Flood avoidance behaviour in Brown Dippers

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Extreme weather events such as tropical cyclones are becoming more frequent, but efforts to understand the impact on wildlife have focused on population-level change rather than the behavioural responses of individuals. In this study, we monitored an individually marked population of Brown Dippers *Cinclus pallasii* in upland Taiwanese streams in order to investigate the movements of these birds following typhoons in 2004, 2012 and 2013. Individuals moved significantly longer distances (i) immediately after floods compared with before and (ii) in typhoon years compared with other years. Most of these movements involved temporary displacement from a major stream to one of its tributaries, where population size and food abundance are typically lower. These results suggest that movements after flooding were not driven by food abundance but that relatively poor quality streams may provide an important refuge for birds following typhoons.

Keywords: typhoon, climate change, tropical cyclone**,** refuge, survival

Extreme weather and natural disasters can dramatically increase extinction risk (Easterling *et al.*, 2000, IPCC, 2014, Vincenzi, 2014). Alongside increasing global temperatures, extreme weather events have become more frequent and severe, and this trend is likely to continue into the next century (IPCC, 2014). Understanding how wildlife responds to these events is therefore a major conservation challenge, but since they are difficult to predict, their impact on animal and plant populations remains poorly understood (Reed *et al.*, 2003, Jenouvrier, 2013, Bailey & Pol, 2016).

The ability to adapt to or escape from the conditions imposed by extreme weather events may be critical for individual survival and population persistence. For example, birds may alter their foraging behaviour when flooding restricts access to feeding sites (e.g. Anich & Reiley, 2010), or when the availability of preferred food is limited by drought (e.g. Steenhof & Kochert, 1985). In other cases, birds may leave their territories to avoid unfavourable conditions. In one extreme example, individual Golden-winged Warblers *Vermivora chrysoptera* were recorded leaving their breeding grounds more than 24 hours before a severe tornadic storm, travelling over 1500 km in five days (Streby *et al.*, 2014). However, these studies are rare, and more research is needed to investigate the movements made by individual birds to escape the effects of extreme weather.

In Taiwan, typhoons have become increasingly frequent (Tu *et al.*, 2009) and can cause devastating floods between June and October (Chiang & Chang, 2011). The Brown Dipper *Cinclus pallasii* is a specialist of fast-flowing streams in upland Taiwan, feeding mainly on aquatic macroinvertebrates (Chiu *et al.*, 2009), and previous studies have shown that extreme flooding following typhoons causes significant reductions in prey density, leading to decreases in population size (Chiu *et al.*, 2008), survival rate (Chiu *et al.*, 2013) and reproductive performance (Hong *et al.*, 2016). Chiu *et al.* (2008) reported the movement of several individuals from a major stream to a small tributary after one flood in 2004, but sample sizes were small. In order to investigate this phenomenon further, we closely monitored the same study population from 2011 to 2014 and compared the location and movements of ringed birds before and after typhoons, and in typhoon years versus other years. We also compared the relationships between discharge, invertebrate density and population size on each stream in order to test whether movements were likely to be driven by food availability.

METHODS

Study area

The study area comprised the Cijiawan stream and its tributary the Yousheng in the Tachia river catchment of central Taiwan (Fig. S1). The Cijiawan is a protected area within Shei-Pa National Park. The drainage areas of the Cijiawan and Yousheng are 77 and 31 km^2, respectively, and records from 2007 and 2008 indicate that maximum flow rates following typhoons were more than twice as high in the former than the latter (Huang *et al.*, 2012). The daily water flow was recorded by the Taiwan Power Company at a site 400 m downstream of the confluence of the Cijiawan and Yousheng throughout the study period. The mean (± SD) daily flow from 2012 to 2014 was 6.1 ± 14.4 m^3s^{-1}, and maximum flows following typhoon years in 2004, 2012, and 2013 were 258.7, 310.8, and 240.5 m^3s^{-1}, respectively. There were no typhoons in 2011 and 2014, and maximum flows in these two years were 21.5 and 58.3 m^3s^{-1}, respectively.

