laid, and effect brood feeding success. Hence, our second metric was the cumulative number of hydrographic peaks that occurred over the duration of the breeding season. Peaks were determined by a sudden increase and decrease in flow that had an amplitude of > 450 cfs (Fig. 2). This volume of flow was chosen because it appeared to be the minimum flow reversal required to dramatically change the bank full width of the river. These values provide an index of predictability of streamflow.

Metric 3: Hydrographic peak post average peak flow. Our third metric was the value of the greatest single hydrographic peak post (after) average peak flow (Fig. 2). Harlequin Ducks incubate through the declining arm of the hydrograph, and spikes in streamflow during this time can wash out nests (Wiggins 2005).

Metric 4: Average flow during incubation. Our fourth metric was the average flow that occurred from beginning to end of the incubation period (15 June-20 July). This metric best reflects conditions females would be foraging in during incubation. We refer to the combination of the four metrics as the spectrum of high and low streamflow severity (Fig. 2).

Statistical Analysis

All analyses were completed using Program R (R Core Team 2013). First, we assessed collinearity between the four metrics of streamflow using Pearson correlation coefficient. We conducted two separate analyses to model reproductive success using the four streamflow metrics previously discussed. First, we ran multiple linear regression to examine the effect of the four streamflow metrics. We examined all combinations of the metrics including univariate and a global model with all four metrics (Burnham and Anderson 2003). Second, we used Akaike's Information Criterion corrected for small sample size (AICc) to rank the models. We used ANOVA to describe variation between years of both arrival date of breeding pairs and first sighting of broods on the stream. We used quartile interpretability of the data (Johnson and VanDerWal 2009). We measured the long term

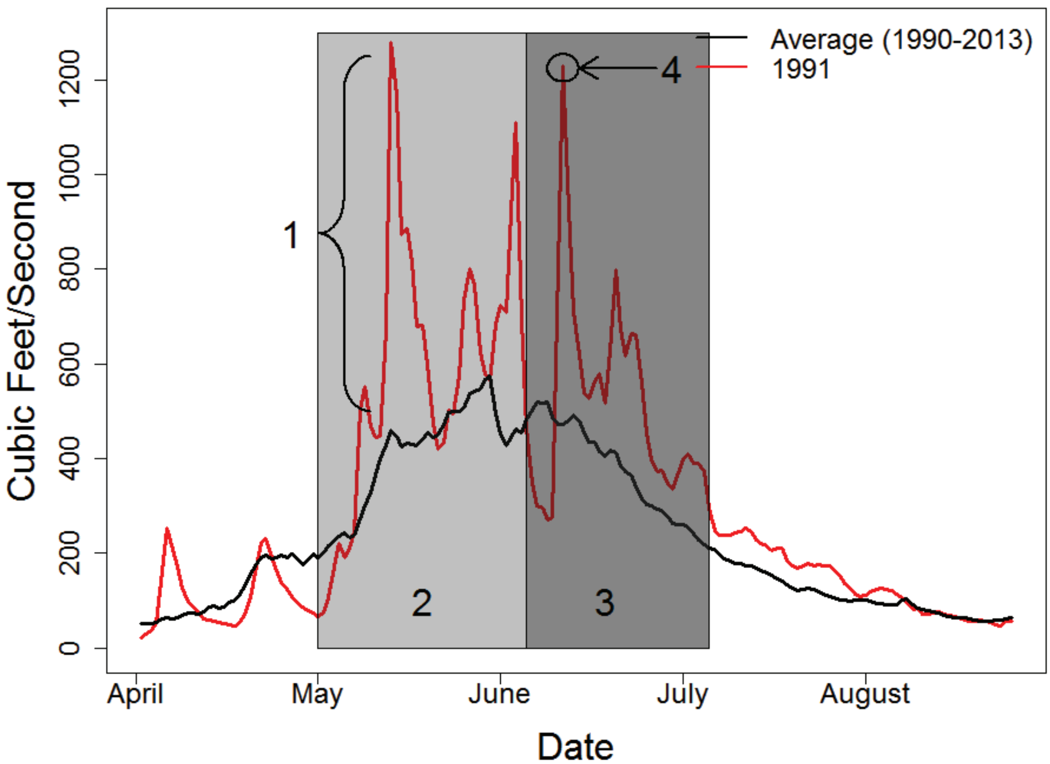

Figure 2. Example of manually extracted hydrograph characteristics used to determine streamflow metrics of Upper McDonald Creek in Glacier National Park, Montana, USA related to Harlequin Duck (*Histrionicus histrionicus*) breeding biology (1 = hydrographic spike represented by amplitude of > 450 cfs; 2 = average streamflow prior to incubation [light shaded area]; 3 = average streamflow during incubation [dark shaded area]; 4 = peak streamflow post historical peak flow). The black line represents average streamflow estimates from 1990-2013, and the red line represents streamflow from 1991.

