Individuality emerging in cap making by sponge crab

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Abstract

To get camouflage successful, an animal and camouflage as a body-part need to be integrated into the environment. When an individual grows, the camouflage is usually modified to maintain integrity. How does the animal maintain the whole body-camouflage system as an individual? We studied the cap making behavior of the sponge crab, *Lauridromia dehaani* that can carry an artificial sponge as a cap. We obtained the behavioral data including repeated samples from the same individual. The multilevel or hierarchical models are often used to deal with the clustered data. However, the evaluation of the appropriateness of the hierarchical model is a challenge in statistical modeling. This is because the hierarchical model is a statistically non-regular model. Here, we apply marginal-level WAIC (Widely Applicable Information Criterion) to assess the appropriateness of the assumption of the hierarchical structure. We found that the hierarchical models remarkably outperformed non-hierarchical ones in decision making of material size and cap making by the crab, although the performance improvements of the models were small for cap hole making. Our analyses revealed that not only large individuals tend to choose and shape large caps, but also the individual-specific bias emerges in the behavior.

Introduction

Animals sometimes use environmental materials to camouflage themselves in their environment. [7] [42] [21] [55]. When the material becomes not appropriate for some reason, for example, because of growth, animals usually make them suitable to maintain the integrity of the body and camouflage. In other words, the body and camouflage would have some uniqueness as a united individual. How can we measure the appropriateness of the assumption of the 'individual' in their behavior? We propose a statistical formulation of how to capture the individuality from the behavioral data. To capture the structure in the clustered data so far, the class of statistical models with hierarchical structure is often used [17]. The data is sometimes called 'pseudo-replicated' because of the violation of the assumption of independent and identical distribution under the non-hierarchical models [40]. The problem can be dealt with appropriately if we explicitly introduce a hierarchical structure into the model such as linear mixed or generalized linear mixed models [24] [56]. However, it has been a challenge to assess the appropriateness of the models because they are non-regular models [48] [38]. In order to infer the true probability distribution using regular models, the maximum likelihood-based framework of the model selection using AIC (Akaike Information Criterion) has been traditionally used. [2] [41]. However, for the non-regular models, one can not approximate the posterior distribution by any normal distribution, so one needs a fully Bayesian approach and WAIC (Widely Applicable Information Criterion) [47] [46]. WAIC can be used for non-regular, non-identifiable, non-realizable models under the identical and independent distribution [48]. Additionally, not only we need the approach, but also we must be careful about how to compute WAIC. It is strongly recommended to compute the marginal-level WAIC which is consistently applicable to the hierarchical and non-hierarchical models instead of typically used conditioned-level WAIC [38]. We took the approach to examine whether the 'individual' specified as hierarchical structure exists in the cap making behavior of marine sponge crabs who make caps or hats for 'concealment strategy' [21].

To conceal themselves in their environment, some brachyuran are known to carry and decorate materials such as Porifera, Ascidiacea, sea anemone, shell, or algae [19] [21]. The majid crabs decorate themselves with some sponges and algae [27] [52] [3] [5] [14]. Crabs of the family Dromiidae [15] [30] [3], Homolidae [53] [49] [50] [9] [11] [20] [21], and Dorippidae [50] [3] [20] are reported to carry sponges and ascidians. It is suggested that these behaviors are mainly camouflage and defense to predators [50] [51] [44] [21]. In particular, the toxic character of sponges is more effective to protect crabs against the attacks of predators [3].

Among these crabs, dromiids can detach sponges or ascidians from the substrate and make caps [15] [29] [30] [32] [33] [34] [31] [35] [36] [37] [50] [25] [20] [21]. The cap has a concave surface on the bottom, and the dromid crabs put it on to their back. Sponge 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) [20] [21]. 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 the crab [30]. It is reported that *Cryptodromia hilgendorfi* use the caps made by many species of sponges, but they particularly prefer the sponge *Suberites carnosus*, and the crabs make sponge caps twice as large as the carapace area. 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 [15] 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 [3], while they can also make caps with paper [15]. However, it should be noted that these studies have not dealt with the problem raised in this study, because the samples for analyses are dataset consisting of one observation from one individual.

In this study, we studied a species of sponge crab: *Lauridromia dehaani* and examined the individuality of their cap making behavior consisting of sponge size choice, sponge removing, hole making. To sample repeated observations from one individual, we repeatedly gave three different sizes of artificial sponges. Our goals of this study are two holds. First, we aim to introduce the hierarchical structure into statistical models. Second, we aim to assess the appropriateness of the assumption by comparing non-hierarchical competing alternative models using marginal-level WAIC.

