Prey Selection by Breeding Brown Dippers *Cinclus pallasii* in a Taiwanese Mountain Stream

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Ming-Chih Chiu, Mei-Hwa Kuo, Chyng-Shyan Tzeng, Cheng-Hsiung Yang, Chao-Chieh Chen, and Yuan-Hsun Sun (2009) Prey selection by breeding Brown Dippers *Cinclus pallasii* in a Taiwanese mountain stream. *Zoological Studies* **48**(6): 761-768. Optimal foraging theory predicts that prey selection by breeding birds is governed by tradeoffs among diverse prey types with different energy gains per unit energy expended. This is particularly so in central-place foragers such as dippers (Cinclidae), which must provision nest-bound young using prey gathered along a linear habitat. In this study, we examined changes in the dietary composition of nestling Brown Dippers *Cinclus pallasii* over the course of the nestling period in the mountainous Dajia River of central Taiwan. Prey preference was associated with prey morphological traits: fish and trichopterans, with relatively large body sizes, were the preferred prey items, while smaller prey such as ephemeropterans, plecopterans, and dipterans were least preferred. However, the nestling dietary composition significantly shifted over the 1st 1/2 of the nestling period, with the proportion of large prey and daily maximum prey size increasing as the nestlings grew. Our data suggest that the increasing energy demands of the nestlings are responsible for the increase in prey size, while nestling gape-size possibly limited the maximum prey size early in the nestling period. These results bear a striking similarity to data reported for other dipper species, implying identical constraints and strategies in nest provisioning. http://zoolstud.sinica.edu.tw/Journals/48.6/761.pdf

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Cost-benefit tradeoffs in delivering prey to nestlings are dynamic and depend on both intrinsic and extrinsic factors. For example, differences in dietary compositions of nestlings result not only from changes in prey availability (Naef-Daenzer et al. 2000) but also from sexually dimorphic traits that lead to differences in the foraging abilities of male and female parents (Kennedy and Johnson 1986). Moreover, begging behavior, physiological demands, and nutritional requirements of nestlings can also affect parental foraging strategies (Moser 1986, Haggerty 1992, Slagsvold and Wiebe 2007, Budden and Wright 2008, Bujoczek and Ciach 2009).

The 5 species of dippers (*Cinclus*) in the world are top predators that inhabit fast-flowing rivers on 5 continents (Voelker 2002). As obligate predators in river systems, their predation presents a potential control on freshwater prey (Ormerod and Tyler 1991); however, they are also sensitive to bottom-up effects from both natural and anthropogenic influences on prey availability (Ormerod et al. 1991, Logie et al. 1996, Buckton et al. 1998). In fact, dippers appear to be so sensitive

to these impacts that they are considered to be indicators of habitat quality in the monitoring and management of lotic systems (Sorace et al. 2002, Strom et al. 2002, Henny et al. 2005). Numerous studies demonstrated strong linkages between dippers and river organisms which comprise their diet (e.g., Taylor and O'Halloran 2001, Buckton and Ormerod 2008), their distribution in relation to prey composition (e.g., Feck and Hall 2004), and dynamic interactions between the occurrence and varying prey abundances (e.g., Chiu et al. 2008). Indeed, because of their occurrence along rivers, where nest provisioning is limited by the need to repeatedly collect and transport prey along this linear habitat, dippers provide an excellent model for which to investigate interactions among prey selection, prey availability, and the tradeoffs that adult birds face when feeding nestlings (Ormerod et al. 1987).