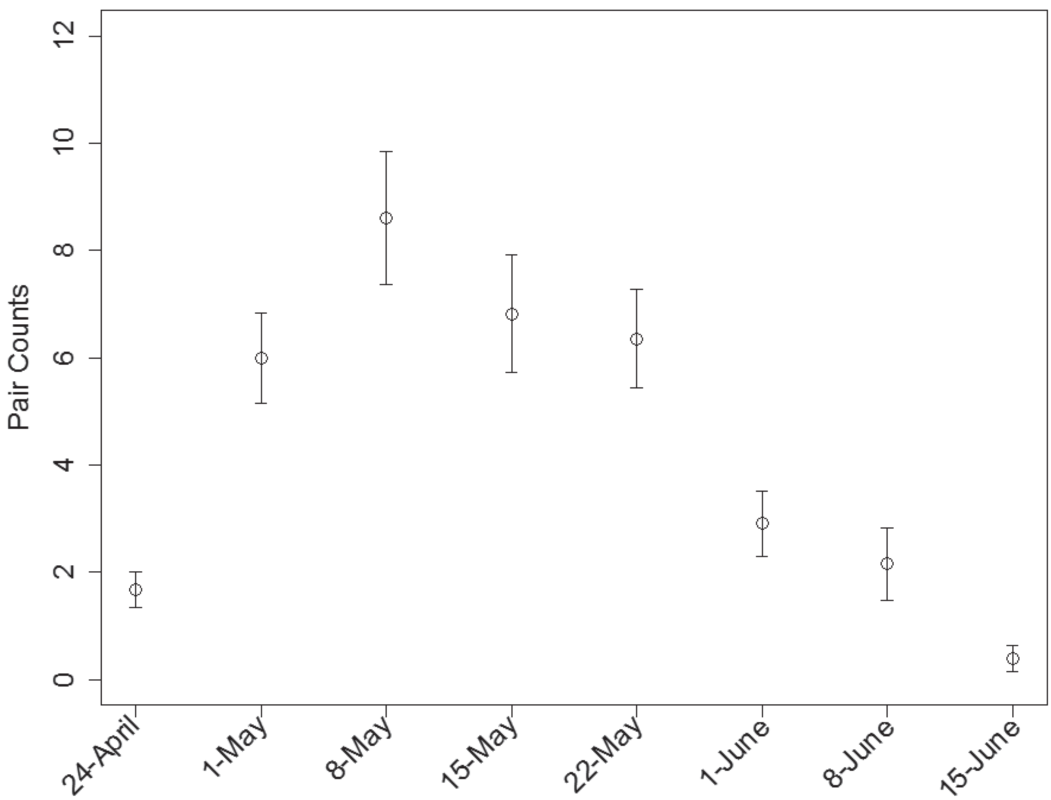

Figure 3. Average weekly pair high counts (± SE) of Harlequin Ducks (*Histrionicus histrionicus*) averaged across 24 years (1990-2013) of survey data in Glacier National Park, Montana, USA.

trend of our hydrographic metrics to better understand how they are changing over time. The earliest historical record of streamflow statistics started in 1912, thus our trend captured a little over a century of time from 1912 to 2015. The trends of streamflow series for each hydrological metric were analyzed with linear regression. All tests were considered significant at $\alpha = 0.05$. All results are presented as mean ± SE unless specified otherwise.

RESULTS

Abundance Data

Between 1990 and 2013, Glacier National Park staff and volunteers conducted 102 spring surveys and 112 brood surveys counting 896 total ducks, 212 pairs, 56 broods, and 278 ducklings. The average number of full surveys in a year was six, (maximum 13, minimum 2). In 3 years of telemetry, we conducted 18 pair surveys with 90 successful detections out of 101 possible radio-marked females that were known to be in the survey area (including repeat sightings between surveys; probability of detection was 89%). Absences, in this case, are considered true absences because each survey was a near complete census of the stream. Due to this high level of detection, we used a detection probability of one in our abundance estimates. We additionally did not account for variation in detection probability between years due to the overlap of trained surveyors and consistency of data collection.

