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RESEARCH ARTICLE

Length of the recovery period after extreme flood is more important than flood magnitude in influencing reproductive output of Brown Dippers (*Cinclus pallasii*) in Taiwan

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ABSTRACT

Due to climate change, extreme weather events are becoming more frequent and severe. These extreme events have been documented to affect avian predators in stream ecosystems. To better understand the mechanisms behind this effect, we used a decade-long dataset from a mountain stream in Taiwan to assess the effects of extreme flooding caused by typhoons on invertebrate abundance in different periods of the year and the resulting effects on reproductive output of an avian predator of these invertebrates, the Brown Dipper (*Cinclus pallasii*). In this study stream, all extreme floods occurred between June and October, and these floods negatively affected invertebrate density. Consequently, average invertebrate density was lowest in October at the end of the typhoon season, and highest 4 mo later. Because invertebrate density increases over time after a flood, the length of the recovery period between floods that occurred between June and October was more important than each flood's magnitude in determining invertebrate density in October. October invertebrate density then positively correlated with invertebrate density, the number of dipper breeding pairs, and the proportion of breeding individuals in the following breeding season, which lasted from January to early April. The effects of lower invertebrate densities in October and then February percolated all the way through the system, affecting laying date, fledgling population, and the next winter's population. Given our results, an increase in the frequency of typhoons, especially late-season typhoons, will have a negative effect on Brown Dipper reproductive output through bottom-up effects in stream ecosystems.

Keywords: aquatic invertebrates, climate change, flooding, stream, Brown Dipper

La longitud del período de recuperación luego de una inundación extrema es más importante que la magnitud de la inundación para determinar el rendimiento reproductivo de *Cinclus pallasii* en Taiwan

RESUMEN

Debido al cambio climático, los eventos climáticos extremos son cada vez más frecuentes y severos. Se ha documentado que estos eventos extremos afectan a las aves depredadoras en los ecosistemas ribereños. Usamos una base de datos de una década de un arroyo de montaña de Taiwán para entender mejor los mecanismos detrás de estos efectos. Evaluamos los efectos de las inundaciones extremas causadas por los tifones en la abundancia de invertebrados en diferentes períodos del año, y los efectos resultantes en el rendimiento reproductivo de una ave depredadora de estos invertebrados, *Cinclus pallasii*. En este arroyo estudiado, todas las inundaciones extremas ocurrieron entre junio y octubre, y estas inundaciones impactaron negativamente la densidad de invertebrados. Consecuentemente, la densidad promedio de invertebrados fue más baja en octubre al final de la estación de tifones y más alta cuatro meses después. Debido a que la densidad de invertebrados aumentó a lo largo del tiempo luego de la inundación, la longitud de este período de recuperación fue más importante que la magnitud de la inundación para determinar la densidad de invertebrados en octubre. La densidad de invertebrados de octubre entonces se correlacionó positivamente con la densidad de invertebrados, el número de parejas reproductivas de *C. pallasii* y la proporción de individuos reproductivos en la próxima estación reproductiva, que duró de enero hasta inicios de abril. Los efectos de una menor densidad de invertebrados en octubre y luego febrero se sintieron a través de todo el sistema, afectando la fecha de puesta, la población de volantones y la población del próximo invierno. Dados nuestros resultados, un incremento en la frecuencia de tifones, especialmente los tifones de fines de la estación, tendrá un efecto negativo en el rendimiento reproductivo de *C. pallasii* a través de efectos de abajo hacia arriba en los ecosistemas ribereños.

Palabras clave: Arroyo, Cambio climático, *Cinclus pallasii*, Inundaciones, Invertebrados acuáticos

INTRODUCTION

Climate change is altering the phenology, distribution, and demographic rates of many species (e.g., Parmesan et al. 2000, Hussell and Brittingham 2003, Lof et al. 2012, Dybala et al. 2013, Jenouvrier 2013). One of the consequences of climate change is that, in addition to an overall warming trend, extreme weather events have become more frequent and severe, and these trends will increase (IPCC 2013). Weather-related disturbances, such as heat waves, droughts, storms, and floods, can change or limit a species' reproduction, distribution, and abundance (Parmesan et al. 2000, McCarty 2001, Elkins 2010). Extreme weather events can thus directly affect the survival and reproduction of individuals, or indirectly affect them by limiting the availability of habitat or other resources (Jenouvrier 2013). Since extreme weather events are rare and difficult to predict, their effects on species' survival and reproduction are still poorly understood (Reed et al. 2003, Jenouvrier 2013).

The 5 species of dipper (*Cinclus*) occur on 5 continents, where they inhabit fast-flowing rivers in which they feed mainly on aquatic macroinvertebrates (Tyler and Ormerod 1994, Ormerod and Tyler 2005). Dippers are sensitive to acidification and pollution, and are therefore considered bioindicators of stream habitats (Ormerod et al. 1985, Tyler and Ormerod 1992, Ormerod and Tyler 1993, Sorace et al. 2002, Morrissey et al. 2004). They are also sensitive to the average air and water temperature, which influences population dynamics and laying dates of White-throated Dippers (*Cinclus cinclus*) (Sæther et al. 2000, Hegelbach 2001, D'Amico et al. 2003). Additionally, dippers are sensitive to extreme weather events: floods can cause their reproduction to fail (Shaw 1978, Price and Bock 1983, Morrissey 2004, Royan et al. 2014), change their foraging behavior and diet (Da Prato 1981, Taylor and O'Halloran 2001), and decrease their survival (Lebreton et al. 1992, Marzolin 2002, Chiu et al. 2013), abundance (Chiu et al. 2008), and distribution (Royan et al. 2015). Changes in flow regime are also associated with changes in the presence and absence of White-throated Dippers (Royan et al. 2013).

A river's flow regime is also one of the key factors affecting macroinvertebrate composition and abundance in stream ecosystems. Based on previous work, we know that extreme floods triggered by typhoons in Taiwan result in a large reduction in macroinvertebrate abundance, which, in turn, causes the numbers (Chiu et al. 2008, Chiu and Kuo 2012) as well as the survival rate (Chiu et al. 2013) of one of their avian predators, the Brown Dipper (*Cinclus pallasii*), to decrease. After such an extreme flooding event, the total abundance of invertebrates generally recovers again over a matter of months (Greenwood and Booker 2014), and the length of this recovery period affects macroinvertebrate abundance and composition (Chiu and Kuo 2012). Thus, the time period between a flood and the Brown Dipper's breeding season may be a crucial factor that determines prey availability, and therefore breeding onset and output.

In this study, we used long-term data on ambient temperatures and flow regimes of streams in Taiwan to investigate the effect of extreme weather events precipitated by typhoons on invertebrate abundance and the abundance and reproduction of the Brown Dipper. In Taiwan, typhoons usually cause extreme floods from June to October (Tu et al. 2009), while the breeding season of the Brown Dipper lasts from January to early April (Hong et al. 2011). We therefore hypothesized that extreme floods would affect the dipper's breeding phenology and reproductive output via bottom-up impacts caused by decreased prey abundance prior to the breeding season, or even lasting into the breeding season. We used information-theoretic model selection methods (Burnham and Anderson 2002) to determine whether ambient temperature, the magnitude of the flood, or the length of the recovery period after the flood influenced invertebrate abundance and, in turn, the abundance and reproductive output of dippers.

