Individuality emerging in cap making by sponge crab

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ABSTRACT

Successful camouflage requires an animal to be integrated into the environment. When an individual grows, the camouflage is usually modified to maintain the integrated state. 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 crab. 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 it is a statistically non-regular model. Here, we for the first time applied marginal-level WAIC (Widely Applicable Information Criterion) to the behavioral data and found that the hierarchical models remarkably outperformed non-hierarchical ones in decision making of material size and cap making by the crab. Our new modeling approach successfully detected the integrated 'individuality' revealed as probabilistic distribution structures in the real world behavioral data.

INTRODUCTION

Animals sometimes use environmental materials to camouflage themselves in their environment (Blanke and Metzinger, 2009; Sonoda et al., 2012; Guinot and Wicksten, 2015; Wilby et al., 2018). When the material becomes inappropriate (e.g., due to growth), animals usually make them suitable to maintain the integrated state of the body and camouflage. In other words, the body and camouflage would have some uniqueness as a united individual. We defined the individuality as some uniqueness in the behavior within an individual and difference across the individuals. How can we measure the appropriateness of the assumption of the 'individual' only using their behavior? In this study, we for the first time formulated the problem as a statistical framework and studied the individuality in the brachyuran species. The crabs are known to carry and decorate materials such as Porifera, Ascidiacea, sea anemone, shell, or algae to conceal themselves in their environment (Guinot et al., 1995; Guinot and Wicksten, 2015). The majid crabs decorate themselves with some sponges and algae (Maldonado and Uriz, 1992; Wicksten, 1993; Bedini et al., 2003; Berke and Woodin, 2008b; De Carvalho et al., 2016). Crabs of the family Dromiidae (Dembowska, 1926; McLay, 1983; Bedini et al., 2003), Homolidae (Wicksten, 1983, 1985, 1986a; Braga-Henriques et al., 2012; Capezzuto et al., 2012; Guinot et al., 2013; Guinot and Wicksten, 2015), and Dorippidae (Wicksten, 1986a; Bedini et al., 2003; Guinot et al., 2013) are reported to carry sponges and ascidians. It is suggested that these behaviors are mainly camouflage and defense to predators (Wicksten, 1986a,b; Thanh et al., 2005; Guinot and Wicksten, 2015). In particular, the toxic character of sponges is effective to protect crabs against the attacks of predators (Bedini et al., 2003). Among these crabs, dromiids can detach sponges or ascidians from the substrate and make caps (Dembowska, 1926; McLay, 1982, 1983, 1991, 1993, 2001b,a,c, 2002, 2009; Wicksten, 1986a; Lavaleye and Den Hartog, 1995; Guinot et al., 2013; Guinot and Wicksten, 2015). The cap has a concave surface on the bottom, and the dromid crabs put it on to their back. The 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) (Guinot et al., 2013; Guinot and Wicksten, 2015).

In order to measure the appropriateness of the assumption of the 'individual' in the cap making behavior, we propose a novel 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 (Galbraith et al., 2010). Data is sometimes called 'pseudo-replicated' because of the violation of the assumption of independent and identically distributed samples under the non-hierarchical models (Reinhart, 2015). Pseudo-replication can be dealt with appropriately if we explicitly introduce a hierarchical structure into the model such as linear mixed or generalized linear mixed models (Zuur et al., 2009; Kagaya and Patek, 2016). However, it has been a challenge to assess the appropriateness of these models because they are statistically non-regular models (Watanabe, 2018; Millar, 2018). 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 traditionally been used (Akaike, 1974; Sakamoto et al., 1986). 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) (Watanabe, 2010b,a). WAIC can be used for non-regular, non-identifiable, non-realizable models under the identical and independent distribution (Watanabe, 2018). 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 (Millar, 2018). 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' (Guinot and Wicksten, 2015).

There has been several researches implying the individual differences in the material preference. In the field research, one study dealt with the preference of dromids to materials for caps and the correspondence between the size of cap to the size of the crab (McLay, 1983). It is reported that *Cryptodromia hilgendorfi* use the caps made from 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 for the size of material and the suitability between the size of crabs and the caps are scarcely investigated. *Dromia personata* mainly uses sponges and ascidians (Bedini et al., 2003), while they can also make caps with paper (Dembowska, 1926). 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. However, it should be noted that these studies have not dealt with the problem raised in this study, because the samples for analyses are datasets consisting of one observation from one individual.