Abundance of breeding pairs on UMC peaked from weeks 17-20 (1 May-21 May), (Fig. 3), with no significant difference among those weeks ($F_{1,41} = 0.15$, $P = 0.701$), and decreased significantly thereafter (mean abundance during week 17-20 = 6.9 ± 1.3 and week 21-23 = 2.1 ± 1.25; $F_{1,27} = 4.67$, $P = 0.038$). The mean number of pairs observed between surveys averaged across years was 4.36 ± 0.75

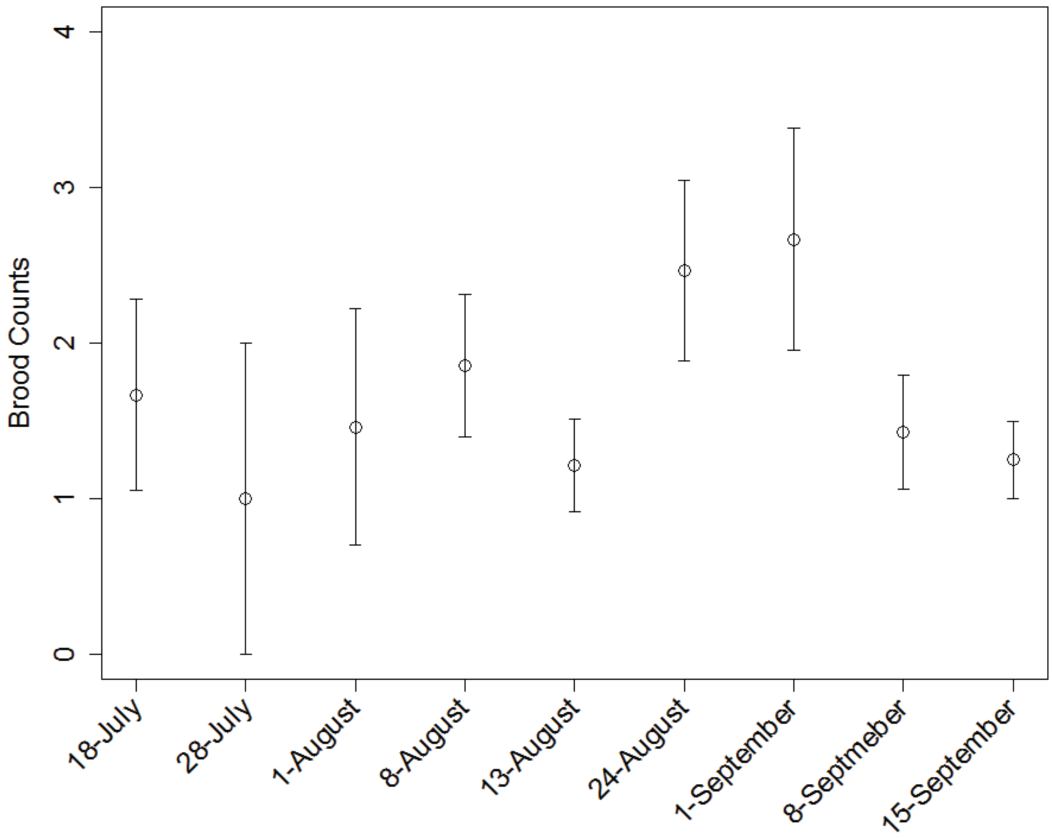

Figure 4. Average weekly brood high counts (± SE) of Harlequin Ducks (*Histrionicus histrionicus*) averaged across 24 years (1990-2013) of survey data in Glacier National Park, Montana, USA.

(median = 4.46; range = 0.40 - 8.60). There were no significant differences in brood abundance observed across the survey period ($F_{10,78}$ = 1.29, P = 0.259; mean = 1.67 ± 0.56; median = 1.46; range = 1.0 - 2.67; Fig. 4). The mean proportion of broods to pairs (reproductive success) across years was 0.25 ± 0.05 (median = 0.24; range = 0.0 - 0.62; Fig. 5).