Population monitoring and colour ringing

Dippers were surveyed along an 8.5 km stretch of the Cijiawan and the same length of the Yousheng from their confluence. The former included a short (1.5 km) section of the Gaoshan, a small tributary which usually holds one or two pairs of dippers near to where it joins the Cijiawan; this was classified as the Cijiawan to simplify the analyses. Surveys were conducted every one or two months (depending on weather conditions and access) from June 2011 to December 2014 (6 surveys in 2011 of the Cijiawan only; 10 surveys of both streams in 2012, 9 in 2013 and 10 in 2014). In 2004, the Cijiawan was surveyed five times (from June to December) and the Yousheng twice (in September and November). Birds were counted by slowly walking along the stream edge and ignoring individuals which flew ahead to avoid double counting; individuals almost invariably double-back once they reach the boundary of their territory and thus fly by the observer (Chen & Wang, 2010, Hong *et al.*, 2016).

A colour ringing programme was conducted from 2011 to 2014 along the Cijiawan and 2012 to 2014 on the Yousheng. Adults were caught in mist nets and given individual colour combinations, mostly in the pre-breeding period (September to December). The entire study area was surveyed for nests at least twice per month from January to March; nests were readily found by following adults carrying nest material or food (Hong *et al.*, 2016). All nestlings were given unique colour ring combinations when 16-18 days old (January to April). During population surveys, the location of all resighted colour ringed birds was recorded on a map to within 50 m.

Invertebrate sampling

Benthic macroinvertebrates were sampled at four sites in each of the two streams every other month from February 2012 to October 2013 and in February, June and October 2014. On each visit, six samples were taken from riffles (where the birds usually feed) within each site using a Surber sampler (area = 30.48 cm x 30.48 cm, mesh size = 250 µm); samples were preserved in 75% ethanol. Specimens were identified at least to genus using published keys (Kang, 1993, Merritt & Cummins, 1996, Kawai & Tanida, 2005). According to Chiu *et al.* (2009), Brown Dippers feed mostly on Trichoptera, Ephemeroptera, Diptera, and Plecoptera in our study area. The mean number of invertebrates from these four taxa caught in the 24 samples (4 sites x 6 samples) was therefore multiplied by a factor of 10.764 (i.e. 10,000 cm^2/[30.48 cm x 30.48 cm] as a measure of invertebrate density in m^2.

Data analysis

The distances moved by colour-ringed individuals before and after flood events were non-normally distributed and so compared using a Wilcoxon signed rank test. Movements before a flood were measured as the distance between an individual's locations on the two population surveys before the flood event. Movements after a flood were measured as the distance between an individual's locations on the surveys in the months immediately before and after the flood event. We also compared the movements after flooding in typhoon years with movements at the same time of year in non-typhoon years (2011 and 2014) using a Mann-Whitney U Test. Movements in non-typhoon years were measured as the maximum distance between an individual's locations during July to September. To exclude cases of natal dispersal and the movements of non-breeding individuals or 'floaters', analyses were restricted to those individuals which were recorded breeding in the year of the flood. To determine how many ringed adults in the breeding population were still present in the study area after flooding, post-flood resighting rate (simply 'resighting rate' hereafter) were calculated by totalling the number of ringed adults resighted after three months of flooding and dividing by the number of all ringed adults present in the previous breeding season.

Wilcoxon signed rank tests were also used to compare the monthly population size and invertebrate density between the Cijiawan and the Yousheng; this was done using the total number of birds recorded on population surveys and the mean invertebrate density per sampling site, respectively, for each month in which the two sets of data (both non-normal) were recorded. Following Chiu *et al.* (2008), simple linear regression was used to investigate the relationships between log-transformed maximum flow, invertebrate density and dipper population size on each stream. Maximum flow was measured in the two month period prior to invertebrate sampling. Dipper counts were taken from population surveys in the same month as invertebrate sampling. All statistical tests were performed using SPSS version 19 (IBM Corp).

