# Relationship between salmon egg subsidy and the distribution of an avian predator

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**ABSTRACT**

As a spatial subsidy, which is the phenomenon of transferring resources from a donor system to a recipient system, anadromous salmonids contribute to the supply of marine-derived nutrients to freshwater and terrestrial systems. Live salmon and salmon carcasses and eggs are utilized by various organisms and affect their abundance and distribution. However, the evaluation of the effect of salmon subsidies on the abundance and distribution of terrestrial animals is biased towards predators or scavengers that utilize spawning adults and carcasses, and few studies have focused on the effect of salmon eggs as a subsidy. To avoid underestimating the function of salmon subsidies, the response to the availability of salmon eggs in various systems should be investigated. Here, we investigated the abundance and feeding behaviour of the brown dipper *Cinclus pallasii*, as salmon egg a consumer, based on the hypothesis that the availability of salmon eggs affects the diet composition and stream distribution of this small predator. In addition, to test whether changes in the abundance of brown dippers are determined by salmon spawning or by other factors, their abundance was compared upstream and downstream of the dam. Brown dippers used salmon eggs during the spawning season (63% of diet composition), and their abundance increased as the number of spawning redds increased. In contrast, this pattern was not observed upstream of the dam. These results suggested that the abundance and stream distribution of brown dippers vary according to the variation in the spatiotemporal availability of salmon eggs.

**Key Words**: resource subsidy, marine-derived nutrients, behavioural ecology, stream ecology, Salmonidae, Pacific salmon.

## 1. INTRODUCTION

Spatial subsidies are a phenomenon in which resources are transferred from a donor system to a recipient system (Polis et al. 1997). Spatial subsidies play a crucial role in biological communities because they affect the abundance and distribution patterns of organisms and the food web structure in the recipient systems by affecting the availability of basal resources (Nakano and Murakami 2001, Kawaguchi et al. 2003, Spiller et al. 2010, Hocking et al. 2013, Terui et al. 2018).

Anadromous salmonids, well-known spatial subsidy representatives, transport marine-derived nutrients and energy to freshwater and terrestrial ecosystems through their migrations (Gende et al. 2002, Schindler et al. 2003, Hocking and Reynolds 2011, Koshino et al. 2013). Salmon subsidies contribute to increasing aquatic invertebrate biomass and freshwater fish abundance in rivers (Wipfli et al. 1998, 1999, Denton et al. 2009). Spawning adults and carcasses are also used as food by terrestrial animals not only in the underwater ecosystem but also in surrounding riparian ecosystems and eventually affect the abundance and distribution of terrestrial scavengers and top predators (Boulanger et al. 2004, Christie and Reimchen 2005, Levi et al. 2012, Field and Reynolds 2013, Walters et al. 2021). Salmon subsidies thus provide insights into how multiple ecosystems are tangled together.

Past investigations on the effects of salmon subsidies on terrestrial organism abundance and distribution have thus far been biased towards predators or scavengers that utilize spawning adults and carcasses (e.g., Boulanger et al. 2004, Christie and Reimchen 2005, Levi et al. 2012, Field and Reynolds 2013, Walters et al. 2021). Considering that terrestrial organisms are provided multiple resources by salmon runs, such as eggs and fry, as well as spawning adults and carcasses (Munro 1941, Willson and Halupka 1995), salmon subsidies may have even more unexpected far-reaching effects. Therefore, a comprehensive understanding of the effect of

64 subsidies on the population and distribution of organisms is important. However, few studies
65 have focused on the effect of salmon eggs as a subsidy on the abundance and distribution of
66 terrestrial animals. It is necessary to clarify the response to the availability of salmon eggs in
67 various systems to avoid underestimating the function of salmon subsidies.