Streamflow

The highest rate of collinearity between streamflow metrics was between the average streamflow during incubation (metric four) and the hydrographic peak post average peak flow (metric three) (r = 0.61). The second highest correlation was between average streamflow prior to incubation and hydrographic peak post average peak flow (r = 0.58). All streamflow metrics were retained for model development. The multiple regression analysis resulted in four models with a ΔAICc < 2 (Table 1). The top two models were Hydrographic Peaks + Average Streamflow Prior to Incubation (R^2 = 0.42, P = 0.003) and Hydrographic Peaks + Average Streamflow During Incubation (R^2 = 0.42, P = 0.003). In both of these models, reproductive success decreased with an increase in frequency of Hydrographic Peaks and increase in volume of streamflow, represented by Average Streamflow Prior To and During Incubation. The remaining two models with ΔAICc < 2 included Hydrographic Peaks Post Average Peak Flow and the variables from the top two models (Table 1). Univariate models showed decreasing proportions of broods to pairs with increasing values of the four metrics of streamflow (Fig. 6), suggesting that streamflow is more deterministic of reproductive success when

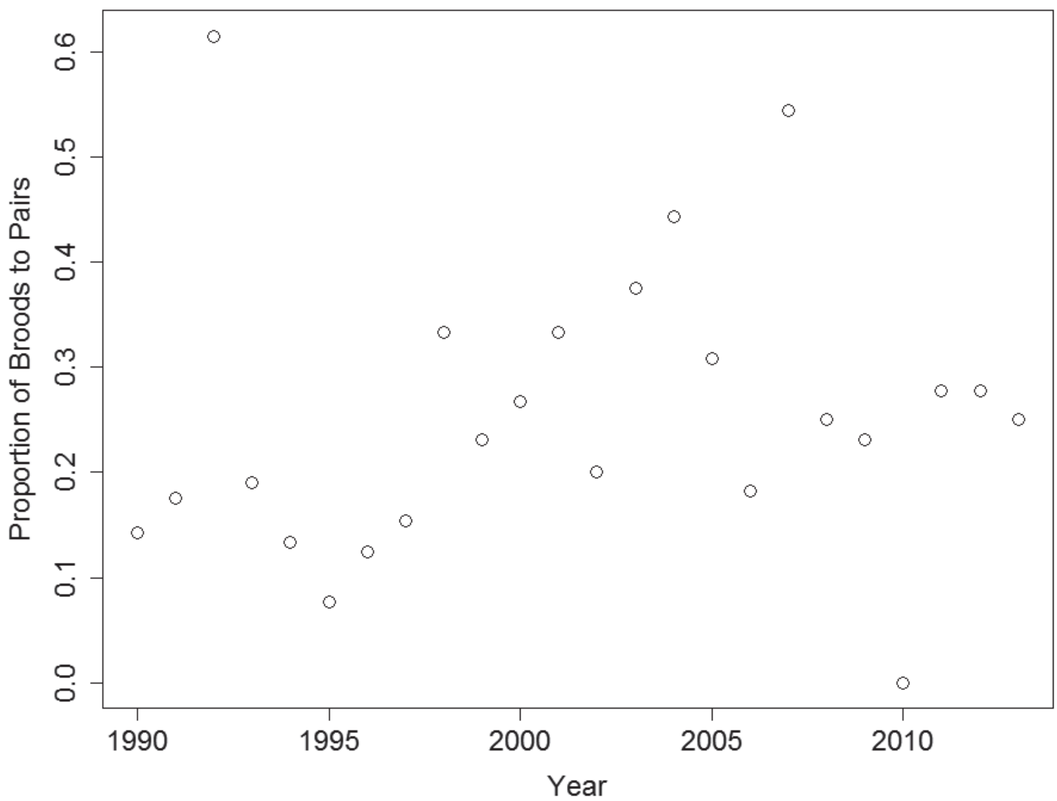

Figure 5. Proportion of pair high counts to brood high counts (reproductive success) of Harlequin Ducks (*Histrionicus histrionicus*) for 24 years (1990-2013) of survey data in Glacier National Park, Montana, USA.

flow levels reach extremes. Harlequin Ducks appear to time important phases in their reproductive life history around streamflow patterns (Fig. 7).

Average Streamflow Prior to Peak Incubation decreased over the last century in the time series model, but the change was not statistically significant ($R^2 = 0.035$, $P = 0.058$, $F_{1,102} = 3.67$, SE = 8.63). The remaining streamflow metrics did not have a significant change over time (Fig. 8; Time Series Linear Regression, (b) $R^2 = 0.005$, $P = 0.46$, $F_{1,102} = 0.55$, SE = 0.18, (c) $R^2 = 0.0001$, $P = 0.915$, $F_{1,102} = 0.011$, SE = 27.23 , (d) $R^2 = 0.016$, $P = 0.196$, $F_{1,102} = 1.695$, SE = 13.46).