METHODS

Study Area and Environmental Variables

Our study was conducted from 2003 to 2014 in the upstream drainage of the Tachia River in central Taiwan, which includes the Cijiawan (also spelled Chichiawan), the Gaoshan, and the Yousheng streams (Figure 1). The watershed covers 77 km^2, and elevation ranges from 1,700 to 2,000 m. Air temperature data is recorded at Siyuan weather station (24.3900°N, 121.3482°E), which is located near the Yousheng Stream, ~5 km from our study area. During the study period, daily mean air temperature ranged from 4.9 ± 4.2°C in January to 16.7 ± 3.1°C in July (mean ± SD). To calculate the winter temperature prior to the Brown Dipper's breeding season, we averaged daily air temperature from December 1 to January 31.

Daily mean water flow, measured in cubic meters per second (m^3 s^{-1}), was recorded by the Taiwan Power Company at a site downstream of the confluence of the Cijiawan and Yousheng streams (Figure 1). From all the daily means, we took the maximum value for each of 2 periods, namely June 1–October 31 and November 1–January 31, and used these maximum values as estimates of maximum summer flow and maximum winter flow, respectively. In other words, we used the water flow from the day with the largest water discharge as a measure of the flood with the largest magnitude, because we assumed a priori that the largest flood would have the strongest impact on the invertebrate fauna. The summer period was

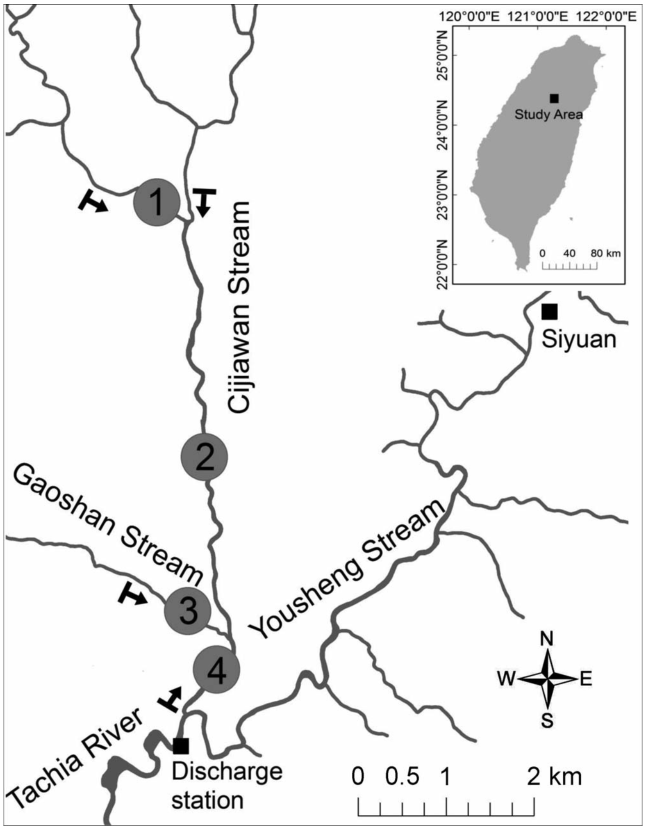

FIGURE 1. Map of the study area in Taiwan, where we examined the influence of extreme floods on Brown Dippers and their macroinvertebrate prey from 2003 to 2014. Circles indicate the 4 macroinvertebrate sampling site locations: 1 = 24.39809°N, 121.30789°E; 2 = 24.37099°N, 121.31096°E; 3 = 24.35824°N, 121.30899°E; and 4 = 24.35460°N, 121.31362°E. The station that recorded water flow (discharge station) was located at 24.34461°N, 121.30653°E. Black arrows indicate the extent of dipper surveys.

chosen because the typical typhoon season in Taiwan usually lasts from June to October (Tu et al. 2009), and the winter period was selected because it precedes the breeding season.

Brown Dipper Population, Breeding, and Food Surveys

Dippers are habitat specialists that occupy a linear territory. In our case, this linear habitat was always a rocky and narrow (5–20 m wide) riverbed with very little vegetation that was always bounded by steep, rocky, vegetated cliffs (Figure 2). The probability of observers visually detecting dippers by walking along a stream is very high. For example, D'Amico and Hemery (2003) showed that 3 visits (i.e. surveys) were sufficient to detect the entire breeding population of White-throated Dippers in mountainous stream habitats.

We conducted monthly population surveys from November to January to census the potential breeding population for the following breeding season. During each survey, we counted individual Brown Dippers by slowly walking along the stream's edge through the entire defined study area (8.5 km), which was one sampling unit. Our study area extended 7 km up the Cijiawan Stream from its confluence with the Yousheng Stream and 1.5 km up the Gaoshan stream from its confluence with the Cijiawan stream (Figure 1).

Individual dippers almost invariably move away from the observer before they "double back" and fly past the observer (and never through the high vegetation adjacent to the riverbed). Therefore, we ignored individuals that flew ahead of the observer to avoid re-counting birds. Each survey lasted from 08:00 to 16:00, with the lower part of the study area covered on the first day, and the upper part on the second day. Further details of and justifications for

TABLE 1. Environmental variables and biotic response variables used in our model selection analysis of the influence of extreme floods on Brown Dippers and their macroinvertebrate prey. Sample size (*n*) is the number of years for which a variable was measured; the sampling period was 2003–2014, thus *n* =12 unless data are missing.

	Abbreviation	Missing years	*n*	Mean ± SD	Min.	Max.
Environmental variables						
Winter temperature (°C)	Winter temp.	—	12	4.8 ± 0.9	3.3	6.3
Maximum summer flow ($m^3\ s^{-1}$)	Summer flow	—	12	223 ± 178	15	610
Maximum winter flow ($m^3\ s^{-1}$)	Winter flow	—	12	7.7 ± 6.9	1.2	24.0
Recovery period (day)	Rec. period	—	12	74 ± 49	6	141
Biotic response variables						
June invertebrate density (m^{-2})	June invert.	2014	11	349 ± 256	61	812
A. August invertebrate density (m^{-2})	Aug. invert.	2014	11	319 ± 339	58	1072
B. October invertebrate density (m^{-2})	Oct. invert.	2014	11	265 ± 238	39	793
C. February invertebrate density (m^{-2})	Feb. invert.	—	12	667 ± 468	237	1864
D. Winter population (individual)	Winter pop.	2003, 2009, 2010	9	40 ± 8	30	55
E. Breeding pairs (pair)	Breed. pair	2009	11	7.6 ± 1.4	6.0	10.0
F. Breeding percentage (%)	Breed. perc.	2003, 2009, 2010	9	38.4 ± 7.3	29.8	48.6
G. First laying date (day)	First laying	2009, 2010	10	18.1 ± 5.6	10.0	28.0
H. Fledgling population (individual)	Fledg. pop.	2003, 2009, 2010	9	15.3 ± 5.4	4.0	23.0

FIGURE 2. Cijiawan Stream, Taiwan, approximately halfway between macroinvertebrate sampling sites 1 and 2 (see Figure 1).

our survey methods, including a detailed description of the dipper's territorial behavior, are given in Chiu et al. (2008) and Chen and Wang (2010).