Previous studies used prey size and availability to characterize prey selection (e.g., Rudolph 1982, Radford and du Plessis 2003, Sundell et al. 2003). Since large macroinvertebrates typically exist at low population densities (Marquet et al. 1990, Strayer 1994, Schmid et al. 2000, Principe 2008), tradeoffs between prey size and prey abundance influence the diets of both adult and nestling birds (Ormerod 1985, Ormerod et al. 1987, Santamarina 1993). In some species, for example, nestlings are fed progressively larger prey items as they grow, suggesting that nutritional requirements of the nestlings are a primary determinant of adult foraging strategy (Moser 1986, Slagsvold and Wiebe 2007). In the White-throated Dipper *C. cinclus*, such effects were demonstrated using fecal analysis (Ormerod 1985, Ormerod et al. 1987). Further dietary shifts with age were also shown in the ontogeny of feeding behavior of recently fledged dippers as foraging proficiency increased (Yoerg 1994 1998). Prey selection is also affected by other prey traits, such as handling costs and vulnerability to capture. Therefore, it is necessary to integrate these multiple traits and constraints into a single behavioral framework in order to completely understand foraging decisions.

Cijiawan Stream, a clear stream in central Taiwan inhabited by Brown Dippers *Cinclus pallasii* Temminck, is the last refuge of an important fish species, the Formosan landlocked salmon *Oncorhynchus masou formosanus* (Jordan and Oshima). The macroinvertebrate community of this stream, therefore, is well-studied due to overall habitat monitoring in an effort to conserve this salmon, making it an ideal location for further studies on dippers (Shieh and Yang 2000, Kuo et al. 2004). Here, Brown Dippers potentially compete with Formosan landlocked salmon for macroinvertebrates, i.e., their major food (Kuo 2008). In this study, we examined the relationship between prey selection of Brown Dippers and the life history traits of several prey taxa in the Cijiawan Stream system, assessing also how the prey selection changed with nestling age. According to previous studies on other dipper species (Ormerod 1985, Ormerod et al. 1987), we hypothesized that: (1) dipper adults should show a higher preference for larger prey to provision their nestlings and (2) the prey size and composition of the nestling diet should shift over the course of at least the 1st 1/2 of the nestling period as the nestling energy demands increase. To test these hypotheses, we observed and quantified vertebrate and invertebrate prey delivered to nestling dippers during a single breeding season. We also conducted surveys on habitat availability of common prey types.

MATERIALS AND METHODS

Study area and Brown Dipper observations

The study was carried out in an upstream drainage of the Dajia River in Taiwan (Fig. 1), with a range of elevation of 1700-2000 m and an area of about 77 km^2 (Chiu et al. 2008). In this river system, we mist-netted and color-banded breeding pairs of Brown Dippers. Nests were located and observed every 2-3 d during incubation to determine the date of hatching, i.e., the 1st day of nest provisioning. Observations were typically made for 6-8 h with a 20× spotting scope from a distance of at least 20 m from sunrise to sunset during Feb. to Apr. 2004. We recorded the types and body sizes of prey delivered, measured by comparison to the adult dipper bill length which was a known size. Based on the fact that fledging typically occurred at 23-25 d post-hatching, the diet of the dippers during the nestling period was divided into 2 periods based on nestling age: 1-13 and 14-25 d. Four prey categories could be identified: dipterans, ephemeropterans/ plecopterans, trichopterans, and fish. Amphibian larvae rarely occurred, and unsystematically, and so we excluded them from further analysis.

Sampling protocols for macroinvertebrates and fish

Aquatic insects were sampled with a Surber sampler (30.48 × 30.48 cm, with a mesh size of 250 μm) at 4 sites near or in dipper territories (Fig. 1). Six replicates, defined as 1 sampling unit for subsequent analyses, were taken from each site in Feb. or Apr. 2004 with respect to the nestling period of each nest. These replicates were sampled randomly in runs and riffles, and then preserved in 70% ethanol in the field. Although Brown Dippers forage in all stream habitats, including marginal habitats, runs and riffles dominate the stream habitats available to foraging dippers during breeding, so the Surber samples should closely reflect prey availability. In the laboratory, we used elutriation to separate the organic matter from inorganic matter. Except for the Chironomidae (which were classified into the Tanypodinae and non-Tanypodinae), all aquatic insects were identified to genus or species according to published keys (Kang 1993, Merritt and Cummins 1996, Kawai and Tanida 2005). We recorded the numbers of organisms in each taxon per sampling unit to provide the density of each taxon, which was in turn combined to give the total abundance of the 3 invertebrate categories that could be recognized in prey carried by dippers, i.e., dipterans, ephemeropterans/plecopterans, and trichopterans.