DISCUSSION

Our results revealed a negative relationship between annual reproductive success (proportion of broods to pairs) of Harlequin Ducks and peaks in streamflow and amount of streamflow prior to incubation. The negative relationship between reproductive success and severe streamflow (e.g., unusual flood timing and duration, unusual high flow and low flow) has long been hypothesized by biologists on Harlequin Duck breeding streams (Kuchel 1977; Reichel 1996; Robertson and Goudie 1999; Wiggins 2005), but reports have all been anecdotal. Streamflow is clearly an important abiotic influence on Harlequin Duck reproduction. This study does not identify the specific mechanism (e.g., limited forage, limited available nest sites, or washed out nests), but suggests a range of hypotheses to be tested to better understand the interaction between streamflow and reproduction. For example, foraging behavior and clutch size could be good indicators that variable streamflow is limiting nutrient uptake and decreasing reproduction in more extreme

Table 1. Candidate models of stream discharge correlation with the proportion of broods to pairs (reproductive success) of Harlequin Ducks (*Histrionicus histrionicus*) on Upper McDonald Creek in Glacier National Park, Montana, USA during breeding seasons 1990-2013.

Streamflow Metrics	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Hydrographic Peaks + Average Streamflow Prior to Incubation	4	-30.36	0	0.24	0.24	20.23
Hydrographic Peaks + Average Streamflow During Incubation	4	-30.18	0.18	0.22	0.46	20.14
Hydrographic Peaks + Average Streamflow Prior to Incubation + Average Streamflow During Incubation	5	-29.15	1.21	0.13	0.59	21.24
Hydrographic Peaks + Peak Hydrographic Value Post Historic Peak Value	4	-28.54	1.82	0.1	0.69	19.32
Hydrographic Peaks + Average Streamflow Prior to Incubation + Peak Hydrographic Value Post Historic Peak Value	5	-27.70	2.66	0.06	0.75	20.52
Hydrographic Peaks	3	-27.65	2.71	0.06	0.82	17.42
Hydrographic Peaks + Peak Hydrographic Value Post Historic Peak Value + Average Streamflow During Incubation	5	-27.55	2.81	0.06	0.87	20.44
Average Streamflow During Incubation	3	-27.08	3.28	0.05	0.92	17.14
Average Streamflow Prior to Incubation + Hydrographic Peaks + Peak Hydrographic Value Post Historic Peak Value + Average Streamflow During Incubation	6	-25.57	4.79	0.02	0.94	21.26
Average Streamflow Prior to Incubation + Average Streamflow During Incubation	4	-24.80	5.56	0.01	0.96	17.45
Peak Hydrographic Value Post Historic Peak Value+ Average Streamflow During Incubation	4	-24.69	5.67	0.01	0.97	17.4
Peak Hydrographic Value Post Historic Peak Value	3	-24.47	5.89	0.01	0.98	15.83
Average Streamflow Prior to Incubation	3	-23.46	6.9	0.01	0.99	15.33
Average Streamflow Prior to Incubation + Peak Hydrographic Value Post Historic Peak Value	4	-22.26	8.1	0	1	16.18
Pre-Incubation Streamflow + Peak Hydrographic Value Post Historic Peak Value + Average Streamflow During Incubation	5	-21.76	8.6	0	1	17.55

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. In our study, one individual nested in three different locations over four years: in Year One she was unsuccessful, in Year Two she was unsuccessful in a new location, in Year Three she was successful in a third location, and in Year Four she reused the same nest as the previous year, but was killed on the nest by a mink. We documented two other females reusing nest sites from a previously successful year. Long term banding data could identify population demographics that could lend insight to this theory.

Our results suggest the severe streamflow metrics are more deterministic of reproductive failure (possibly through limits on nest initiation or early nest persistence), and that reproductive success is more variable at moderate and low flows and influenced by other mechanisms than streamflow alone, allowing a greater number of nests to persist past the early stages. It is unclear what biological factors limit Harlequin Duck abundance, but some studies have identified predation and competition with fish as possible limiting factors (Heath *et al.* 2006; LeBourdais *et al.* 2009). 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). We documented pine marten (*Martes Americana*), American mink (*Neovision vison*), red squirrel (*Tamiasciurus hudsonicus*), and gray wolf (*Canis lupis*) preying on the eggs of Harlequin Ducks. Further investigation is needed on the mechanism of the relationship between streamflow and predation on limiting reproductive success.