68 Dippers (Aves: Cinclidae) are riparian birds that mainly feed on aquatic invertebrates by
69 diving into the water (Eguchi 1990, Taylor and O'Halloran 1997, 2001) and which are known to
70 use salmon eggs in available rivers and seasons (Goodge 1959, Obermeyer et al. 1999, 2006,
71 Whitehorne 2010, Reimchen 2017). For example, the American dipper *Cinclus mexicanus* can
72 achieve high reproductive success, represented as fecundity and juvenile growth, by foraging on
73 *Oncorhynchus* eggs (Obermeyer et al. 2006, Tonra et al. 2016). The population size of the white-
74 throated dipper *C. cinclus* in Norway may also benefit from eating salmon fry because it was
75 correlated with the annual density of salmon fry (Nilsson et al. 2018). Because dippers, which
76 are not scavengers, are not affected by the amount of carcasses – in addition to their well-studied
77 relationship with salmon, as noted above – they are the most suitable model species for
78 examining the effect of salmon egg subsidies on the abundance and distribution of terrestrial
79 animals. The brown dipper *C. pallasii*, which is distributed in Asia (Hong et al. 2019), preys on
80 salmon eggs and juvenile salmon (Murata 1900). However, its actual status has never been
81 evaluated quantitatively, and the relationship with salmon subsidies has long been overlooked.

82 We therefore investigated the abundance and diet composition of the brown dipper in
83 the Shiretoko Peninsula of Hokkaido, northern Japan, where the spawning migrations of salmon
84 are well observed, based on the hypothesis that the availability of salmon subsidies drives the
85 diet composition and stream distribution of this small predator. In addition, by comparing the
86 abundance of brown dippers above and below dams where salmon cannot run upstream during
87 peak salmon spawning runs, we tested whether changes in the abundance of brown dippers are

determined by salmon spawning or by other factors. More specifically, it was predicted that salmon spawning would cause a shift in the diet of brown dippers to salmon eggs and an increase in the abundance of brown dippers by altering the distribution of food resources, while no such pattern occurs upstream of the dam.

## 2. MATERIALS AND METHODS

### 2-1. Study site

Four streams located in the Shiretoko Peninsula were selected for the present survey (Figure 1). Natural spawning sustains pink salmon *Oncorhynchus gorbuscha* and chum salmon *O. keta* populations in these streams (T. Yamada, unpublished data). The release of juvenile chum salmon has been conducted only in the Mosekarubetsu stream, and in-stream harvesting does not occur in all streams. The central part of the Shiretoko Peninsula has been designated as a World Natural Heritage site since 2005, partially because of the close relationships between the marine and terrestrial ecosystems sustained by the anadromous migration of pink salmon and chum salmon (IUCN 2005). The upper reaches of the studied streams are included in the Shiretoko World Natural Heritage site. Rivers and streams in the Shiretoko Peninsula are highly fragmented by more than 330 artificial dams (Takahashi et al. 2005), which is no exception in all selected streams. Study sections were set up in each stream from the mouth of the stream to the proximal dam. The Chienbetsu stream was surveyed up to the second proximal dam because many salmon pass through the first proximal dam. The length of the study section was 289.4, 348.2, 154.9, and 211.3 m in the Chienbetsu stream, Funbe stream, Mosekarubetsu stream, and Shoji stream, respectively.

112 **2-2. Field survey**

113 Temporal changes in the abundance and diet of brown dippers were evaluated from August to
114 September 2021. Field observations were conducted in one or two streams per day for a total
115 effort of five days at every 9- or 10-day interval in each stream. In the observation protocol, one
116 investigator (T. Yamada) walked along the study section from the lower to the upper reach,
117 counting the number of brown dippers. To avoid recounting birds, the investigator checked
118 where the flying individuals stopped and ignored individuals who flew ahead of the investigator,
119 expecting territorial individuals to characteristically 'double-back' when pushed to the ends of
120 their territory (Chiu et al. 2008).

