Customizing material into embodied cap by sponge crab

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Abstract

Getting camouflaged with environmental material can improve survivability of animals. How animals select and fit some material into their body design remains unclear. To address the question, we examined the cap making behavior of the sponge crab, *Lauridromia dehaani* that carries a natural sponge as a cap. We analyzed their preference to the size of artificial sponge, the whole area size of the cap that the crabs cut off, and its hole size of the caps that the crabs customize to make it suitable for their body. Three different sizes of artificial sponge were given to the crabs experimentally so that they chosen one sponge among them. We video recorded the process of the cap making behavior, and measured the size of caps. Although a particular fixed behavioral pattern was observed in the cap making behavior, the choice and hole size considerably varied even in a single individual. To fully consider the individuality, we constructed statistical models including hierarchical models. We infered the posterior distributions of the parameters in several models, and built up the predictive distributions of the models by a Bayesian approach. The model selection based on WAIC (Widely-Applicable Information Criterion) and posterior information from the models revealed that large individuals tended to choose large sponges with the variability specific to each individual. Furthermore, the individual-specific tendency was found in the relationship of the carapace width and the cap hole size. These analyses imply that the crabs update the cap making behavior by recalibration, given that they have to molt to become large. These findings might give a new insight into body extending capability of crustaceans.

Key words: embodiment, camouflage, sponge crab, hierarchical Bayesian approach, tool making

Introduction

Extending body by attaching some living or non-living material obtained from the environment is widespread in the animal kingdom. After some material is attached, it is often to be assimilated into a whole body in vertebrates and invertebrates (Blanke and Metzinger, 2009; Sonoda et al., 2012; Wilby et al., 2018). Even if the material is not appropriate to the design by themselves, animals can make them suitable by processing and customizing them (Hunt, 1996). However, how animals select suitable material and how they process them to embody the material under controlled experimental condition, remain obscure.

The behavior of the marine crabs decorating themselves can offer a clue to address the questions. They are known to use materials such as Porifera, Ascidiacea, or algae. The majid crabs decorate themselves with some sponges and algae (Maldonado and Uriz, 1992; Wicksten, 1993; Bedini et al., 2003; Berke and Woodin, 2008; De Carvalho et al., 2016). Crabs of the family Dromiidae (Dembowska, 1926; Mclay, 1983; Bedini et al., 2003), Homolidae (Wicksten, 1985; Braga-Henriques et al., 2011; Capezzuto et al., 2012), and Dorippidae (Bedini et al., 2003) are reported to carry sponges and ascidians. It is suggested that these behaviors are mainly camouflage and defense to predators (e.g. Thanh et al., 2005). In particular, the toxic character of sponges is more effective to protect crabs against the attacks of predators (e.g. Bedini et al., 2003).

Among these crabs, dromids can detach sponges or ascidians from the substrate and make caps (Dembowska, 1926; McLay, 1983). The cap has concave surface on the bottom, and the dromid crabs put it on to their back. The crabs have a fixed spine on the propodus of the fourth and fifth pairs of the pereiopods, and the dactylus can move opposite direction, so they can use the legs just like chelae to grasp and stretch the cap (Fig. 1A).

In the field research, one study dealt with the preference of dromids to materials for caps and the correspondence of the size of cap to the size of crab (McLay, 1983). It is reported that *Cryptodromia hilgendorfi* use the caps made by many species of sponges, but they prefer the sponge *Suberites carnosus,* and the crabs make sponge caps twice as large as the carapace area. In the research, natural sponges were used for making caps and the hole size was not measured.

In the experimental research, the preference to the size of material and the suitability between the size of crabs and the caps are scarcely investigated. Dembowska (1926) reported qualitatively that the size of caps made by *Dromia personata* (reported as *D. vulgaris*) with paper is as large as the size of those that the crabs originally carried. *Dromia personata* mainly uses sponges and ascidians (Bedini et al., 2003), while they can also make caps with paper (Dembowska, 1926).

In this study, we focused on a species of sponge crab: *Lauridromia dehaani*. In order to experimentally control the sponge size and its condition, we gave different sizes of artificial sponges to the crabs. We examined the relationship of the carapace size with the size of sponge the animal select, the size of cap holes, and the time they took for cap making. To explore and extract the patterns from these relationships with the individuality specific to each animal, we constructed the statistical models implementing the individuality as hierarchical structure in the parameters. We applied the models to the data and computed the posterior distribution of the parameters by a Bayesian approach. The predictabilities of the multiple models were evaluated by the widely applicable information criterion (WAIC, Watanabe, 2010), because it can be applicable to the cases that the posterior distribution of the parameters does not resemble any normal distribution such as hierarchical Bayesian models(Watanabe, 2018).

Materials and methods

Animal collection

From December 2015 to April 2017, 38 individuals (20 males, 18 females) of *Lauridromia dehaani* (Brachyura: Dromiidae) were obtained from the Sakai fishing port, Minabe town, Wakayama prefecture, Japan (33° 44'N, 135° 20'E). We conducted the experiments in the tanks at Shirahama Aquarium, Seto Marine Biological Laboratory, Kyoto University (33° 41'N, 135° 20'E), from December 2015 to June 2017. Before the experiments, all individuals were maintained in the tanks (19.5–23.8 $°C$) of the aquarium more than two days to make them get used to the environment. We measured the carapace width of them (Fig. 1B), and the individuals were divided into five classes whether they lacked any of the fourth and fifth pereiopods: (A) only one of them was absent, (B) either of both side were absent, (C) both of the fourth and fifth of each side were absent, (D) more than three were absent, (O) none of the fourth and fifth pereiopods were absent. In this study, the specimens that classed B or D were not collected, so that we just used the categories, A, C, and O.

Experimental setup and procedure

We cut the melamine sponge into three classes of size (S: 20 mm × 30 mm × 40 mm, M: 30 mm × 60 mm × 85 mm, L: 30 mm × 140 mm × 150 mm). Each sponge was put pseudorandomly to the either sides and the center behind of the cage (700 mm × 470 mm × 190 mm, Fig. 1C), which floated in the tank. Then, crabs were introduced to the front center of the cage, thereby the distance between each sponge and the crab was equal.

We checked whether the crab carried any sponge once a day in the morning. If it did, we collected the sponge, otherwise the crab and the three sponges remained in the cage. When the crab did not carry any sponge for five days, we stopped the experiment. First we performed one experiment for one individual, but five experiments for one individual after February 2017 to examine the individuality of the behavior. We throughly desiccated the sponges that the crabs processed, measured the whole area of them, and the area of the hole (Fig. 2) by taking pictures from 46 cm above the sponges.

