Variation in Prey Size Selectivity of Fingerling Chum Salmon (*Oncorhynchus keta*) in Sea Life: Effects of Stomach Fullness and Prey Abundance

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Prey size selection by fingerling chum salmon (*Oncorhynchus keta*) was studied with respect to variations in the stomach fullness of fish and their estimated prey abundance in the coastal waters of the Japan Sea off northern Honshu, Japan. Fingerlings mainly fed on zooplankton, and their diets consisted of two size groups of major prey taxa. Fingerlings showed two behavioral patterns: selective foraging for the larger prey and non-selective foraging. The effects of prey abundance on the selectivity of fish were different between the size groups. Fingerlings intensified their foraging selectivity with a increase in the abundance of larger prey. On the contrary, the abundance of smaller prey did not influence the prey size selectivity. The stomach fullness of fish was also positively correlated with the prey size selectivity. Since the abundance of larger prey and the stomach fullness of fish varied independently of each other, both are considered to be important factors affecting the prey size selection and diet composition of fingerling chum salmon in the sea.

INTRODUCTION

Changes in prey selectivity of predators in relation to status of prey and (or) predator are well known in various taxa of animal (see Stephens and Krebs 1986). For teleost fish, prey selection has been studied intensively on visual and particulate feeders, which feed on planktonic or epibenthic prey one at a time or no more than a few at a time (see Durbin 1979; Ringler 1979a; Sawara 1987; Gerking 1994). Previous studies pointed out factors affecting prey selection, such as size and abundance of prey (e.g., Ivlev 1965; Werner and Hall 1974; O'Brien et al. 1976) and size (or developmental stage) and stomach fullness of fish (e.g. Ivlev 1965; Hart and Ison 1991; Hart and Gill 1992).

Salmonids are recognized as visual and particulate feeders (see Gerking 1994), and juvenile chum salmon (*Oncorhynchus keta*) feed on zooplankton in their sea life (Salo 1991; Higgs et al. 1995). Juvenile chum salmon feed opportunistically on most prey species (LeBrasseur 1996; Peterson et al. 1982; Brodeur and Pearcy 1990), but selectively on larger prey (LeBrasseur 1969; Bailey et al. 1975; Healey 1980, 1991; Simenstad and Salo 1982; Cordell 1986). On the other hand, temporal and geographical variations in the size of dominant prey have been observed for juvenile chum salmon (Manzer 1969; Kaeriyama 1986), which suggests that the prey size selectivity of juvenile chum salmon is variable. Nevertheless, little information is available on variation in the prey size selectivity of juvenile chum salmon, except for the ontogenetic change with development from the fry stage to the fingerling stage (Suzuki et al. 1994).

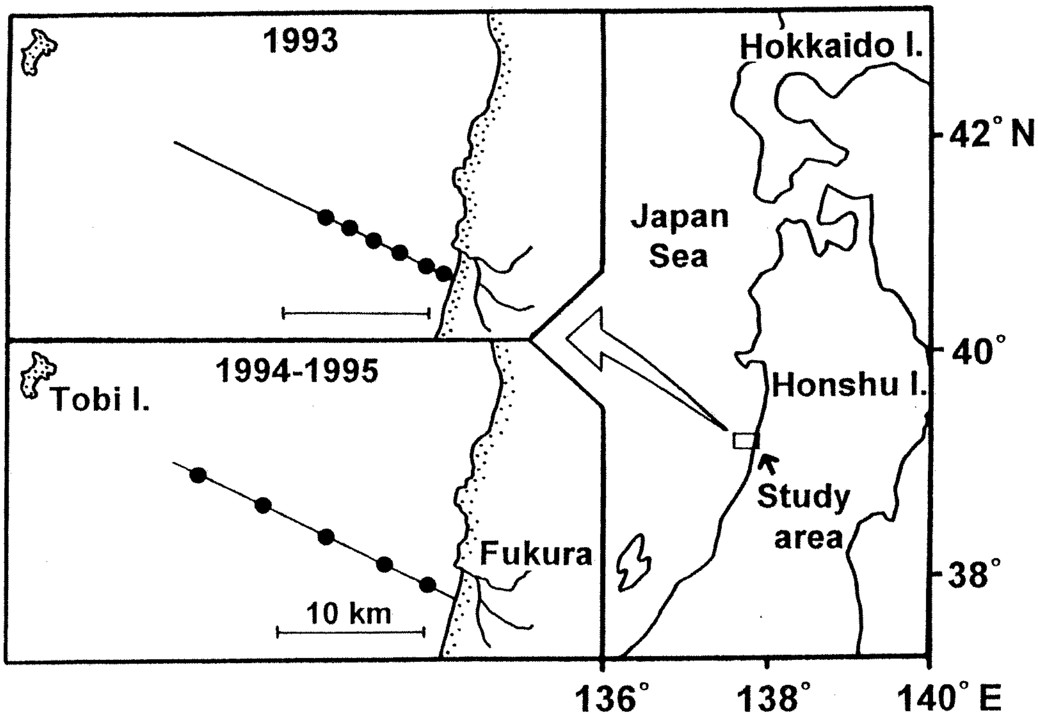
This paper examines variations in prey size selection of fingerling chum salmon with respect to their stomach fullness and prey abundance using data collected from fingerling chum salmon inhabiting the coastal waters of the Japan Sea off northern Honshu Island.