121 The date of the count survey was the same as that of the diet survey, and the count
122 survey was conducted before the diet survey was conducted. In the diet survey, when the
123 investigator found an individual, they approached it at an observable distance and checked the
124 diet composition and age category (adult or juvenile) using binoculars (MONARCH 10 × 42;
125 Nikon, Tokyo, Japan). The age category was classified by the presence or absence of juvenal
126 plumage. The contents of the dipper's diet were classified into four categories: aquatic insects,
127 terrestrial insects, algae, and salmon eggs. If no observable individuals were found, no
128 observations were made. The diet survey was conducted only once per individual at each
129 observation cycle; the observation time ranged from 1-11 minutes.

130 Salmon spawning redds were also visually counted on the same day as the above
131 observation procedures to obtain an index of the availability of salmon eggs. Pink salmon exhibit
132 "probing", a periodic and short-term migration behaviour between the sea and multiple drainages
133 (Thedinga et al. 2000, Morita 2021). If many individuals exhibit probing, salmon abundance
134 cannot be a direct indicator of the number of spawners; therefore, we used the number of
135 spawning redds as an indicator of the number of spawners. Spawning redds were visually judged

as the area of disturbed gravel or bright (denuded) areas among the periphyton-covered gravel (Ortlepp and Mürle 2003, Pedersen et al. 2009). We also measured the stream surface area of the study section only once in each section during the study period.

The abundance of brown dippers was also surveyed upstream of dams in the selected stream at the end of September 2021 during the peak spawning period of pink salmon, except in the Chienbetsu stream, where the dam has a fishway allowing migration to the upper reaches. Additional study sections were set up at approximately 400 m from the dam in each case. An investigator walked from the dam to the upstream end of the study section counting the number of dippers, as was the case in the lower reach survey. This survey was conducted on the same day in the fifth cycle of the count survey mentioned above. We also measured the stream surface area of the study section only once in each stream.

**2-3. Statistical analysis**

The dependence on salmon eggs during the salmon spawning period, classified based on the presence of spawning redds, was evaluated by discriminating the dipper's age by fitting a generalized linear mixed model (GLMM) to the diet data per individual. In the analysis, the dominance ratio of salmon eggs in the diet composition was used as a response variable following a binomial distribution. Age category was tested as an explanatory variable, considering observation cycle ID and stream ID as random intercepts. When the 95% confidence intervals (95% CI) of the estimated coefficient values did not overlap between age categories, we considered the differences significant.

A relationship between the availability of salmon eggs (represented as the number of spawning redds) and the brown dipper abundance was also estimated by fitting GLMMs to the dipper count data as a response variable assuming a Poisson distribution. The number of

spawning redds and time in the day when the survey was started were used as the candidate explanatory variables, considering log-transformed stream surface area as an offset term and observation cycle ID and stream ID as random intercepts. To avoid multicollinearity, variance inflation factors (VIFs) were calculated before the analysis; all variables had values less than 5, the threshold indicative of troubling collinearity for regressions (Sheather 2009). Akaike's information criterion (AIC) was used for model selection (Burnham and Anderson 2002). If several plausible models had $\Delta AIC \leq 2$, the optimal model was selected according to the principle of parsimony (Burnham and Anderson 2002).

Since resource availability may affect organism distribution (e.g., Dingle and Drake 2007, Dingle 2014), it was also expected that the dipper abundance differed between the upper and lower reaches of the dam. Brown dipper abundance in the fifth observation cycle was compared between the lower reaches and the upper reaches of the dam by fitting the count data to a GLMM considering log-transformed stream surface area as an offset term and the stream ID as a random intercept. When the 95% CI of the estimated coefficient values did not overlap between the study sections, we considered the differences significant.

All data analyses were conducted with R v. 4.2.3 (R Core Team 2022) using glmmTMB v. 1.1.3 (Brooks et al. 2017) for GLMMs.