Materials & 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, 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 x 30 mm x 40 mm, M: 30 mm x 60 mm x 85 mm, L: 30 mm x 140 mm x 150 mm). Each sponge was put pseudo-randomly to either sides and the center behind of the cage (700 mm x 470 mm x 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 trial for one individual (n = 30), but five trials for one individual after February 2017 (n = 8) to examine the individuality of the behavior. We thoroughly desiccated all the sponges that the crabs processed, measured the whole area of them, and the area of the hole by taking pictures from 46 cm above the sponges.

To confirm the cap making behavior is not different from the behavior in the detailed report [15] [30], We video recorded the behavior from the two crabs (4.30 cm and 7.19 cm of the carapace width for each). They are used only for this recording in the aquarium (310 mm x 180 mm x 240 mm). The recording was continued more than three hours after they were into the aquarium with the sponge. We repeated the recording 5 times for each crab.

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 constructed the models that explicitly include 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 [43]. 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 in Stan. Whether the sampling was converged was diagnosed by trace plots and quantitatively via the Gelman-Rubin convergence statistic, R_{hat} [18]. All of the draws were judged to converge when $R_{hat} < 1.10$.

We compared the predictive performances of the models using WAIC. To give the essence 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 1). It should be emphasized that WAIC must be computed with the marginalization of the parameters assigned to each individual (marginal-level WAIC) to construct a predictive distribution. [48] [38]. 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. WAIC is an estimator of the generalization error of the models to the true models generating data. We assessed the model predictability by this WAIC, not by the conditional-level WAIC which is beginning to be used without the consideration of this point. We did in the same way in all hierarchical models built in this study.

All the computations were performed in the statistical environment R [39], and the Stan codes for each model were compiled and executed through the R package *rstan* [43].

behavioral choice of material size (model 1_1)

The crabs did not choose S size sponge and unexpectedly abandoned the choice itself. Therefore, we in a post hoc way formulated the tendency to a choice of a certain sponge $\mu[n, m]$ ($m = 1, 2, 3$ for M, L, no choice, respectively). The μ 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 inferred as the comparison with the M size choice,

$$\mu[n, 1] = 0,$$
$$\mu[n, 2] = a_{choice_L}[ID[n]] + b_{choice_L} * Cwidth[n] + c_{choice_L} * LegLack[n],$$
$$\mu[n, 3] = d_{choice_0} + e_{choice_0} * Cwidth[n] + f_{choice_0} * LegLack[n],$$
$$n = 1, ..., N_{act}.$$

N_{act} is the total number of behavioral acts. ID represents animal identity. It should be noted that we could not collect repeated data from some animals. The local parameters $a_{choice_L}[ID[n]]$ are the intercepts for each individual. The parameter d_{choice_0} does not include individuality because the number of no choice was small. The $a_{choice_L}[ID[n]]$ 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 and removing (model 2_1)

The probability $\phi[n]$ for the decision whether the animal cut off the sponge is 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,

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

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 also set as

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

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 an integer to apply this model. The rounding process was judged to have no impact on 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 predictor. 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,

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

$$log(\lambda_{day}[n]) = b_{day}[ID[n]],$$

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

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

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

Results

Cap making using an artificial sponge

The behavior was video recorded specifically from the two crabs other than the individuals for the behavioral experiments to be described in the following sections. They usually grasped either side of the sponge by the second and third pereiopods (Fig. 1A). They tore off small pieces of the sponge by chelae (Fig. 2A upper left, upper right, Supplementary movie 1). Sometimes they moved to another side of the sponge. By repeating these behaviors, the crabs made the groove to cut off the clod of sponge. On average, it took about 50 minutes for the crabs to cut the clod, and in 9 trials, the crabs started digging as soon as they finished removing. Next, the crabs made a hole by tearing off small pieces of sponge (Fig. 2A bottom). It took 11 minutes to dig the hole on average. 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 the second and third pereiopods from the cap and began to carry it (Fig. 2B, C). 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 night and it took up to five hours. When the crabs rotated their body, the direction of the rotation was maintained along with the sponge. 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.

We will describe the results of the modeling the variables (1) cap choice, (2) removing size, (3) cap hole size, and (4) time for cap making, in the next sections.

Cap choice

All the 38 animals did not choose the S size sponge, and 7 animals abandoned the cap making behavior itself (Fig. 3A). Therefore, we defined the choice as the random variable taking three behavioral choices, M or L or no choice. The hierarchical model assuming individuality in the model 1_1 (Fig. 3A, B) remarkably outperformed the non-hierarchical one in terms of WAIC (-2.13 to 0.87, Fig. 3A-D Table. 1). The posterior probability of the behavioral choices, were more widely variable in the model 1_1 than 1_6 depending on the individual difference specified as a_{choice_L} (Fig. 3B). The probability of choice sampled from the posterior distribution is visualized in white lines (Fig. 3A,C). For example, although the animal indicated with the white arrowhead (Fig. 3A) is small, but preferably selected the size L. In either case of hierarchical or non-hierarchical model, the behavioral choice of the sponges was better explained by the carapace width (Fig. 3A,C), suggesting larger crabs tended to choose L size sponge rather than M size. However, the crabs whose carapace width becomes larger than about 9 cm did not choose the sponges.