MATERIALS AND METHODS

Study Area

This study was conducted in the Japan Sea off the coast of Fukura, northern Honshu Island, Japan, during March and May in 1993-1995 (Fig. 1). Six stations were located along a southeast-to-northwest transect in the area in 1993. The distances from the shore line to each station ranged from 1 km to 10 km. In 1994 and 1995, five stations (2-20 km offshore) were located on the transect. The depth at the stations ranged from 12 m to 120 m. Temperature and salinity of surface water measured at each stations varied between 8.5-14.3°C and 18.5-34.1‰ in the sampling period during the 3 years.

Fig. 1 Location of the study area and the sampling stations (dots) in 1993 and 1994-1995 in the coastal waters of the Japn Sea off Fukura, northern Honshu Island, Japan



Juvenile Chum Salmon

Juvenile chum salmon were collected with a surface trawl net, which was operated by two vessels. The net was 8 m wide and 4 m deep at the mouth and equipped with 25-34 mm (stretched) mesh in the body and 7.5 mm mesh in the cod end. The net was towed parallel to the shore line at a speed of 4 km/h. The net was towed for thirty minutes at each station in 1993. Three sets of 15 minute tows at each station were carried out in 1994 and 1995. Most collections were made in the morning. Catches were anaesthetized in MS-222 and preserved in buffered 10% formalin-seawater solution aboard, following which samples were transferred to 70% etanol solution in 1994 and 1995.

Fishes were sorted to species, measured FL (fork length) and wet weight recorded (nearest 0.1 mm and 0.01 g, respectively). We selected juvenile chum salmon larger than 50 mm FL (the size chum salmon change their developmental stage from fry to fingerling (Kaeriyama 1986)) for our analyses. Young chum salmon (larger than 120 mm FL) were not caught in this study.

Zooplankton

Zooplankton samples were collected using a Norpac net (0.45 m diameter, 0.33 mm mesh size) twice (before and after the fish collection) in 1993 and 3 times (after fish collection) in 1994 and 1995 at each station. The Norpac net was towed vertically from 20 m to the surface. At the stations where depth was less than 20 m, the net was towed from the bottom. Filtered water volume was measured using a flow meter (Rigosha Co. Ltd., Japan). The samples were fixed in 10% buffered formalin-seawater solution.

Zooplankton samples were sorted to the lowest possible taxonomic level and life history stage and the number of each taxon was recorded. Abundance of zooplankton was defined as density per cubic meter. The percent composition and abundance of zooplankton at each station were expressed as the mean value of the sets within a station. Body length and body width of zooplankton were measured to the nearest 0.01 mm on a random sample of 50 individuals in each taxon. Assuming that the form of zooplankton was a cylinder, we calculated a volume of zooplankton as a size index of each taxon.

We estimated a food environment of fingerlings from daytime zooplankton collections. However, juvenile salmon generally start feeding at dawn (Bailey et al. 1975; Godin 1981; Kaeriyama 1986) and diel vertical migration of zooplankton is common (see Raymont 1983), suggesting that the food environment would change temporally. Thus, to compare abundance of prey between dawn and day, we collected zooplankton at dawn at some stations in

1995. The abundance of two prey groups (described in the next section) did not differ significantly by time of collection except for a single case (Table 1), suggesting that our estimation is reliable.