We are confident that our surveys resulted in a complete (or almost complete) census of the dipper population present at the time. Furthermore, we calculated the repeatability (Krebs 1999) of the 3 monthly censuses, which yielded a relatively high repeatability of 0.859 (95% CI: 0.814–0.926, $n = 27$ mo). Most of the remaining variation was due to some floater individuals that moved rather than remaining on territories during the prebreeding season. We wanted to obtain the potential breeding population during the prebreeding season, so we included floaters. Therefore, we used the maximum (instead of the mean) number of dippers counted during the 3 monthly surveys as our estimate of the winter population.

During the breeding season, dippers typically nest on cliff ledges, in natural or artificial cavities, and under bridges (Severinghaus et al. 2010, Hong et al. 2011). We conducted at least 2 breeding surveys per month for dipper nests from January to March by slowly walking along the streams and following birds with binoculars when they flew to their nests. Dippers are territorial, with a typical distance between adjacent nests of 500–1,000 m in Taiwan, with variation explained by food abundance (Chen and Wang 2010). Because of our prior winter population censuses (see above) and our constant observations during the breeding season, it was highly unlikely that we missed any nests of pairs that continuously occupied a territory. We thus determined the number of breeding pairs as the total number of nests into which a female placed eggs. In some years, a few pairs built a nest but then abandoned it before laying eggs; these "attempted nests" were not included in our number of breeding pairs. In a few cases, we observed a second brood within the same breeding season, but we never observed a pair building a second nest in another location. Since most breeding adults (and some of the floaters) were color-banded, we were able to ascertain if a pair moved to another location. We then used the number of breeding pairs to calculate the breeding percentage as (2 × breeding pairs) / winter population.

Once a nest was found, we observed the nest every 3–5 days to determine the breeding status. We determined the laying date by direct observation or by backdating from the hatching date or based on nestling weight (Hong et al. 2011). For each nest, we counted the number of days from January 1 until a nest contained the first egg. We then averaged the laying dates of the first 2 nests for our variable of first laying date, because we believed that an average from 2 nests would be a more reliable estimate of the onset of laying for the entire population.

For accessible nests, we counted the number of almost-fledged nestlings when we banded them at 18–20 days of age. We carefully observed inaccessible nests to count the fledglings when they left the nest. Over our study years, the percentage of such inaccessible nests ranged from 0% to ~12%, averaging ~6%. We thus determined the fledgling population as the total number of fledglings produced by all the nests.

To examine the main food source for dippers, we sampled benthic macroinvertebrates using a Surber sampler (area = 30.48 cm × 30.48 cm, mesh size = 250 μm) at 4 sites (Figure 1) every 2 mo from February 2003 to February 2014. All intervals were sampled in all years, except December, which was only sampled in 2003, 2004, and 2006. In each sampling period, we took 6 samples from each site at randomly selected locations within runs and riffles. Samples were preserved in 75% ethanol. We identified most individuals to genus or species using published keys (Kang 1993, Merritt and Cummins 1996, Kawai and Tanida 2005). According to Chiu et al. (2009), dippers in Taiwan feed mainly on large invertebrates, primarily Diptera, Ephemeroptera, Plecoptera, and Trichoptera. To estimate food abundance per square meter (m^{-2}), we multiplied the mean number of invertebrates of these 4 taxa caught in the 24 samples (4 sites × 6 samples) by a factor of 10.764 (i.e. 10,000 cm^2 / [30.48 cm × 30.48 cm]) in order to derive an estimate of invertebrate density. In our model selection analysis, we then used only June, August, October, and February invertebrate density (Table 1).

Because typhoon-triggered floods are known to affect the dipper's invertebrate prey, we also determined the recovery period as the number of days between the date of the most recent flood during the typhoon season from June to October and the date when invertebrates were sampled in October for the first time at the end of the typhoon season. A flood was defined as a maximum water

TABLE 2. Ranking of all possible models for 8 biotic response variables (see definitions in Table 1) of Brown Dippers and their macroinvertebrate prey to factors influenced by extreme flood events in Taiwan, 2003–2014. Models are ranked by the difference from the top model in Akaike's Information Criterion corrected for small ample size (ΔAIC_c) and Akaike weight (w_i). The parameter count (K) and model deviance ($-2\log L$) is also shown. Models with substantial support ($\Delta\text{AIC}_c < 2$) are in bold font. Response variables with positive relationships are in roman font; italic font indicates negative relationships.

Response	Independent variables	Selected variables	R^2	K	$-2\log L$	ΔAIC_c ^{a}	w_i
A. Aug. invert.	Summer flow ^{b}, rec. period ^{b}, June invert.	***Summer flow*** ^{b}	**0.53**	**3**	**−27.00**	**0.00**	**0.394**
		Summer flow ^{b} **+ Jun. invert.**	**0.70**	**4**	**−32.05**	**0.19**	**0.359**
		Jun. invert.	0.37	3	−23.78	3.22	0.079
		Jun. invert. + rec. period	0.58	4	−28.25	3.99	0.054
		Null model	0.00	2	−18.76	4.31	0.046
		Summer flow + rec. period	0.53	4	−27.05	5.18	0.030
		Rec. period	0.24	3	−21.76	5.24	0.029
		Summer flow ^{b} + Jun. invert. + rec. period	0.70	5	−32.14	7.43	0.010
B. Oct. invert.	Summer flow, rec. period, Aug. invert.	**Rec. period**	**0.76**	**3**	**−5.09**	**0.00**	**0.722**
		Rec. period + Aug. invert.	0.81	4	−7.71	2.62	0.195
		Rec. period + *summer flow*	0.77	4	−5.43	4.90	0.062
		Summer flow	0.47	3	3.71	8.80	0.009
		Rec. period + Aug. invert. + summer flow	0.82	5	−7.99	9.67	0.006
		Aug. invert.	0.39	3	5.33	10.42	0.004
		Null model	0.00	2	10.72	11.88	0.002
		Aug. invert. + *summer flow*	0.50	4	3.01	13.34	0.001
C. Feb. invert.	Winter temp., winter flow, Oct. invert.	**Oct. invert.**	**0.49**	**3**	**−4.52**	**0.00**	**0.718**
		Null model	0.00	2	2.92	3.51	0.124
		Winter flow + Oct. invert.	0.50	4	−4.62	5.14	0.056
		Winter temp. + Oct. invert.	0.49	4	−4.52	5.24	0.053
		Winter flow	0.02	3	2.74	7.26	0.019
		Winter temp.	0.00	3	2.88	7.40	0.018
		Winter temp. + winter flow	0.02	4	2.70	12.50	0.001
		Winter temp. + *winter flow* + Oct. invert.	0.50	5	−4.62	12.50	0.001
D. Winter pop.	Oct. invert., winter pop. ^{c}, fledg. pop.	**Fledg. pop.**	**0.73**	**3**	**−28.11**	**0.00**	**0.734**
		Null model	0.00	2	−18.90	2.20	0.244
		Oct. invert.	0.03	3	−19.10	9.01	0.008
		Winter pop. ^{c}	0.02	3	−19.04	9.07	0.008
		Winter pop. ^{c} + fledg. pop.	0.85	4	−32.33	9.78	0.006
		Oct. invert. + fledg. pop.	0.75	4	−28.62	13.50	0.001
		Oct. invert. + *winter pop.* ^{c}	0.03	4	−19.10	23.00	0.000
		Oct. invert. + winter pop. ^{c} + fledg. pop.	0.89	5	−34.07	50.00	0.000
E. Breed. pair	Oct. invert., Feb. invert., winter pop.	**Oct. invert.**	**0.68**	**3**	**−30.84**	**0.00**	**0.516**
		Oct. invert. + winter pop.	**0.85**	**4**	**−37.55**	**0.48**	**0.404**
		Null model	0.00	2	−20.64	5.40	0.035
		Oct. invert. + *Feb. invert.*	0.69	4	−31.06	6.98	0.016
		Feb. invert.	0.26	3	−23.37	7.47	0.012
		Winter pop.	0.25	3	−23.25	7.58	0.012
		Feb. invert. + winter pop.	0.60	4	−28.90	9.13	0.005
		Oct. invert. + Feb. invert. + winter pop.	0.85	5	−37.67	12.40	0.001