Cutting and removing behavior

After the choice of M or L size sponge, the crabs decided to remove the extra part of the sponge or not (Fig. 4). Here we model how much the crabs removed the sponge. The removed sponge showed three patterns (Fig. 4B). They cut off (1) the four corners of the sponge, (2) one corner of it elliptically, (3) two corners of it linearly. The twenty three crabs skipped cutting in 33 trials.

The removing behavior showed two paths. One path was that the crabs decided to remove the sponge and then decided how much they remove the sponge. The other path was that they skipped removing, and 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. 4C).

The WAIC score of the hierarchical model 2_1 was -2.08 and the score of counterpart non-hierarchical model 2_6 was 7.40 (Fig. 4D, Table 1). The tendency of decreasing of removed size can be recognized when the choice is fixed to L size in the predictive density of both of the models (Fig. 4C,D).

Cap hole and body size

The six crabs just cut the sponge and did not dig. We modeled the cap hole size as a random variable subjected to the gamma distribution with the log link function (Fig. 5). The cap hole size increased with the carapace width, as well as the model with the individuality best performed in the predictability (Table 1). WAIC of the hierarchical model 3_1 (4.45) is smaller than that of the counterpart non-hierarchical model 3_2(4.54) (Fig. 5A,B, Table 1). The individual with the arrowhead made relatively large cap holes(Fig. 5A), indicating the individual bias of the behavior.

Time for making process

We modeled the time for making (from the choice of sponge to carrying) as a random variable subjected to zero-inflated distribution (Fig. 6). 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. However, the hierarchical model 4_1 outperformed the model 4_2 as the non-hierarchical model (WAICs, 1.10 and 1.28 respectively).

Discussion

We modeled the four variates, (1) choice of sponge size, (2) removed size, (3) cap hole size, and (4) time for making, as random variables with the hierarchical structures. When these models were compared with the non-hierarchical versions of the models, marginal-level WAICs [38] favored hierarchical models in all of the four variates. Therefore, our assumption of individuals for the behavioral data is considered to be appropriate in terms of the model predictability.

Functional role of cap

It is expected that the crabs extending their body in order to camouflage and defend themselves [15] [30] [3] with repellent effect of the sponge [12]. In particular, some homolid crabs are reported to carry not only sponges or ascidians but also sea anemones [13], and they drive away their predators with these materials [9]. In addition, it is observed that sponge crabs carry not only sponges or ascidians but also sea anemones [19] [25] or bivalve shells [51] [20] [21]. As Bedini et al. [3] 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.

Many similarities were observed in the cap making behavior of *L. dehaani* with other crabs such as *D. personata* and *C. hilgendorfi* [15] [30]. From the video recordings, we described all of the cap making behavioral sequence, 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 [30], 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 [15] 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. A 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. For example, the adult males of *Oregonia gracilis* tended to decorate less than the juveniles or adult females and this would be because of the energetic cost of the adult males to maintain their large claws increases and they could not pay the cost for decorating [4]. In this experiment, the size of the crabs that did not carry caps was larger than that carried caps. 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 individual 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 [15] 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.

Integrated 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 [6] [22] [54]. Although hermit crabs cannot 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 [42].

Among vertebrates, the primates such as chimpanzees and gorillas (e.g. [8], [10]) and the birds such as crows [23] [28] have been studied as tool users. On the other hand, among invertebrates, it is known that octopuses use coconuts as defensive tools [16] and insects, for instance bumblebees, are able to perform the task in which they have to use surrounding materials [26]. Some crustacean, such as green crabs and American lobster are able to perform instrumental conditioning [1] [45]. Our findings demonstrated that not only the crabs can modify the cap size depending on the current body size during the inter-molt period, but also they have an individual bias emerging in the behavioral data captured in the hierarchical models. Although the possibility can not be excluded that the source of the bias is from genetic properties, we propose a possibility that unique experience through interactions with their environments would develop the individuality not reset by the molt cycle.