Diet Analyses

Stomach contents from up to 30 specimens were analyzed for each station; Obrebski and Sibert (1977) suggested that the full range of dietary organisms is usually found in a sample of 30 fish.

Stomachs were opened and the entire contents were weighed (wet weight) to the nearest 1mg. A relative stomach weight (SCI) was used for an index of the stomach fullness of fingerlings: $SCI=100 \times SCW/(BW-SCW)$; where SCW and BW are the weight of stomach contents and fish body weight, respectively.

Food items were identified to the lowest possible taxonomic level and life history stage, and the number of each taxon was recorded. Diet composition was expressed as percent number at each station. Only prey taxa contributing more than 5% to the diet composition at a station were used in our prey selectivity analysis. However, fish larvae and an amphipod, *Themisto japonica*, were omitted because they were not collected by the Norpac net. Accordingly, we excluded three stations where fish larvae and *Themisto japonica* were dominant (>50%) in the diet composition.

Prey taxa were divided into two size groups according to their mean sizes (Fig. 2). The smaller taxa, such as *Evadne nordmanni, Podon leuckarti*, euphausiid calyptopis larvae, and *Oikopleura* spp. are called small prey. The larger taxa, such as euphausiid furcilia larvae, polychaetes, *Calanus sinicus*, and *Neocalanus plumchrus* copepodid V stage (*Neocalanus plumchrus* CV) were classified as large prey.

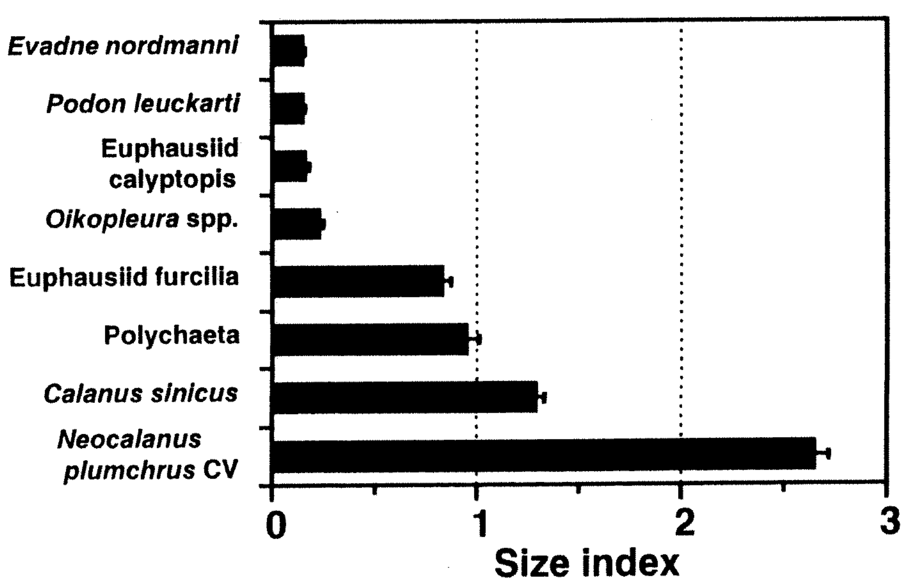
Selectivity for the prey groups by fingerlings was measured by the Rank Preference Index (Johnson 1980) for each station. Following this method, we compared differences in selectivity among food items without influence of inclusion or exclusion of a specific food item.

Table 1. Comparisons between abundance of prey (average ± S.E., N=3) collected at dawn and that collected in day at each station by one-way ANOVA. The values of abundance were log-transformed.

Date	Station[a]	Large prey			Small prey		
		Dawn	Day	p	Dawn	Day	p
Apr. 12, 1995	10	4.13 ± 0.17	3.27 ± 0.26	*	6.05 ± 0.21	5.94 ± 0.29	NS
Apr. 28, 1995	10	2.36 ± 0.47	3.34 ± 0.12	NS	5.58 ± 0.60	6.59 ± 0.36	NS
Apr. 28, 1995	20	4.65 ± 1.22	6.04 ± 1.15	NS	7.38 ± 1.05	5.84 ± 0.61	NS
May 09, 1995	10	2.00 ± 0.34	1.14 ± 0.29	NS	6.73 ± 0.23	6.75 ± 0.41	NS
May 10, 1995	20	1.95 ± 0.09	2.50 ± 0.39	NS	6.07 ± 0.29	6.74 ± 0.26	NS

a: The numbers indicate distance (km) from the shore to the stations.
*: $p<0.05$, NS: $p>=0.05$

Fig. 2 Average body size of the major prey taxa of fingerling chum salmon. The horizontal lines indicate standard errors. The size index is indicated as volume of prey, whose shape is assumed to be a cylinder.