RESULTS

168 dippers were colour-ringed from 2011 to 2014 (120 on the Cijiawan, 48 on the Yousheng) and 75 were colour-ringed on the Cijiawan in 2003 and 2004. Across three main flood events caused by typhoons, 19 individuals were recorded making unusually long movements (i.e. greater than the mean territory length of 1045 m, Chen and Wang 2010) but remaining within the study area (Table 1, Fig. 1). 16 individuals moved from the lower Cijiawan to the lower Yousheng, and 3 birds moved from the lower to the upper Yousheng (Fig. 1). These movements represent 25.0%, 15.0% and 38.9% of the Cijiawan breeding population moving to Yousheng after flooding in 2004, 2012 and 2013, respectively (Table 1). All 19 individuals returned to their original territories within two months of the flood. The resighting rate of all ringed adults ranged from 86.7 to 88.2% three months after floods in 2004, 2012 and 2013. In 2014 when the flood was relatively small, only one bird (5.5% of the Cijiawan breeding population) was recorded making a long movement and the resighting rate was 92.6% (Table 1).

The mean (± SD) distance moved by individuals after floods (3766 ± 851 m) was significantly longer than that moved before (198 ± 136 m; n = 19, Z = -3.823, P < 0.001) and also longer than movements in non-typhoon years (440 ± 890 m; n = 15, U = 9.000, P < 0.001). If excluding the single individual which made a long-distance movement in 2014, the mean distance moved in non-typhoon years was only 214 ± 174 (n = 14). Furthermore, the dipper population size on the Cijiawan decreased during each flood event (only 8.3, 34.3, and 14.8% of the population in the previous month remained during the floods in 2004, 2012, and 2013, respectively), while that on the Yousheng remained stable or increased dramatically (100 and 213.3% of the previous month's population in 2012 and 2013; Fig. 2). By contrast, the dipper population on the Cijiawan was relatively stable in summer 2011 when no typhoon occurred and 92.6% remained during a small flood in 2014 (Fig. 2). Outside of flooding events, the population on the Cijiawan (31.5 ± 8.1) was always significantly greater than that on the Yousheng (20.3 ± 6.2; n = 27, Z = -4.824, P = 0.003).

The invertebrate density in the Cijiawan (395 ± 301 m^{-2}) was significantly higher than that in the Yousheng (246 ± 167 m^{-2}; n = 13, Z = -2.411, P = 0.016). There were significant negative correlations between discharge and invertebrate density in both streams (Cijiawan: n = 13, r^2 = 0.76, P < 0.001; Yousheng: n = 13, r^2 = 0.70, P < 0.001; Figs 3a-3b). However, the relationship between invertebrate density and population size differed between the two streams; there was a significant positive correlation in the Cijiawan (n = 13, r^2 = 0.47, P = 0.009) but no significant correlation in the Yousheng (n = 13, r^2 = 0.06, P = 0.497; Figs 3c-3d).

DISCUSSION

Brown Dippers moved significantly greater distances following flood events caused by typhoons than in the period prior to flooding and also in the equivalent period of non-typhoon years. Most movements were from the relatively large population on the Cijiawan, the main stream, to a significantly smaller population on its tributary, the Yousheng; the remainder were movements upstream within the Yousheng, all in 2012 when flooding was severe in both steams. All movements were temporary, with individuals returning to their original territories within two months of the flood. Other individuals disappeared from the Cijiawan during flood events, especially those living in the upstream section, and may have moved further upstream beyond the study area (Fig. S1) where the discharge is presumably smaller. However, in summer 2011 and 2014, the population on the Cijiawan was relatively stable and showed high site fidelity (only one individual made a long-distance movement), supporting the idea that unusually long movements were trigged by floods rather than seasonal movements. This is one of very few studies providing clear evidence of individual birds moving atypical distances to avoid the effects of typhoons. Others have described escape behaviour or the use of refugia during or after cyclones (White Jr *et al.*, 2005, Streby *et al.*, 2014) and similar behaviour has been described in freshwater fish (Koizumi *et al.*, 2013).