## 3. RESULTS

A total of 69 brown dipper individuals, 356 redds, and 1093 pink salmon individuals were observed during our survey. Feeding behaviour was monitored in 4 individuals (3 adults and 1 juvenile) in the pre-spawning period and in 18 individuals (10 adults and 8 juveniles) in the

183 spawning period from the three streams, except for the Mosekarubetsu stream, where close
184 observation could not be made.

185 The diet composition changed between the salmon pre-spawning and spawning periods
186 (Figure 2A; Appendix S1; Table S1). The percentage of salmon eggs in the diet was up to 63%
187 (Figure 2A) during the latter period. The brown dippers basically used only small baits in the
188 water and did not peck salmon carcasses. Regarding the dependence on salmon eggs among age
189 groups estimated by GLMM fitting, adults had a higher ratio of salmons eggs in their diets than
190 juveniles, although a significant difference was not found (Figure 2B; Table 1).

191 In the abundance survey, the GLMM including the number of spawning redds as the
192 explanatory variable had the lowest AIC value (Table 2). The brown dipper abundance positively
193 correlated with the number of spawning redds in the selected model (Figure 3; Table 1). The
194 comparison between abundances in the upper and lower sections of the dam showed that the
195 abundance in the lower section was clearly higher than that in the upper section (Figure 4; Table
196 1).

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198

199 **4. DISCUSSION**

200 This study demonstrates for the first time that salmon eggs are the dominant dietary item for the
201 brown dipper during the salmon spawning season and that the abundance and stream distribution
202 of terrestrial vertebrate species can be predicted by the number of spawning redds used to
203 represent the availability of salmon eggs. In addition, brown dipper abundance during the peak
204 spawning season differed significantly between upstream and downstream of the dam, with the
205 downstream abundance being higher. It is therefore indicated that the distribution of brown
206 dippers varies according to variation in the spatiotemporal availability of salmon subsidies. One

207 of the typical theories of the spatial distribution of animal populations is the ideal free
208 distribution, which assumes that individuals are free to move among sites (Fretwell and Lucas
209 1969), and our results may be explained by this theory. The reason is that brown dippers did not
210 use the site upstream of the dam (without salmon subsidies) even when their density was high
211 downstream of the dam.

212 While salmon eggs serve as an important food source for brown dippers, the salmon
213 spawning behaviour of digging up the riverbed leads to a reduction in the abundance of aquatic
214 invertebrates that are prey for brown dippers (Minakawa and Gara 2003, Moore and Schindler
215 2008). Since the energy value per salmon egg is higher than that per individual aquatic
216 invertebrate (Obermeyer et al. 2006, Whitehorne 2010), the positive effect of egg-eating may
217 outweigh the negative effect of reduced eating of aquatic invertebrates. In fact, juvenile weight
218 and mortality in the American dipper in salmon spawning reaches are known to be higher and
219 lower than those in the non-spawning reaches (Obermeyer et al. 2006). Further verification is
220 required to clarify whether these findings may be supported in the present system.

221 The abundance of aquatic invertebrates varies greatly with the season (Rundio and
222 Lindley 2008) and declines with flooding (Chiu et al. 2008, McMullen and Lytle 2012).
223 Accordingly, the decrease in aquatic invertebrate abundance leads to a decline in brown dipper
224 abundance and survival (Chiu et al. 2008, 2013). Pink salmon, chum salmon, and masu salmon
225 running up Japanese rivers spawn during the summer, fall and winter (Kuzishchin et al. 2009,
226 Kovach et al. 2012, Quinn 2018, Iida et al. 2021). Since summer and fall are typhoon seasons in
227 East Asia, salmon subsidies may compensate for the decline in aquatic invertebrates. In addition,
228 dippers sometimes prey on salmon fry (Ormerod 1985, Ormerod and Tyler 1986, 1991,
229 Obermeyer et al. 2006). Since most salmon fry mainly emerge during spring and summer
230 (Pavlov et al. 2008, Kirillov et al. 2018, Yamada et al. 2022), salmon fry may be used as a food

resource by dippers during this period. Therefore, spawning by anadromous salmonids may compensate for declines in the abundance of aquatic invertebrates during various seasons.