RESULTS

Prey Size Selection

Fingerling chum salmon showed two behavioral patterns: selective foraging for larger prey and non-selective foraging. The large prey were ranked higher in selectivity than the small prey in 17 of the stations (Table 2); in seven other stations, the ranks of selectivity were tied or not significantly different ($F_{1,2}$=2.00, p=0.293). These variations in the prey size selectivity of fingerlings did not depend on relative abundance of prey, because the ranks of the small prey in zooplankton composition were consistently higher than those of the large prey.

In the following analyses, the rank of selectivity for the small prey was used for an index of prey size selectivity of fingerlings, since the rank of the large prey was constant as rank 1 among stations; the rank 1 and the rank 2 indicated non-selective and selective foraging, respectively.

Factors Affecting the Prey Size Selection

We used three factors i.e., the abundance of the large prey, that of the small prey, and the stomach fullness of fingerlings (SCI) to evaluate effects on the variation in the prey size selectivity of fingerling chum salmon. these three factors varied independently from one another in this study (Table 3). A significant positive relationship between the rank of selectivity for the small prey and the abundance of the large prey indicated that fingerling chum salmon intensified foraging selectivity with an increase in the availability of the large prey (r_s =0.616, p<0.001, Fig. 3). On the contrary, the abundance of the small prey was not related to the variation in the selectivity of the small prey (r_s = -0.331, p>0.05, Fig. 4). The SCI was positively correlated with the rank of selectivity for the smaller prey (r_s =0.556, p<0.01, Fig. 5), showing a tendency for fingerlings to forage selectively as they became satiated.

Table 2. Ranks of the large prey (LP) and the small prey (SP) in the zooplankton compositions (percent by number), in the diet compositions (percent by number), and in selectivity of fingerling chum salmon at each sampling station.

Year	Date	Station[a]	Zooplankton composition		Diet composition[b]		Selectivity[c]		N[d]
			LP	SP	LP	SP	LP	SP	
1993	Apr. 28	1	2	1	1.4	1.6	1	2	7
1993	Apr. 28	2	2	1	1.0	2.0	1	2	28
1993	Apr. 28	4	2	1	1.0	2.0	1	2	4
1993	Apr. 28	8	2	1	1.0	2.0	1	2	30
1993	May 18	2	2	1	2.0	1.0	1	1	3
1993	May 18	6	2	1	2.0	1.0	1	1	3
1994	Mar. 22	2	2	1	2.0	1.0	1	1	3
1994	Apr. 7	2	2	1	1.8	1.2	1	2	28
1994	Apr. 7	5	2	1	1.0	2.0	1	2	4
1994	Apr. 21	2	2	1	2.0	1.0	1	1	15
1994	Apr. 21	5	2	1	2.0	1.0	1	1	15
1994	Apr. 21	10	2	1	1.8	1.2	1	2	26
1994	Apr. 21	15	2	1	1.0	2.0	1	2	6
1994	Apr. 21	20	2	1	1.0	2.0	1	2	5
1995	Apr. 12	2	2	1	1.0	2.0	1	2	12
1995	Apr. 12	10	2	1	1.0	2.0	1	2	2
1995	Apr. 28	2	2	1	1.0	2.0	1	2	22
1995	Apr. 28	10	2	1	1.3	1.8	1	2	4
1995	Apr. 29	15	2	1	2.0	1.0	1	1	3
1995	May 9	10	2	1	1.5	1.5	1*	2*	2
1995	May 9	15	2	1	1.0	2.0	1	2	11
1995	May 9	20	2	1	1.0	2.0	1	2	30
1995	May10	2	2	1	1.1	1.9	1	2	8
1995	May 10	5	2	1	1.1	1.9	1	2	27

[a]: The numbers indicate distance (km) from the shore to the stations.