Invertebrate density was negatively correlated with the severity of flooding, supporting previous findings from the same catchment (Chiu *et al.*, 2008). However, there was no significant relationship between invertebrate density and the population size of dippers on the Yousheng, where invertebrate density was significantly lower than on the Cijiawan. This suggests that the movements of birds from the main stream to its tributary were not driven by flood-induced decreases in food availability. Instead, it may be that foraging behaviour is adversely affected by high water levels and this has been suggested in studies of the closely related White-throated Dipper *Cinclus cinclus*: the shallow riffles favoured for feeding become unavailable (Da Prato, 1981, O'Halloran *et al.*, 1990). Furthermore, because the drainage area of the Cijiawan is more than double that of the Yousheng, the former becomes turbid more quickly after heavy rainfall (Fig. S2) and this may be the cue causing dippers to adopt flood avoidance behaviour.

Surprisingly, resighting rates after floods were relatively high. The dipper population on the Cijiawan, for example, almost recovered in one or two months after flooding. It may be that the escape movements reported here increase the survival probabilities of dippers during these extreme discharges (Fig. S3). However, floods also decreased invertebrate density in the following breeding season, especially typhoons occurring late in the year (Hong *et al.*, 2016). A previous study showed that the breeding population size would decrease on the Cijiawan if invertebrate density was low, and some adults abandon reproduction and disappear (Hong *et al.*, 2016). This phenomenon suggests that the reduction in annual survival rates caused by flooding as reported in Chiu *et al.* (2013) does not happen immediately, but instead results from longer-term impacts mediated through food abundance.

The use of the Yousheng as a refuge during typhoons has important implications for the management of riverine ecosystems. While the lower population size and invertebrate density of this unprotected stream indicate that habitat quality is relatively poor for dippers and their prey, this part of the catchment may be crucial for its wildlife during flood events. These results support previous suggestions that catchment connectivity is vital for population persistence in freshwater species and that protection and management should operate at the catchment level (Davidson *et al.*, 2012, Koizumi *et al.*, 2013).

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Table 1. The number of breeding pairs of Brown Dippers in two streams and the number of individuals which made long-distance but temporary movements after floods. Each individual has a serial number, shown in Fig. 1. Post-flood resighting rate indicates the proportion of ringed adults in the breeding population which were present in the study area three months after each flood.

	Breeding pairs		From Cijiawan to	Movement within	Resighting rate (%)
	Cijiawan	Yousheng	Yousheng	Yousheng	after flooding
2004	12	-	6	0	88.2 (15/17)
2012	10	5	3	3	86.7 (13/15)
2013	9	6	7	0	88.0 (22/25)
2014	9	6	1	0	92.6 (25/27)

Figure legends

Figure 1. The movements of Brown Dippers after floods in (a) 2004, (b) 2012, and (c) 2013. Black circles show each individual's original territory; white circles show their temporary locations after floods. (d) The movements of Brown Dippers in summer 2014. Black circles show each individual's location in July; white circles show their locations in September 2014.

Figure 2. The monthly maximum discharge and population dynamics of Brown Dippers in the Cijiawan and Yousheng from June 2011 to December 2014 and several months in 2004.

Figure 3. The relationship between discharge and invertebrate density in the (a) Cijiawan and (b) the Yousheng from 2012 to 2014 (n = 13), and the relationship between invertebrate density and the number of Brown Dippers in (c) the Cijiawan and (d) the Yousheng from 2012 to 2014 (n=13).