Supplementary information

The movie of cutting and digging behaviors were attached 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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Figure legends

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 cap making behavior consists of cutting to change the size of the cap, digging to change the size of the hole, and carrying. (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.
Figure 3. The choice of sponge size with the posterior predictive distributions. (A)The predictive distribution with the data points of the behavioral choices, which are M or L size choices or abandon of the choices, in the graded color map of the hierarchical model assuming

the individuality. The dotted lines connecting the square points represent the data from the same individual repeatedly. For example, the individual pointed by the white arrowhead preferred the L size sponge repeatedly even if this animal is small. The white lines are ten samples in decreasing order from the highest posterior density of the parameter representing the probability of the choice L and no choice when compared with the choice M. (B)The structure of the model 1_1 in a graphical model. The a_{choice_L} is the latent parameters (N_{animal}) assigned to each individual to specify the hierarchy. The variables whose first letter are written in capital and small letters represent observed data (N_{act}) and parameters to be estimated, respectively. (C)The predictive distribution of the choices of the non-hierarchical model 1_6. Note that the variability of the choice probability in white curved lines is smaller than the model 1_1. (D)The model structure of the model 1_6 in a graphical model. The predictive performances measured in WAIC indicates that the model 1_1 of the hierarchical model(-2.13) remarkably outperformed the WAIC of the model 1_6(0.85).

Figure 4. The predictive distributions of how much sponge was removed. (A)The outline of the removing process from the choice of the sponge, removing(part of animals skipped this behavior), to the hole making. (B)The three patterns of cutting. Upper: cutting the four corners; Middle: cutting elliptically; Bottom: cutting linearly. The crabs removed the white area and started making a cap with the dotted area. (C)Upper plot: The predictive distribution of the hierarchical model 2_1. The white dotted lines connect the data points from the same individual. When the animals choose the M size sponges, almost all of the animals except for one individual decided not to remove the sponge, whereas they removed the sponge in relation to their body sizes when they choose the L size sponges. Lower plot: The predictive distribution visualized by re-scaling the color density of the expanded area in the upper plot except for the zero in the y-axis. (D)The predictive distribution of the non-hierarchical model 2_6. The bright area mismatches the data points except for the non-removing points. Note that the WAIC of the hierarchical model (-2.08) is remarkably smaller than the non-hierarchical one (7.40).

Figure 5. The predictive distributions of the cap hole size. (A)The hierarchical model. The data points connected with the white dotted lines are from one individual. Predictably, the larger size of crabs made the larger size of holes. The difference of the WAIC scores is about 0.1, thus the hierarchical model is more predictable than the non-hierarchical one. The improvement of the predictability might show that relatively small room for the individuality other than the body size to determine the cap hole size.

Figure 6. The predictive distributions of the time the crabs took for cap making. (A)The hierarchical model. 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. (B)The non-hierarchical model. (C)The outline of the cap making until carrying. Both of the models assume that the mean parameter is constant while the carapace width changes. We applied the zero-inflated Poisson model to the time variable. The hierarchical model outperformed non-hierarchical one in terms of WAIC(1.10 and 1.28 respectively), indicating the assumption of the individual would be appropriate for this data.

response variable	model	hierarchical structure	explanatory variables	link function	distribution	WAIC	dWAIC	plot
Choice	1_1	intercept_L	CW_L, Leg_L, CW_NO, Leg_NO	softmax	categorical	-2.13	0.00	Fig.4A
Choice	1_2	intercept_L	CW_L, CW_NO	softmax	categorical	-1.87	0.26	-
Choice	1_3	intercept_L	-	softmax	categorical	-0.88	1.25	-
Choice	1_4	intercept_L	Leg_L, Leg_NO	softmax	categorical	-0.78	1.35	-
Choice	1_5	-	CW_L, CW_NO	softmax	categorical	0.85	2.99	Fig.4C
Choice	1_6	-	CW_L, Leg_L, CW_NO, Leg_NO	softmax	categorical	0.87	3.01	-
Removed size	2_1	intercept_1, intercept_2	CW, Choice	logit, log	ZIP	-2.08	0.00	Fig.5A
Removed size	2_2	intercept_2	Choice	logit, log	ZIP	0.81	2.89	-
Removed size	2_3	intercept_2	CW, Choice	logit, log	ZIP	0.86	2.95	-
Removed size	2_4	intercept_2	-	logit, log	ZIP	1.23	3.32	-
Removed size	2_5	intercept_2	CW	logit, log	ZIP	1.37	3.46	-
Removed size	2_6	-	CW, Choice	logit, log	ZIP	7.40	9.48	Fig.5B
Removed size	2_7	-	CW	logit, log	ZIP	10.05	12.13	-
Removed size	2_8	-	-	logit, log	ZIP	12.55	14.63	-
Cap hole size	3_1	intercept	CW	log	gamma	4.45	0.00	Fig.6A
Cap hole size	3_2	-	CW	log	gamma	4.54	0.08	Fig.6B
Cap hole size	3_3	-	CW, Gender	log	gamma	4.69	0.24	-
Cap hole size	3_4	intercept	-	log	gamma	4.71	0.26	-
Cap hole size	3_5	-	CW	identity	normal	4.75	0.30	-
Cap hole size	3_6	intercept, cw	CW	log	gamma	6.18	1.73	-
Time for making	4_1	intercept_2	CW	logit, log	ZIP	1.10	0.00	Fig.7A
Time for making	4_2	intercept_2	-	logit, log	ZIP	1.28	0.18	-
Time for making	4_3	-	-	logit, log	ZIP	1.28	0.19	Fig.7B
Time for making	4_4	-	Choice	logit, log	ZIP	1.30	0.20	-
Time for making	4_5	-	CW	logit, log	ZIP	1.38	0.28	-
Time for making	4_6	-	CW, Choice	logit, log	ZIP	1.72	0.62	-