In this study, we investigated a species of the sponge crab: *Lauridromia dehaani* and examined the individuality of their cap making behavior. To sample repeated observations from one individual, we repeatedly gave three different sizes of artificial sponges. 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 hierarchical structures. We introduced hierarchical structures into statistical models, and assessed the appropriateness of the assumption by comparing non-hierarchical competing alternative models using marginal-level WAIC (Millar, 2018). When these models were compared with their non-hierarchical versions of the models, WAIC values 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. We added the carapace width as an explanatory variable to the model. Therefore, it should be noted that our novel detection of behavioral individuality as probabilistic distribution structure does not mean the individual difference explained by the carapace width or other correlative variables to the width. We propose that the individuality would be acquired through the unique reciprocal interaction of the crabs with their environment.

METHODS

Animal collection

From December 2015 to April 2017, 40 individuals (21 males, 19 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 on 38 individuals (20 males, 18 females) and video recorded for 2 individuals (4.30 cm and 7.19 cm of the carapace width for each) 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 for more than two days for acclimation. We measured their carapace width (Fig. 1B), and divided them into five classes depending on whether they lacked any of the fourth and fifth pereiopods: (A) only one of them was absent, (B) either or both sides 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 prepared the melamine sponges of 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). The S size was smaller than all crabs, whereas the L size was larger than all crabs. Each sponge was put pseudo-randomly to either sides and the back 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 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 their whole area of them, and the area of the concave part dug by the crab from the pictures taken 46 cm above the sponges.

To confirm that the cap making behavior is similar to the behavior in the detailed report (Dembowska, 1926; McLay, 1983), We video recorded the behavior from the two crabs. They were used only for this recording in the aquarium (310 mm × 180 mm × 240 mm). The recording lasted more than three hours after they were put 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 behavioral aspects: (1) choice of sponge size (6 models), (2) cutting behavior (8 models), (3) cap hole making behavior (6 models), and (4) time until carrying the sponge (6 models). In each case, we constructed the models that explicitly included 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, 2018). We used non-informative uniform priors for the parameters unless otherwise explicitly described. The performed sampling from the posterior distributions using No-U-Turn Sampler (NUTS), which is implemented as a Hamiltonian Monte Carlo (HMC) sampler in Stan. Sampling convergence was diagnosed by trace plots and quantitatively via the Gelman-Rubin convergence statistic, R_{hat} (Gelman et al., 1992). All of the draws were judged to converge when $R_{hat} < 1.10$.

We compared the predictive performances of the models using WAIC (Watanabe, 2018, 2010b). To provide an overview of the models, we will explain only the best-performing models in terms of WAIC in this section. The other models were, 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 (Watanabe, 2018; Millar, 2018). In our case, we were 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 R statistical environment (R Core Team, 2018), and the Stan codes for each model were compiled and executed through the R package *rstan* (Stan Development Team, 2018).

behavioral choice of material size (model 1_1)

The crabs did not choose S size sponges and unexpectedly abandoned the choice itself. Therefore, we formulated the tendency toward the choice of a certain sponge $\mu[n,m]$ ($m = 1,2,3$ for M, L, no choice, respectively). The μ is linked to the linear predictor in terms of the carapace width, $CarapaceWidth[n]$ and the degree of leg lack, $LegLack[n]$. The choice for M size was fixed to zero, and the parameters of the other two choices were inferred as the comparison with the M size choice,

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

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 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 $a_{choice_{Ls}}$,

$$
\begin{aligned}
a_{choice_L}[k] &\sim Normal(a_{choice_{L0}}, a_{choice_{Ls}}),\\
k &= 1,\ldots,N_{animal}.
\end{aligned}
$$

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

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

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, $CarapaceWidth[n]$ and selected sponge size, $Choice[n]$,

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

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},

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

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

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

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

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

The parameters $d_{cut}[ID[n]]$ are 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},