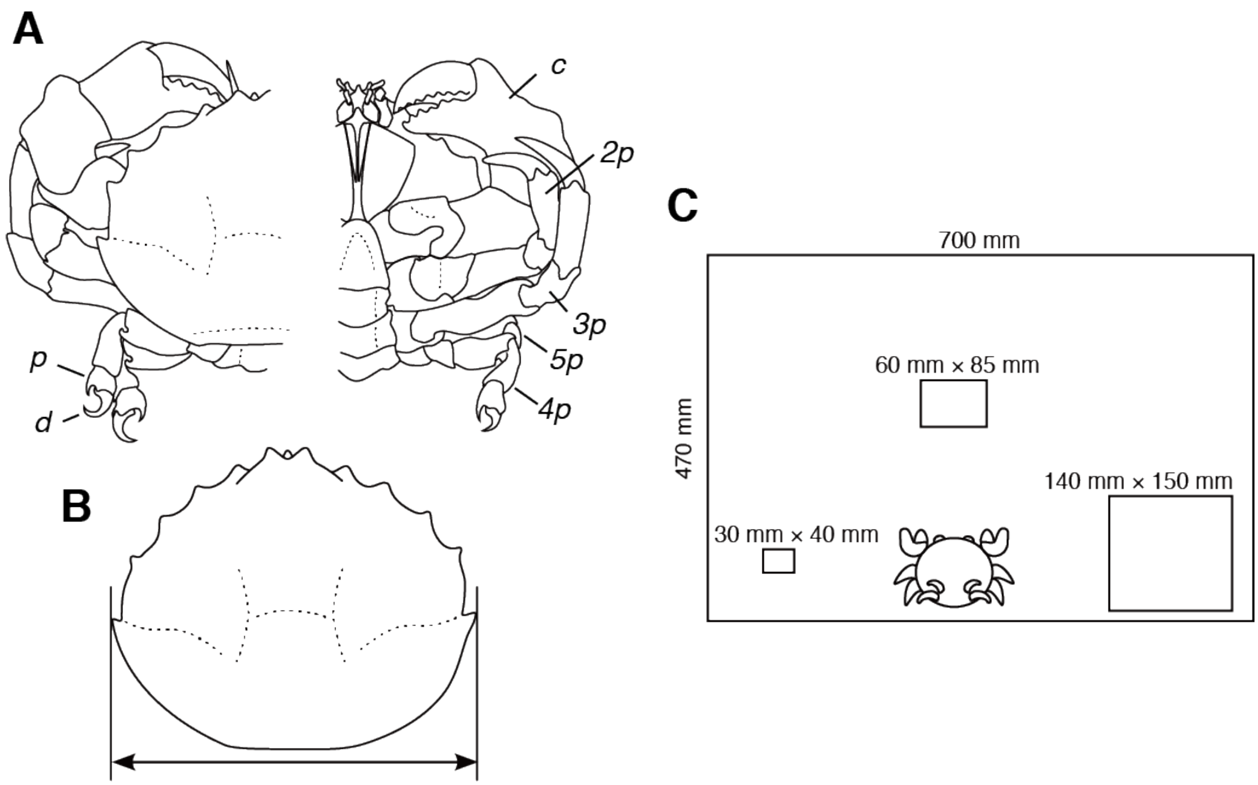

Figure 1: **Experimental animal and setup.** (A) A drawing of *Lauridromia dehaani*; p—propodus of fifth pereiopod; d—dactylus of fifth pereiopod; c—chela (1st pereiopod); 2p—second pereiopod; 3p—third pereiopod; 4p—fourth pereiopod; 5p—fifth pereiopod; (B) carapace width; (C) position of the three different sizes of sponge and the crab in the experiment.

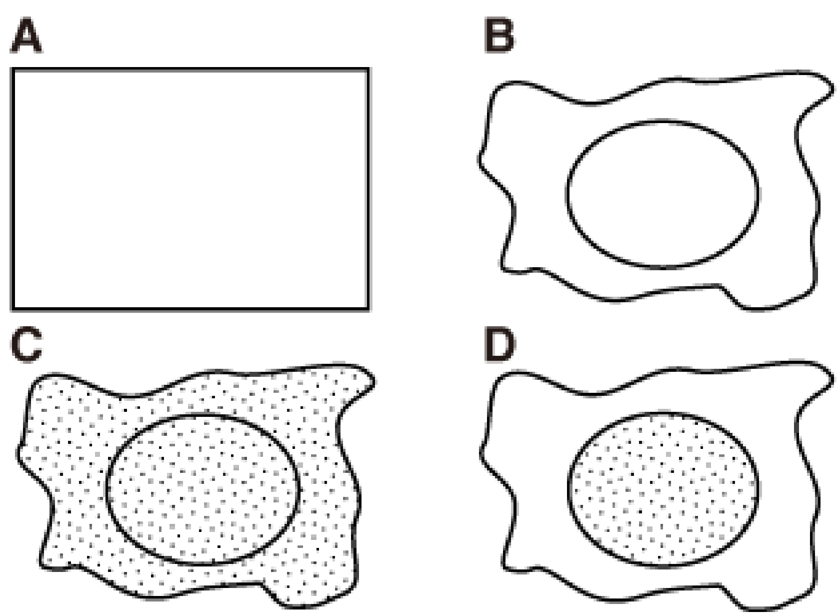

Figure 2: **The examples of the area of sponge.** (A) a sponge before process; (B) after process; (C) the whole area of this sponge; (D) the area of the hole.

Statistical modeling

In order to quantify and extract the structure of the behavioral aspects including individuality, we explored 26 statistical models constructed for the four different aspects of the behavior: (1) choice of sponge size (6 models), (2) cutting behavior (8 models), (3) cap hole making behavior (6 models), (4) time until carrying the sponge (6 models). In either case, we have constructed the models that explicitly includes individuality as the hierarchical (or multi-level) models and computed the posterior distribution of the parameters. We implemented the models in a probabilistic programming language Stan (Stan Development Team, 2017; Matsuura, 2016). We used non-informative uniform priors for the parameters unless it is explicitly described. The performed sampling from the posterior distributions using No-U-Tern Sampler (NUTS), which is implemented as a Hamiltonian Monte Carlo (HMC) sampler. Whether the sampling was converged was diagnosed by trace plots and quantitatively via the Gelman-Rubin convergence statistic, R_{hat} (Gelman and Rubin, 1992). All of the draws were judged to converge when $R_{hat} < 1.10$.