Harlequin Ducks appear to time important phases in their reproductive life history around streamflow patterns. Based on current models, climate change is expected to have significant impacts on streamflow across the west in the next 50 to 75 years, po-

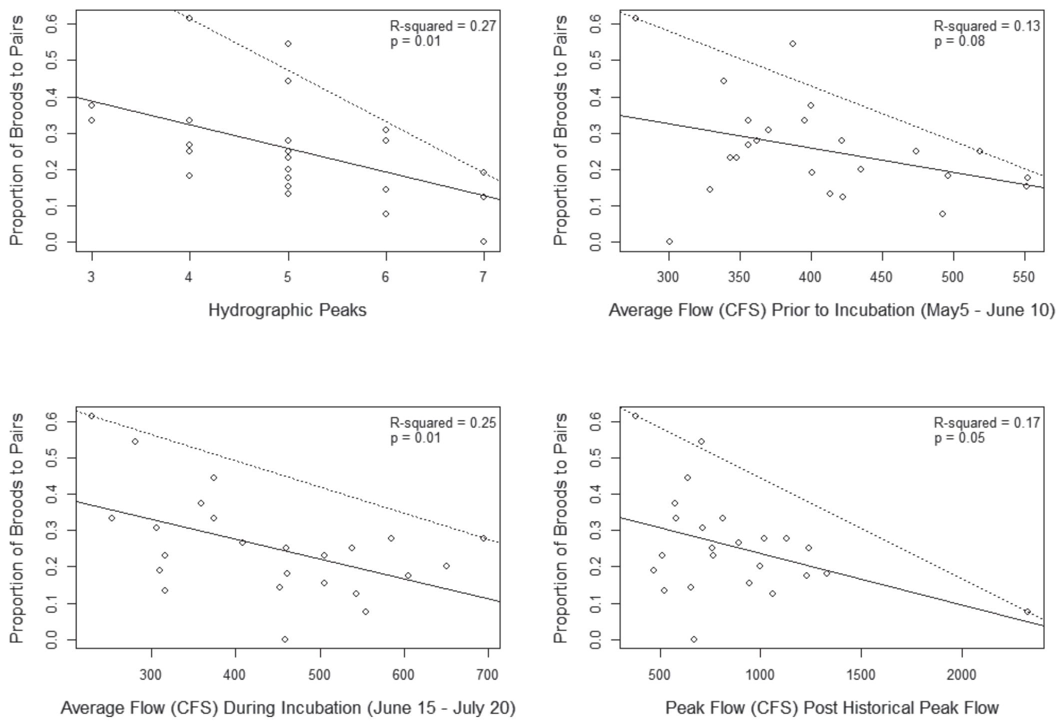

Figure 6. Plots representing the relationship of the proportion of broods to pairs (reproductive success) and the four streamflow metrics (hydrographic peaks, average flow prior to incubation [5 May-10 June], average flow during incubation [15 June-20 July], and peak flow post historical peak flow) for Upper McDonald Creek in Northwest Montana, USA. Flow given in cubic feet per second. The solid line is the fitted mean of the regression model. The dotted line represents the model fitted to the 95th quartile values of the proportion of broods to pairs.

tentially exacerbating the severe streamflow factors that limit Harlequin Duck reproductive success (Stewart *et al.* 2005; Goode *et al.* 2013). Our first streamflow severity metric (average streamflow prior to incubation) may increase substantially, given that peak runoff is expected to occur earlier in the spring. By pushing peak runoff earlier into the spring, there could be an overall increase in flow during the arrival and egg-laying periods. Increases in early discharge can reduce foraging efficiency in females preparing to lay and delay egg laying until historical nest sites become available. A good example of this kind of streamflow came in May of 2018, streamflow on UMC was at sub-flood stage for the entire month and turbidity was very high. In July, when brood surveys are conducted, 20 single females were counted indicating massive reproductive failure. Only one brood was observed in three surveys before wildfires restricted access. However, our modeling of the trend of this metric indicates that average flow prior to incubation has been gradually decreasing. It is unclear as to why our time series of streamflow conditions does not reflect projections of streamflow that have been made for the Pacific Northwest region (Stewart *et al.* 2004; 2005; Goode *et al.* 2013; Surfleet and Tullos 2013). Likely explanations are that these predictive models do not reflect variability at more local scales, and our historical time series of coarse streamflow measurements may not yet be reflecting the predicted changes.