Three fish species, namely *Formosania lacustre* (Steindachner), *Oncorhynchus masou formosanus*, and *Onychostoma barbatula* (Pellegrin), were counted during the daytime in late May to early June 2004 by snorkeling surveys (Chung et al. 2007, Chung et al. 2008). Water clarity for visual censuses was consistently good in the stream. The streams were divided into sections, with dams or abrupt changes in the channel gradient forming the upper and lower boundaries of each section. Each snorkeling
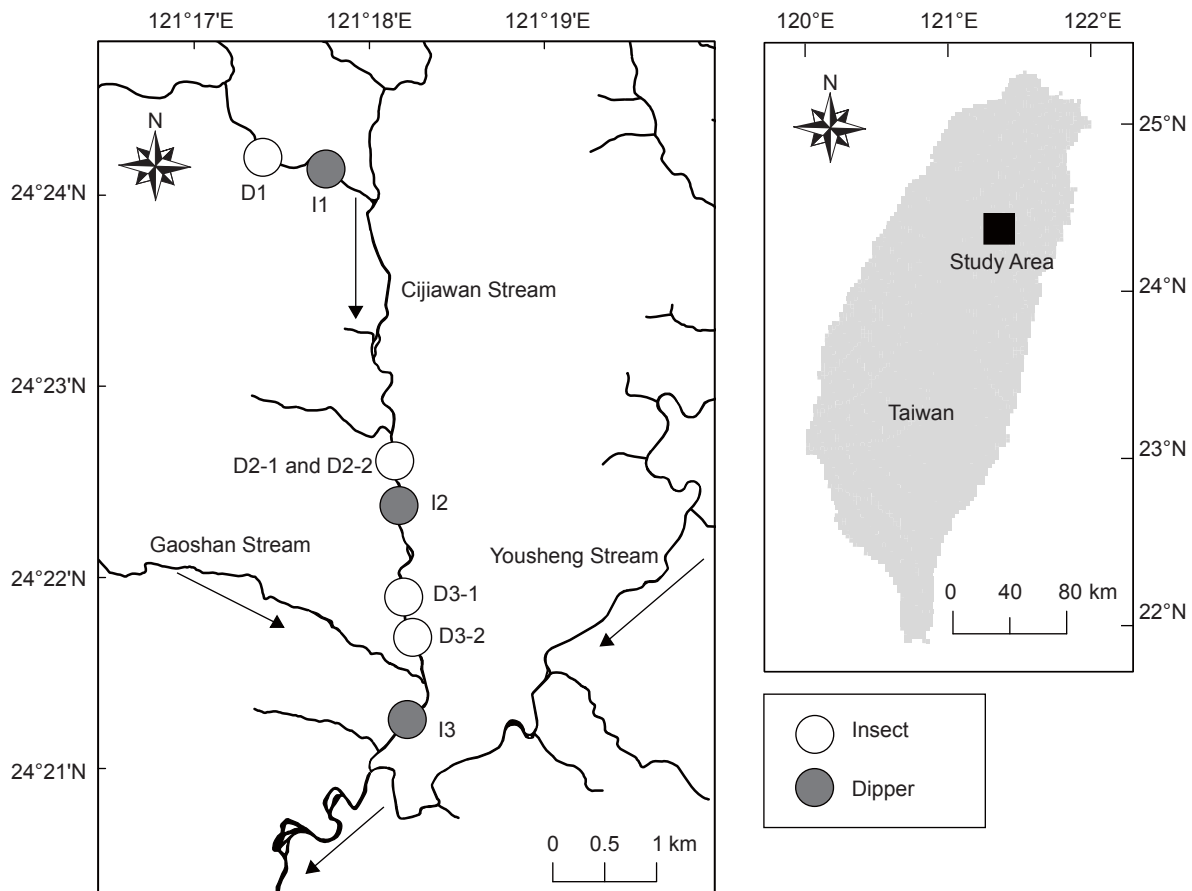