TABLE 2. Continued.

Response	Independent variables	Selected variables	R^2	K	−2log$L$	ΔAIC$_c$ [a]	w_i
F. Breed. perc.	Oct. invert., Feb. invert., winter pop.	**Oct. invert. + *winter pop.***	**0.85**	**4**	**−37.55**	**0.00**	**0.705**
		Oct. invert.	0.50	3	−26.94	3.41	0.128
		Feb. invert.	0.43	3	−25.73	4.63	0.070
		Null model	0.00	2	−20.64	4.91	0.060
		Winter pop.	0.25	3	−23.25	7.10	0.020
		Feb. invert. + *winter pop.*	0.60	4	−28.90	8.65	0.009
		Oct. invert. + Feb. invert.	0.55	4	−27.92	9.64	0.006
		Oct. invert. + Feb. invert. + *winter pop.*	0.85	5	−37.67	11.90	0.002
G. First laying	Winter temp., Feb. invert., winter pop.	***Feb. invert.***	**0.87**	**3**	**−32.58**	**0.00**	**0.935**
		Winter temp. + Feb. invert.	0.88	4	−33.16	5.42	0.062
		Feb. invert. + *winter pop.*	0.84	4	−28.42	12.20	0.002
		Null model	0.00	2	−11.79	16.50	0.000
		Winter temp.	0.00	3	−11.84	20.70	0.000
		Winter pop.	−0.22	3	−9.98	23.40	0.000
		Winter temp. + Feb. invert. + winter pop.	0.85	5	−29.11	23.50	0.000
		Winter temp. + winter pop.	−0.21	4	−10.08	30.50	0.000
H. Fledg. pop.	Feb. invert., breed. pair, first laying	***First laying***	**0.74**	**3**	**61.32**	**0.00**	**0.739**
		Feb. invert. + first laying	0.83	4	57.39	3.27	0.144
		First laying + breed. pair	0.78	4	59.81	5.69	0.043
		Feb. invert.	0.48	3	67.46	6.14	0.034
		Null model	0.00	2	73.33	7.21	0.020
		Breed. pair	0.37	3	69.15	7.83	0.015
		Feb. invert. + first laying + breed. pair	0.89	5	53.63	11.51	0.002
		Feb. invert. + breed. pair	0.57	4	65.78	11.67	0.002

[a] The AIC$_c$ values of the top models are as follows: A. Aug. invert. = –17.6; B. Oct. invert. = 4.3; C. Feb. invert. = 4.9; D. Winter pop. = –14.1; E. Breed. Pair = –20.0; F. Breed. perc. = –19.6; G. First laying = –22.6; H. Fledg. pop. = 72.1.

[b] For this analysis, summer flow and recovery period were defined for the period from June 1 to the invertebrate sampling date in August.

[c] The winter population of the previous year.

flow of >100 m^3 s^{-1}, which was a convenient threshold because the 3 yr without a typhoon, and thus without a flood, were 2003, 2010, and 2011, with maximum flows of 15, 58, and 41 m^3 s^{-1}, respectively, while all other years had at least 1 typhoon, with the smallest resulting maximum flow being 141 m^3 s^{-1} in 2005. The largest maximum flow of 610 m^3 s^{-1} occurred in 2004. For years without a flood, we used the beginning of the typhoon season (June 1) as the starting date for the recovery period.

Data Analyses

We tested for various reasonable relationships among the 4 environmental variables and 8 biotic responses (Table 1) using multiple linear regression. To achieve a normal distribution for each variable, all independent variables and response variables (i.e. all variables in Table 1) were log-transformed prior to all analyses (see Chiu et al. 2008), except for August invertebrate density and fledgling population, which required a Box-Cox transformation (Krebs 1999) to achieve a normal distribution (one-sample Kolmogorov-Smirnov test or Shapiro-Wilk $P > 0.05$).

For each biotic response variable (i.e. the dependent variable) listed in Table 2 by capital letters A–H, we first used all of the other 12 variables listed in Table 1 as independent variables (the correlation matrix for all variables is given in Appendix Table 4). However, in each case, only a few variables made an important contribution according to AIC$_c$ value and Akaike weight (w_i; see below). Therefore, in the second step, we selected the 3 independent variables from among the 12 variables presented in Table 1 which (1) were the most important according to ΔAIC$_c$, but also (2) were most likely to influence the response variable using prior knowledge

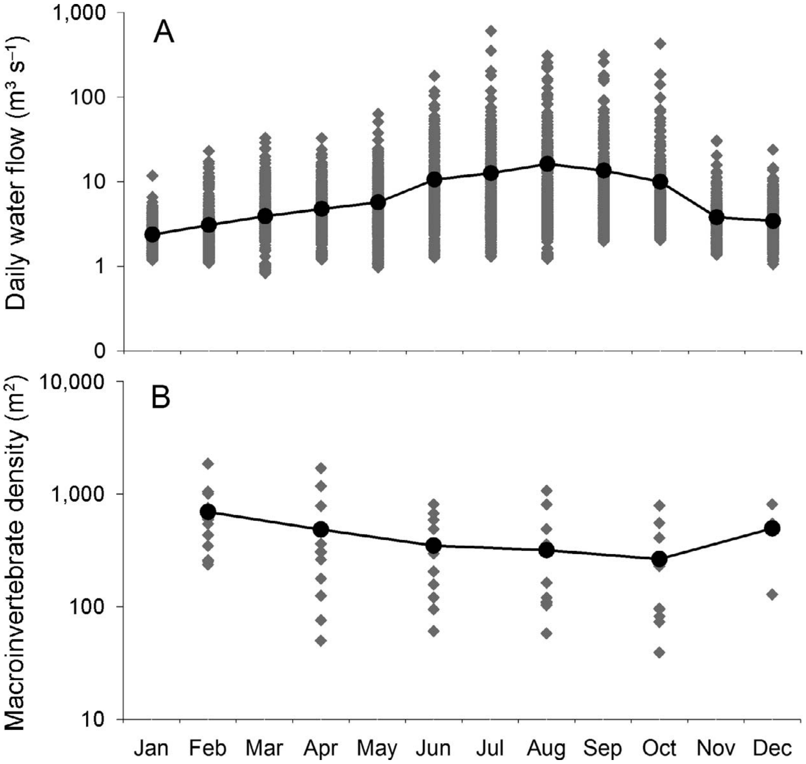

FIGURE 3. (A) Daily mean water flow ($n = 4{,}384$), and **(B)** bimonthly macroinvertebrate density averaged over the 4 sampling sites (see Figure 1) for the entire study period of 2003–2014 (except December, which was only sampled in 2003, 2004, and 2006 and averaged over these years). Black lines and points show trends and means of log-transformed flow and macroinvertebrates.