We compared the predictabilities of the models using WAIC (Watanabe, 2010). To give the essense of the models, we will explain only the best performed models in terms of WAIC in this section. The other models are, for example, without the explanatory variables or without the individuality (Table 2). It should be noted that WAIC can be computed in different ways depending on what we want to predict the data (Watanabe, 2018). In our case, we are interested in the prediction of a new data when we get a new individual and get a new behavioral act instead of the prediction of a new behavioral act from the individuals sampled in this study. Therefore, for the hierarchical models, we have to integrate out the parameters applied to each individual. We performed numerical integration of the local parameters defining the hierarchy to average out. For facilitating the understanding of this point in more simpler linear models, see the post(http://rpubs.com/katzkagaya/460937).

All the computations were performed in the statistical environment R(R Core Team, 2018) and the Stan codes for each model were compiled and executed through the R package *rstan* (Stan Development Team, 2017). All the source codes and data are available from a gist repository (https://gist.github.com/kagaya/3188dd0a4571b068e501aeef9863e255).

behavioral choice of material size (model 1_1)

The tendency to a choice of a certain sponge $\mu[n, m]$ ($m = 1, 2, 3$ for M, L, no choice, respectively) is expressed as the linear predictor in terms of the carapace width, $Cwidth[n]$ and the degree of leg lack, $LegLack[n]$. The choice for M size was fixed to zero, and the parameters of other two choices were infered as the comparison with the M size choice.

$$\mu[n,1] = 0$$

$$\mu[n,2] = a_{choice_L}[ID[n]] + b_{choice_L} * Cwidth[n] + c_{choice_L} * LegLack[n]$$

$$\mu[n,3] = d_{choice_0}[n] + e_{choice_0} * Cwidth[n] + f_{choice_0} * LegLack[n]$$

$$n = 1, ..., N_{act}$$

N_{act} is the total number of the behavioral acts. ID represents animal identity. The local parameters $a_{choice_L}[ID[n]]$ are the intercepts for each individual. The parameter $d_{choice_0}[n]$ does not include individuality as represented, because the choice of "no choice" observation was only from one individual. The $a_{choice_L}[ID[n]]$ as a random variable is subjected to normal distribution with the mean $a_{choice_{L0}}$ and standard deviation $a_{choice_{Ls}}$.

$$a_{choice_L}[k] \sim Normal(a_{choice_{L0}}, a_{choice_{Ls}})$$

$$k = 1, ..., N_{animal}$$

The actual choice $Choice[n]$ is subjected to the categorical distribution via the softmax function.

$$Choice[n] \sim Categorical(softmax(\mu[n,])), n = 1, ..., N_{act}$$

cutting behavior (model 2_1)

The probability $\phi[n]$ for the decision whether the animal cut off the sponge can be linked to the linear predictor with the terms of carapace width, $Cwidth[n]$ and selected sponge size, $Choice[n]$.

$$\phi_{cut}[n] = InverseLogit(a_{cut}[ID[n]] + b_{cut} * Cwidth[n] + c_{cut} * Choice[n]), n = 1, ..., N_{act}$$

The parameters $a_{cut}[ID[n]]$ are the intercepts for each individual. The $a_{cut}[k]$ is subjected to the normal distribution with the mean a_{cut_0} and the standard deviation a_{cut_s}.

$$a_{cut}[k] \sim Normal(a_{cut_0}, a_{cut_s}), k = 1, ..., N_{animal}$$

The prior of a_{cut_s} is subjected to the half t distribution.

$$a_{cut_s} \sim Student\_t^{+}(4, 0, 50)$$

How much the animal removed the sponge on average $\lambda[n]$ also can be linked to the linear predictor with the same terms by the log link function.

$$log(\lambda_{cut}[n]) = d_{cut}[ID[n]] + e_{cut} * Cwidth[n] + f_{cut} * Choice[n], n = 1, ..., N_{act}$$

The parameters $d_{cut}[ID[n]]$ is the other intercepts for each individual. The $d_{cut}[k]$ is subjected to the normal distribution with the mean d_{cut_0} and the standard deviation d_{cut_s}.

$$d_{cut}[k] \sim Normal(d_{cut_0}, d_{cut_s}), k = 1, ..., N_{animal}$$

The prior of d_{cut_s} is subjected to the half t distribution.

$$d_{cut_s} \sim Student\_t^{+}(4, 0, 10)$$

Altogether, the measured quantity of how much the animal removed the sponge as the response variable $Removed[n]$ is subjected to the zero-inflated poisson distribution (ZIP) with the parameters $\phi_{cut}[n]$ and $\lambda_{cut}[n]$.

$$Removed[n] \sim ZIP(\phi_{cut}[n], \lambda_{cut}[n]), n = 1, ..., N_{act}$$

When the crab skipped cutting behavior, the $Removed[n]$ was set to zero even if the sponge size is smaller than the defined sizes of M or L due to measurement error. Additionally, the $Removed[n]$ was rounded to integer to apply this model. The rounding process was judged to have no impact to the data distribution.

cap hole making (model 3_1)

To examine how the cap hole size $HoleSize[n]$ is explained by the carapace width $Cwidth[n]$, the gamma distribution was chosen to represent non-negative hole size data. The shape and rate parameters were given as follows,

$$HoleSize[n] \sim Gamma(shape, shape/exp(a_{hole}[ID[n]] + b_{hole} * Cwidth[n])), n = 1, ..., N_{act}$$

where the rate parameter was given as the shape over the log linked linear predicter. The $a_{hole}[ID[n]]$ are the intercepts for each individual. The $a_{hole}[k]$ is subjected to the normal distribution with the mean a_{hole_0} and the standard deviation a_{hole_s}.

$$a_{hole}[k] \sim Normal(a_{hole_0}, a_{hole_s}), k = 1, ..., N_{animal}$$

time for making (model 4_1)

We assumed that the time for making until the animal carries the sponge, $Days[n]$, which is similar to the $Removed[n]$ case, is subjected to the ZIP distribution.

$$\phi_{day}[n] = InverseLogit(a_{day})$$

$$log(\lambda_{day}[n]) = b_{day}[ID[n]] + c_{day} * Cwidth[n]$$

$$b_{day}[k] \sim Normal(b_{day_0}, b_{day_s}), k = 1, ..., N_{animal}$$

$$Days[n] \sim ZIP(\phi_{day}[n], \lambda_{day}[n]), n = 1, ..., N_{act}$$

As described above, we also considered the individuality so that the parameters $b_{day}[ID[n]]$ were incorporated into this model.