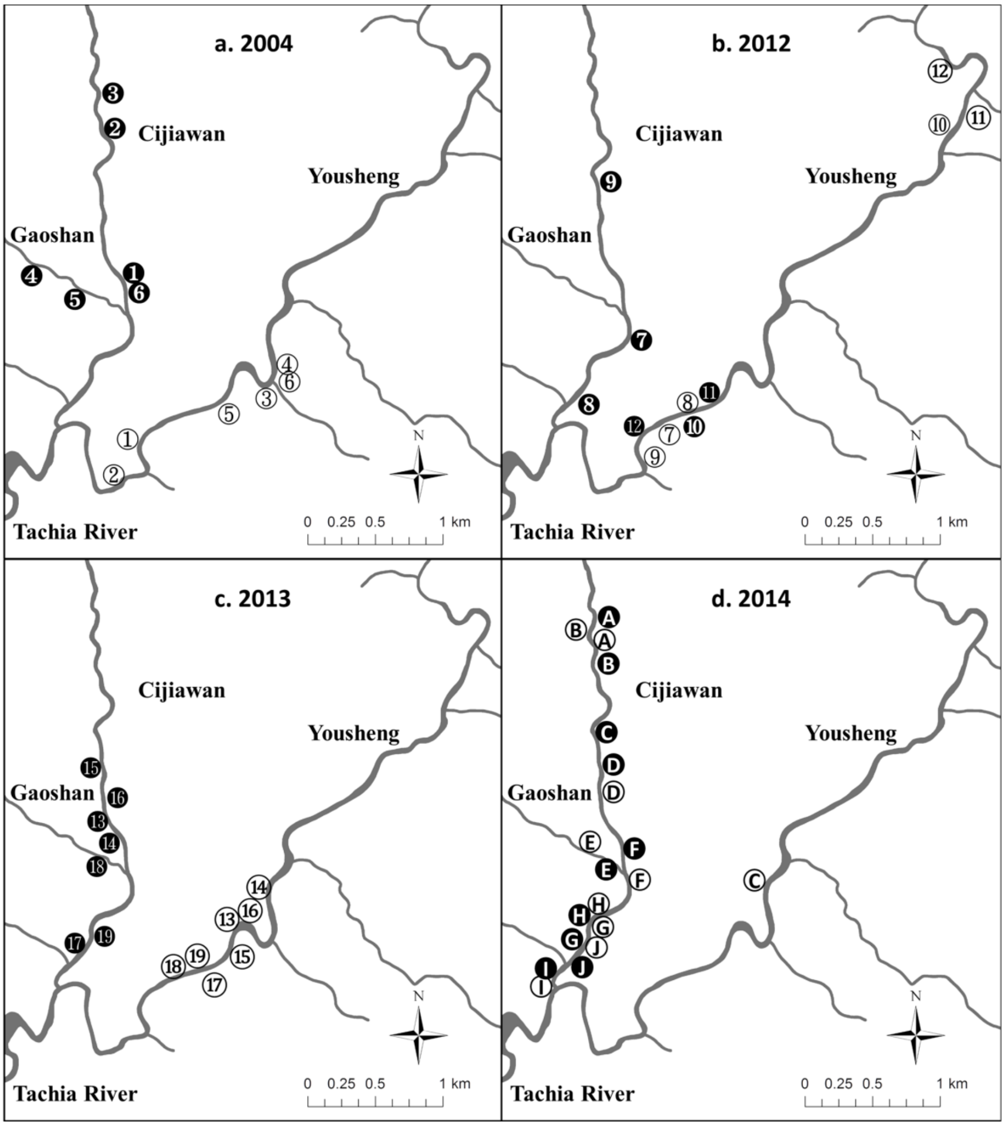
a. 2004
b. 2012
c. 2013
d. 2014
Cijiawan
Yousheng
Gaoshan
Tachia River
N
0 0.25 0.5 1 km

Figure 1.