Fig. 1. Map of the upstream drainage of the Dajia River, showing locations of 5 nests and their corresponding sites for sampling aquatic insects in central Taiwan from Feb. to Apr. 2004 (I1 for D1, I2 for D2-1 or D2-2, and I3 for D3-1 or D3-2). Arrows indicate the direction of flow of the streams.

survey began at the downstream end of a section (~300 m long) and was completed in a single upstream pass. During each count, 2 trained snorkelers, who moved parallel to each other, swam slowly upstream along the middle of the channel and counted fish outwards and towards the bank nearest to them to avoid double-counting. Snorkelers recorded the numbers of each fish species on slates and paused periodically at the end of a section to relay the information to a data recorder on the bank. Density data for *F. lacustre*, *Onc. masou formosanus* (2-8 cm in length), and *Ony. barbatula* (< 15 cm in length) were combined into a total abundance of the fish category for each section for subsequent analyses.

Data analyses

Jacobs's electivity index (*E*) of Brown Dippers at each nest for each prey category was calculated following the formula given below (Jacobs 1974):

$$E_i = \frac{(R_i - P_i)}{(R_i + P_i - 2R_iP_i)} \; ;$$

where R_i is the proportion of prey items of category *i* in the nestling diet at a given nest, and P_i is the proportion of the abundance of category *i* in the corresponding stream habitat. Negative values (-1.0-0) indicate avoidance of a given prey type, whereas positive values (0-1.0) indicate its preference. Values of Jacobs's electivity index are categorized into no preference as 0 ± 0.15, slight preference or avoidance by ± 0.16-0.40, moderate preference or avoidance by ± 0.41-0.80, and strong preference or avoidance by ± 0.81-1.00 (Morrison 1982, Loiselle and Blake 1990, Riehl and Adelson 2008).

We performed Friedman's test (PROC RREQ, SAS Institute 1999) on the effect of prey category on the proportion of items in the diet. Rank-sum multiple comparisons (PROC RANK and PROC GLM, SAS Institute 1999) among proportions of items in each prey category were carried out, when significant effects of the prey category on the variable were found. The effect of the prey category on the percentage frequency of occurrence in deliveries through an identical analysis protocol was considered to be validation, since the frequency of occurrence is a useful additional index of prey contributions by number to the dipper diet (Ormerod 1985). Finally, the same procedure was also used for the effect of prey category on its electivity index, in order to confirm

that large prey, i.e., trichopterans and fish, were preferred by the dipper. Statistical significance was set to alpha = 0.05.

We used regression models to check the increasing alterations in composition of large prey and prey size present over the course of at least the 1st 1/2 of the nestling period. First, the daily nestling diets were related to nestling ages of the 1st or 2nd 1/2 of the nestling period using a linear regression model (PROC REG, SAS Institute 1999). Second, the linear regression model was exploited to describe the relationship between the daily maximum prey size of deliveries and nestling age over the course of the 2 half-nestling periods, respectively. The significance level of these regressions was set to 0.05.

RESULTS

Our data comprised 5412 identified prey items from a total of 47 nest-days, with the body sizes of 2015 items measured over a total 26 nest-days. In this set of field observations, there were a total of 2500 deliveries with at least 1 identified prey item during the dipper breeding season. Data were collected from 5 nests that successfully fledged more than 1 young (Fig. 1).

