

Trait correlations and genetic variation among populations in parental care  
in the burying beetle *Nicrophorus quadripunctatus*

ヨツボシモンシテムシにおける養育行動の個体群間変異の探索と  
形質間相関の解明（英文）

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## **Abstract**

Parental care is a prime example of altruism and has evolved across a wide range of taxa. Although parental care is common in mammals, birds, fishes and some invertebrate groups, there is considerable variation in reproductive effort (called parental investment) among species. Understanding the factors underlying the origin and maintenance of the variation contributes to uncovering the ultimate drivers of the emergence of complex family life and social behavior. Theoretical and empirical studies have shown that the optimal amount of parental investment for offspring exceeds that of its parent, and consequently the power balance between the parents and offspring determines the amount provided. Previous studies have reported individual traits in parents and offspring can influence investment, though in reality a set of coevolved traits in both parties will contribute to determine the optimal investment level. Hence, it is essential to investigate the correlation between multiple traits, and how this is related to the variation in parental investment. Herein, I use natural intraspecific variation in the amount of parental investment in a burying beetle *Nicrophorus quadripunctatus* to investigate the links between this variation and multiple parent and offspring traits. Results suggest that there was a genetic basis to parental feeding capacity and offspring solicitation ability, as I found a variation in post-hatching food feeding among populations. I also clarified how this variation is linked to the interrelationships among multiple traits on feeding amount. Variation in investment is particularly important for evolution, and these findings will help us understand the evolution of offspring rearing behavior.

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## **General Introduction**

Parental care is a prime example of altruism and an important life history trait to understand the evolution of family life and social behavior (Davies et al. 1992). Parents spend time and energy on care for their offspring to increase offspring survival and quality. The parental expenditure is called parental investment (Davies et al. 1992). Parental care has evolved multiple times across a wide range of taxa and there is notable variation in the amount of parental investment among species (Smiseth, 2012). Understanding the mechanism generating the variation contributes to explain the patterns in parental care as well as uncovering the evolutionary process underlying the elaboration of parental care.

Parents of many animals invest time and resources for guarding and provisioning their offspring (Davies et al. 1992). The amount of provisioning is an important aspect of parental investment and affects the offspring body size and numerous life history traits of the species (Woodward et al. 2005). Optimization theory (Charnov, 1974; Stephens & Krebs, 1986) predicts surrounding biotic and abiotic environment will determine the optimum amount of provisioning, and thus there will be genetic variation in the amount of parental provisioning among populations. However, no empirical studies have explored genetic variation in the amount of parental provisioning, although it has a substantial impact on offspring traits. This is somewhat surprising, since the genetic variation in pre-hatching investment for an egg and a fetus has been intensively studied (Snell-Rood et al. 2010).

Burying beetles (*Nicrophorus*) are well-studied model systems for parental care in insects, as they provide elaborate parental care including offspring provisioning (Clutton-Brock, 2012). *Nicrophorus* beetles use the carcasses of small vertebrates as a food resource for their larvae. After discovery of the carcass, females develop their ovaries and lay eggs in the soil near the carcass (Eggert and Müller 1997; Scott 1998). After hatching, the larvae crawl to the carcass and obtain food by begging for pre-digested carrion from their parents (who remain with the carcass) or by directly feeding from the carcass themselves. Although parental food provisioning is not necessary for larval survival, it improves offspring survival and increases body size dramatically (Eggert *et al.* 1998). The body size of adult beetles may differ among populations. For instance, the pronotum width in *N. quadripunctatus* is known to differ between Kyoto and Hokkaido populations (Nisimura *et al.* 2002; Atakura & Ueno, 1985). Thus, there may be variation in parental provisioning among populations.

Therefore, in this study, to clarify how increased the amount of provisioning occurs when selective pressures of different environments are applied, we used two populations of intra-species with different amount of provisioning. We investigated whether variation of the amount of provisioning is genetic, multiple parent and offspring traits influencing provisioning amount between population.