Salmon spawning abundance is disturbed by several human activities, such as dam construction and fisheries (Finney et al. 2000, Romakkaniemi et al. 2003, Nakamura and Komiyama 2010). This study shows for the first time that the distribution patterns of small terrestrial predators are determined by the supply of salmon eggs, indicating that the disruption of natural spawning may have unexpected effects on the abundance and distribution of terrestrial salmon egg consumers. Future studies are needed to examine the effects of these anthropogenic restrictions of the salmon egg subsidy on the abundance and distribution of terrestrial consumers.

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**CONFLICT OF INTERESTS STATEMENT**

None declared.

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## TABLES

**Table 1.** Results of GLMMs testing effects of age category (adult/juvenile) on the salmon egg ratio in brown dipper diets and number of spawning redds and presence/absence of salmon (below/above dam) on brown dipper abundance.

| Response variable | Fixed effect | Estimate | Std. Error | z value |
|---|---|---|---|---|
| Salmon egg ratio in dipper diets | Intercept | 0.61 | 1.02 | 0.60 |
| | Age -Juvenile | -1.83 | 0.91 | -2.00 |
| Dipper abundance | Intercept | -6.59 | 0.24 | -27.64 |
| | Number of redds | 0.02 | 0.01 | 3.15 |
| Dipper abundance during peak spawning period | Intercept | -8.41 | 0.71 | -11.89 |
| | Section -Below dam | 2.73 | 0.74 | 3.69 |

**Table 2.** Results of model selection. AIC corresponds to Akaike information criteria; ΔAIC is the difference between the AIC of that model and that of the model with the lowest AIC. Bold indicates the best model. Redds, number of spawning redds; Time, survey start time.

| Model | logLik | AIC | ΔAIC |
|---|---|---|---|
| **Redds** | **-37.92** | **83.84** | **0.00** |
| Redds + Time | -37.71 | 85.42 | 1.58 |
| Null | -40.63 | 87.26 | 3.42 |
| Time | -40.27 | 88.55 | 4.71 |

432 **FIGURE CAPTIONS**

433

434 **Figure 1.** Map of the study area located on the Shiretoko Peninsula. The blue lines indicate the
435 streams surveyed.

436 **Figure 2.** (A) Composition of brown dipper diets during the salmon pre-spawning and spawning
437 periods. AI: aquatic invertebrate, TI: terrestrial invertebrate, A: algae, and SE: salmon egg. (B)
438 Mean predicted marginal effects of age category on the salmon egg ratio in brown dipper diets.
439 The translucent boxes indicate 95% CIs. Grey circles denote each observed value.

440 **Figure 3.** Mean predicted marginal effects of the number of spawning redds on brown dipper
441 abundance. The 95% CI is denoted by dotted lines.

442 **Figure 4.** Mean predicted marginal effects of salmon occurrence on brown dipper abundance
443 during the peak spawning season. The translucent boxes indicate 95% CIs. Grey circles denote
444 each observed value.

