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Effects of flooding on avian top-predators and their invertebrate prey in a monsoonal Taiwan stream

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SUMMARY

1. The effects of flooding on top predators are poorly understood globally, but particularly in monsoonal streams. We therefore attempted to assess how inter-annual and intra-annual variations in flood magnitude affected an obligate riverine predator, the brown dipper (*Cinclus pallasii*), and its invertebrate prey, in the mountain Tachia River, Taiwan. Major flooding in one of the study years (2005) allowed an insight into the effects of abnormally large flows.
2. The abundance and biomass of insects, and the abundance of dippers, decreased steadily from 2003 to 2005 as flood magnitude grew, but then increased in 2006 when more typical discharge returned. Dipper abundance, insect abundance and insect biomass were all strongly positively inter-related, but negatively related to discharge. Insect biomass, rather than abundance, was more useful in predicting brown dipper abundance.
3. Aquatic insect composition fluctuated among sampling years, revealed by non-metric multidimensional scaling, and these fluctuations were also related to discharge. In turn, dipper abundance and the mean body size of aquatic insects declined with the shift in insect composition as flow increased.
4. These data illustrate how discharge fluctuations can have pronounced effects on top predators in streams, mediated in this case by fluctuating prey abundance. While contributions from bird movement, breeding performance and mortality were not clearly differentiated, our data reveal how dippers have strategies to accommodate varying discharge in river systems. We suggest that the effects of floods on dippers should be taken into account when using this group as indicators of river quality.

Keywords: aquatic insects, brown dipper, floods, flow regime, mountain streams

Introduction

The important linkages between aquatic and terrestrial food webs are increasingly recognized (Polis, Anderson & Holt, 1997). Not only riparian bird assemblages are subsidized by aquatic insect emergence (Nakano & Murakami, 2001), but some species also have evolved as top freshwater predators that prey directly on fish or riverine macroinvertebrates (Davis, 1982; Eguchi, 1990). As a result, birds can be affected both by habitat conditions in freshwaters, and by bottom-up processes that arise through prey abundance and availability. In turn, impacts on freshwater organisms can have important effects on the population dynamics of riparian birds.

In rivers, macroinvertebrates are the primary food for dippers of the genus *Cinclus* whose five species inhabit fast-flowing rivers on five continents (Ormerod, 1985; Ormerod, Efteland & Gabrielsen, 1987; Feck & Hall, 2004). As top predators in river systems, they potentially affect prey abundance (Ormerod & Tyler, 1991), but also are sensitive to

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variations in prey quantity and quality that occur both naturally and through aquatic habitat degradation (Ormerod *et al.*, 1991; Logie *et al.*, 1996; Buckton *et al.*, 1998). Indeed, these effects on dippers are so well defined that they have been widely proposed as indicator species in the monitoring and management of lotic systems (Sorace *et al.*, 2002; Strom, Ramsdell & Archuleta, 2002; Feck & Hall, 2004). However, such studies on the population dynamics and distribution of dippers rarely consider the effect of flooding (but see Price & Bock, 1983), which can be a major disturbance in river systems. There are very few studies that have considered how flood frequency, magnitude or timing affect riparian predators in general.

Fluctuations in flow are key features in the dynamics of macroinvertebrates (Lake, 2000; Wood, Agnew & Petts, 2000; Bêche, Mcelravy & Resh, 2006; Chaves *et al.*, 2008), and numerous studies have shown the impacts of flooding on macroinvertebrate numbers (Scrimgeour & Winterbourn, 1989; Olsen & Townsend, 2005; Suren & Jowett, 2006). Throughout the duration of flooding, macroinvertebrates are influenced by direct impacts of flow (Holomuzki & Biggs, 1999, 2000; Beckmann, Scholl & Matthaei, 2005) and by the indirect effects of substrate movement or changes in bedform (Cobb, Galloway & Flannagan, 1992). Floods reduce abundance and taxon richness of macroinvertebrates (Brewin, Buckton & Ormerod, 2000; Gjerløv, Hildrew & Jones, 2003), and cause condition-dependent alteration to community structure and functional organization (Nicole *et al.*, 2004; Snyder & Johnson, 2006). As a consequence, floods can exert considerable influence on macroinvertebrates, and in turn affect dippers.