[b]: The rank of prey item is indicated by mean value of fingerlings at each station.

[c]: The rank of selectivity is indicated by the Rank Preference Index (Johnson 1980).

[d]: The number of fish examined at each station.

*: Ranks are not significantly different using ANOVA (p>=0.05).

Table 3. Relationship between the abundance of the large prey (LP), that of the small prey (SP), and the stomach fullness (SCI) of fingerling chum salmon among the sampling stations (N=24). The values of abundance were log-transformed.

Variables		r	P
LP	SP	-0.083	0.702
LP	SCI	0.150	0.485
SP	SCI	0.248	0.243

Fig. 3 Relationship between abundance of the large prey and the rank preference index of the small prey. r_s indicates Spearman's rank correlation coefficient. ***: $p<0.001$.

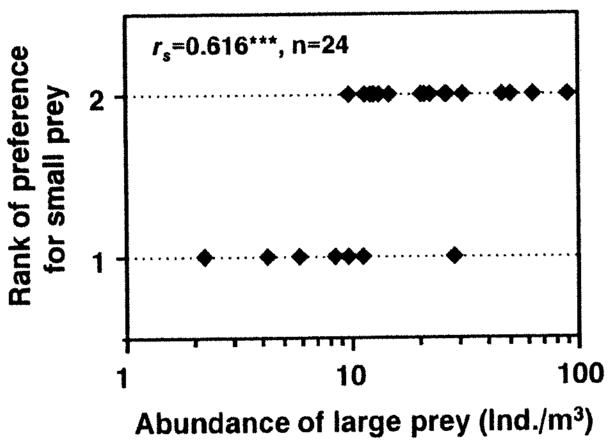


Fig. 4 Relationship between abundance of the small prey and the rank preference index of the small prey. r_s indicates Spearman's rank correlation coefficient. NS: $p>=0.05$.

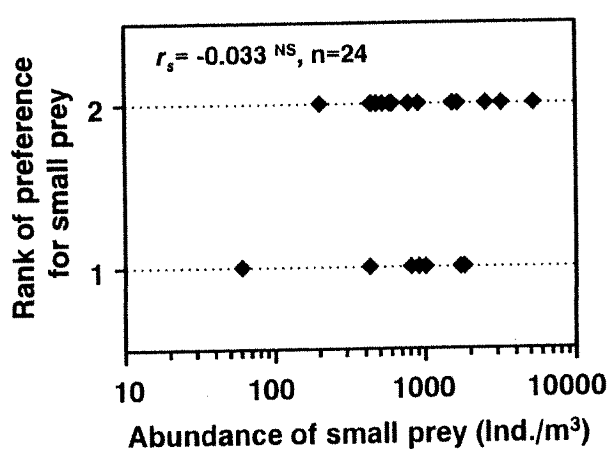
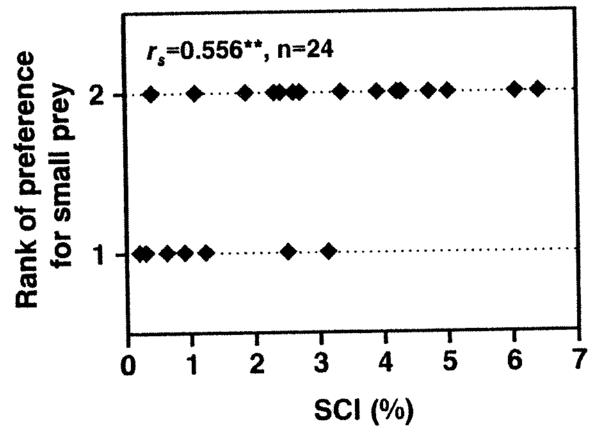


Fig. 5 Relationship between stomach fullness of fingerling chum salmon and the rank preference index of the small prey. The stomach fullness is indicated by SCI (relative weight of stomach contents per body weight). r_s indicates Spearman's rank correlation coefficient. **: $p<0.01$.



DISCUSSION

Estimation of Prey Abundance

We assumed that fingerling chum salmon inhabit near-surface waters shallower than 20 m in depth. However, there has been little research directed at determining vertical distribution of juvenile salmon at sea. Burgner (1991) concluded that salmon generally occur in near-surface waters by reviewing research and commercial high-seas salmon fisheries information. For chum salmon, both young and adult fish mostly swam above the 20-24m layer in the North Pacific Ocean from spring to autumn (Manzer 1964; Machidori 1967; French et al. 1971; Ogura and Ishida 1995).