## **Chapter 1**

### **Interpopulation genetic variation in parental and offspring traits affecting the amount of provisioning**

#### **Introduction**

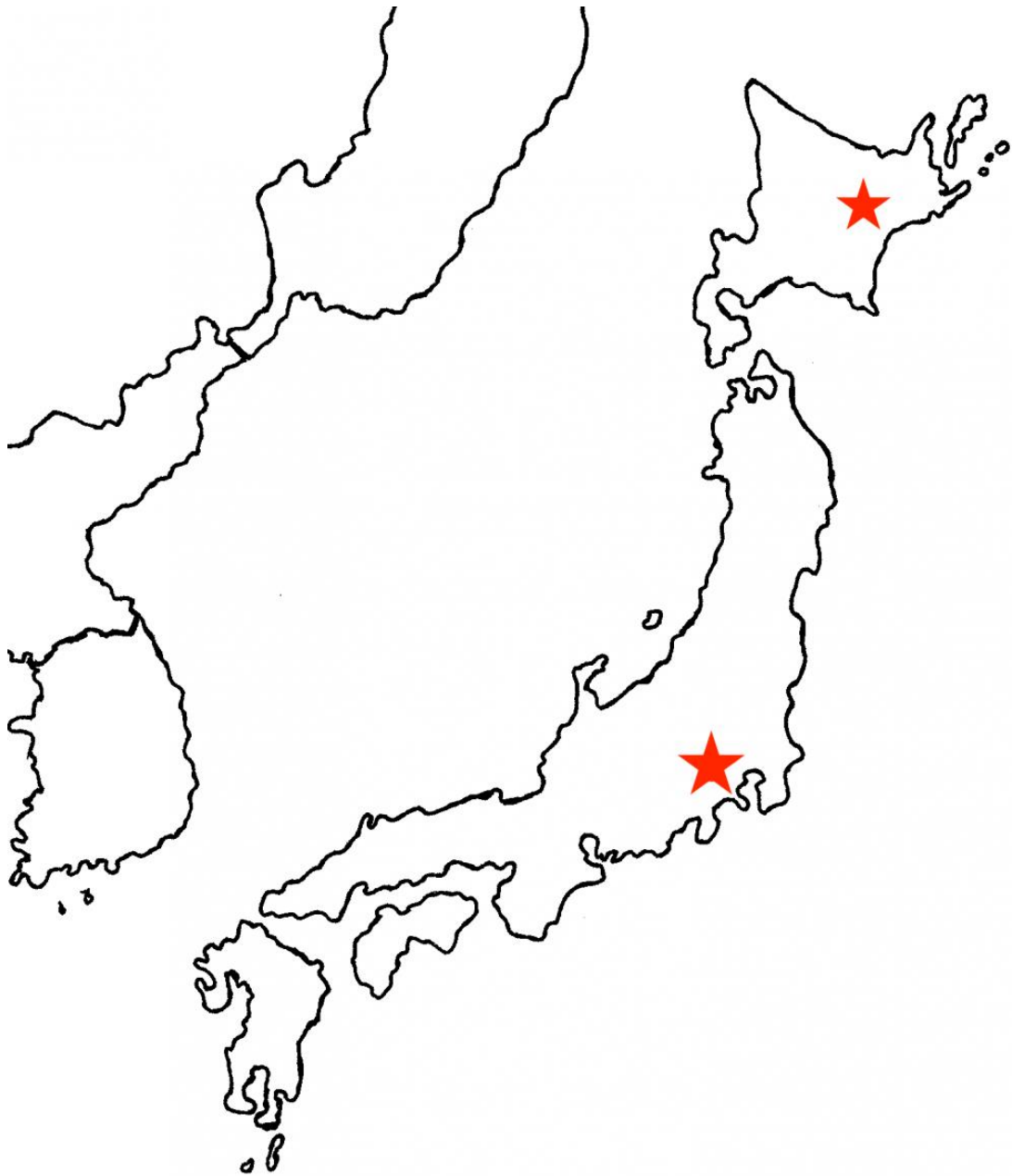
The amount of offspring provisioning is typically determined through parent-offspring interactions (Royle et al. 2002). Since parents and offspring have conflicting interests in the optimal amount of provisioning for each offspring (Godfray, 1995; Godfray & Johnstone, 2000), investment is determined by the power balance between the two parties. Offspring of many species solicit food by emitting begging signals and parents respond to it by changing the amount of provisioning to the offspring (Parker & Macnair, 1979; Hussell, 1988; Kolliker, 2003). Identifying the interpopulation variation in the amount of provisioning contributes to understand how parent and offspring trait values are linked with the evolutionary dynamics of provisioning.

In the present study, I investigated relationship between the variation in the amount of provisioning and interrelationship among the parent and offspring traits in *N. quadripunctatus*. First, I compared adult body size of wild beetles between two populations. Second, I investigated inheritance of this variation using laboratory rearing experiments. Finally, I compared multiple parent and offspring traits that potentially affect the amount of provisioning.

## **Materials and methods**

### *Collection of insects in the field*

To clarify differences between species in the field, adults of all beetle species were trapped by plastic cup traps (122 mm diameter, 111 mm depth) baited with a piece of chicken (40 g), which were installed in sites 1.5 m above the ground on the trunks of trees. Ten traps were installed <300 m apart in an evergreen forest in Hachioji Tokyo (35°40'09.4"N 139°13'00.0"E) and Shibechea Hokkaido (44°43'07.9"N 142°15'01.2"E) (Fig. 1). Beetles at these two locations are known to differ in adult size (Katakura & Ueno, 1985). After one day, all trapped insects were removed. The beetles were maintained individually in small transparent plastic cups (height 4 cm, diameter 6 cm) at 20±1°C under a 14:10 h light: dark cycle and fed 200 mg of freshly killed mealworms (*Zophobas atratus*) three times a week.



**Fig. 1. Study populations**

The star marks show the places where traps were set to collect beetles.

*Comparison of adult body size among populations*

Body size of individuals collected in wild was measured to compare adult body size between natural populations. We measured pronotum width of female and male



parents as a proxy for body size using an electronic Vernier caliper (Mitutoyo Corp., Kanagawa, Japan) with an accuracy of 0.1 mm. Individuals maintained in the laboratory were measured in the same way to compare adult body size in the laboratory and the field.