In Taiwan, brown dippers (*Cinclus pallasii* Temminck) occur along clear streams, such as the Chichiawan. Since this stream is the last refuge of Formosan landlocked salmon (*Oncorhynchus masou formosanum*), aquatic insects have been well studied with respect to their assemblage structure and for water quality monitoring (Shieh & Yang, 2000; Kuo, Chiu & Shieh, 2004). In addition, previous observations have shown that brown dippers mostly feed on aquatic insect larvae (Eguchi, 1990). Here, we assess the distribution and abundance of brown dippers in this same river system. We hypothesized that a low abundance of brown dippers represented their response to high-flow events mediated through their close trophic linkage with aquatic insects. By surveying the fluctuations of brown dipper population and the biomass/abundance of aquatic insects during a prolonged period of varying discharge, we expected that support for this hypothesis would arise from close relationships among flood pattern, insect biomass or numbers, and the abundance of brown dippers.

Methods

Study area and brown dipper monitoring

The study was conducted in the upstream drainage of the Tachia River in central Taiwan, including Chichiawan Stream and Gaoshan Stream (Fig. 1), with a catchment area of 77 km^2 and an altitudinal range of 1700–2000 m. The rural catchment is occupied by the Shei-Pa National Park, a popular tourist area that also contains fruit and vegetable farms.

Because the spring rainy season and the following summer typhoons cause floods, discharge is recorded

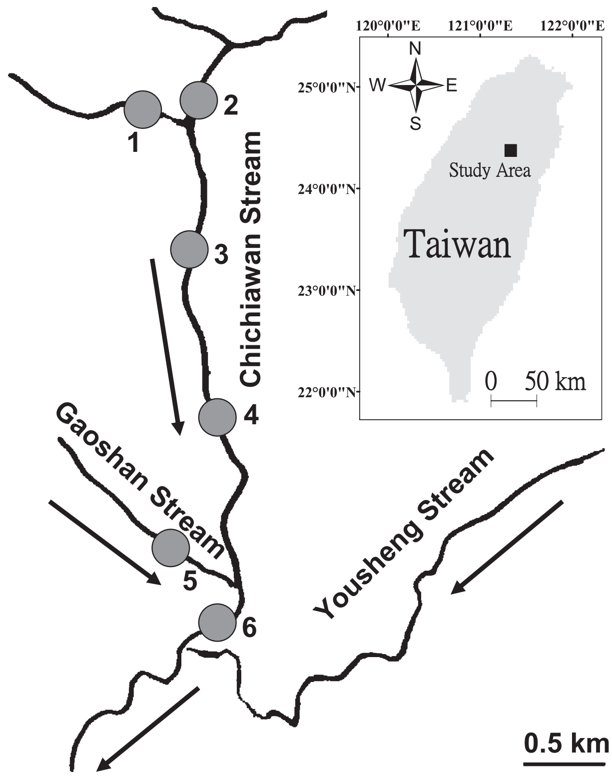

Fig. 1 Map of upstream drainage of the Tachia River and location of six sampling sites in central Taiwan. Arrows indicate flow directions of streams.