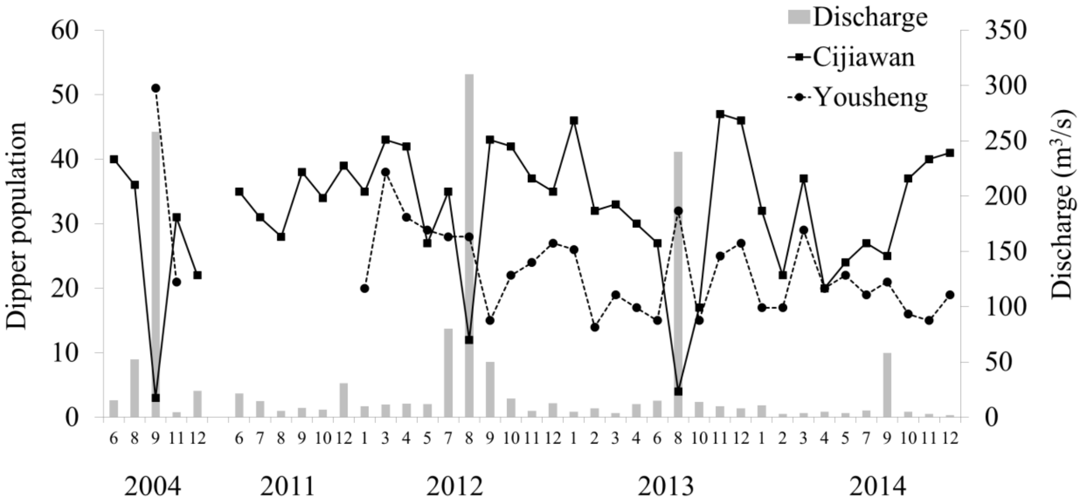
Discharge
Cijiawan
Yousheng
Dipper population
Discharge (m³/s)
60
50
40
30
20
10
0
350
300
250
200
150
100
50
0
6 8 9 11 12 6 7 8 9 10 12 1 3 4 5 7 8 9 10 11 12 1 2 3 4 6 8 10 11 12 1 2 3 4 5 7 9 10 11 12
2004
2011
2012
2013
2014

Figure 2.

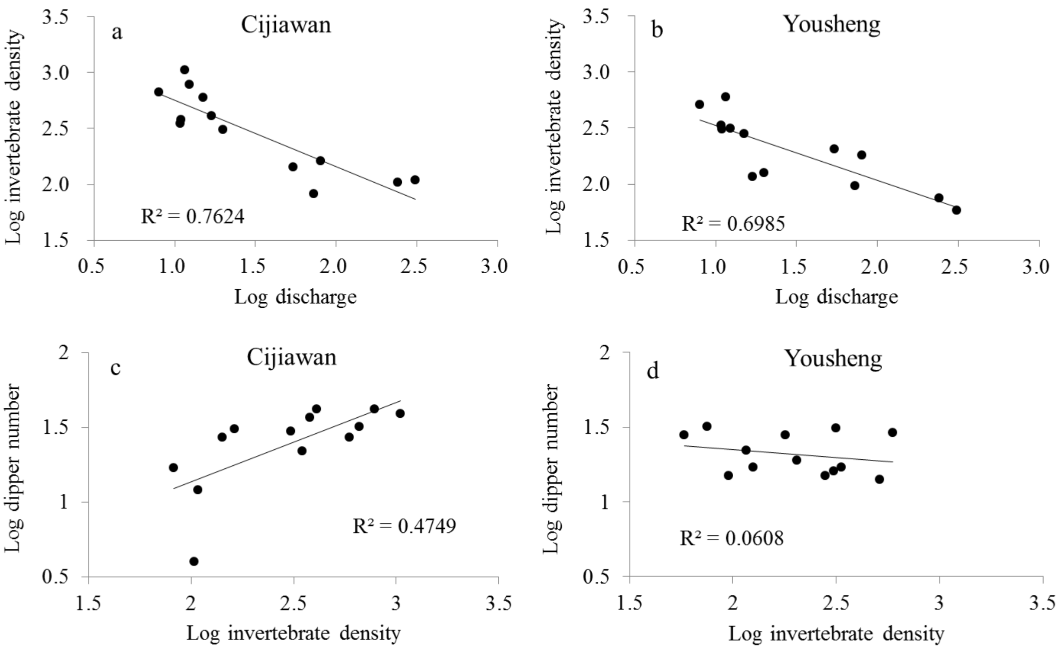
a
Cijiawan
Log invertebrate density
Log discharge
R² = 0.7624
b
Yousheng
Log invertebrate density
Log discharge
R² = 0.6985
c
Cijiawan
Log dipper number
Log invertebrate density
R² = 0.4749
d
Yousheng
Log dipper number
Log invertebrate density
R² = 0.0608