(see Introduction and Methods). We thus followed Burnham and Anderson's (2002) suggestion to only test for relationships which make biological sense and restricted our analysis to testing only the most ecologically reasonable models. For each response variable (Table 2), we then tested the 8 candidate models resulting from all of the possible combinations of the 3 independent variables plus the null (intercept only) model.

We ranked models based on Akaike's Information Criterion adjusted for small sample size (AIC_c). We accepted only those models with a $\Delta AIC_c < 2$ as having "substantial" support (Burnham and Anderson 2002, Grabowska-Zhang et al. 2011, Majić et al. 2011). If there was model selection uncertainty (i.e. >1 model with $\Delta AIC_c < 2$), we averaged the accepted high-ranking models to obtain parameter estimates. To assess the relative importance of each predictor, we also calculated the relative variable importance (RVI) by summing the Akaike weights (w_i) for all of the accepted models with each selected variable (Burnham and Anderson 2002), thereby ranking variables by importance according to their contribution to the entire set of accepted models. We conducted all model ranking and model averaging procedures with the MuMIn package (Bartoń 2012) applied in program R 3.1.0 (R Core Team 2012).

RESULTS

During the study period, there were 15 flooding events with a water flow of $>100\ m^3\ s^{-1}$, each lasting from 1 to 3 days (Figure 3A, Appendix Figure 6). These floods all occurred between June and October, while the water flow during the remaining months was comparatively low and stable. The higher magnitude of water flow was mirrored by a decrease in invertebrate density; the period from June to October had the lowest mean invertebrate densities (Figure 3B).

Each of the 8 response variables was effectively predicted by models with only 1 or 2 predictors (Table 2). For 5 of the 8 response variables, only 1 independent variable had substantial model support as a correlated variable, while the breeding percentage was correlated with 2 independent variables. For the 2 remaining response variables, August invertebrate density and breeding pairs, 2 candidate models had substantial support. Table 3 presents the results from averaging these 2 models. Using the relative variable importance as a measure, summer flow was more strongly correlated with August invertebrate density than was June

TABLE 3. Results of model-averaging the top models ($\Delta AIC_c < 2$) with >1 variable selected to determine the influence of extreme floods on Brown Dippers and their macroinvertebrate prey in Taiwan, 2003–2014 (see Tables 1 and 2 for corresponding capital letter labels and variable definitions). Coeff. = coefficient of explanatory variable; SE = unconditional standard error; CL = 95% confidence limit; RVI = relative variable importance.

Response	Coeff.	Estimate	SE	Lower CL	Upper CL	RVI
A. Aug. invert.	(Intercept)	2.363	0.241	1.85	2.87	
	Summer flow [a]	−0.148	0.050	−0.26	−0.04	1.00
	June invert.	0.126	0.058	−0.01	0.26	0.48
E. Breed. pair	(Intercept)	0.251	0.366	−0.51	1.01	
	Oct. invert.	0.146	0.035	0.06	0.23	1.00
	Winter pop.	0.412	0.160	0.02	0.80	0.44

[a] For this analysis only, summer flow was defined for the period from June 1 to the invertebrate sampling date in August.

invertebrate density, and October invertebrate density had a higher correlation with breeding pairs than winter population. All of the correlations with substantial support in Table 2 are depicted graphically in Figure 4.

To summarize the information contained in Tables 2 and 3 and Figure 4, we constructed a flow diagram depicting the directions of the relationships (Figure 5). Higher summer flow and lower June invertebrate density were associated with lower August invertebrate density (Table 2, Figure 4A), but summer flow was of greater importance (Table 3). Only the length of the recovery period positively influenced October invertebrate density (Table 2, Figure 4B). October invertebrate density positively influenced February invertebrate density (Table 2, Figure 4C), and higher February invertebrate density was related to an earlier laying date (Table 2, Figure 4G), which then led to a higher fledgling population (Table 2, Figure 4H). Therefore, the influence of the recovery period filtered all the way down to the fledgling population in the subsequent spring breeding season. The fledgling population then had a positive effect on the population in the following winter (Table 2, Figure 4D), which in turn had a positive influence on the number of breeding pairs in the subsequent breeding season (Table 2, Figure 4E-2). However, the number of breeding pairs was influenced more by the October invertebrate density before the breeding season (Tables 2 and 3, Figure 4E-1) than by the winter population just before the breeding season (Tables 2 and 3, Figure 4E-2). Finally, more individuals of the entire population bred (i.e. the breeding percentage was higher) if the October invertebrate density was higher (Table 2, Figure 4F-1), but fewer individuals of the entire population bred (i.e. the breeding percentage was lower) if the winter population was higher (Table 2, Figure 4F-2).

DISCUSSION

Our long-term study monitored the population and breeding parameters of the Brown Dipper, as well as its invertebrate prey and some weather-related variables which might have influenced this study system, for more than a decade. The strengths of this particular study system are that (1) population counts of dippers are highly accurate because of the visual openness and constrained linear shape of the habitat; (2) dippers feed mainly on aquatic macroinvertebrates, which can be reliably sampled; and (3) this study and other studies have demonstrated the strong influence of water flow on this macroinvertebrate community. Therefore, the correlations summarized in Figure 5 are most likely causal relationships, although correlative evidence is naturally always open to alternative explanations.

Previous studies have shown negative correlations between water flow, invertebrate density, and dipper populations (Chiu et al. 2008), and the negative influence of extreme flooding on dipper survival (Chiu et al. 2013). In addition to using a temporally longer dataset, our study also provides a comprehensive and more mechanistic understanding of how extreme flooding affects the reproductive output and subsequent abundance of dippers.