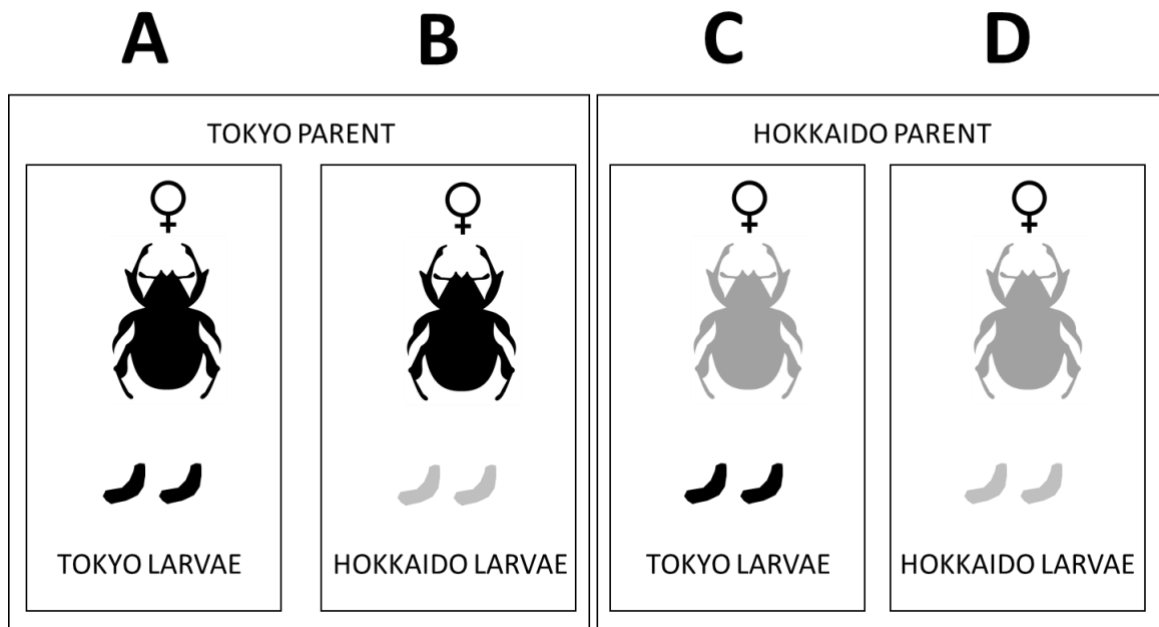
### *Experimental procedure*

Adult beetles reared in the lab were randomly assigned to one of four experimental groups for a cross-fostering experiment (see below). There was no statistically significant difference in the body size of female parents between experimental groups ( $P > 0.05$ , t-test with Bonferroni correction). Pairs of non-sibling, same-aged male and female beetles were randomly selected, and each pair was placed in a plastic cup (height 8 cm, diameter 15 cm) with moist peat. They were provided with 4.0 g of a whole-body mouse carcass (Cyber Cricket, Shiga, Japan). In our pilot study, pairs successfully bred larvae on this size of carcass. The beetles in the plastic cups were kept in a dark incubator at  $20 \pm 1^\circ\text{C}$  for 72 h. During this period, female beetles laid eggs in the soil near the carcass. Then, the female and the carcass were transferred to a second, new plastic cup with moist peat. The male beetles were removed from the original plastic cup at this stage because parental care by male parents has no effect on larval growth or survival under laboratory conditions (Smiseth et al. 2005). The eggs were left to hatch in the original plastic cup. Hatching of larvae was checked at two-hour intervals, and newly hatched larvae were used for experiments.

### *Cross-fostering experiment*

To compare the parental feeding capacity and offspring solicitation ability among populations, we performed a cross-fostering experiment between Tokyo and Hokkaido populations. Four conditions were set and a cross-fostering experiment was conducted (Fig. 2).

At the time of hatching, two larvae were transferred to a carcass with its foster mother and reared under the same conditions as above. The ages of foster parents were the same as natal parents. Larval body weight was measured 120 h after being transferred onto the carcass, because larvae disperse away from the carcass at 120 h (Takata et al. 2013). Each of the four conditions consists of parents from Tokyo or Hokkaido, and two offspring from either locality in various combinations (Fig. 2).



**Fig. 2.** Experimental design of cross-fostering experiment. Tokyo parents and larvae are shown in black and Hokkaido parents and larvae in grey.

### *Statistical analysis*

Generalized linear models (GLM) were used to compare wild and laboratory reared adult body size. In analyses of differences between populations, body size was treated as a response variable assuming a Gaussian distribution, with population and the interaction between these terms. The interaction term was excluded from subsequent analysis, because it did not have a significant effect.