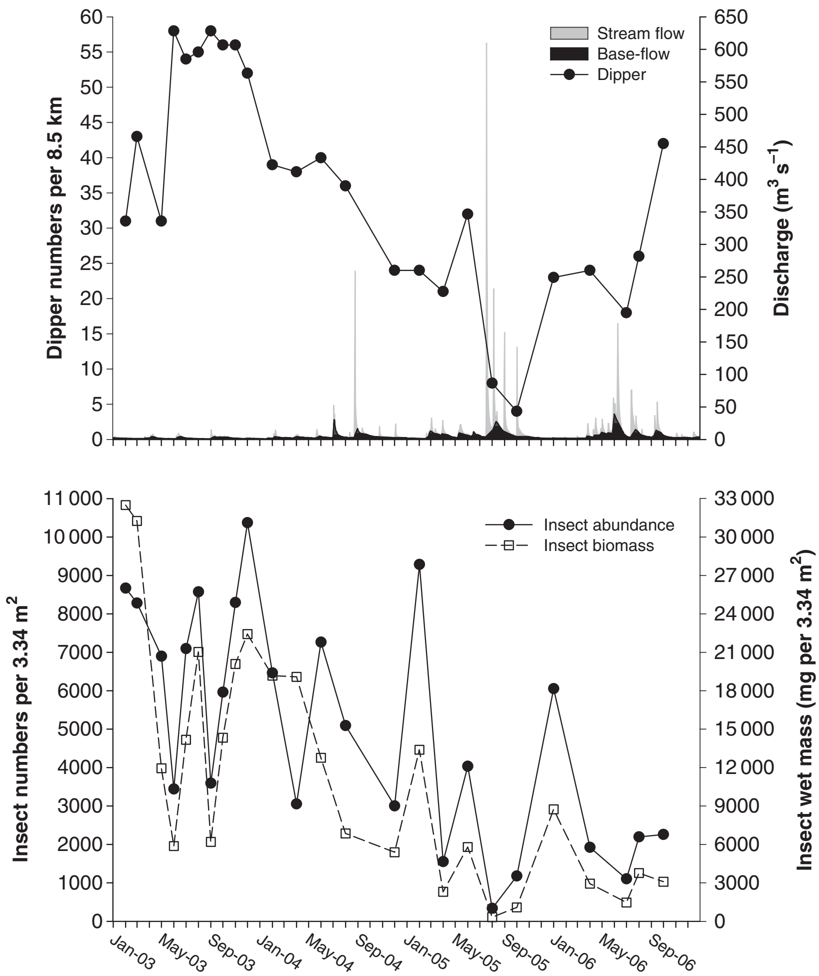

Fig. 2 Daily discharge of stream flow and base-flow, abundance of dippers along the stream bank and abundance and biomass of aquatic insects per sampling unit in the upstream drainage of the Tachia River between February 2003 and October 2006.

at a site downstream of the confluence of Chichiawan Stream and Yousheng Stream by the Taiwan Power Company. Stream flows with discharge more than 10 $m^3 s^{-1}$ were considered floods (Suren & Jowett, 2006), given a mean base-flow of 4.9 $m^3 s^{-1}$ and calculated using 'BFLOW filter' of the Web-based Hydrograph Analysis Tool (WHAT) system (Lim *et al.*, 2005) (Fig. 2).

Six sampling sites were selected for macroinvertebrate monitoring to encompass the whole survey area for brown dipper (Fig. 1), stretching 7 km along Chichiawan Stream from its confluence with Yousheng Stream and 1.5 km along Gaoshan Stream from its confluence with Chichiawan Stream. We used binoculars to monitor dipper abundance on 25 occasions from February 2003 to October 2006, and censuses were made on foot from the stream edge. To avoid recounting birds, we ignored individuals that flew ahead of us, expecting territorial individuals characteristically to 'double-back' when pushed to the ends of their territory.

Sampling protocol for macroinvertebrates

Benthic aquatic insects were sampled using a Surber sampler (area = 30.48 cm × 30.48 cm, mesh size = 250 μm) in the adjacent occasions as the dipper surveys. Six samples were taken from each site on each sampling occasion at randomly selected locations in runs and riffles. A total of 36 samples at each sampling time were defined as one sampling unit for subsequent analyses. Samples preserved in 70% ethanol in the field were brought back to the laboratory, where they were elutriated to separate organic matter from inorganic material. All aquatic insects were identified to genus or species (Kang, 1993; Merritt & Cummins, 1996; Kawai & Tanida, 2005) expect for Chironomidae, which were classified into

Tanypodinae and non-Tanypodinae only. Finally, we recorded total number of individuals and wet weight of organisms in each taxon per sampling unit.