Prey category significantly affected the fraction of prey items in the diet (Friedman's test, $\chi^2 = 10.68$, $p = 0.0136$), with the fraction of trichopterans significantly higher than that of other prey taxa based on pair-wise comparisons (Fig. 2). The same significant influence of prey category on the percentage frequency of occurrence in deliveries (Friedman's test, $\chi^2 = 10.68$, $p = 0.0136$) and a consistent ranking among the 4 prey categories with the fraction of prey items in the diet were found. The electivity indices for trichopterans and fish were also significantly higher than those of the other prey types (Fig. 2), with electivity varying significantly among prey taxa (Friedman's test, $\chi^2 = 14.04$, $p = 0.0029$). Although large fish were considered to have greater escape activity than intermediate-sized trichopterans, the former were apparently preferred by dippers. The 2 less-preferred prey, ephemeropterans/plecopterans and dipterans, had moderate avoidance and high availability, but small body sizes (Fig. 2).

The fraction of large prey presented to nestlings was positively related to nestling age during the 1st 1/2 of the nestling period, but not beyond then (Fig. 3). The daily maximum prey size increased during the 1st 13 d of the nestling

period, reaching a plateau at the end of the 1st 1/2 of the nestling period (Fig. 4). Taken together, these data show that the change in diet was correlated with nestling age for at least the 1st 1/2 of the nestling period, such that the proportion of large-bodied prey and daily maximum prey size increased over time.

DISCUSSION

Nestling diet

Direct nest observations showed that macroinvertebrates, primarily trichopterans, were the major prey provisioned to nestling dippers, supporting previous studies using fecal analysis (Ormerod 1985, Ormerod et al. 1987). Trichopterans and fish were characterized by larger, softer bodies, and these were preferred by Brown Dippers despite their lower abundances. Differences in body size between trichopterans and other invertebrate taxa suggest that prey size, which is directly correlated with energetic content, is a key feature in food selection (Ormerod 1985, Santamarina 1993). However, adult dippers consume smaller prey than the nestlings (Ormerod 1985, Ormerod et al. 1987), and non-breeding adult dippers frequently prey on small invertebrates such as those in the Simuliidae and Baetidae (Ormerod and Tyler 1991). Similarly, studies on optimal foraging strategies of other bird species found that nestlings are frequently fed larger prey items (Rudolph 1982, Carlson 1983). We suggest that while adult dippers can consume their prey when captured, they must carry the prey over a distance to feed nestlings. In turn, adults may carry larger prey items to compensate for the flight costs between foraging sites and the nest.

Prey preference and traits

Although prey size is a commonly used index of quality, prey abundance has a major effect on rates of encounter by predators. Since large-bodied prey are usually less abundant than small-bodied prey, this creates a tradeoff between search time and prey quality for the dipper. Our results show that dippers selected prey based on size rather than abundance. In addition to being of a high quality, large-bodied prey may also be easier to detect, reducing the search time (e.g., Naef-Daenzer and Keller 1999). Brown Dippers are often observed foraging for large prey by diving, a