Table 1. Summary of model structures and the predictive performances. Abbreviations, intercept_L: intercept in the linear predictor (LP) for the choice of L; intercept_1: intercept in the LP for the decision of cutting; intercept_2: 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: choice whether to cut the sponge; Gender: gender of the animal; intercept_2: intercept in the LP for the mean of the days to carrying; Choice: choice of sponge size; ZIP: Zero-inflated Poisson distribution; WAIC: Widely-Applicable Information Criterion; dWAIC: the difference of the WAIC of the model and the best-performed model.

Figure 1

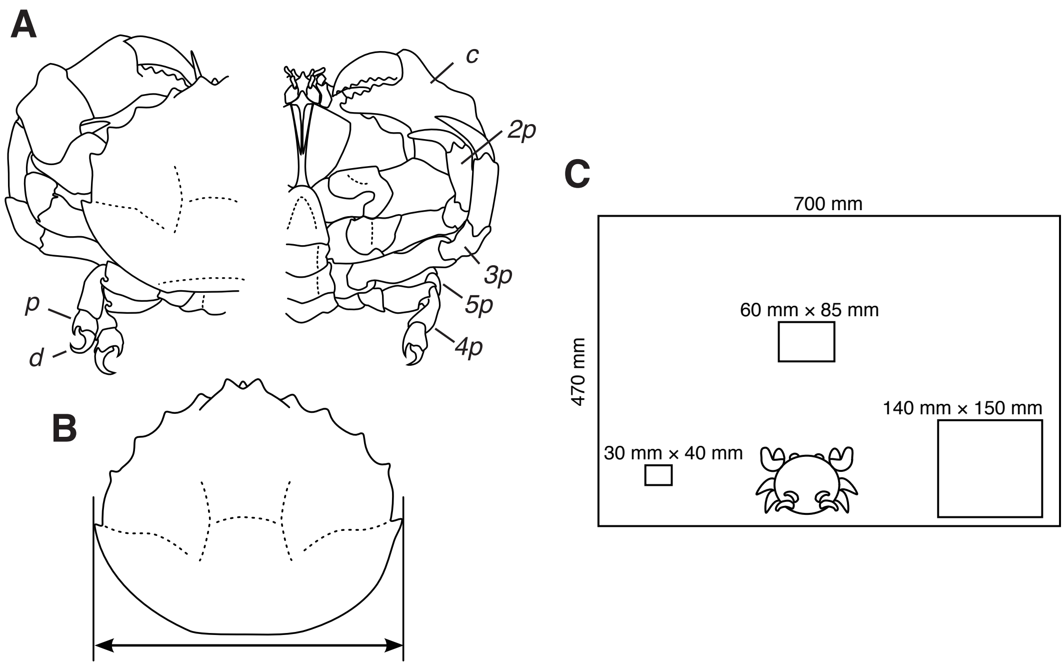

A
c
2p
3p
5p
4p
p
d
B
C
700 mm
470 mm
60 mm × 85 mm
140 mm × 150 mm
30 mm × 40 mm