Data analyses

Linear regression (PROC REG, SAS Institute, 1999) was used to check for linearity of relationships between dipper abundance as the dependent variable and monthly mean discharge of stream flow, abundance and biomass of aquatic insects as independent variables. We also examined relationships between the abundance and biomass of aquatic insects and monthly mean discharge. Statistical significance was determined at alpha = 0.05. In addition, we computed Akaike's Information Criteria (AIC) for all possible subsets of multiple regression models (PROC REG, SAS Institute, 1999) to estimate the potential influence of monthly mean stream-flow discharge (x_1) plus abundance (x_2) and biomass (x_3) of aquatic insects on dipper abundance (y). AIC is a likelihood-based tool for optimal model selection determined by the lowest AIC (Akaike, 1974). All variables were $\log_e$-transformed for simple and multiple regression analyses.

The subsequent analyses were exploited to examine relationships among change in insect assemblage structure, discharge, dipper abundance and mean body size (ratio of biomass to abundance) of aquatic insects over the sampling duration. First, we used non-metric multidimensional scaling (MDS, Clarke & Warwick, 2001) with a Bray-Curtis similarity matrix on $\log_e(X + 1)$-transformed taxon abundance data by PRIMER software (Clarke & Warwick, 2001) to ordinate all sampling units. In our MDS plot in two-dimensional space, the stress value less than 0.2 indicated significance (Clarke & Warwick, 2001). Secondly, scores along two MDS axes of 25 sampling units throughout the study period were separately related to $\log_e$-transformed stream flow using linear regression, and $\log_e$-transformed dipper abundance and mean body size of aquatic insects were also separately regressed against the axis with higher prediction for stream flow. Again the alpha value was set at 0.05.

Results

Daily flow discharges varied greatly during the study period of 4 years, ranging from 1.2 to 609.7 $m^3 s^{-1}$. Yearly mean discharges increased from 2.6 in 2003, with only one flood occurring throughout the whole year, to 14.5 $m^3 s^{-1}$ in 2005 (the year with the most frequent flood events: 112) and then decreased to 10.8 $m^3 s^{-1}$ in 2006. Peak discharge and the number of floods in 2005 were the largest in local discharge history. Yearly mean base-flow increased from 2.2 to 5.9 $m^3 s^{-1}$ between 2003 and 2005, with base-flow discharge of 5.9 $m^3 s^{-1}$ continuing into 2006.

From 2004 to 2006, spring discharges and flood peaks were obviously lower than summer discharges and the biomass and abundance of aquatic insects decreased with summer floods (Fig. 2). The abundance of aquatic insects recovered more rapidly than their biomass after floods, although the biomass even gradually declined from 2003 to 2006. The abundance of brown dippers also decreased through time up until 2006 (Fig. 2).

Linear regression analyses revealed significant negative relationships between dipper abundance and discharge ($P < 0.05$), with greater run-off accompanied by lower dipper abundance (Fig. 3). There were significant positive relationships between dipper abundance and the abundance/biomass of their aquatic insect prey (Fig. 3). Insect prey was also significantly related to flow discharges (Fig. 4). Based on the coefficient of determination (r^2), insect biomass appeared to be a better predictor for dipper abundance than insect abundance (Fig. 3). This was further confirmed by multiple regression models; according to the AIC criterion, the model using insect biomass alone appeared to be optimal (Table 1).

From the MDS plot (Fig. 5), insect assemblage structure changed from 2003 to 2005, and shifted back in 2006. This structural shift seemed to correspond more to axis 1 than to axis 2. During this period, discharge explained significant variation along MDS axis 1, but not axis 2 (Fig. 6). In turn, dipper abundance and the mean body size of aquatic insects were both negatively related to MDS axis 1 (Fig. 7).