The second metric (number of hydrographic peaks during the breeding season) is more difficult to predict. Streamflow has been modeled to become more unpredictable with greater variation due to an increase of rain and snow events (Surfleet and Tullos 2013), but it is difficult to predict when this variability will occur temporally. The third metric (hydrographic

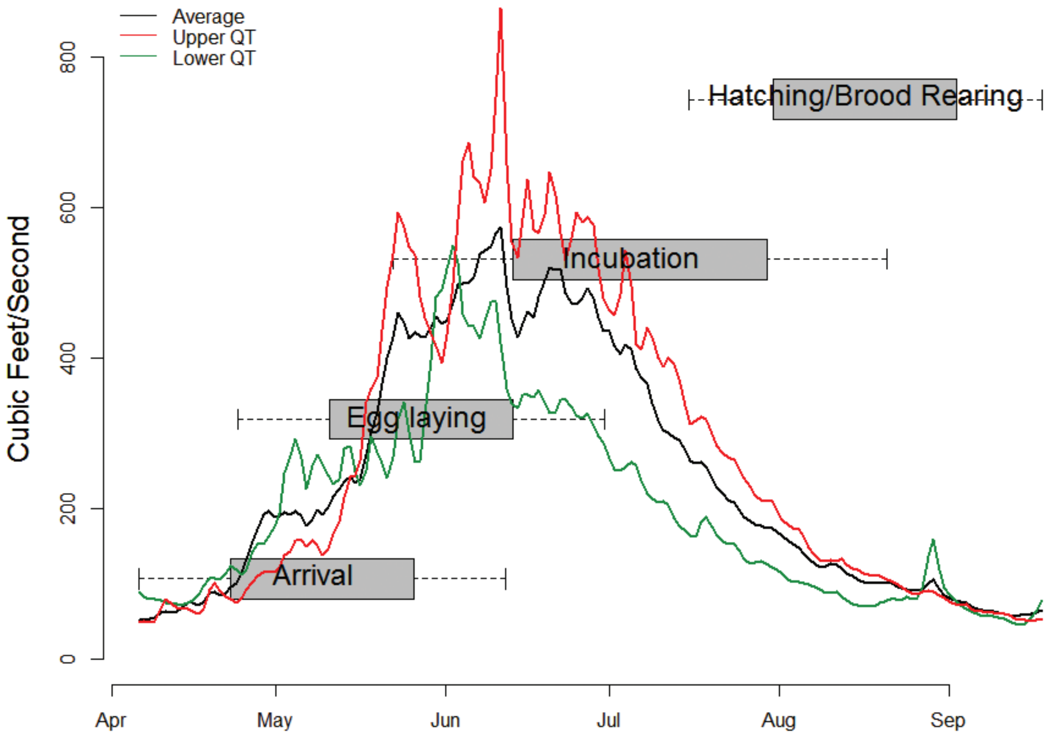

Figure 7. Graph represents hydrographs of historical average (black line) taken from streamflow data (1990 to 2013), average high severity (redline) taken from the upper quartile of high severity years from the linear regression, and average low severity (green line) taken from the lower quartiles of the linear regression. The streamflow values are taken for Swiftcurrent Creek and corrected for the watershed area of Upper McDonald Creek in Northwest Montana, USA. The grey boxes reflect the average dates of four different phases of reproduction of Harlequin Ducks; (arrival, laying, incubation, and hatching, adapted from Kuchel 1977), and the dotted lined represents the 1.5 quartile outside of the mean.

peaks post average peak flow) is expected to increase in frequency through time as the effects of climate change become more pronounced (Goode *et al.* 2013). Substantial increases in peak flow over time pose the greatest risk to flooding nests. Harlequin Ducks have been observed nesting in the same place year after year (Chubbs *et al.* 2000; Smith 2000; W. Hansen, pers. obs.) usually within 1 m of the stream's edge. In our study, eight of 10 nests were located equal to or less than 1 m from water at the time of discovery (the exceptions were 25 m and 220 m from water). This distance varied during the incubation period as streamflow varied as a result of the spring discharge. Harlequin Ducks select nest sites close to the stream edge, presumably to allow quick escape from predators, and seem to reuse the same locations in subsequent years based on previous experience. Unpredictable changes in peak flow can render previous experience unreliable. Although, due to the variability of nest distance from water documented in other studies (Bruner 1997; Smith 2000), it is conceivable that Harlequin Ducks may have an adaptive strategy to deal with high water events, and further study is needed to understand the variation in nest site distance to stream.