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

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 of the sponge was removed as the response variable $Removed[n]$, which fits 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 $CarapaceWidth[n]$, the gamma distribution was chosen to represent non-negative hole size data. The shape and rate parameters were given as follows

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

where the rate parameter was given as the shape over the log linked linear predictor, $a_{hole}[ID[n]]$ are the intercepts for each individual, and $a_{hole}[k]$ fits 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 lasted until the animal carries the sponge, $Days[n]$, fits the ZIP distribution, which is similar to the $Removed[n]$ case,

$$\phi_{day}[n] = InverseLogit(a_{day}),$$
$$log(\lambda_{day}[n]) = b_{day}[ID[n]],$$
$$b_{day}[k] \sim Normal(b_{day_0}, b_{day_s}), k = 1, ..., N_{animal},$$
$$Days[n] \sim ZIP(\phi_{day}[n], \lambda_{day}[n]), n = 1, ..., N_{act}.$$

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 of the two crabs was video recorded to confirm the behavioral sequence of cap making using an artificial sponge. They usually grasped either side of the sponge by the second and third pereiopods (Fig. 1A), and 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 portion of sponge. On average, it took about 50 minutes to cut the portion, and the crabs started digging as soon as they finished removing in 6 trials. Next, the crabs made a hole by tearing off small pieces of sponge (Fig. 2A bottom, Supplementary movie 2). It took 11 minutes on average to dig the hole. Then, the crabs rotated their body backward in order to catch it with the fourth and fifth pereiopods while they kept the portion grasped 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 with 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 stayed under the sponge during digging to make a hole. In the next sections, 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

None of the 38 animals choose the S size sponge, and 7 animals abandoned the cap making behavior altogether (Fig. 3A). Therefore, we defined the choice as the random variable taking three behavioral choices, i.e. M, 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 (0.87 to -2.13, Fig. 3A-D, Table. 1). The posterior probability of the behavioral choices was more widely variable in the model 1_1 than in model 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, it 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 larger than about 9 cm carapace width did not choose the sponges.

Cutting and removing behavior

After the choice of M or L size sponge, the crabs decided whether to remove the extra part of the sponge (Fig. 4A). Here, we modeled how much of the sponge was removed by the crabs ($N_{animal} = 30$). The removed sponge showed three patterns (Fig. 4B). They cut off (1) the four corners of the sponge, (2) one corner of it elliptically, or (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 of the sponge they remove. 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 decrease 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

Six crabs just cut the sponge and did not dig. We modeled the cap hole size made by the 30 crabs 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, and the model considering individuality performed best in predictability (Table1). WAIC of the hierarchical model 3_1 is smaller than that of the counterpart non-hierarchical model 3_2 (4.45 and 4.54, respectively)(Fig. 5A,B, Table 1). The individual with the arrowhead (Fig. 5A) made relatively large cap holes, indicating the individual bias of the behavior.

Time for making process

We modeled the time for making (from the choice of sponge to carrying) by 32 crabs as a random variable subjected to zero-inflated distribution (Fig. 6). No obvious relation was found 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 non-hierarchical model 4_2 (WAIC values, 1.10 and 1.28 respectively).

DISCUSSION

Functional role of cap

It is expected that the crabs extend their body in order to camouflage and defend themselves (Dembowska, 1926; McLay, 1983; Bedini et al., 2003) with the repellent effect of the sponge (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; Guinot et al., 1995; Lavaleye and Den Hartog, 1995), which they use to drive away their predators. (Braga-Henriques et al., 2012). In addition, it is observed that sponge crabs carry bivalve shells (Wicksten, 1986b; Guinot et al., 2013; Guinot and Wicksten, 2015). As Bedini et al. (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 there were no materials with the toxic chemicals available in this study.