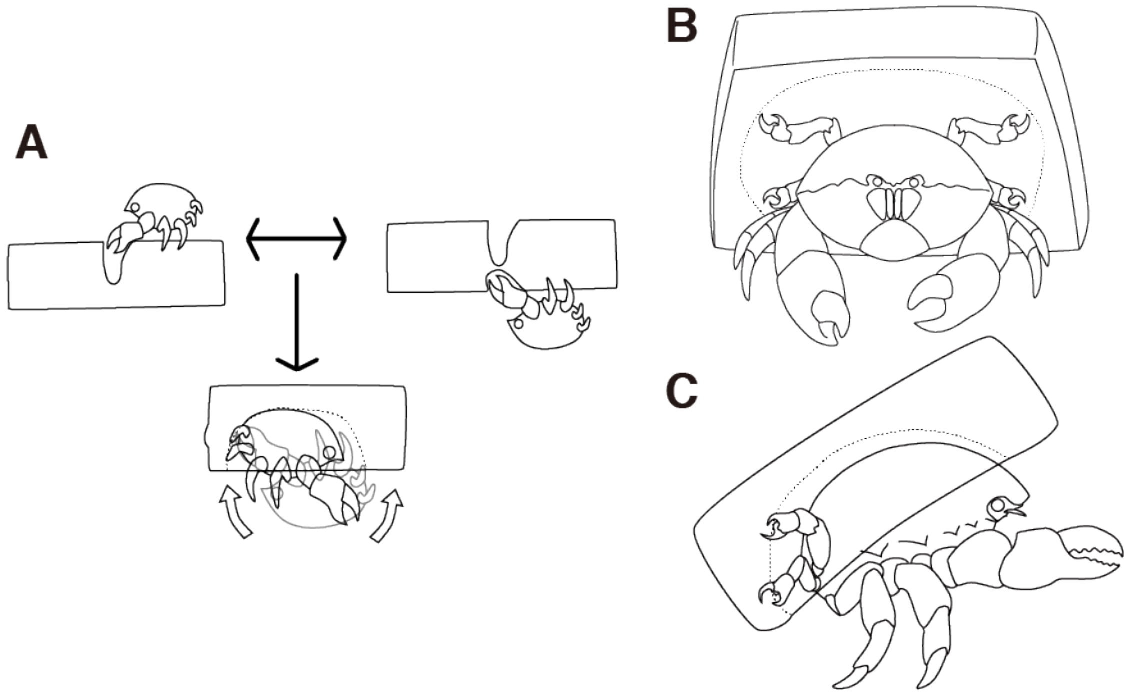

Figure 3: **The cap making behavior consists of cutting to change size of cap, digging to change size of hole, and carrying to extend the body.** (A) The cap making behavior. *L. dehaani* grasps either side of the sponge and tears off small pieces of sponge to make the groove. After cutting the clod of sponge, the crab makes the hole on it. Then the crab rotates their body backward and grasps it by the fourth and fifth pereiopods. It often happened that the crab rotated their body forward and dug it repeatedly to make the hole larger. (B–C) The carrying behavior of the crab. It carries a cap made from an artificial sponge. (B) Frontal view; (C) Right side of the crab; The tips of dactylus of the fourth and fifth pereiopods elongate in opposite directions and grasp the sponge tightly.

Results

Cap making behavior

The crabs usually made their caps at night. They usually grasped either side of the sponge by the second and third pereiopods (Fig. 1A). They teared off small pieces of sponge by chelae (Fig. 3A upper left, upper right, S1). Sometimes they moved to another side of sponge. By repeating these behaviors, the crabs made the groove to cut off the clod of sponge. After cutting, the crabs made a hole by tearing off small pieces of sponge (Fig. 3A bottom, S2). It took 14 minutes to dig the hole on average (3 individuals, 7 trials). The chelae of larger crabs tore off larger pieces of sponge. Then the crabs rotated their body backward in order to catch it by fourth and fifth pereiopods while they kept the clod grasping by second and third pereiopods. Finally, the crabs released second and third pereiopods from the cap, and began to carry it (Fig. 3B, C). The

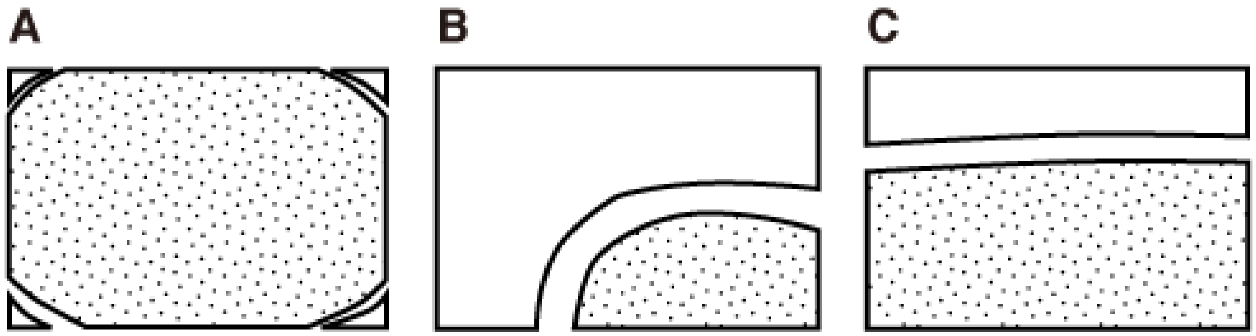

Figure 4: **The patterns of cutting**; (A) cutting the four corners; (B) cutting elliptically; (C) cutting linearly; The crabs carried the dotted area.

tip of dactylus of fourth and fifth pereiopods elongates in opposite directions each other permitting to grasp the caps tightly. In the digging behavior, it often happened that they rotated their body forward and dug it to make the hole larger. They repeated this process up to eleven times per one night and it took up to five hours. Only one crab stopped the cutting behavior in halfway and changed the position of the sponge to remove. The other crabs never showed such a trial-and-error behavior in cutting. When the crabs rotated their body, the direction of the rotation was maintained along with the sponge.

On average, it took 50 minutes for the crabs to cut the clod (2 individuals, 10 trials), and almost all the crabs started digging as soon as they finished cutting. The cut sponge showed three patterns (Fig. 4). They cut off (1) the four corners of the sponge, (2) one corner of it elliptically, (3) two corners of it linearly. While the crabs cut the sponge, they actively moved around the sponge. In contrast, they persistently kept under the sponge during digging to make a hole. Sometimes the crabs did not show the behavior. Only one crab just cut the sponge and did not dig, 18 crabs skipped cutting in 28 trials, and 5 individuals abandoned the both of the behaviors in 5 trials.

Cap choice

The behavioral choice of the sponges was better explained by the carapace width (Fig. 5). The larger crabs tended to choose L size sponge. However, the crabs whose carapace width becomes larger than 9 cm did not choose the sponges. The parameters b_{choice_L} and e_{choice_0} for the carapace width were estimated to be larger than zero, whereas the c_{choice_L} and f_{choice_0} for the degree of leg lack overlapped zero. The percentiles of the parameters were summarized (Table. 1).