costlier strategy than wading-and-pecking (Eguchi 1990). In our study, dippers frequently dove to catch large prey to feed nestlings, despite the low availability and high catch cost of the prey. Optimal foraging theory predicts that animals should adopt a certain foraging strategy so as to maximize the net energy intake (McArthur and Pianka 1966, Schoener 1971), suggesting that increased prey quantity cannot always compensate for lower prey
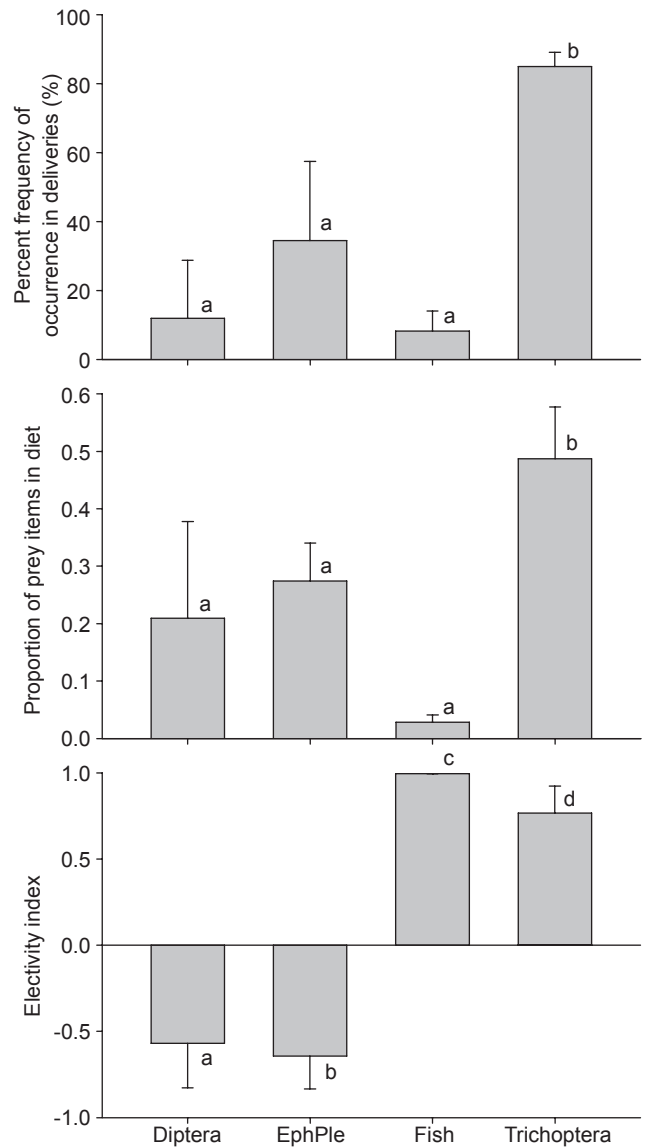

Fig. 2. Mean values plus standard errors of prey-item proportion in the nestling diets, percentage frequency of item occurrence in deliveries, and Jacobs's electivity index ($n = 5$ dipper nests) for dipterans, ephemeropterans/plecopterans (EphPle), fish, and trichopterans. Bars with the same letter do not significantly differ by rank-sum multiple comparisons ($p < 0.05$).

quality.

Prey profitability is a function of prey quality and handling time. For invertebrates, body size, exoskeleton hardness, and distastefulness are associated with higher handling costs (Sherry and McDade 1982). For a given prey size, therefore, chitinous prey are more costly than those of lower hardness. In addition, antipredator behavior of prey animals may also influence their vulnerability (e.g., Laurila 2000, Lingle et al. 2005). Some invertebrate prey respond to dipper predators with escape behaviors by either moving away or drifting in the flow, while others display less-active avoidance tactics (Jenkins and Ormerod 1996). Compared to rapidly swimming fish, however, there was no apparent difference in escape activity of these invertebrate prey. In the present study, larger prey such as trichopterans were often characterized by both lower exoskeleton hardness and less-effective antipredatory behavior.