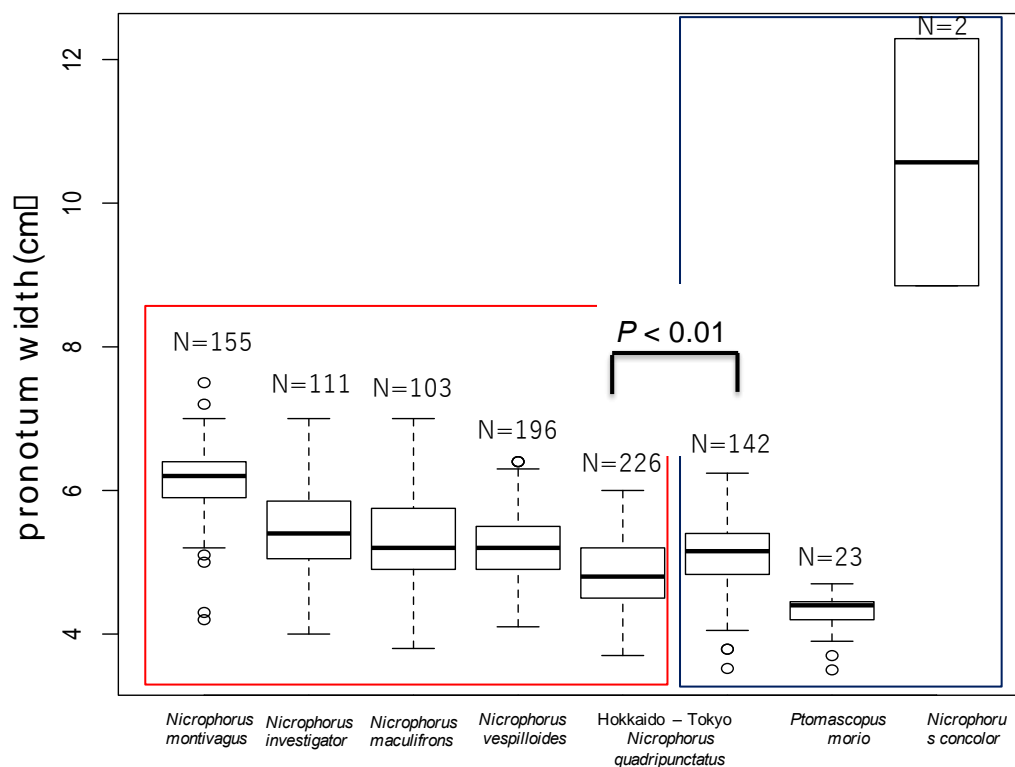
To investigate the relationship between parental feeding capacity and offspring solicitation ability, we analysed the difference in body weight between larvae raised in each experimental group. In analyses comparing experimental groups, larval body weight at 120 h old was treated as a response variable assuming a Gaussian distribution, and population and pronotum width of female parents and its interaction were treated as explanatory variables. Then, the interaction term was excluded from this analysis, because it did not have a significant effect. All GLMs were conducted using R 3.1.1 (R core team 2018), and p-values were calculated using likelihood ratio tests.

## **Results**

### *Comparison of field populations*

Species compositions were different between the two populations. Four and three Nicrophorinae species including *N. quadripunctatus* were collected in Hokkaido and Tokyo population respectively. The notable difference in competitive circumstances

for *N. quadripunctatus* was the number of similar sized competing species. In the Hokkaido population, *N. quadripunctatus* had two similar sized species, *N. vespilloides* and *N. maculifrons*, both of which had superior body size to *N. quadripunctatus*. In the Tokyo population, however body sizes were distinctly different among species [add anova/tukey to show this here]and no species had overlapping body size with *N. quadripunctatus*, (Fig. 3).

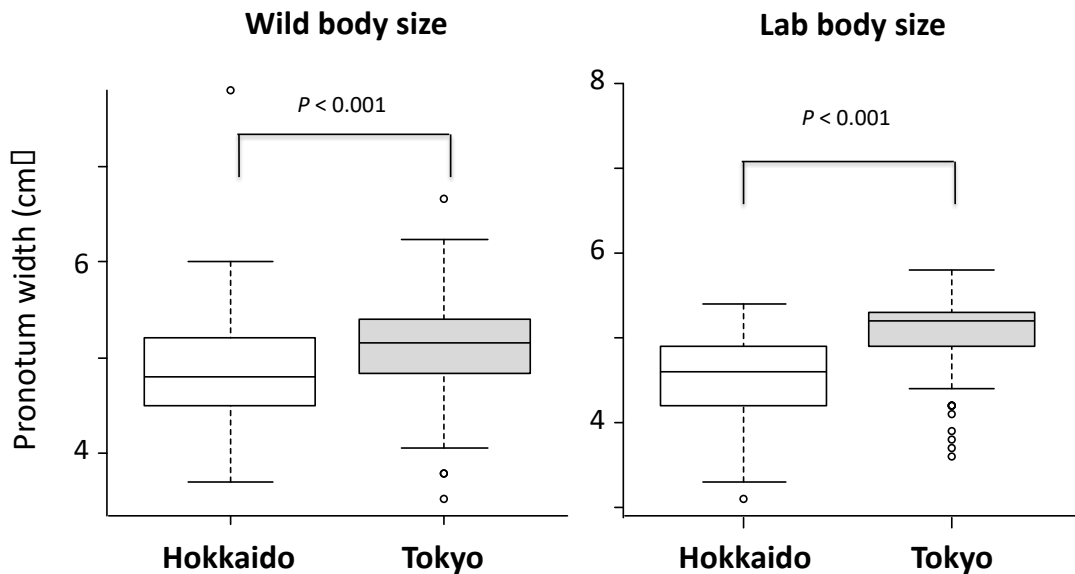


**Fig. 3 Body size of the burying beetles trapped in Hokkaido and Tokyo populations**

The y-axis shows the pronotum width of beetles. The red-boxed panel collected in Hokkaido (*Nicrophorus montivagus*, *N. investigator*, *N. maculifrons*, *N. vespilloides*, *N. quadripunctatus*). The blue-boxed panel collected in Tokyo (*Nicrophorus*

*quadripunctatus*, *Ptomascopus morio*, *Nicrophorus concolor*)

Body size was different between Hokkaido and Tokyo populations in the field caught *N. quadripunctatus*. The pronotum width of the wild beetles in Tokyo was larger than the wild beetles in Hokkaido (GLM: estimate = 4.85644,  $\chi^2 = 149.788$ , d.f. = 0.03242,  $P < 0.001$ ). The difference in body size was approximately 5 %. The variation was also observed between Tokyo and Hokkaido sourced beetles reared in the lab (GLM: estimate = 0.53419,  $\chi^2 = -20.611$ , d.f. = 287,  $P < 0.01$ ; Fig. 4) indicating there is a genetic basis to the difference in body size.