First, if the initial population of macroinvertebrates sampled in June was higher, the population sampled in August was also higher. Second, logically, invertebrate density in August was negatively influenced by summer flow, especially if the summer flow was a major flood. This influence of water flow (and especially extreme water flow) on macroinvertebrate communities has also been demonstrated in previous studies (Chiu et al. 2008, Chiu and Kuo 2012). Furthermore, Chiu and Kuo (2012) showed that, after a typhoon-triggered flood, invertebrate density increased over time. Consequently, the length of the recovery period was the only important variable in our study that determined invertebrate density in October, at the end of the typhoon season, while a flood's magnitude had no influence on invertebrate density in October. This result meant that October invertebrate abundance was lower when extreme flooding was caused by a typhoon later in the typhoon season than if the flooding occurred earlier in the typhoon season. We also demonstrated that

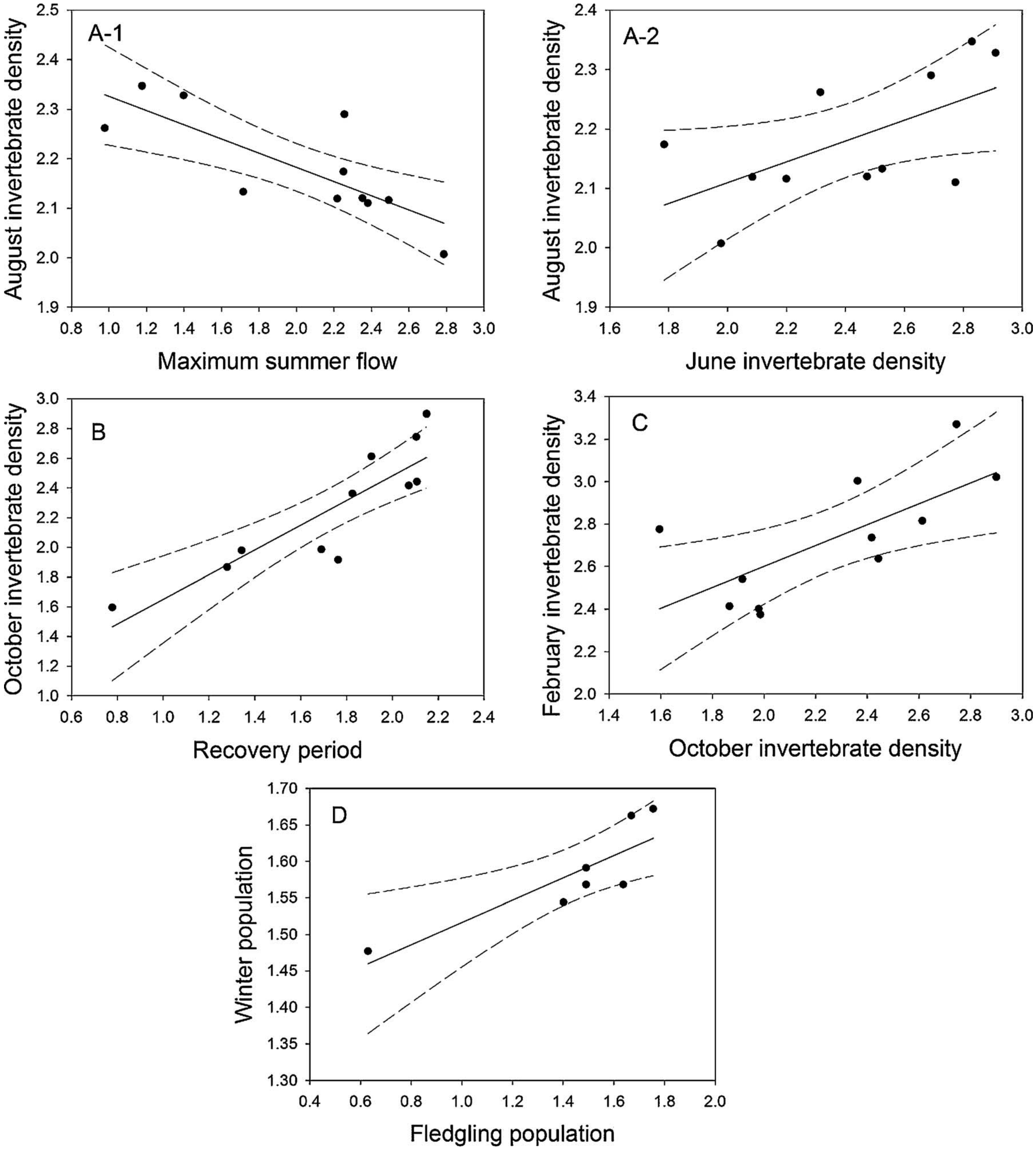

FIGURE 4. Linear regression means and 95% confidence intervals for each of the top models shown in Table 2 (see Tables 1 and 2 for corresponding capital letter labels). For panels **A-2, E-2,** and **F-2,** we show only the univariate regression of the independent variable on the response variable as a useful visual representation, even though the full additive model as shown in Table 2 consists of the regression of 2 independent variables on the response variable.

invertebrate abundance in October influenced all of the subsequent breeding parameters and outputs of dippers (Figure 5). Therefore, flood timing was more influential than flood magnitude on Brown Dipper breeding.

Interestingly, a higher proportion of individuals bred if October invertebrate density was higher; presumably, the higher food supply improved individual condition (Wendeln and Becker 1999, Cubaynes et al. 2011, Lehikoinen et al. 2011, Reichert et al. 2012, Millon et al. 2014). Alternatively, the higher food supply may have decreased territory size, thus allowing more individuals to breed (Chen and Wang 2010). However, a lower proportion of individuals bred if the winter population was higher, suggesting that the total number of territories was limiting. Dippers also could have been limited by the number of suitable nest sites (Loegering and Anthony 2006, Sever-