The prey abundance was not significantly different between dawn and day at most stations. This result was supported by previous studies on the diel vertical distribution of major prey taxa found in this study. Euphausiid calyptopis larvae do not show diel vertical migration (Iguchi 1995). *Evadne nordmanni* and *Podon leuckarti* inhabited near-surface water throughout the day (Onbe 1974). This distribution pattern is also observed with *Neocalanus plumchrus* CV in the spring (Fulton 1973; Taka et al. 1982). *Calanus sinicus* and euphausiid furilia larvae migrate down below the range of our zooplankton sampling, but they descend to this habitat before dawn (Hirakawa et al. 1990; Uye et al. 1990; Taki et al. 1996). For *Oikopleura* spp., there is little information of diel vertical migration; however, Shiga (1985) reported that their vertical distribution is governed by hydrographic conditions and that they are homogeneously distributed when the water column is vertically mixed. Since the water column had not yet stratified throughout this study period (Suzuki and Fukuwaka, unpublished data), the vertical distribution of *Oikopleura* spp. would not change greatly on a daily basis.

Factors Affecting Prey Size Selectivity

Fingerling chum salmon showed two behavioral patterns: selective foraging for large prey and non-selective foraging. Selection for a larger prey has been previously observed in various particulate planktivore fishes, including chum salmon (see Sawara 1987; Salo 1991; Gerking 1994; Higgs et al. 1995). Size is recognized as one of the most important characteristics of prey affecting selection in particulate planktivores (Kislalioglu and Gibson 1976). It has been suggested that selection for larger prey can be attributed to their higher visibility (Ware 1972; Confer and Blades 1975) and a higher rate of energy intake per prey item (Werner and Hall 1974; Ringler 1979b).

Fingerlings foraged selectively for large prey with increasing abundance of the large prey, irrespective of the abundance of the small prey. Indicies for measurement of foraging selectivity, in general, can vary depending on the relative abundance of prey items in the environment and on the relative number of prey in the diet. In this study, however, the relative abundance of prey in the environment was not related to the variation in prey size selectivity, because small prey were consistently more abundant than large prey in the environment. Selective foraging for large prey resulted when fingerlings fed more on large prey than small prey. Consequently, the observed variation in prey size selection by fingerling chum salmon reflects a foraging behaviour of particulate planktivore fishes where frequency of predation on small prey was higher when large prey were relatively rare irrespective of the abundance of small prey (Sunaga 1970, 1971; Eggers 1982).

Selective foraging was indicated by fingerling chum salmon that contained a relatively large amount of food in their stomachs. Ivlev (1965), Hart and Ison (1991), and Hart and Gill (1992) examined the effect of stomach fullness on prey selection of particulate feeding fishes by observing their foraging behaviour directly until fish reach satiation. They demonstrated that as fish approached satiation, they became highly selective and ate only preferred prey. Although we could not clarify the level of hunger when the fingerlings started feeding, previous studies suggest that the rate of preferred prey in diet would increase with an increase of stomach fullness.

Sawara (1987) suggested that a change in prey selection with prey abundance may only reflect the change with fish stomach fullness, since he speculated that the best index that fish can use to evaluate prey abundance would be their stomach fullness and that feeding intensity in general would relate positively to prey availability. Contrary to this hypothesis, we demonstrated that prey abundance and stomach fullness independently affect prey selection, which is consistent with the experimental study by Hart and Ison (1991).

Although we could not clarify a ecological and physiological explanation for the variation in prey size selectivity of fingerling chum salmon from this empirical study, some quantitative experiments have succeeded in explaining the prey selection of particulate planktivore fishes functionally or causally (e.g., Werner and Hall 1974; O'Brien et al. 1976; Ringler 1979b; Hart and Gill 1992). Such a study is needed to further understanding of prey selection by fingerling chum salmon.

CONCLUSIONS

The present study indicated that prey size selectivity by fingerling chum salmon in sea life is variable. We pointed out both extrinsic and intrinsic factors, such as abundance of a larger prey and stomach fullness of fish as important factors affecting the variation. These two factors were positively related to the selectivity for a larger prey.

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