Figure 3.

Supplementary material

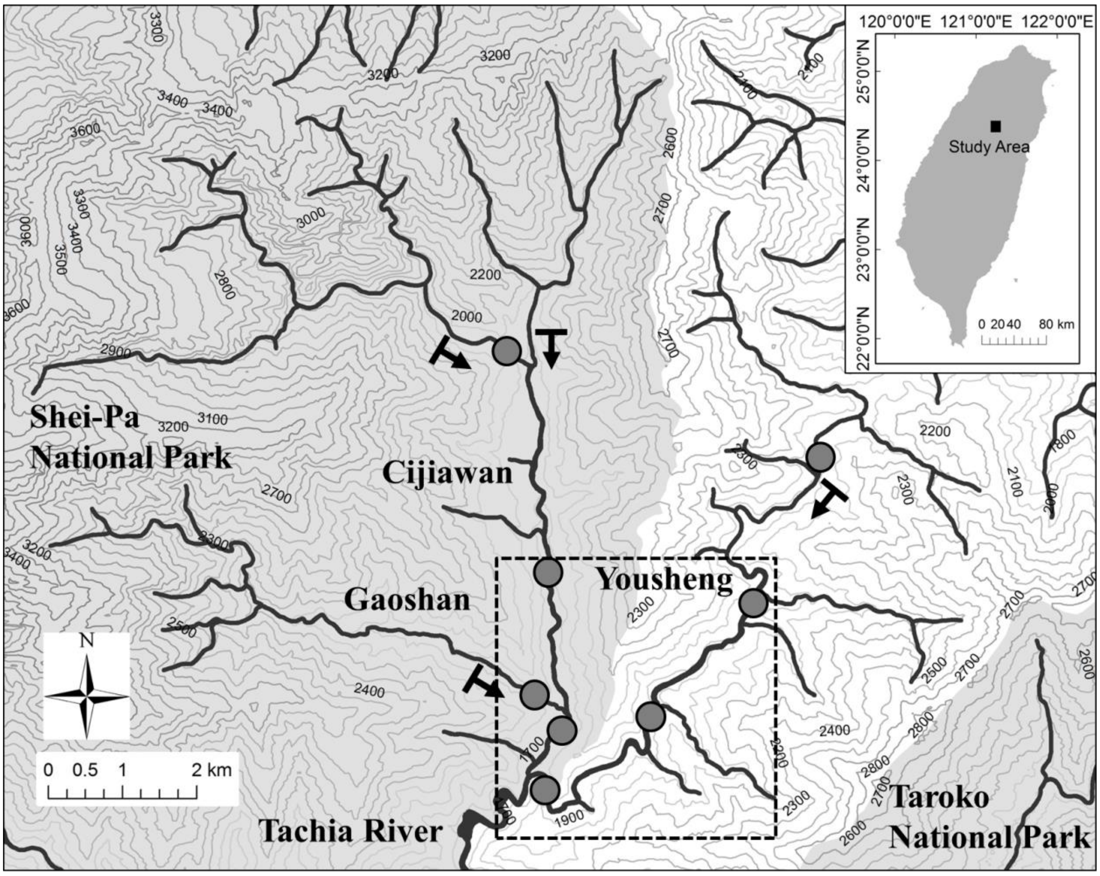

Figure S1

Map of the study area in central Taiwan. The drainage areas of the Cijiawan (including Gaoshan) and Yousheng are 77 and 31 km^2, respectively. Arrows indicate the range of Brown Dipper population surveys which started from the confluence of the Cijiawan and Yousheng. In addition to the streams we surveyed (Cijiawan, Yousheng, and Gaoshan), other tributaries were too small to support dippers in normal conditions. Circles are the eight invertebrate sampling sites. The contour lines give altitude in m. The shaded area shows the range of the Shei-Pa National Park.