Discussion

Response of dippers to flow regime

In combination, these data reveal how severe flood conditions, associated with disproportionately large effects during monsoons or typhoons, affect not only

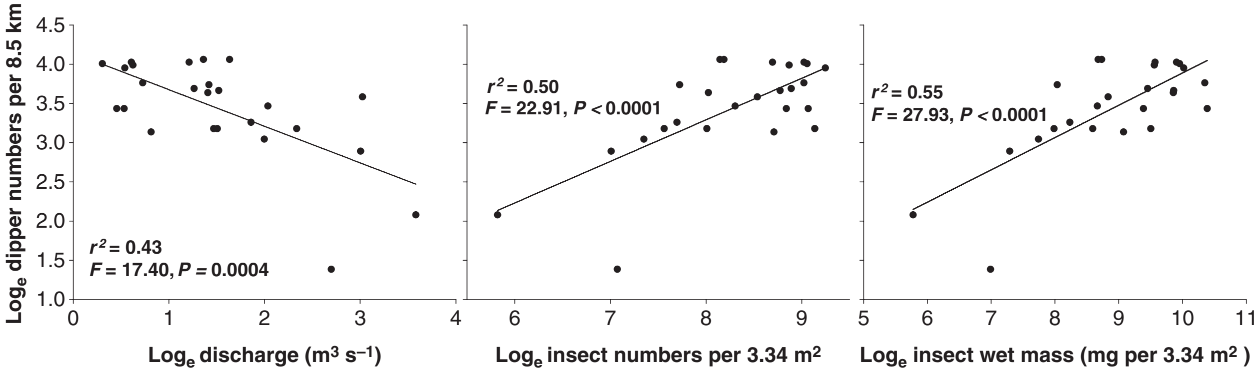

Fig. 3 Abundance of brown dippers along the stream bank in relation to mean monthly discharge of stream flow, abundance and biomass of aquatic insects per sampling unit (n = 25).

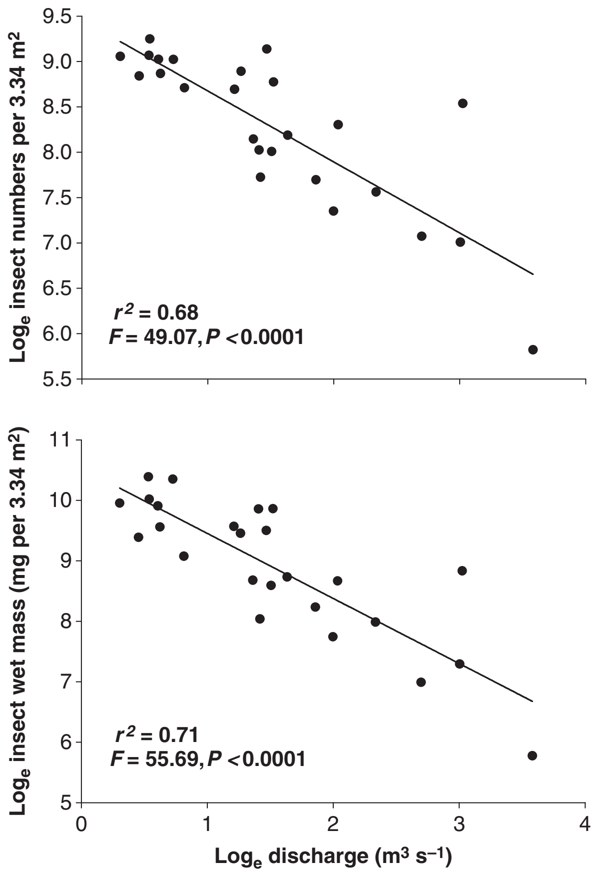

Fig. 4 Abundance and biomass of aquatic insects per sampling unit in relation to monthly mean discharge of stream flow (n = 25).

aquatic invertebrates, but can have cascading effects also on predatory organisms at higher trophic levels. While relationships among dippers, their prey and discharge appeared clear from our study, the underlying processes were not investigated. Several mechanisms are possible, and include bird movement into adjacent tributaries, reduced adult survival during floods, and impaired breeding. Anecdotal evidence supports at least two of these hypotheses.