Figure 2

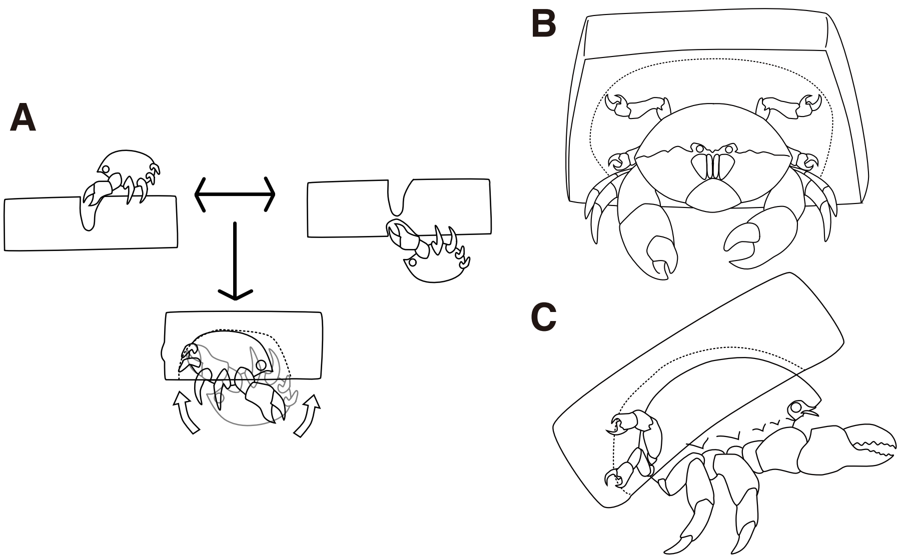


Figure 3

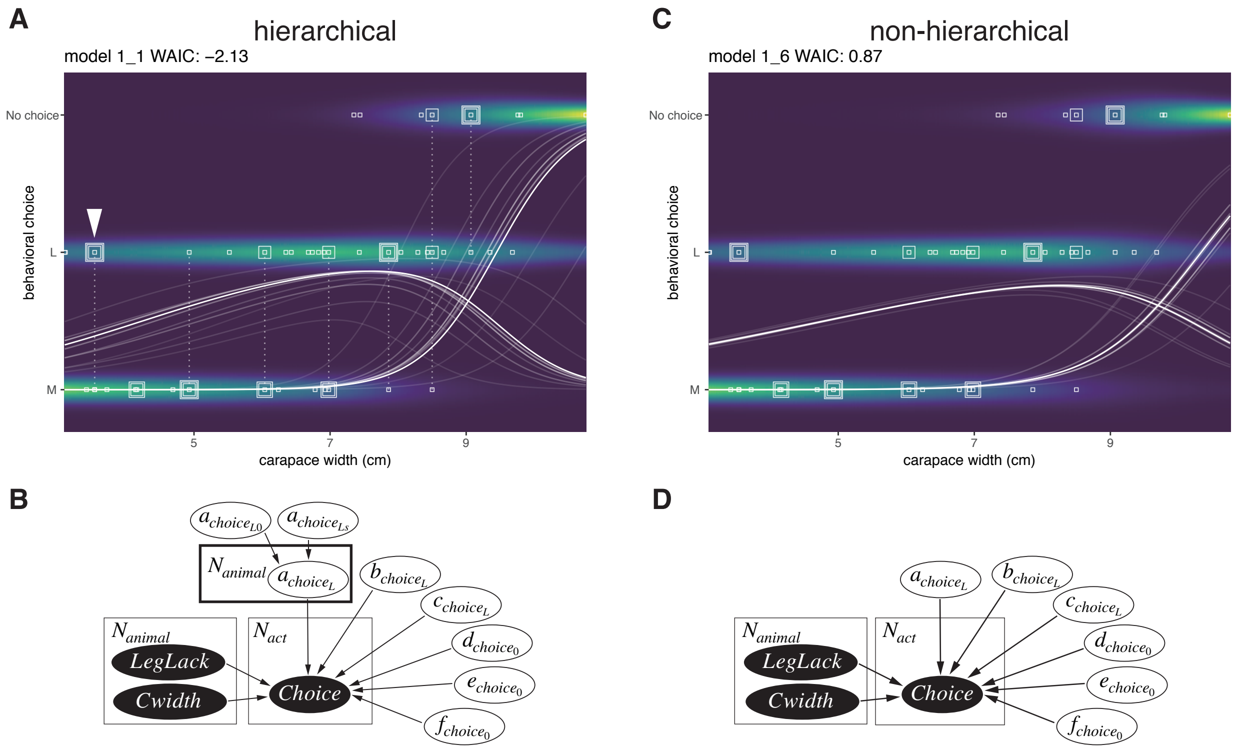

A
hierarchical
model 1_1 WAIC: −2.13
No choice
L
M
behavioral choice
5
7
9
carapace width (cm)
C
non-hierarchical
model 1_6 WAIC: 0.87
No choice
L
M
behavioral choice
5
7
9
carapace width (cm)
B
$a_{choice_{L0}}$
$a_{choice_{Ls}}$
N_{animal}
a_{choice_L}
b_{choice_L}
c_{choice_L}
d_{choice_0}
e_{choice_0}
f_{choice_0}
N_{animal}
LegLack
Cwidth
N_{act}
Choice
D
a_{choice_L}
b_{choice_L}
c_{choice_L}
d_{choice_0}
e_{choice_0}
f_{choice_0}
N_{animal}
LegLack
Cwidth
N_{act}
Choice