Foraging tradeoffs during the nestling period

Observations of prey deliveries to nests revealed that trichopterans and fish were the preferred prey collected by adults for nestlings, with prey size increasing over the nestling period. This is consistent with similar results of previous studies on dippers and other birds (Ormerod 1985, Moser 1986, Slagsvold and Wiebe 2007). Two factors might determine the composition of prey fed to nestlings: changing nutritional requirements over the course of the nestling period, and resource limitations in the habitat. In other bird species, females respond to increased energy demands in nestlings by decreasing brooding time and increasing foraging time as nestlings become more homeothermic, while increasing the number and size of prey brought to the nest (Haggerty 1992). Several authors suggested that the size of the nestling's gape acts as an upper limit on prey size (Moser 1986, Slagsvold and Wiebe 2007). In our study, this limit was reached early in the nestling period, consistent with previous dipper research (Ormerod 1985). Anecdotal evidence also supports this hypothesis: we observed adult dippers occasionally misjudging nestling handling ability and delivered overly large prey, which was either discarded or consumed by the adults themselves. Changes in prey availability can also affect the diets of avian predators (e.g., Naef-Daenzer et al. 2000, Prugh 2005, Lin et al. 2007). However, prey would less likely present rapid dynamic changes on a short time scale, and dipper breeding occurs before seasonal floods result in dramatic declines in their prey (Chiu et al. 2008).
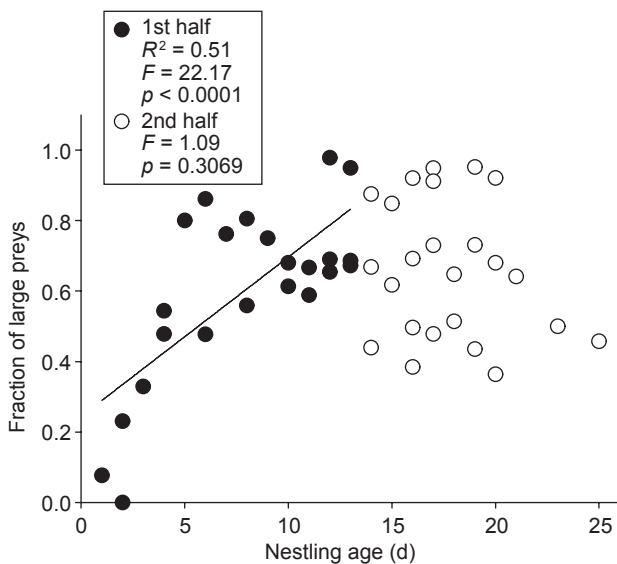

Fig. 3. Fraction of large prey among the delivered items in relation to nestling age over the course of the 1st nestling period (*n* = 23 nest-days) or the 2nd nestling period (*n* = 24 nest-days).
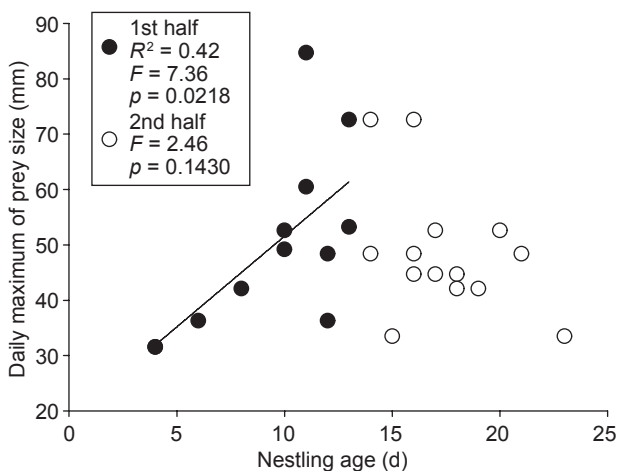

Fig. 4. Daily maximum size of delivered prey in relation to nestling age over the course of the 1st nestling period (*n* = 12 nest-days) or the 2nd nestling period (*n* = 14 nest-days).

CONCLUSIONS

Through telescopic observations, our study revealed that prey morphology influences dipper foraging behavior and the shift in prey size and composition in nestling diet over the course of 1st 1/2 of the nestling period. These results also

suggest identical constraints on central place foraging and loading strategies as in other dipper species. However, the immediate observations used in this study suffer from a number of short-comings. In contrast to a higher resolution in prey taxonomic level of fecal analysis (Ormerod 1985), this method, due to a limited observation time for each delivery, provides lower resolution of prey identification to maintain the identification accuracy to a reasonable level. Nevertheless, additional information on the behavior of dippers can be obtained through this observation method.

As the foraging for nestling Brown Dippers depended on prey size, large prey such as juveniles of Formosan landlocked salmons were highly preferred in our stream system. Hence, our study lends further weight to calls for consideration of possible trophic paths which reduce recruitment for the conservation of Formosan landlocked salmon which is at risk of extinction.

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