Table 1 All possible subsets of multiple regression models on relationships of dipper abundance (numbers per 8.5 km along the stream bank) with monthly mean discharge of stream flow (m^3 s^{-1}), abundance (numbers per 3.34 m^2) and biomass (mg wet mass per 3.34 m^2) of aquatic insects

Variables in model	F	P	r^2	AIC
Discharge	17.40	0.0004	0.43	−34.11
Insect abundance	22.91	<0.0001	0.50	−37.31
Insect biomass	27.93	<0.0001	0.55	−39.90
Discharge and insect abundance	11.72	0.0003	0.52	−36.16
Discharge and insect biomass	13.57	0.0001	0.55	−38.11
Insect abundance and biomass	13.37	0.0002	0.55	−37.92
Discharge, insect abundance and biomass	8.63	0.0006	0.55	−36.12

AIC, Akaike's Information Criteria.

First, banded dippers found outside the study area during flood periods suggested lateral movement to adjacent, smaller tributaries or other rivers. Specifically, eight (banded) dippers were located in a nearby, less-disturbed stream after flooding caused by typhoon 'Ali' in August 2004. After the August typhoons of 2004 and the July typhoon of 2005, at least four and three individuals, respectively, returned to their original breeding sites the following January. Elsewhere, floods have been

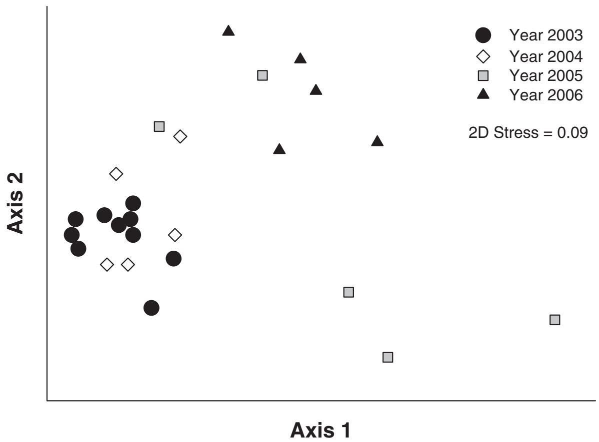

Fig. 5 MDS ordination of 25 sampling units based on Bray-Curtis similarities for log (X + 1)-transformed abundance of aquatic insects.