Figure 4

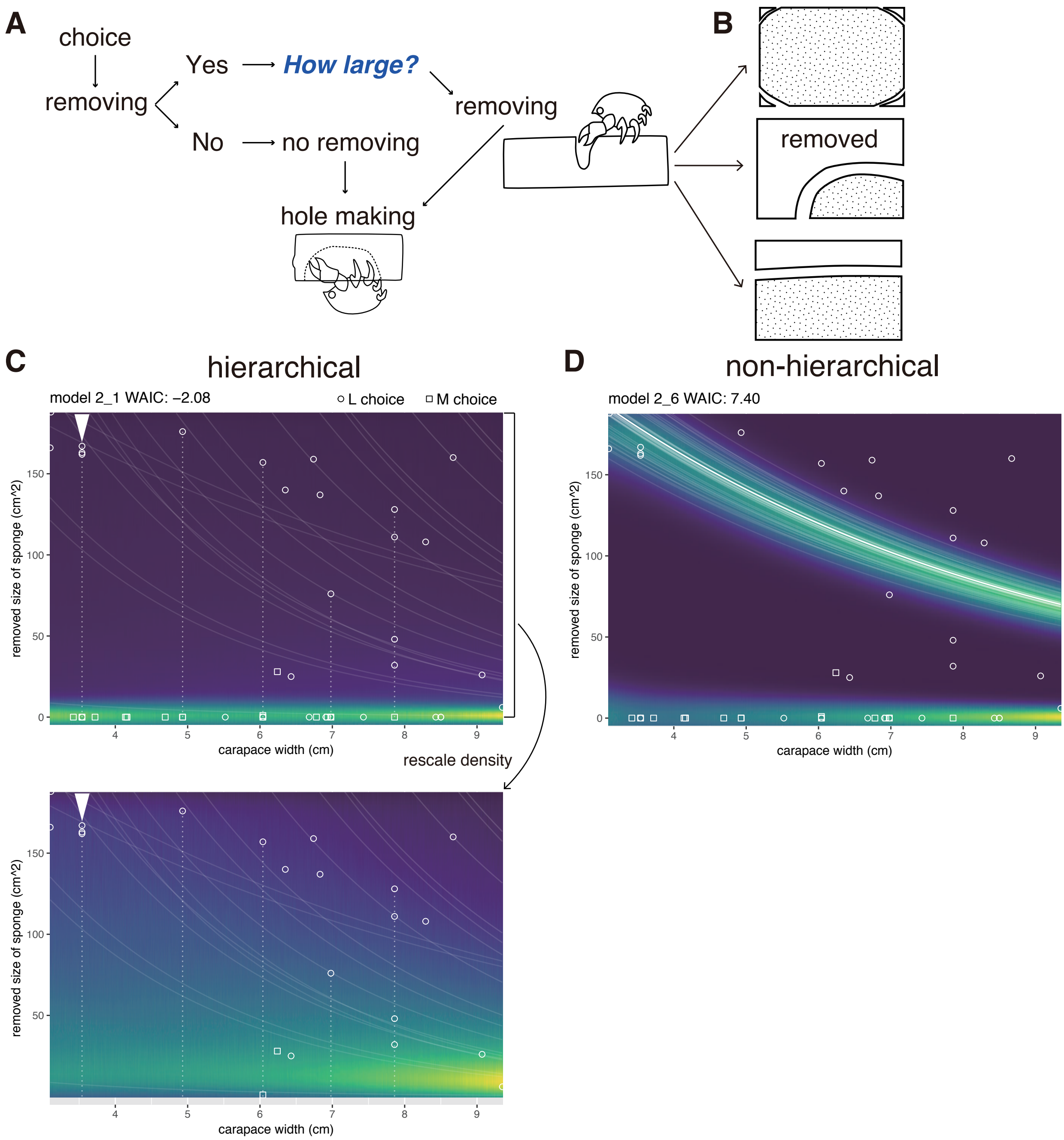

A
choice
removing
Yes
How large?
removing
No
no removing
hole making
B
removed
C
hierarchical
model 2_1 WAIC: −2.08
L choice
M choice
removed size of sponge (cm^2)
carapace width (cm)
rescale density
D
non-hierarchical
model 2_6 WAIC: 7.40