445

**FIGURES**

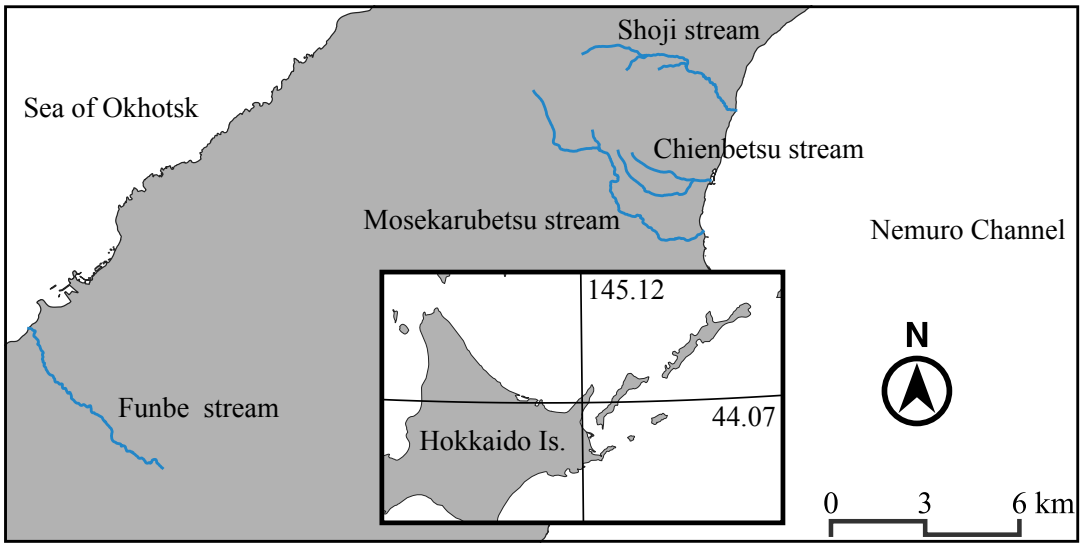


**Figure 1.**

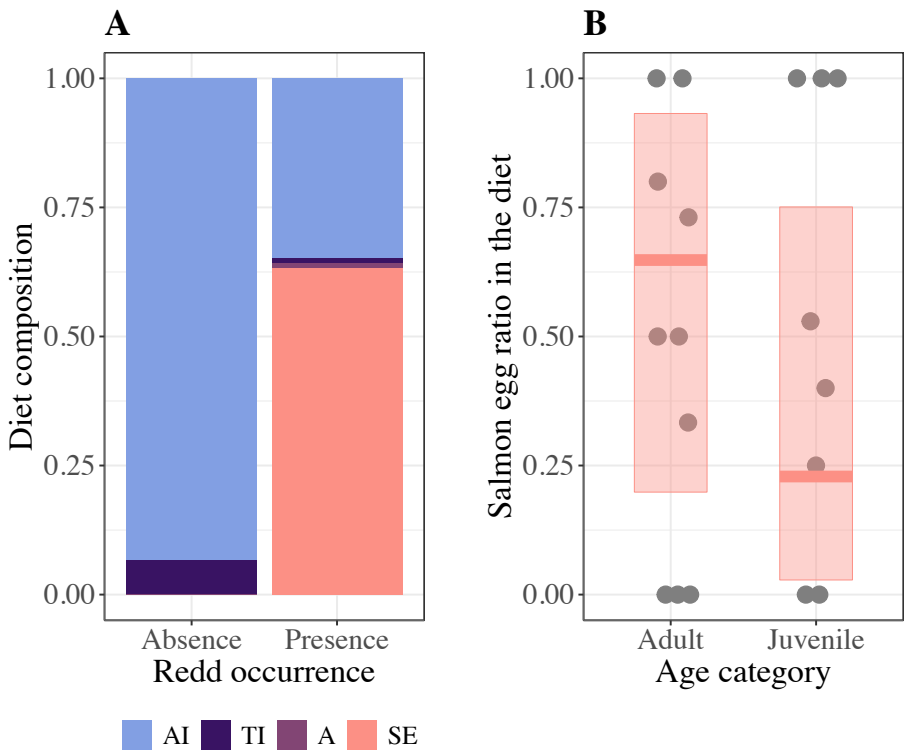
A
B
1.00
0.75
0.50
0.25
0.00
Diet composition
Absence
Presence
Redd occurrence
Salmon egg ratio in the diet
Adult
Juvenile
Age category
AI
TI
A
SE