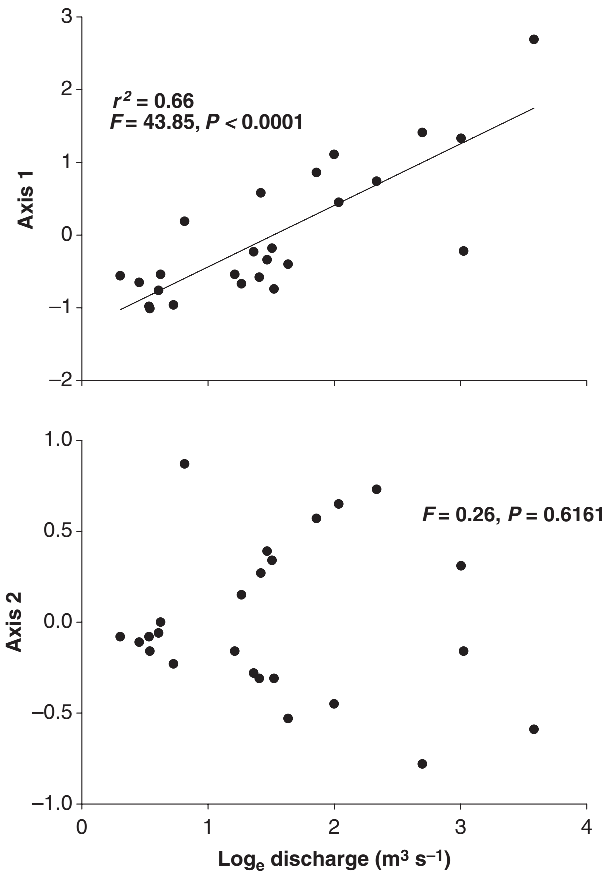

Fig. 6 Scores of sampling units along two MDS axes in relation to monthly mean discharge of stream flow (n = 25).

reported to have a range of behavioural effects on dippers that include immediate behavioural change, such as alterations in feeding, diving and prey use

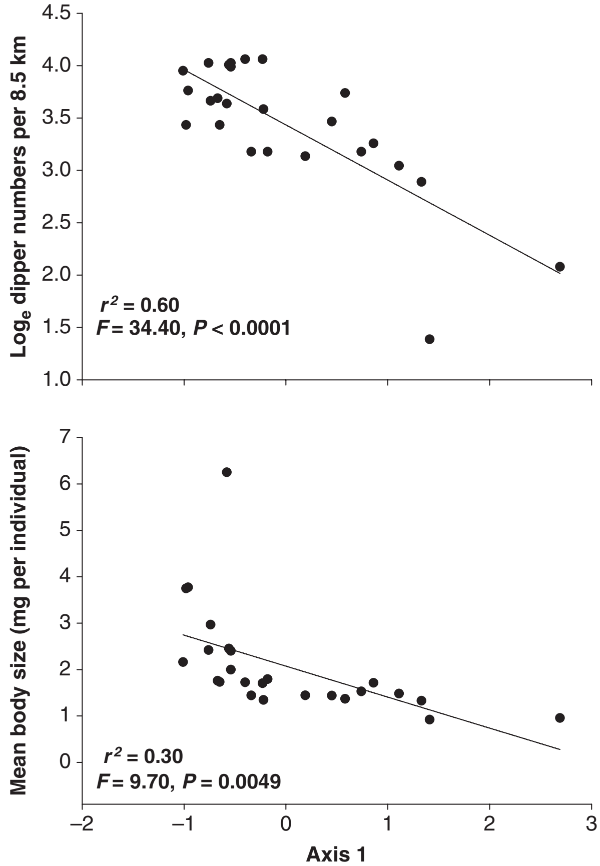

Fig. 7 Mean body weight of aquatic insects per sampling unit and dipper abundance along the stream bank in relation to scores of sampling units along MDS axis 1 (n = 25).

(Da Prato, 1981; Taylor & O'halloran, 2001), or altitudinal migrations into or away tributaries (Morrissey, 2004; Morrissey, Bendell-Young & Elliott, 2004).

Secondly, some variations in breeding performance between years with contrasting discharge were detected. Each year, dippers in Taiwan breed in January–April before the typhoon season of July–October. In January–April of 2003 and 2004, 10 and 12 nests with 12 and 15 fledglings, respectively, were located in the study area. In 2005 only six nests with four fledglings were observed, with nesting success remaining low into 2006 (eight nests with 13 fledglings). Although these effects were probably of too short a duration to reduce population size, over longer time scales, reduced adult and first-year survival in dippers have been linked to winter flooding (Clobert, Lebreton & Marzolin, 1990; Wilson, 1996). In Colorado, high run-off in spring was implicated in reduced numbers of American dippers in winter (Price & Bock, 1983). Whatever the exact mechanism, all of these results indicate that dippers are at risk of adverse effects under increased flow, and must have a range of short-term (i.e. proximate) or longer-term (ultimate) strategies to maintain survival.