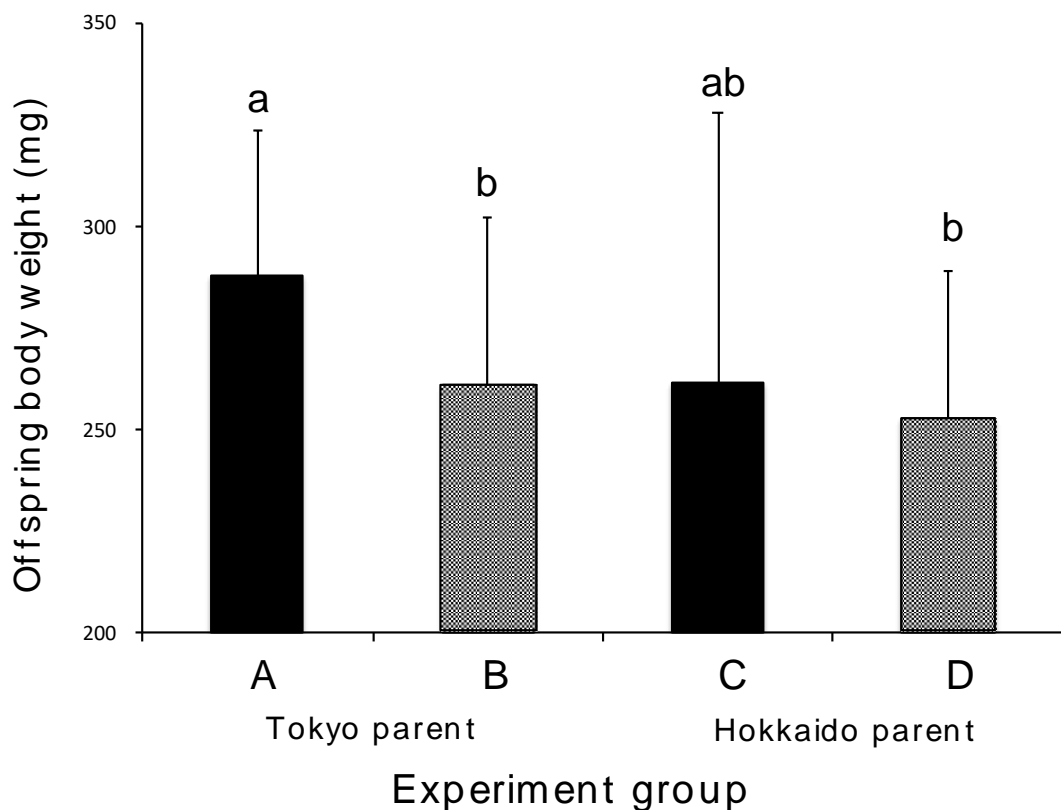


**Fig. 4. Genetic variation in body size between populations**

Box plot showing pronotum width of laboratory bred adult beetles originating from Hokkaido and Tokyo populations. White bars indicate Hokkaido and gray bars indicate Tokyo. Lab data for Hokkaido and Tokyo populations were collected from 50 male and 50 female beetles, and 50 male and 50 female beetles respectively.

*Results of cross-fostering experiment*

Offspring body size was significantly affected by the combination of parental and offspring source population (ANOVA:  $F_3 = 6.288$ ,  $P < 0.001$ ). For Tokyo-larvae, Tokyo-mothers bred larger larvae (though this was marginally non-significant) than Hokkaido-mothers (Tukey-test:  $P = 0.056$ ), however, this effect was not observed when they bred Hokkaido larvae (Tukey-test:  $P = 0.740$ ). Tokyo-larvae grew into larger size than Hokkaido-larvae when they were raised by Tokyo mothers (Tukey-test:  $P = 0.0089$ ), however, this effect was not observed when they were raised by Hokkaido mothers (Tukey-test:  $P = 0.827$ )(Fig. 5).



**Fig. 5. Genetic variations in parental feeding capacity and offspring solicitation ability**

A • B group is Tokyo parent group. C • D group is Hokkaido parent group. Black bars indicates Tokyo offspring. Gray bars indicate Hokkaido offspring.

## **Discussion**

In many species with parental care, parental provisioning has a remarkable impact on offspring life history. In the present study, we found between population difference in the amount of parental provisioning in *N. quadripunctatus*. The variation is found in the field population as well as under laboratory conditions, suggesting that it has a heritable basis. The cross-fostering experiment revealed that the variation is caused by the genetic variation in both parental feeding capacity and offspring solicitation ability between populations. These results suggest that both parent and offspring traits affect the amount of parental investment.