**Figure 2.**

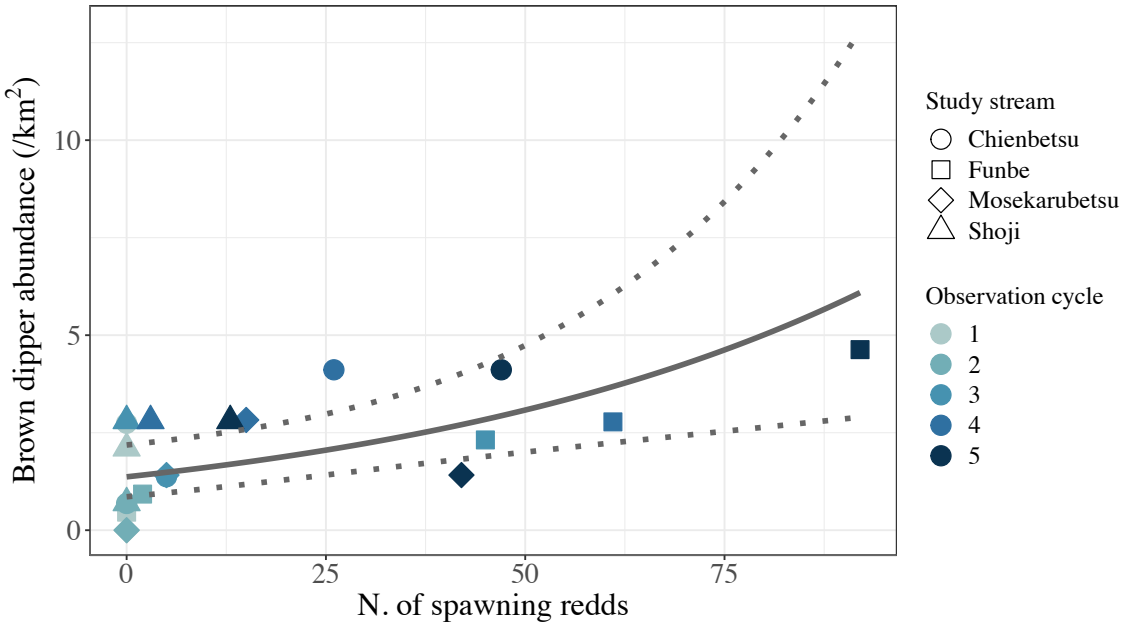
Brown dipper abundance (/km$^2$)
10
5
0
0
25
50
75
N. of spawning redds
Study stream
Chienbetsu
Funbe
Mosekarubetsu
Shoji
Observation cycle
1
2
3
4
5

**Figure 3.**

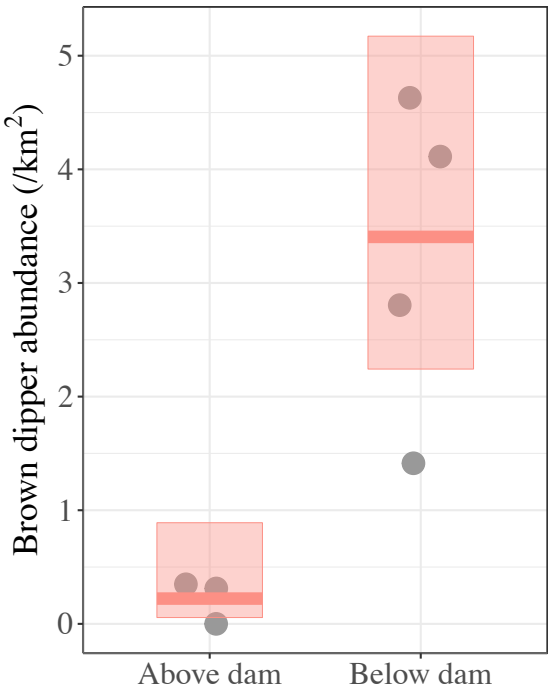


**Figure 4.**