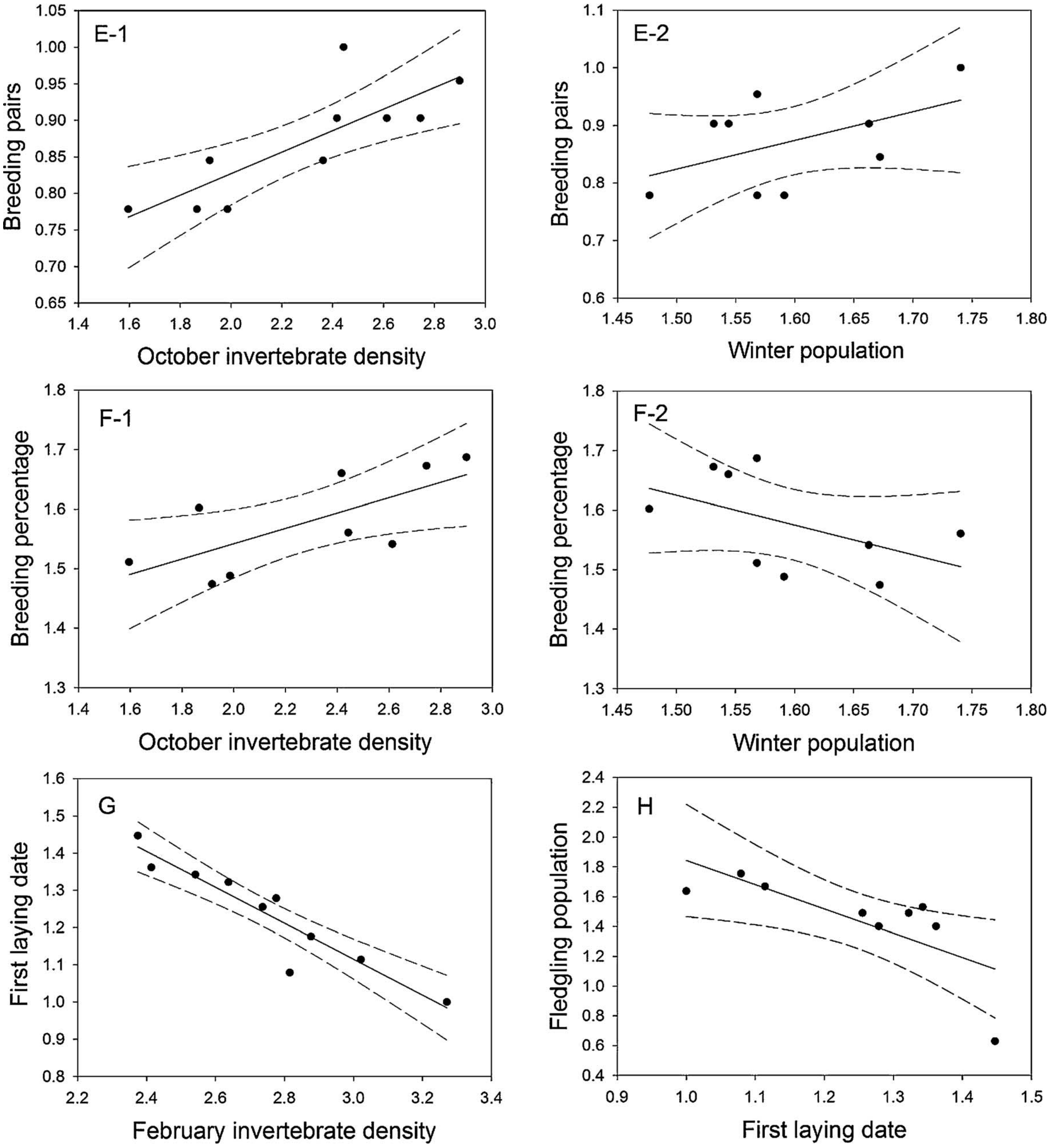

FIGURE 4. Continued.

inghaus et al. 2010). Dippers in our study usually began building their nests in December, but started as early as mid-November in a few years. Thus, competition for territories and nest sites began long before breeding. Similar observations were made by Price and Bock (1983), who reported that the poorest average reproduction occurred in the year with the largest study population of American Dippers (*Cinclus mexicanus*).

In our study population, a sufficiently high number of successful fledglings managed to survive during the summer and autumn to supplement the next winter's population and the next spring's number of breeding pairs (Figure 5). Similar results have been documented for other species (e.g., Sillett et al. 2000, Sæther et al. 2002). Demographic responses to interannual variations in weather may be a typical pattern revealed with large datasets (e.g., Dugger et al. 2016).

A species' laying period usually coincides with favorable weather conditions or seasonal peaks in food abundance. In many regions, these favorable periods are shifting with higher spring temperatures, and species are adjusting their phenology accordingly (e.g., Van Noordwijk et al. 1995,

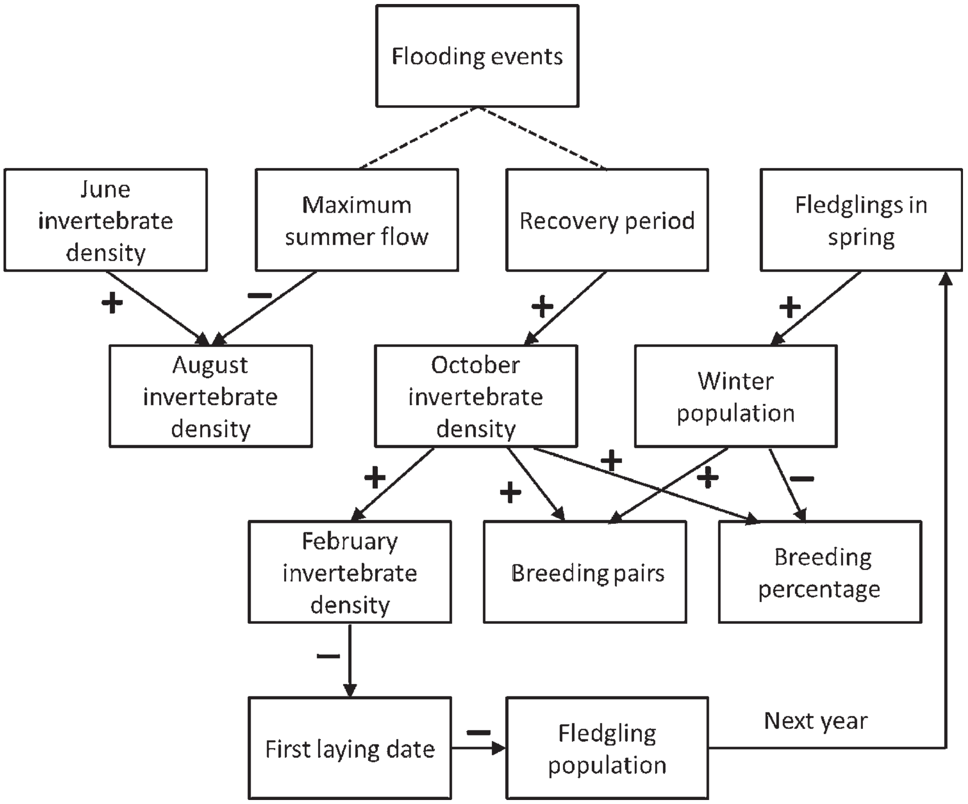

FIGURE 5. Summary of the relationships among the environmental variables and the biotic responses of dippers and invertebrate communities in Taiwan, 2003–2014 (see Tables 1, 2, and 3). Plus and minus signs indicate positive and negative relationships. The dashed lines indicate 2 different effects of the same flooding event.

Parmesan and Yohe 2003). Brown Dippers begin to breed in January, which is the coldest month in our study area, but is also when stream invertebrates have recovered from floods caused by typhoons, and this timing further allows fledglings sufficient time to mature before the next typhoon season. Unlike the findings of several other studies on dippers (Sæther et al. 2000, Hegelbach 2001, D'Amico et al. 2003), winter temperature had no influence on invertebrate density or laying date in our study (Table 2). Perhaps the effects of temperature were masked by the significant effects of flooding, although we found no statistical effect of temperature. The only other variable that we examined which had no discernable influence on our study system was maximum winter flow (Table 2). The most likely explanation for this result is that the period of winter flow does not include the typhoon season and therefore has a much lower and more stable flow regime, with little influence on invertebrate density (Figure 3).

Many studies of dippers and other bird species have demonstrated the positive influence of higher food abundance on laying dates and fledgling populations, and of earlier laying dates on clutch sizes and fledgling populations (e.g., Price and Bock 1983, Van Noordwijk et al. 1995, Morrissey 2004, Visser et al. 2006, Lehikoinen et al. 2011; but see Wilson 1996). Surprisingly, the fledgling population was correlated only with the first laying date and not with the number of breeding pairs within the same breeding season (Table 2H). Since other studies have found a positive relationship between the number of breeding pairs and the total number of fledglings that they produce (e.g., Holland and Yalden 2002, Millon et al. 2014), our result is somewhat surprising. The positive correlation between the number of breeding pairs and the number of fledglings produced explained only 34% of the variation in our model. Thus, there was some effect, but the effect was small compared with the effect of first laying date, especially given the fact that adding the number of breeding pairs into the model with first laying date added only another 6% of explained variation.