Figure 5

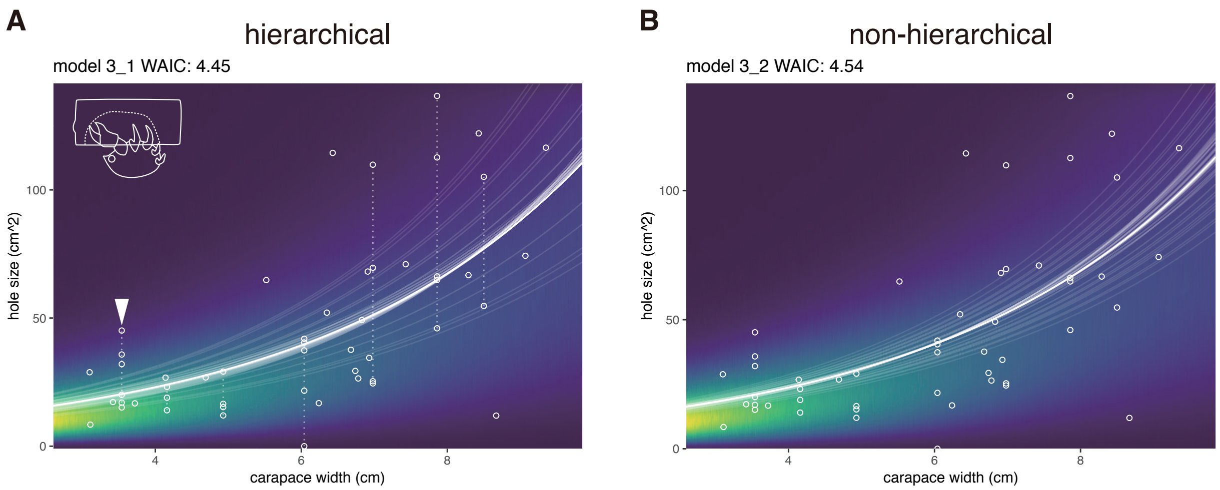
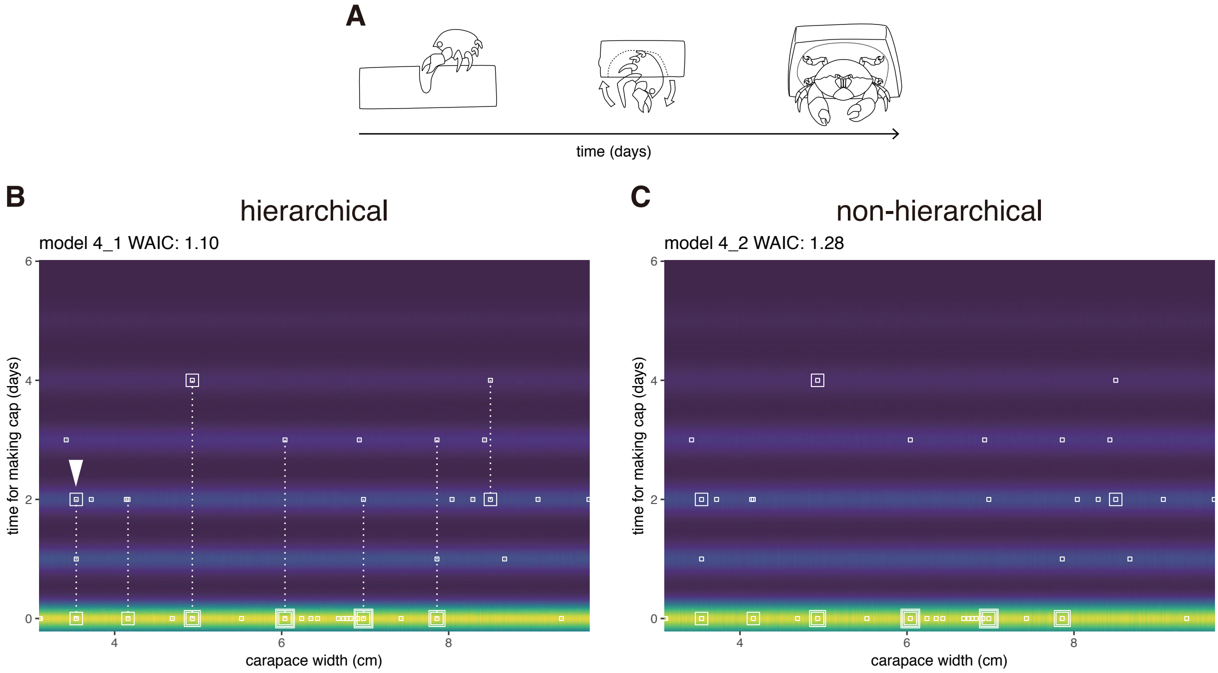

A
hierarchical
model 3_1 WAIC: 4.45
hole size (cm^2)
100
50
0
4
6
8
carapace width (cm)
B
non-hierarchical
model 3_2 WAIC: 4.54
hole size (cm^2)
100
50
0
4
6
8
carapace width (cm)

Figure 6


A
time (days)
B
hierarchical
model 4_1 WAIC: 1.10
time for making cap (days)
carapace width (cm)
C
non-hierarchical
model 4_2 WAIC: 1.28
time for making cap (days)
carapace width (cm)