Our fourth metric (average streamflow during incubation) is expected to decrease (Stewart *et al.* 2005). 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, and these streams may become dry or have insufficient flow for ducklings to navigate

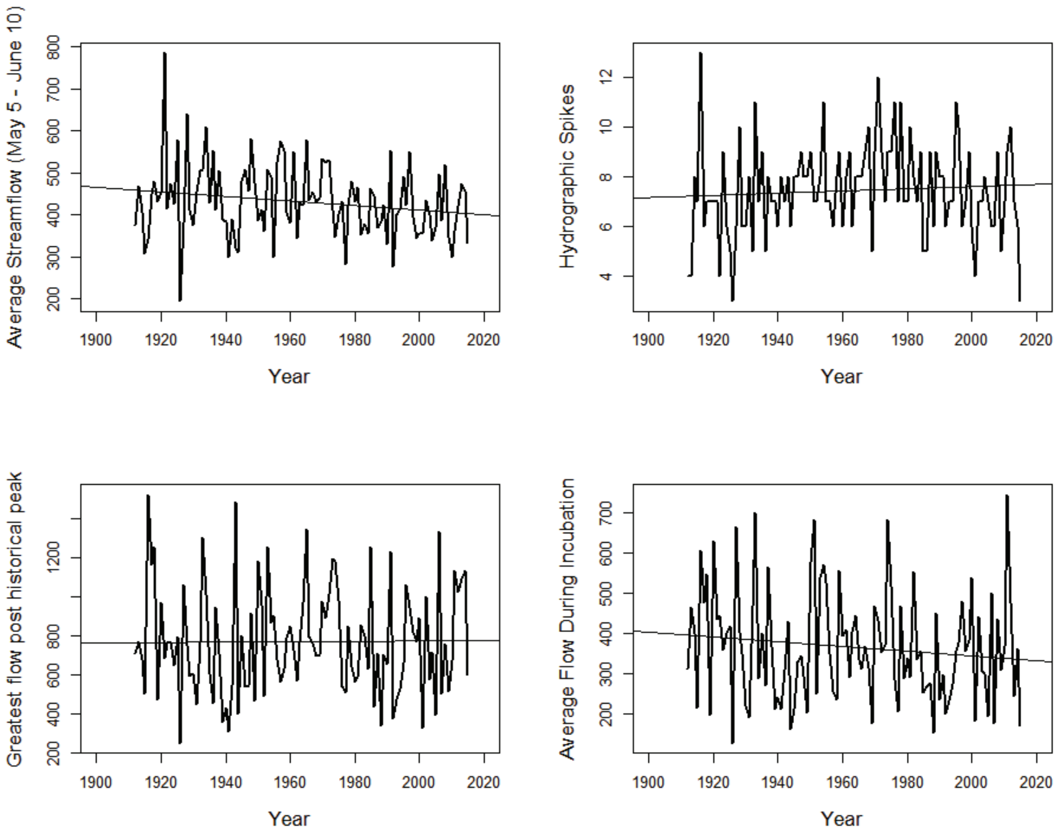

Figure 8. Timeseries of estimated hydrographic metrics of Upper McDonald Creek in Glacier National Park, Montana, USA from 1912-2015 (the straight line represents the trend of the series).

or avoid predators. As suggested by Kuchel (1977), our telemetry data showed that back water habitat is an important feature during early brood rearing. Reproductive success of Harlequin Ducks is generally thought of as boom or bust. Our study demonstrates that boom years are linked to annual decrease in streamflow severity; and predicted increases in frequency of annual streamflow severity may reduce the number of boom years in the future (Stewart *et al.* 2005; Goode *et al.* 2013; Surfleet and Tullos 2013). The GNP Harlequin Duck subpopulation is the densest breeding population in the lower 48 states (Harlequin Duck 2014). We have documented up to 20 breeding pairs in our study area. Most streams and rivers in Western Montana and Idaho have densities ranging from 0.05 to 0.91 pairs per stream kilometer (Reichel and Genter 1996). Due to the unique life history of Harlequin Ducks, repopulation of these streams is slow and likely depends on multiple boom years. Dispersal to new streams is thought to be very low (Cooke *et al.* 2000).

Our results together with climate predictions indicate a high likelihood of increasing challenges to Harlequin Ducks breeding in GNP in the future. While this study only applies to the McDonald Creek watershed in GNP, hydrological conditions are likely important determinants of Harlequin Duck reproductive success throughout their range given the inextricable link between their breeding habitat and lotic variables. An important next step in the conservation of Harlequin Ducks is to collect robust vital rates at all life stages (survival, viability, immigration and emigration) to model population growth rates along a continuum of streamflow severity.

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