In the present study, I did not directly quantify the amount of parental provisioning. However, previous studies in burying beetles suggested that the larval body weight reflects the amount of provisioning obtained by the offspring. Furthermore, unlike other *Nicrophorus* species, parental feeding is important for survival of first instar larvae in *N. quadripunctatus*.( Eggert et al. 1998). Therefore, I can reasonably conclude that the difference in larval body size is caused by the variation in amount of provisioning to each larva.

The discovery of genetic variation in the amount of parental provisioning among populations and indication that this variation is determined by both parent and offspring traits links previously demonstrated laboratory-based knowledge to the

variation observed in the field. Previous studies in birds showed that even within a population there is variation between parental feeding capacity and offspring solicitation ability(Lock et al, 2004). However, previous studies focused on genetic co-variance between the parent and offspring traits assuming the stable equilibrium amount of parental provisioning(Lock et al, 2004). Thus, no studies have investigated how the equilibrium amount of provisioning shifts, i.e. the relationship between the variation in provisioning amount and traits expressed in parent and offspring. My results suggest that the evolutionary shift in provisioning amount is altered by differences in both parent and offspring traits.

The increase in parental provisioning is closely linked to elaboration of parental care. My results suggest that the equilibrium level of provisioning is different among populations and is strongly correlated with genetic variation in parental capacity of provisioning and offspring ability to solicit food. When selecting pressure of different environments, this research leads to clarifying the process of the amount of provisioning increase of how the amount of provisioning is determined between the parent and the offspring and the increase in the amount of provisioning occurred.



## **Chapter 2**

### **Comprehensive comparison of multiple parent and offspring traits influencing provisioning amount**

#### **Introduction**

The amount of parental provisioning is a quantitative trait and influenced by multiple parent and offspring traits (Haskell, 1994). For instance, color and shape of offspring mouth, and loudness of begging affect the provisioning amount in birds (Harper, 1986). These traits are typically exaggerated compared to species without parental provisioning (Kilner & Himde, 2012). However, no studies have investigated the evolutionary dynamics of the traits, since previous studies have focused on a pair of interacting parent and offspring traits and their co-evolution. Selection may act on equally on the related traits, and changes in trait value proceed simultaneously. Or, selective force may act unequally among the related traits, and changes in trait value proceed in a step-wise manner.

In burying beetles, the amount of parental provisioning is influenced by multiple traits. For instance, number and body size of offspring affect provisioning amount by shaping number of competitors and competitive ability for parental provisioning (Benowitz, 2017). During begging, larvae keep waving their legs and tapping parental mouth parts while raising their heads. A recent study showed that length of the larval leg is one of the traits which influences the provisioning amount (M. Takata et al, unpublished data), but whether this is the only trait remains unclear.

In the present study, the traits which potentially influence provisioning amount were compared between Hokkaido and Tokyo populations to reveal their evolutionary dynamics. I investigated interpopulation variation of the following six traits: number of eggs as related to number of larvae, volume of eggs as determinant factor for larval size at hatching, lengths of larval fore-, middle- and hind-legs, and larval head widths as an indicator of larval body size.

## **Materials and methods**

### *Experimental procedure*

To compare parental and offspring traits related to quantitative variation in feeding volume, eggs and larvae were obtained by indoor breeding of the F1 generation beetles obtained from outdoor collected parents. Breeding was done in a plastic container with moist peat and mouse carcass as in Chapter 1.

### *Traits influencing provisioning amount measurement*

To measure the number of eggs and egg size, I collected all the eggs from each parent from Tokyo and Hokkaido populations at 72 hours and 92 hours after breeding. I collected 100 eggs laid by each 100 parents. The lengths of their major and minor axes were measured. To measure the character of the 1st instar larva hatched from these eggs, I placed eggs on individually wet filter paper and hatched the larva. 1st instar larvae were collected within an hour of hatching. I measured the size of the head and the length of the 1-3 legs for 1st larvae instars. The lengths of the egg, larval head, and legs were measured using light microscopy (cellSens Standard Olympus software

version 1.6, Olympus Optical Co., Tokyo, Japan) to an accuracy of 0.01 mm.