Several similarities were observed in *L. dehaani* cap making behavior compared with other crabs such as *D. personata* and *C. hilgendorfi* (Dembowska, 1926; McLay, 1983). From the video recordings, we described the complete cap making behavioral sequence, and the sponge crabs were found to process both natural sponges and artificial sponges in a similar way. However, *C. hilgendorfi* took 30 to 45 minutes to make (McLay, 1983), but *L. dehaani* took longer times (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. During longer time scales, there was no clear positive correlation between the size of crabs and the days to make caps (Fig. 8, Table 1). Dembowska (Dembowska, 1926) qualitatively reported that younger *D. personata* make caps faster than older individuals. We counted the days the crabs took to make caps, but the time resolution would be too small to detect a correlation. A further study measuring time with increased time resolution such as minutes to hours might detect the correlation. Additionally, further controlled experiments for testing time and 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 cause 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 adult males to maintain their large claws increases and they could not pay the cost for decorating (Berke and Woodin, 2008a). In this experiment, crabs that did not carry caps was larger than those that carried caps. When they grow up to some extent, their number of predators would be limited and the energetic cost to make caps might increase, so 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 (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 that fit 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. Contrastingly, no individuals carried the S sponge in this study, because it was too small for all of the crabs to carry. It is likely that younger and smaller crabs than those 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, 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 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 (Sonoda et al., 2012). Among vertebrates, primates such as chimpanzees and gorillas [e.g. Boesch and Boesch (1990); Breuer et al. (2005) , birds such as crows (Hunt, 1996)Matsui and Izawa (2017) have been studied as tool users. Additionally, among invertebrates, it is known that octopuses use coconuts as defensive tools, (Finn et al., 2009) and insects such as bumblebees, are able to perform task in which they have to use surrounding materials (Loukola et al., 2017). Some crustaceans, such as green crabs and American lobsters are able to perform instrumental conditioning (Abramson and Feinman, 1990; Tomina and Takahata, 2010).

The cap making and carrying behavior can be considered a tool making and using behavior (Guinot and Wicksten, 2015). When considering the tight reciprocal coupling of the nervous system, body and environment (Pfeifer et al., 2007) permitting successful behavior, we hypothesized that unique relationships would emerge in the behavioral data. Our novel statistical formulation and precise inference of the predictability of the models clarified not only can the crabs modify the cap size depending on the current body size during the inter-molt period, but they also have an individual bias emerging in the behavioral data captured by comparing the hierarchical models with the non-hierarchical ones. Although the possibility that the bias is coming from genetic properties can not be excluded, we propose that unique experiences through reciprocal interactions with their environment would develop the individuality not reset by the molt cycle.

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 portion of sponge, the crab makes the hole to fit the back. To make the hole the crab rotates their body backward and grasps it by the fourth and fifth pereiopods. (B–C) The carrying behavior of the crab. It carries a cap made from an artificial sponge. (B) Frontal view and (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 data points of the behavioral choices, which are M or L size choices or abandon of the choices, in a graded color map of the hierarchical model assuming individuality. Points connected by dotted lines points represent data from the same individual. 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 of the sponge was removed. (A) 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) Hierarchical model. Data points connected by white dotted lines are from one individual. Predictably, larger size crabs made the larger size holes. The difference of WAIC scores is about 0.1, thus the hierarchical model predict better than the (B) non-hierarchical one. The improvement of 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) Hierarchical model. Days that the animal took until carrying the sponge as a function of carapace width are shown with points and those from the same individual are connected by dotted lines. (B) The non-hierarchical model. (C) Outline of the cap making until carrying. Both of the models assume that the mean parameter is constant while the carapace width changes.

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.3A
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.3C
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.4A
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.4B
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.5A
Cap hole size	3_2	-	CW	log	gamma	4.54	0.08	Fig.5B
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.6A
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.6B
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.