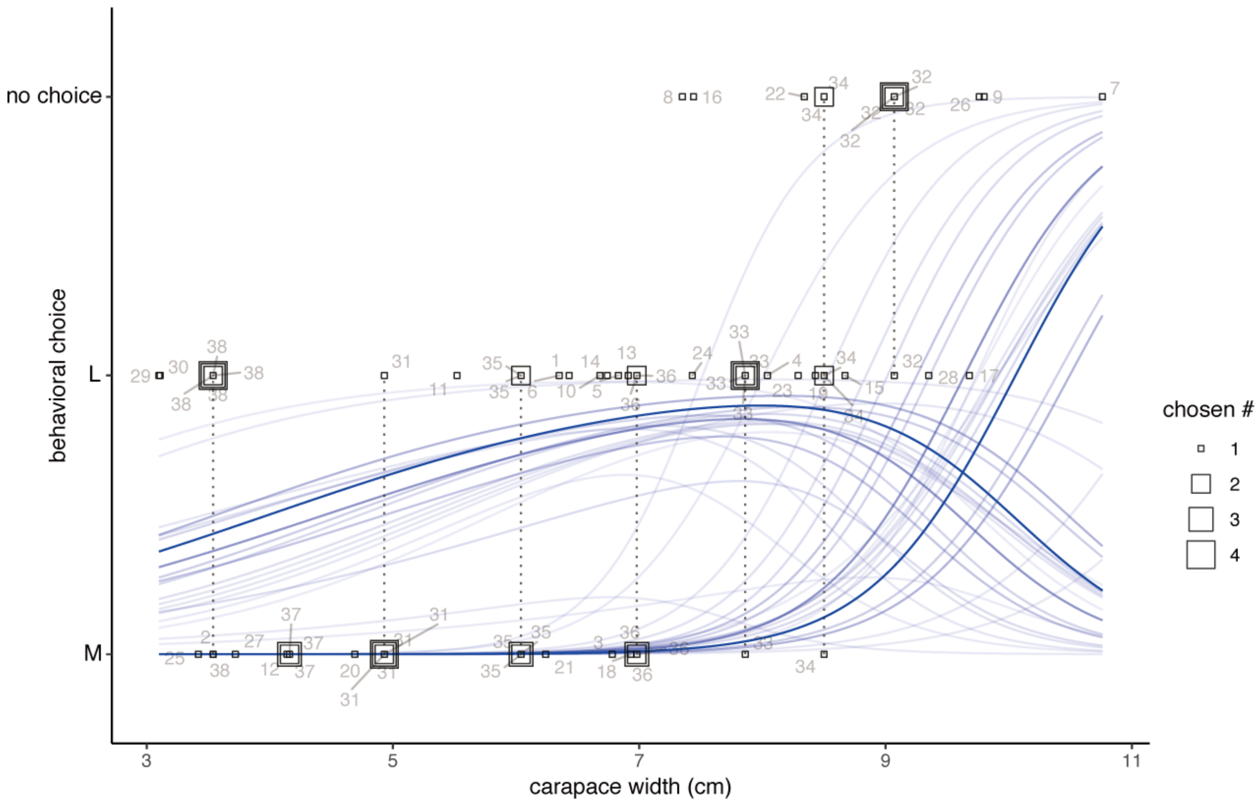

Figure 5: **The larger crabs selected larger sponges, but when the size becomes larger than about 9 cm, they abandoned the choice itself.** The blue lines constructed from ten samples from the poterior distribution of the parameters on the best performed model 1_1 (Table 1, 2) and represent the probabilities of the choices when compared with the choice of M size sponge. .

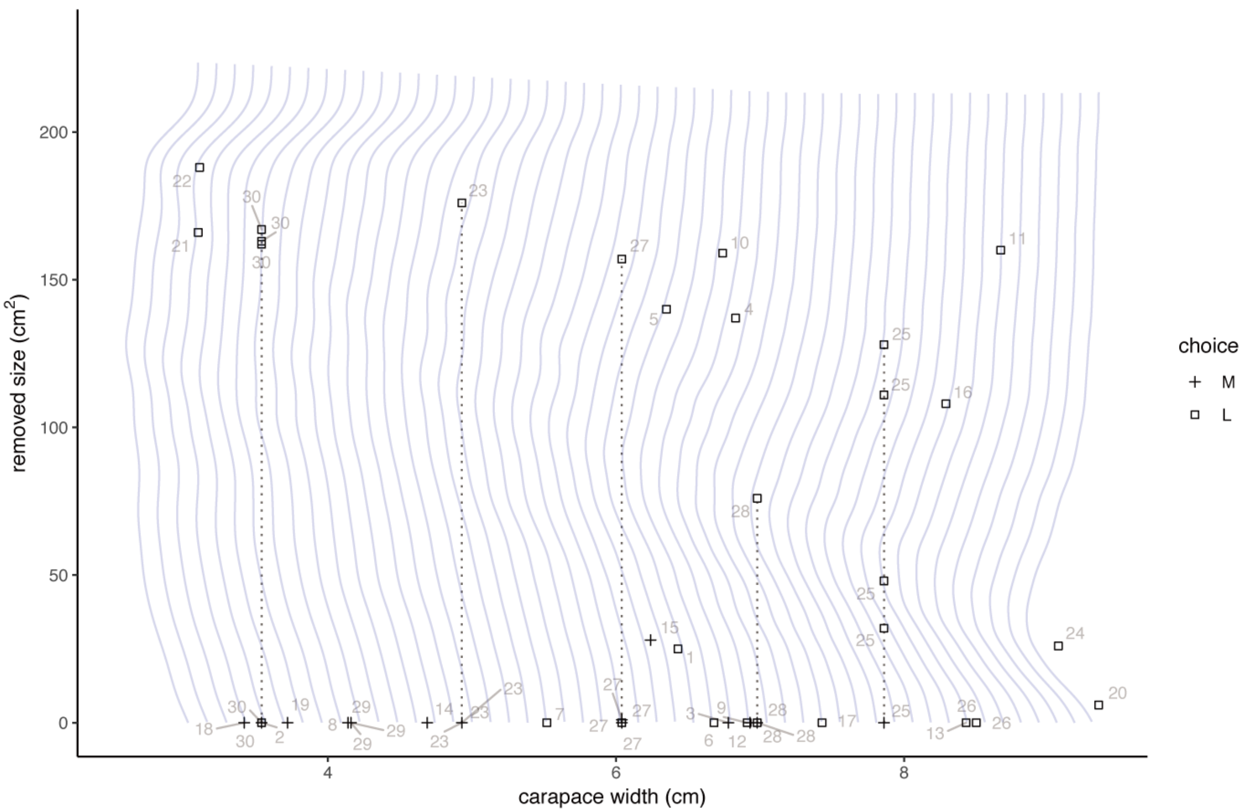

Figure 6: **How much the sponge was removed by cutting by the animals decreases with the carapace width increases.** When the animals choose the M size sponges, almost all of animals decided not to remove the sponge, whereas they removed the sponge in relation to their body sizes when they choose the L size sponges. The dotted lines connect the points from one individual and the labels close to the open squares indicate IDs of the individuals. The blue lines indicate the posterior distribution of the λ_{cut} in the best performed model 2_1 (Table 1, 2) when the choice is fixed to L size sponge.