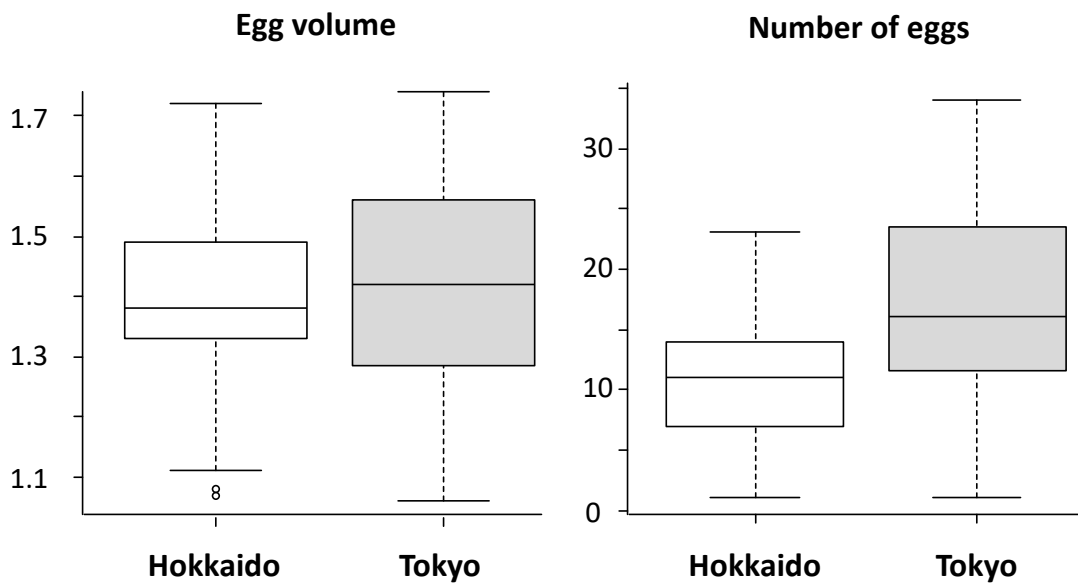
### *Statistical analysis*

Generalized linear models (GLM) were used to investigate variation in traits influencing provisioning among populations. The number of eggs, the egg size, and the characters of the larva were used as response variables, and the experimental group and ID of the genetic parent of the larva were treated as explanatory variables assuming a Gaussian distribution, with population.

## **Results**

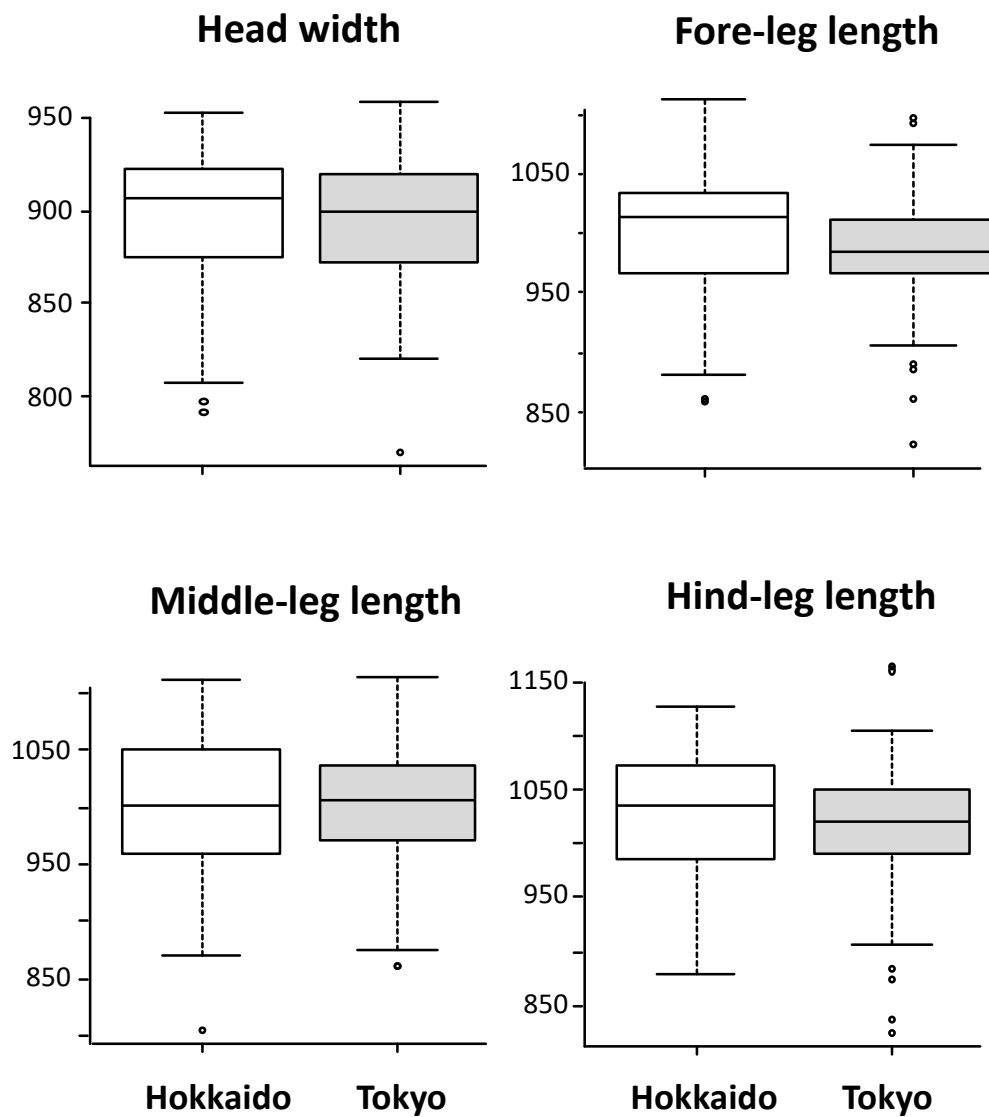
### *Traits influencing provisioning amount measurement*

The size of the egg did not differ between the two different populations (GLM: estimate = 0.03645,  $\chi^2 = -0.028201$ , d.f. = 83, P = 0.318). The number of eggs was different between the two different populations, and was higher in the Tokyo group (GLM: estimate = 6.8328,  $\chi^2 = -1256.7$ , d.f. = 106, P < 0.01). There was no difference between the population in larval head width, which is an index of body size (GLM: estimate = 0.5167,  $\chi^2 = -11.441$ , d.f. = 173, P = 0.924). The trait characteristics of the larval legs determine the feeding amount (unpublished data) but of these, only the length of the fore-leg differed between the two different populations, being shorter in the Tokyo population (GLM: estimate = -15.297,  $\chi^2 = -10028$ , df = 173, P = 0.044). There was no difference in the length of the middle leg (GLM: estimate = -1.540,  $\chi^2 = -101.64$ , d.f. = 173, P = 0.857) or hind leg (GLM: estimate = -1.540,  $\chi^2 = -101.64$ , d.f. = 173, P = 0.857; Figs. 6, 7).