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Figure 1

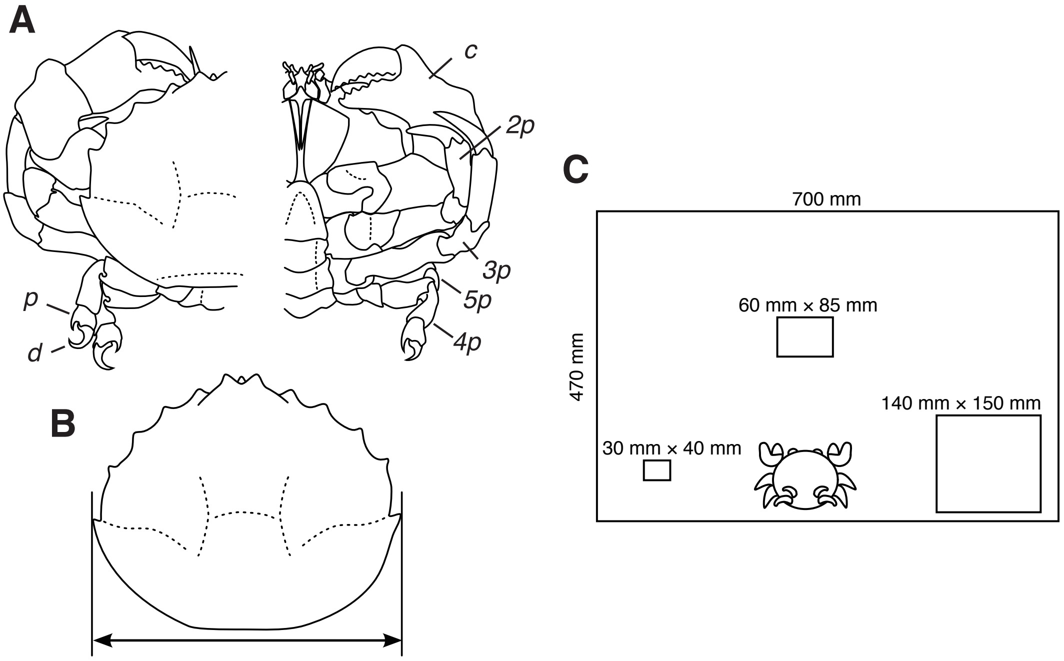

A
c
2p
3p
5p
4p
p
d
B
C
700 mm
470 mm
60 mm × 85 mm
140 mm × 150 mm
30 mm × 40 mm