In some years, stochastic factors, such as bad weather or predators, cause breeding failures (Hong et al. 2011, Y.-H. Sun personal observation) and thus diminish the influence of the number of breeding pairs on the production of fledglings. On the other hand, during years when breeding started early (usually years with no floods before the breeding season), a few pairs produced 2 clutches, thus increasing the total number of fledglings. These double broods may explain why the fledgling population was positively correlated with first laying date, but not with the number of breeding pairs.

As always, correlational evidence is open to alternative explanations. For example, February invertebrate density could conceivably be correlated with a third variable that also influences first laying date (cf. Table 2); perhaps higher temperatures in February cause both higher invertebrate densities and earlier laying dates. In lieu of another explanation, we conclude that bottom-up effects percolate all the way through our study system, from floods to invertebrate density to dipper abundance. A similar bottom-up effect of benthic prey distribution has also been implicated in the distributional shifts of an Arctic duck (Sexson et al. 2016).

Given our results, it is highly likely that an increase in the frequency and severity of extreme climatic events, such as typhoons, will have a negative effect on both the stream invertebrate communities and their main avian predator, the Brown Dipper. These conclusions, naturally, assume no evolutionary adaptation of the invertebrates or the Brown Dipper to these future environmental changes (Visser 2008, Hendry et al. 2010).

The Brown Dipper is the only dipper species which lives in a region that is frequently affected by typhoons. Because typhoons hit Taiwan annually, severe river floods are common (Chen and Chen 2003), and the number and severity of these typhoons is predicted to increase due to climate change (Allan and Soden 2008, Elsner et al. 2008). Typhoons in the western North Pacific are becoming more intense and longer-lasting (Webster et al. 2005, Chiang and Chang 2011). In Taiwan, records show that rainfall from typhoons of all intensities has increased significantly, while other rainfall, particularly lighter rain, has tended to decrease (Tsai and Huang 2011, Tu and Chou 2013, Chu et al. 2014). The intense rainfall from typhoons usually causes extreme flooding of streams, and these floods have increased in magnitude (Appendix Figure 6; Chang et al. 2011, Chiang and Chang 2011, Chiu and Kuo 2012). Given our results, we can thus make a tentative prediction that climate change will negatively impact the Brown Dipper's reproductive output in Taiwan due to increased frequency and severity of floods. Interestingly, if an increase in typhoon frequency were also to be associated with a shift toward earlier or later typhoon occurrence, then the effects on the Brown Dipper would correspondingly change. Naturally, other effects of climate change, such as higher summer temperatures, heat waves, or droughts, may also affect the dipper's food and breeding output, but through different mechanisms.

Streams and rivers not only satisfy human need for freshwater, but also harbor one of the earth's most biodiverse ecosystems. Climate change already affects them, and will increasingly do so (Cumming et al. 2012, Royan et al. 2013). Our results add to the mounting evidence that, at least in the short term, many biological communities will be negatively affected by the impacts of climate change and, in particular, extreme weather events resulting from climate change.

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Author contributions: Y.-H.S. conceived the idea, design, and experiment (supervised research, formulated question or hypothesis); S.-Y.H. and M.-C.C. performed the experiments (collected data, conducted the research); S.-Y.H. and B.A.W. wrote the paper (or substantially edited the paper); Y.-H.S., M.-C.C., and M.-H.K. developed or designed the methods; and S.-Y.H. and B.A.W. analyzed the data.

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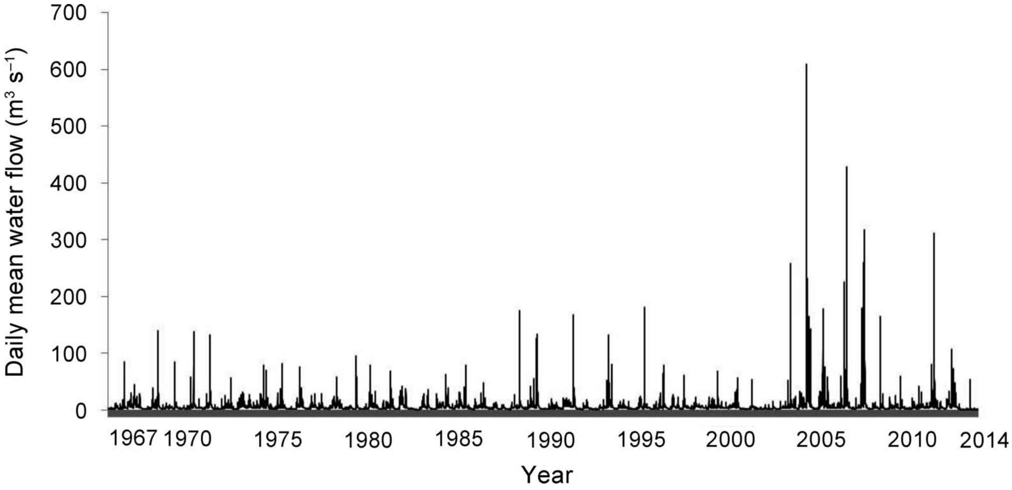
APPENDIX TABLE 4. Pearson correlation coefficient matrix for the 13 variables used in our analyses of the effects of extreme flood events on Brown Dippers and their macroinvertebrate prey in Taiwan, 2003–2014 (see Table 1 for variable definitions).

	Winter temp.	Summer flow	Winter flow	Rec. period	June invert.	Aug. invert.	Oct. invert.	Feb. invert.	Winter pop.	Breed. pair	Breed. perc.	First laying	Fledg. pop.
Winter temp.	1.000												
Summer flow	0.267	1.000											
Winter flow	0.388	0.281	1.000										
Rec. period	−0.297	−0.719	0.126	1.000									
June invert.	−0.535	−0.282	0.109	0.048	1.000								
Aug. invert.	−0.407	−0.726	−0.043	0.488	0.605	1.000							
Oct. invert.	−0.086	−0.687	0.139	0.873	0.117	0.622	1.000						
Feb. invert.	0.097	−0.482	0.001	0.452	0.211	0.461	0.701	1.000					
Winter pop.	−0.410	−0.449	−0.232	0.317	0.148	0.147	0.113	−0.145	1.000				
Breed. pair	−0.297	−0.879	−0.221	0.802	0.128	0.750	0.810	0.466	0.502	1.000			
Breed. perc.	0.033	−0.421	−0.045	0.495	−0.046	0.600	0.710	0.657	−0.502	0.496	1.000		
First laying	0.039	0.340	−0.108	−0.425	−0.317	−0.598	−0.756	−0.935	0.109	−0.524	−0.617	1.000	
Fledg. pop.	−0.183	−0.270	−0.033	0.439	0.155	0.385	0.688	0.692	0.850	0.609	0.435	−0.858	1.000



APPENDIX FIGURE 6. Daily mean water flow ($m^3\ s^{-1}$) recorded at the confluence of the Cijiawan and Yousheng streams as they flow into the Tachia River, Taiwan, 1967–2014.