Cutting behavior

The cutting behavior showed two paths. One path was that the crabs decided to cut off the sponge and then decided how much they cut off the sponge. The other path was that they skipped cutting off, then they started digging. For the first path, the non-zero data points indicating the removed size of the sponge decreased with the increase of the carapace width. For the second path, the data points are positioned at zero (Fig. 6). Our statistical analysis showed that the best performed model in terms of WAIC, was the model including the individuality. The probability to choose performing cutting behavior was neither explained by the carapace width (b_{cut} in Table 1), nor the selected sponge (c_{cut} in Table 1). On the other hand, the removed size was well explained. The smaller size of crabs tended to remove larger size of sponge to make caps (e_{cut} in Table 1). Additionally, the removed size was more remarkably explained by the chosen sponge size, because the 2.5 percentile of the f_{cut} was estimated to be larger than zero (Table 1). When the crabs chose the L size sponge, they tended to choose the first path. On the other hand, when they chose the M size sponge, in most cases they did not showed the cutting behavior except for only one behavioral act.

Cap hole and body size

Among individuals carrying sponges, we compared the carapace width with the area size of cap hole. The size increased with the carapace width (Fig. 7). Moreover, the model with the individuality best performed in the predictability (Table 2). The 2.5 percentile of the parameter b_{hole} was even larger than zero (Table 1).

Time for making process

There were no obvious relation between the carapace width and the number of days until the crabs carried the first cap, and a number of crabs had carried the cap by next day. The expected days to carrying was 0.611 on the best performed model (Fig. 8).

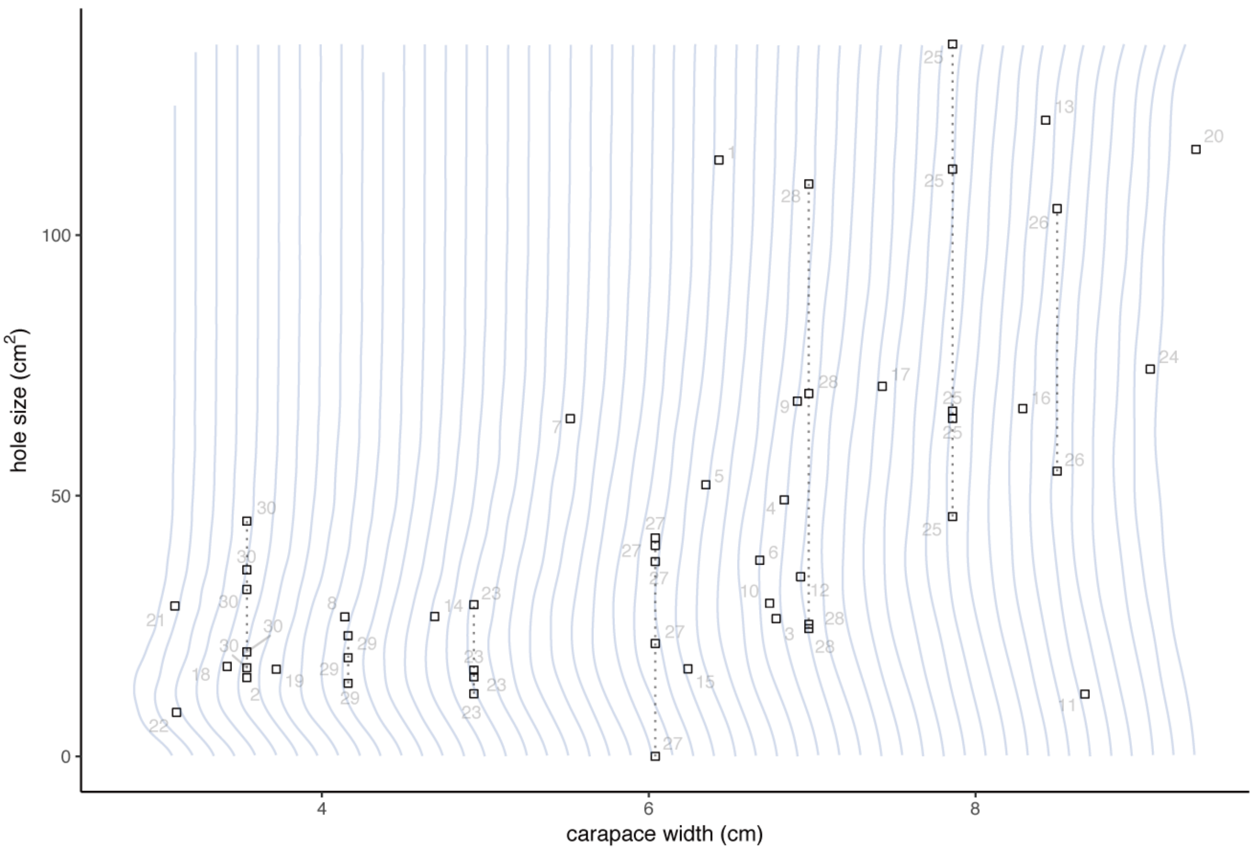

Figure 7: **The larger size of crabs made larger size of holes.** The ID numbers of the individuals are also shown close to the data points. The blue lines are infered predictive distribution on the best performed model 3_1 (Table 1, 2). The larger size of crabs made larger size of holes. Additionally, the probablistic deviation becomes larger when the size of crabs become larger.