Figure 2

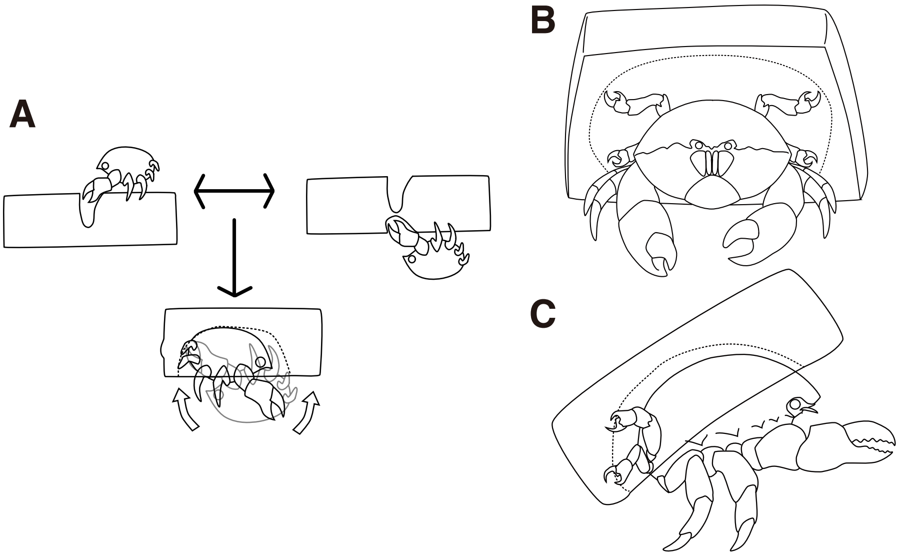
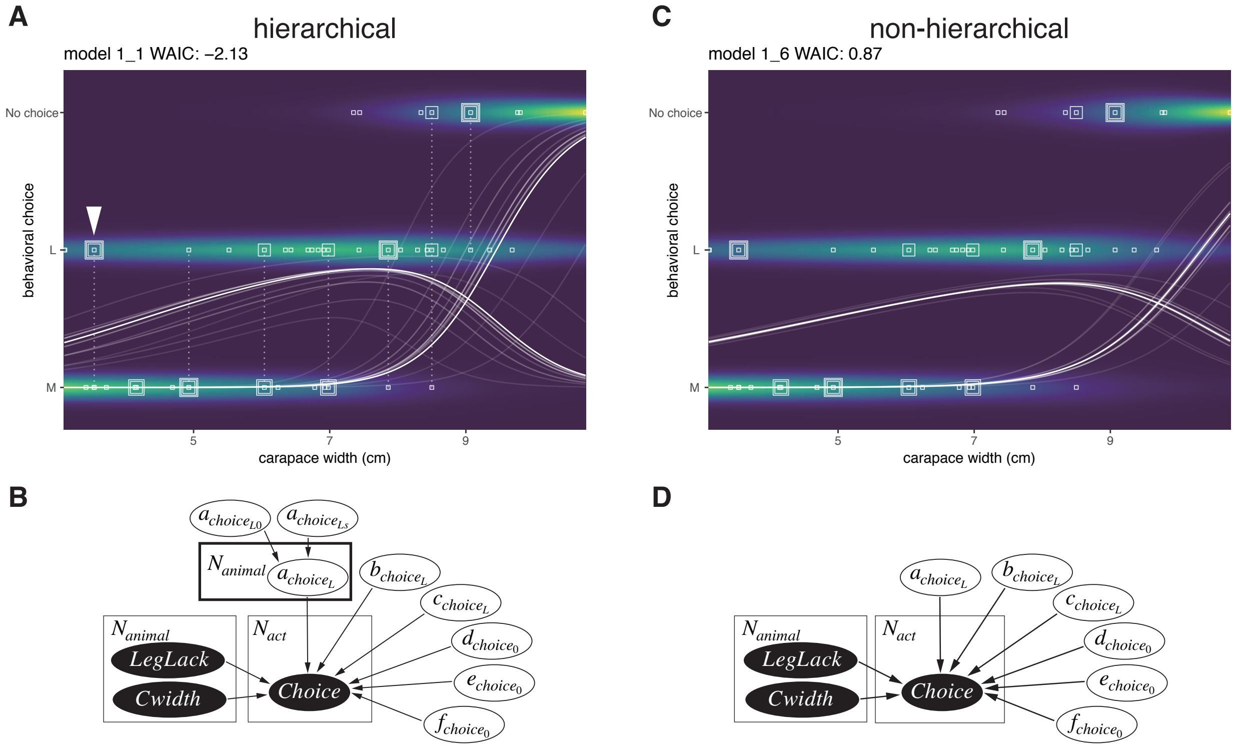


Figure 3


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}
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LegLack
Cwidth
N_{act}
Choice