Relationships between dippers and aquatic insects

Aquatic insects are recognized as an important factor influencing the abundance of dippers, for which they are major prey. This is true of brown dippers, and aquatic insects, dominate the prey of brown dippers in our study area and elsewhere (Y. H. Sun, unpubl. data; Buckton & Ormerod, 2008) They also constitute the majority of macroinvertebrates in our streams wherever waters are clear. Previous reports have illustrated that the diet of dippers elsewhere is formed dominantly from aquatic insects (Ormerod, 1985; Ormerod & Tyler, 1991; Tyler & Ormerod, 1992). With lower food supply, dipper presence or abundance decreases (Ormerod *et al*., 1986; Tyler & Ormerod, 1992; Feck & Hall, 2004), while territory area increases in dippers and other birds (Kodric-Brown & Brown, 1978; Hixon, Carpenter & Paton, 1983; Vickery, 1991). These effects could well explain the patterns observed here following flooding.

Interestingly, dipper abundance in our streams was more strongly related to the biomass than the abundance of aquatic insects, and a shift in the assemblage structure towards smaller mean body-sizes co-occurred with a decrease in dipper abundance. From 2003 to 2005, further observations revealed a steady decline of dippers as prey biomass fell, and this effect was larger than that caused by prey abundance (Fig. 2). Such effects might be explained by a range of factors including prey selection and energetic demands. Thus, outside the breeding season, dippers often take small prey such as Simuliidae and Baetidae (Ormerod & Tyler, 1991) However, large prey such as trichopteran larvae become particularly important during the breeding season, and only they can support sufficient transfer to satisfy the energy demands of growing nestlings (Ormerod, 1985; Ormerod *et al*., 1987; Feck & Hall, 2004). Large prey, in our streams as elsewhere, were a key determinant of benthic biomass (see below).

Flooding effects on aquatic insects

The biomass and abundance of aquatic insects both responded to stream discharge during this study: aquatic insects were significantly reduced in response to floods. However, flooding effects on macroinvertebrates could be short-term, and most evidence suggests they can recover rapidly (Fisher *et al*., 1982; Hendricks, Willis & Snyder, 1995; Scarsbrook, 2002). The high resilience of many members of the benthic fauna contributes to the evolutionary adaptation of their life cycles, and to specific traits that accommodate flood effects (Lytle & Poff, 2004). As a rule, r-selected taxa, that is those characterized generally by short life-span and small body size (Pianka, 1970), can overcome more rapidly the effects of flood instability through their strong reproductive ability. In our results, the abundance of aquatic insects recovered rapidly as flow declined in 2005, but biomass did not return fully to pre-flood levels in part because of subsequently reductions during additional severe floods (Fig. 2). Furthermore, a shift in assemblage structure of aquatic insects with increased discharge during the sampling period appeared to result in a relative decline of taxa with large body sizes. Under the unstable conditions caused by severe floods, among which the largest departures from seasonally normal flows are unpredictable, opportunistic insect taxa can become numerically dominant in stream invertebrate communities (Wallace, 1990).

Overview

In the past two decades, the use of dippers as indicators for habitat quality has received much attention in Europe (Ormerod *et al*., 1991; Logie *et al*., 1996; Sorace *et al*., 2002) and North America (Strom *et al*., 2002; Feck & Hall, 2004; Henny *et al*., 2005). However, to our knowledge, there have been no related reports in Asia. The use of dippers as biological indicators of stream invertebrate quality or general river quality is based on the fundamental relationship between this bird and its macroinvertebrate prey. In the present study, flood-induced fluctuations in abundance and biomass of aquatic insects and shifts in their assemblage structure significantly influenced the abundance of brown dipper. We suggest that it is essential to take the impact of inter-annual and intra-annual fluctuations of mountain streams into account when using dipper abundance to assess habitat quality. This is of great importance in areas like Taiwan, where snowmelt or typhoons cause flow variations that might have catastrophic effects on stream insects over very short time scales.

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