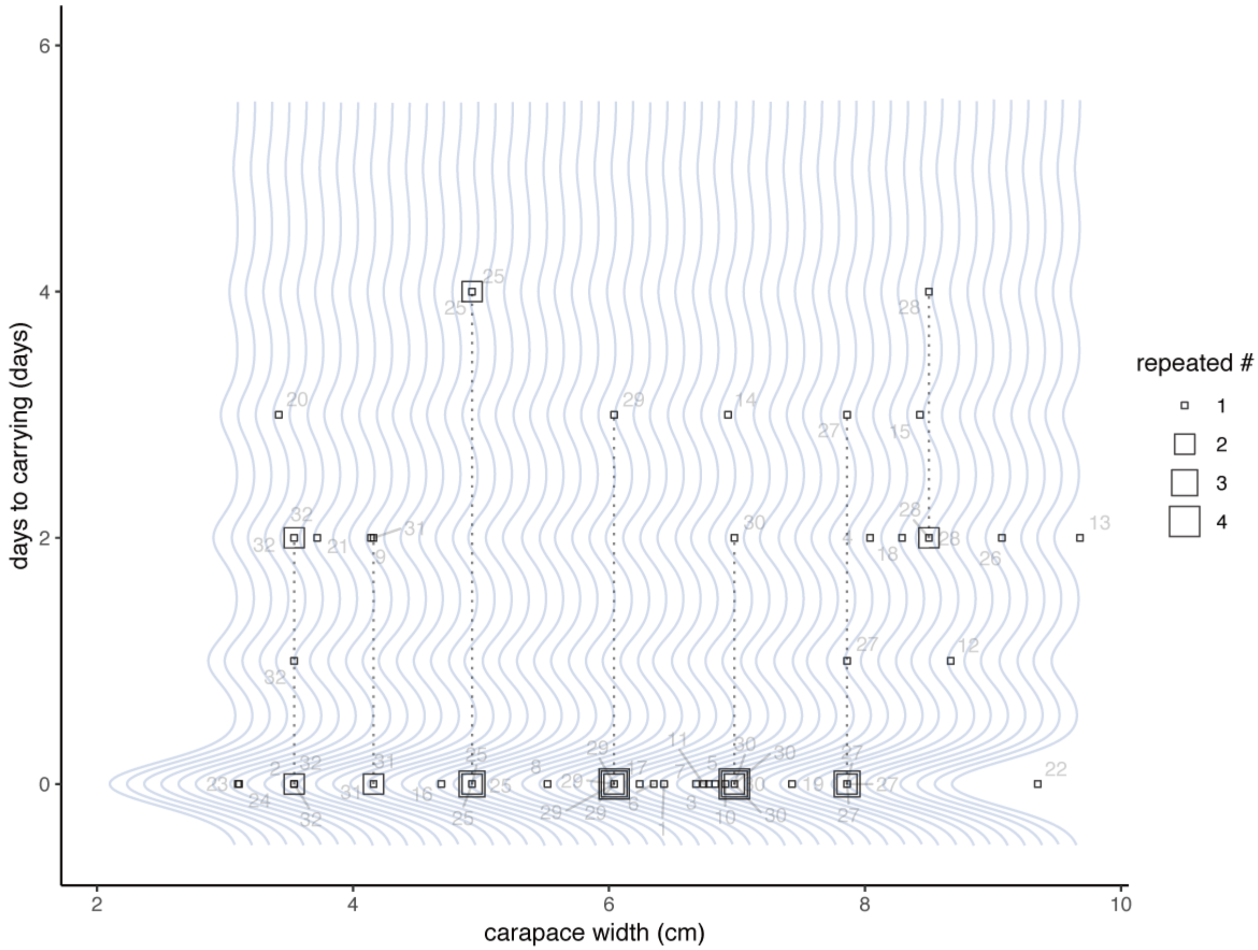

Figure 8: **How many days does it took for the crabs does not change with the carapace width.** The days that the animal took until carrying the sponge as a function of the carapace width are shown with the points and those from the same individual are connected with dotted lines and labels. The model with the carapace width as a explanatory variable was the best performed model. The blue lines represent the predictive distribution on the best performed model 4_1 (Table 1, 2).

Table 1: **The percentiles from the posterior distributions of the major parameters in the best performed models.**

behavioral aspects	parameters	2.5 percentile	50 percentile	97.5 percentile
choice	b_{choice_L}	0.115	0.721	1.970
	c_{choice_L}	-3.11	-0.264	1.914
	e_{choice_0}	1.233	2.467	4.885
	f_{choice_0}	-1.909	0.306	2.329
cutting	b_{cut}	-1.998	0.063	3.107
	c_{cut}	-27.64	-0.894	6.896
	e_{cut}	-0.645	-0.212	0.280
	f_{cut}	3.391	6.270	8.625
hole making	b_{hole}	0.168	0.273	0.378
days to carrying	c_{day}	-0.151	0.010	0.173

Table 2: **Models and their predictive performances quantified by WAIC.** Abbreviations used in the table are as following: intercept_L— intercept in the linear predictor (LP) for the choice of L; intercept_1(cutting section)—intercept in the LP for the decision of cutting; intercept_2(cutting section)—intercept in the LP for the mean of the removed size of the sponge; cw—slope in the LP for the carapace width; CW—carapace width; Leg—degree of the leg lack; _L and _NO—parameters for L sponge and no choice, respectively; Choice (cutting section)—choice whether to cut the sponge; Gender— gender of the animal; intercept_2 (days to carrying section)—intercept in the LP for the mean of the days to carrying; Choice (days to carrying section)—choice of sponge size.

response variable	model	individual difference	explanatory variables	link function	distribution	WAIC
choice	1_1	intercept_L	CW_L, Leg_L, CW_NO, Leg_NO	softmax	categorical	-2.01
	1_2	intercept_L	CW_L, CW_NO	softmax	categorical	-1.87
	1_3	intercept_L	-	softmax	categorical	-0.88
	1_4	intercept_L	Leg_L, Leg_NO	softmax	categorical	-0.78
	1_5	-	CW_L, CW_NO	softmax	categorical	0.85
	1_6	-	CW_L, Leg_L, CW_NO, Leg_NO	softmax	categorical	0.88
cutting	2_1	intercept_1, intercept_2	CW, Choice	logit, log	ZIP	-1.91
	2_2	intercept_2	CW, Choice	logit, log	ZIP	0.88
	2_3	intercept_2	Choice	logit, log	ZIP	0.99
	2_4	intercept_2	-	logit, log	ZIP	1.24
	2_5	intercept_2	CW	logit, log	ZIP	1.37
	2_6	-	CW, Choice	logit, log	ZIP	7.40
	2_7	-	CW	logit, log	ZIP	10.04

response variable	model	individual difference	explanatory variables	link function	distribution	WAIC
	2_8	-	-	logit, log	ZIP	12.53
hole making	3_1	intercept	CW	log	gamma	4.34
	3_2	-	CW	log	gamma	4.54
	3_3	-	CW, Gender	log	gamma	4.69
	3_4	intercept	-	log	gamma	4.71
	3_5	-	CW	identity	normal	4.75
	3_6	intercept, cw	CW	log	gamma	6.43
days to carrying	4_1	intercept_2	CW	logit, log	ZIP	0.99
	4_2	intercept_2	-	logit, log	ZIP	1.05
	4_3	-	-	logit, log	ZIP	1.28
	4_4	-	Choice	logit, log	ZIP	1.28
	4_5	-	CW	logit, log	ZIP	1.30
	4_6	-	CW, Choice	logit, log	ZIP	1.38