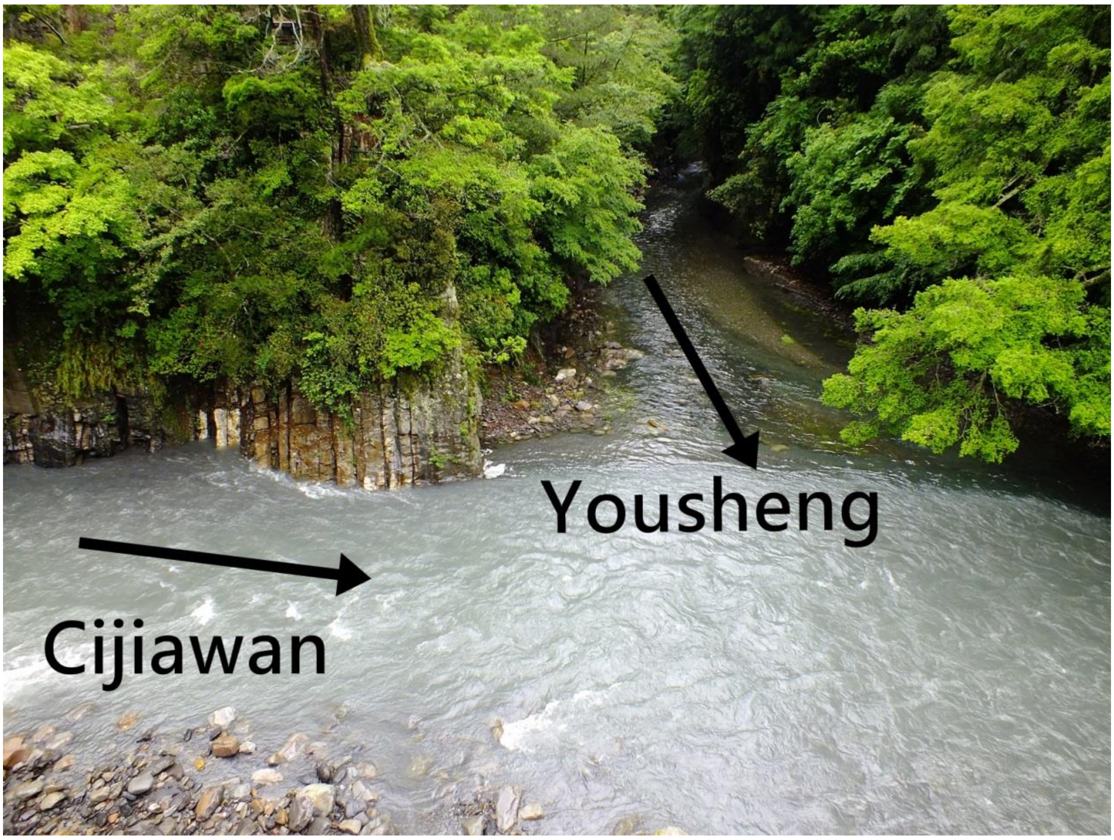

Figure S2

Following heavy precipitation, the Cijiawan became turbid faster than the Yousheng. Arrows indicate flow direction. (Photo by Shiao-Yu Hong)

Figure S3

The flooding which was caused by a typhoon in the middle section of the Cijiawan in August 2012. Typhoon floods are usually triggered by 1-3 days of intensive rainfall and then subside after two weeks. (Photo by Cheng-Hsiung Yang)