Figure 4

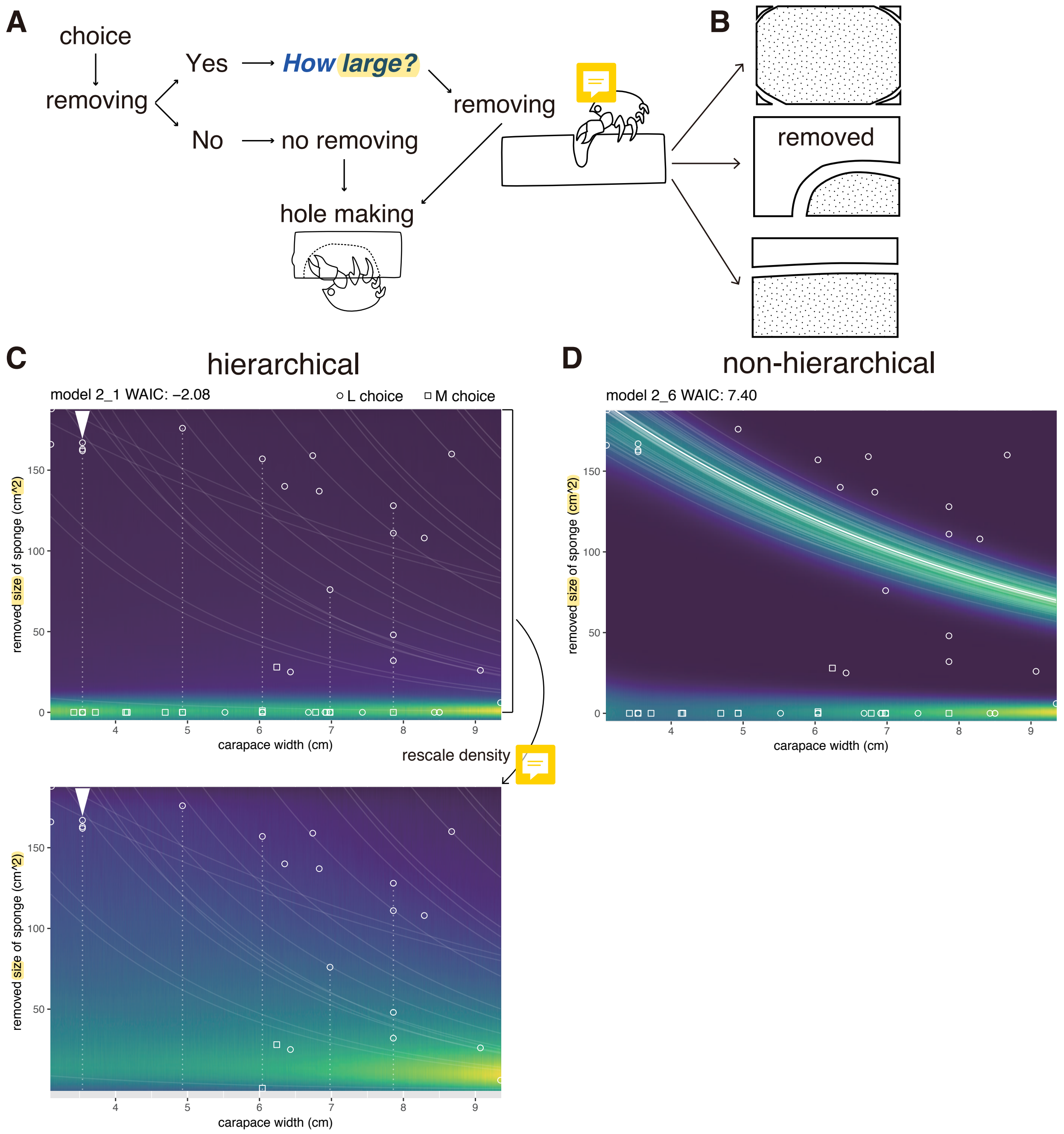

A
choice
removing
Yes
How large?
No
no removing
hole making
removing
B
removed
C
hierarchical
model 2_1 WAIC: −2.08
○ L choice
□ M choice
removed size of sponge (cm^2)
0
50
100
150
4
5
6
7
8
9
carapace width (cm)
rescale density
D
non-hierarchical
model 2_6 WAIC: 7.40
removed size of sponge (cm^2)
carapace width (cm)