Discussion

Functional role of cap

It is expected that the crabs extending their body in order to camouflage and defend themselves (Dembowska, 1926; McLay, 1983; Bedini et al., 2003) with repellent effect of the sponge (e.g. Cariello and Zanetti, 1979). In particular, some homolid crabs are reported to carry not only sponges or ascidians but also sea anemones (Chintiroglou et al., 1996), and they drive away their predators with these materials (Braga-Henriques et al., 2011). As Bedini et al. (2003) expected, the main impulse of camouflaging crabs is to cover themselves even if the materials do not contain certain repellent chemicals. Similarly, the crabs in this study would carry caps to hide their body with top priority. One individual lacking third, fourth, and fifth pereiopods of the right side even carried the cap once during five trials. The crabs may prefer toxic materials, but no materials with the toxic chemicals available in this study. It is observed that sponge crabs carry not only sponges or ascidians but also sea anemones (Lavaleye and den Hartog, 1995) or lamellibranch shells (Wicksten, 1986), and it should be noted that *L. dehaani* in Shirahama aquarium sometimes carries not a few materials such as alcyonacean corals of the families Nephtheidae and Acanthogorgiidae or the cephalothorax of the exuvium of slipper lobster (*Scyllarides squamosus*).

Many similarities were observed in the cap making behavior of *L. dehaani* with other crabs such as *D. personata* and *C. hilgendorfi* (Dembowska, 1926; McLay, 1983). The crabs *C. hilgendorfi* make the caps usually during the night, and McLay (1983) expected that this is because making caps at night is probably less risky. It is likely that *L. dehaani* make caps at night for the same reason. From the video recordings we described all of the cap making behavioral sequence (Fig. 3), and the sponge crabs were found to process both natural sponges and artificial sponges in a similar way. However, in *C. hilgendorfi* it took 30 to 45 minutes for making and donning (McLay, 1983), but *L. dehaani* took longer times for making (50 minutes). In contrast to the case of *C. hilgendorfi*, *L. dehaani* repeated digging behavior up to eleven times, suggesting that there might be species specificity in the making time. In the larger time scales, there was no clear positive correlation between the size of crabs and the days to make caps (Fig. 8, Table 1). Dembowska (1926) qualitatively reported that the younger *D. personata* make caps earlier than old individuals. We counted the days the crabs took to make caps, but the time resolution would be too large to detect the correlation. Further study measuring the time with less time resolution such as minutes to hours might detect the correlation. Additionally, further controlled experiments for testing the time and the risk sensitivity will be required.

Making cost and size choice: why the crab abandoned carrying sponge?

There are not so many marine animals showing the decorating behavior, because this behavior would compel the animal to pay the energetic cost (Berke and Woodin, 2008). For example, the adult males of *Oregonia gracilis* tended to decorate less than the juveniles or adult females, and this would be because the energetic cost of the adult males to maintain their large claws increases and they could not pay the cost for decorating. In this experiment, the size of the crabs that did not carry caps was larger than that carried caps (Fig. 5). When they grow up to some extent, the number of predators for them would be limited and the energetic cost to make caps might increase so that larger individuals would not make the caps.

Another possibility for why the crabs abandoned carrying sponge is that the sponges used in this experiment were smaller than those of necessary size for the crabs. Dembowska (1926) reported that the proportion of caps to the size of *D. personata* tended to decrease with the size of the crabs, and considered that this was because there were few sponges fitting to the large crabs. Similarly, the large crabs that abandoned the choice itself, would carry the cap if the sponge size would be larger than the L size sponge. In contrast, there were no individuals that carried the S sponge in this study. This may be because it was too small for all of the crabs to carry. It is likely that the crabs younger and smaller than those we used in this experiment would carry the S sponge.

The degree of lack of carrying legs is considered not to decrease the probability of sponge choice, because the posterior distribution of the parameter f_{choice_0} largely overlaps zero (Table 1). This might support that the advantages of carrying sponge overcome the disadvantages even if they lack the legs for carrying.

Assimilated extended body

To make the living or non-living materials suitable to the animal body design, the animals choose and sometimes customize the material. Hermit crabs are well known to prefer specific shells (Bertness, 1980; Hazlett, 1981; Wilber, 1990). Although hermit crabs can not modify the shells by themselves, for example, the terrestrial hermit crabs, *Coenobita rugosus*, are suggested to recognize and learn the shape of extended shells and the surrounding terrain. When the experimenter attached a plastic plate to change the shell size, the hermit crabs adapted to the new shell by swiftly changing their walking behavior (Sonoda et al., 2012). In our study, we demonstrated that not only the crabs chose the size of sponges (Fig. 5), but also they cut off the suitable size of sponge (Fig. 6) and made the suitable size of hole in the sponge (Fig. 7).

Moreover, in either case of the statistical models, the models including the individuality outperformed the other models without it in terms of the model predictability. In order to control the quality and size of the sponges, we used artificial sponges in this experiment. Although the sponge was artificial, they have the great potential of making caps fitting to their own body. We finished the trial when the crab carried the cap, but sometimes observed the individuals showing modification by digging after they carry caps. Hence, it is likely that if we continue recording, the animals will be able to obtain more suitable sponge caps.

Among vertebrates, the primates such as chimpanzees and gorillas (e.g. Boesch and Boesch, 1990; Breuer et al., 2005) and the birds such as crows (Hunt, 1996; Matsui and Izawa, 2017) have been studied as tool users. On the other hand, among invertebrates, it is known that octopuses use coconuts as defensive tools (Finn et al., 2009) and insects, for instance bumblebees, are able to perform the task in which they have to use surrounding materials (Loukola, et al., 2017). Some crustacean, such as green crabs and American lobster are able to perform instrumental conditioning (Abramson and Feinman, 1990; Tomina and Takahata, 2010). Our findings demonstrated that the crabs can update the cap size depending on the current body size during inter-molt period. It is observed that the sponge crab repeatedly modified the cap to fit it to their body. Therefore, the crabs have a potential to learn to know the body size and perform the cap making behavior. Additionally, it is probable that the crabs also take advantages of the shape and the size of the body itself as a guide. Almost all of the cutting behavior did not include the trial-and-error process, suggesting that some topdown mechanisms might unlerlie the behavior. Further behavioral and neurophysiological experiments can clarify how they recognize their own body design such as size and shape, and how the information is integrated into making embodied cap.

Supplementary information

The movie of cutting and digging behaviors were attatched as supplementary movies.

All the source codes and data are available from a gist repository, https://gist.github.com/kagaya/3188dd0a4571b068e501aeef9863e255.

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Competing interest

We have no competing interest.

Authors' contributions

Keita Harada conceived the experimental design and performed the experiments. Katsushi Kagaya performed statistical modeling. KH and KK wrote the paper.

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