**Fig. 6. Variations in egg volume and number among populations**

Left: box plot showing egg volume among population; right: box plot showing variation in egg number between populations. White bars indicate Hokkaido and Gray bars indicate Tokyo. Egg volume data for Hokkaido and Tokyo population were from 44 clutches (735 eggs), 41 clutches (472 eggs) respectively. Number of egg data for Hokkaido and Tokyo population were from 51 clutches and 57 clutches respectively.



**Fig.7. Variation in traits influencing provisioning amount between populations**

Box plots showing among population variation in various offspring traits. White bars indicate Hokkaido and Gray bars indicate Tokyo. Sample size for Hokkaido and Tokyo population were from  $n = 100$  and  $n = 76$  individuals respectively.

## **Discussion**

In the present study, I found that not all but some of the traits have genetic variation between the populations with quantitative variation in the provisioning amount. The number of eggs (which is related to number of larvae) and egg volume (a determinant of offspring size at hatching) were larger in the Tokyo population, which also exhibits a higher offspring-provisioning amount. The number of eggs (which is related to number of larvae) and egg size (which determines offspring size at hatching) were larger in the Tokyo population where the provisioning amount is higher. However, the larval leg length (which affects the strength of the begging signal) was smaller in Tokyo than Hokkaido. There was no difference in larval body size between the populations. These results suggest that shift in the equilibrium level of provisioning produces the different selection pressures among the related traits.

In organisms in which parental feeding is essential for the survival of offspring, traits and sizes of beak and feeding responses to them, such as feeding traits, have acquired traits affecting feed amount. The present study revealed that by paying attention to multiple traits related to provisioning amount we find observations suggesting that increase in feeding amount is caused by evolution of traits related to provisioning amount. However, it is necessary to compare also the population with variation in provisioning amount. Whether or not the provisioning amount is correlated with the traits that we found the linkage here will provide evidence for whether the variation in the provisioning amount always cause selection on the traits or which traits will be under selection can not be predicted by the variation. Until now, there are no models to predict the evolutionary dynamics of traits when there are multiple traits

affecting feeding amount, which is an important viewpoint for thinking about the evolution of sophisticated nursing behaviors. The result of this research leads to clarifying the evolutionary process of multiple traits.

Recently, artificial selection experiments have shown which traits respond to selection (Jarrett et al. 2017). The artificial selection is a powerful technique to reveal short term selection responses. However, patterns in traits responding / not responding to selection may not match with the patterns observed in the field, because the populations are under selection for a much longer time scale, and response in one trait changes selection pressure to other traits. It is also important to investigate the genetic changes which have occurred on the evolutionary time scale. Thus, using both techniques is fruitful to reveal evolutionary dynamics of the parent and offspring traits.

The increase in feeding amount is closely related to the evolution of advanced offspring rearing behavior. Our results indicate that the increase in feeding amount is increased not by all traits associated with feeding amount but by evolution of one trait. By looking at a plurality of traits related to feeding amount, it becomes possible to clarify the process of trait evolution.

## **General Discussion**

Parental care is closely linked to a change in investment amount and a trait variation related to feeding amount. In this study I use laboratory rearing experiments and field-based comparisons of the burying beetle *N. quadripunctatus* to investigate how evolution of traits relating to parental investment can explain observed differences in body size between populations.

In Chapter 1, it was revealed that genetic variation in feeding volume are likely linked to selective pressures of different environments. In Chapter 2, it was revealed that only one part of the traits associated with feed volume affects feeding variation. This research not only explains the patterns of offspring rearing activities that are presently found, but also helps us to understand the evolution of fostering behavior and further contributes to the elucidation of evolution of family life and social behaviour.

In order to discuss the evolutionary process of the increase in feed quantity in more detail, we have to clarify some remaining questions. As mentioned in the discussion in Chapter 1, beetles are mostly dependent on the feeding amount from the parent at the first instar, but even in the absence of the feeding behavior from the parent, the offspring is self-feeding at the 2-3 instar. It is possible to survive without parental feeding. Therefore, it is necessary to actually observe feeding frequency, feeding time, and feeding amount, and I would like to consider them for our future work. In addition, as a result of Chapter 2, the traits of Hokkaido, which is smaller in feeding amount than Tokyo, has a longer first leg in offspring to use when feeding. There is a possibility



that offspring competitiveness and competition among offspring are related to this. Therefore, there is a need to clarify the frequency of parental care and the defense time to competitors of parents. Finally, it is important to investigate how multiple traits related to feeding quantities respond when variation occurs on evolutionary time scales, and the results of this research should make it possible to develop a model to predict these evolutionary dynamics.

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