Figure 5

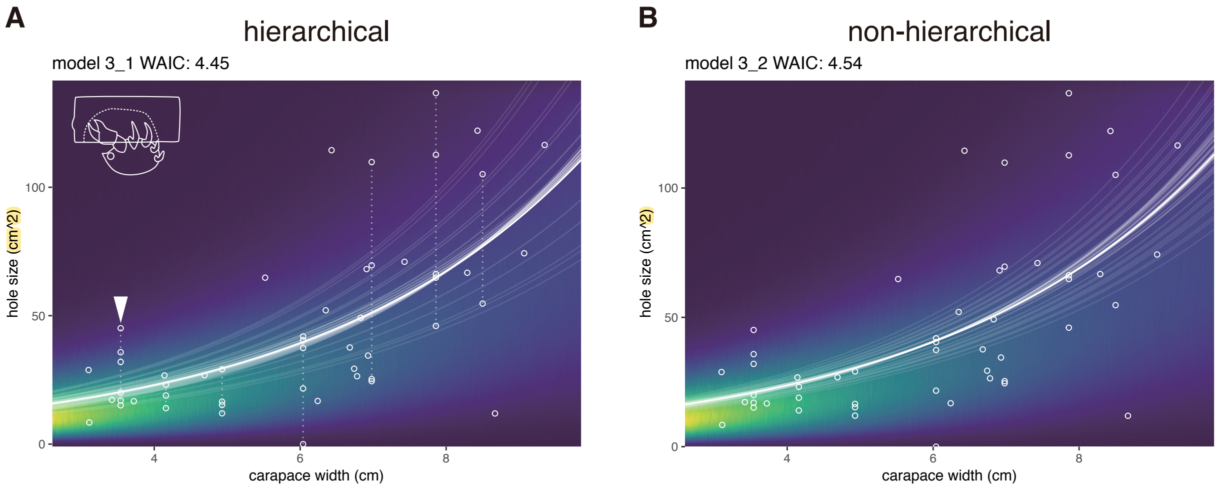
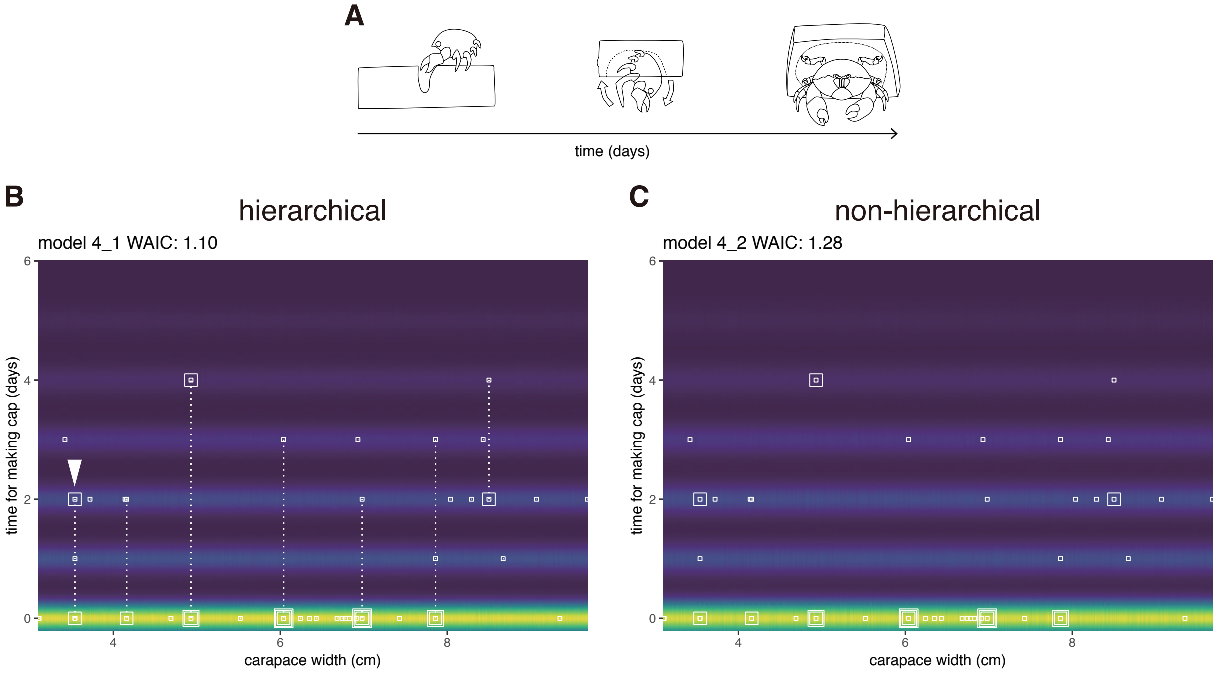

A
hierarchical
model 3_1 WAIC: 4.45
hole size (cm^2)
carapace width (cm)
0
50
100
4
6
8
B
non-hierarchical
model 3_2 WAIC: 4.54
hole size (cm^2)
carapace width (cm)
0
50
100
4
6
8

Figure 6


A
time (days)
B
hierarchical
model 4_1 WAIC: 1.10
time for making cap (days)
0
2
4
6
carapace width (cm)
4
6
8
C
non-hierarchical
model 4_2 WAIC: 1.28
time for making cap (days)
0
2
4
6
carapace width (cm)
4
6
8