

# Heritability estimations of ammonia tolerance and survival of ridgetail white prawn *Exopalaemon carinicauda*\*

Ding LÜ<sup>1, 2, 3, #</sup>, Chengsong ZHANG<sup>1, 2, 3, #</sup>, Yang YU<sup>1, 2, 3</sup>, Jianhai XIANG<sup>1, 2, 3</sup>, Fuhua LI<sup>1, 2, 3, 4, \*\*</sup>

<sup>1</sup> Key Laboratory of Experimental Marine Biology, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China

<sup>2</sup> Laboratory for Marine Biology and Biotechnology, Pilot National Laboratory for Marine Science and Technology (Qingdao), Qingdao 266237, China

<sup>3</sup> Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao 266071, China

<sup>4</sup> The Innovation of Seed Design, Chinese Academy of Sciences, Wuhan 430072, China

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**Abstract** Ridgetail white prawn *Exopalaemon carinicauda* is an important economic marine species in China. To improve the germplasm quality of cultured *E. carinicauda*, for the first time, we estimated the heritability of ammonia tolerance and survival of *E. carinicauda*, covering 263 full-sib families in multiple generations. Analysis models including binary linear animal model (BLA), binary linear sire-dam model (BLSD), probit threshold animal model (PTA), and probit threshold sire-dam model (PTSD) were used. The estimated heritability of tolerance to ammonia in different models ranged from 0.09 to 0.22, and that of survival rate ranged from 0.06 to 0.16. Concerning the tolerance to ammonia, both the PTSD and BLSD models showed comparatively better prediction accuracies (0.48 and 0.47, respectively) than PTA and BLA models (0.40 and 0.26, respectively), while to the survival rate, all four models presented relatively low predictive abilities (0.16–0.26). This study provided important information for the future breeding program of *E. carinicauda*.

**Keyword:** heritability; *Exopalaemon carinicauda*; tolerance to ammonia; survival rate

## 1 INTRODUCTION

The ridgetail white prawn, *Exopalaemon carinicauda* (Crustacean: Decapoda: Palaemonidae), is an economically important marine prawn, distributed naturally along China's coast and the west coast of the Korean Peninsula (Li et al., 2003). With fast growth, strong reproduction ability, wide environmental adaptability, and delicious meat, it is one of the most important species in both aquaculture and fishery activities in China. However, farming on this species mainly relies on the capture of post-larvae or parent prawns from coastal areas, and this primitive method depletes wild resources (Bashirullah et al., 1989) and introduces the risk of pathogen dissemination, especially virulent viruses and bacteria (Lightner et al., 1998), which has led to serious economic loss in shrimp industry around the world (Flegel, 2009; Thitamadee et al., 2016). Besides, culturing wild prawns without artificial breeding

greatly restricted the production efficiency. To continue developing aquaculture industry of *E. carinicauda*, genetic improvement on the main economic traits is particularly important.

Ammonia, especially nonionic ammonia, is the most common toxic environmental factor in aquaculture, due to direct discharge of cultivated animals and ammonization of residual feed and excrement (Armstrong et al., 1978; Yu and Hirayama, 1986). It was reported that high concentrations of ammonia can lead to harmful effects on cultured prawns, such as reducing growth (Chen and Kou, 1992; Chen and Lin, 1992a, b), weakening immune

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\*\* Corresponding author: fhli@qdio.ac.cn

# Ding LÜ and Chengsong ZHANG contributed equally to this work and should be regarded as co-first authors.

system (Liu and Chen, 2004; Wang and Chen, 2005) and increasing mortality (Chen et al., 1990; Lin et al., 1993). Therefore, tolerance of prawns to ammonia stress is an important trait, which enables them to be adaptive to relatively high concentration of ammonia thus to raise the production. Additionally, the output of *E. carinicauda* depends greatly on the survival rate during cultivation.

Selective breeding is a basic approach for genetic improvement in aquatic species, which offers an opportunity of continuous genetic gain, and can be multiplied and expressed in a huge number of progenies in aquatic species (Gjedrem et al., 2012). In the past decade, numerous shrimp selective breeding programs in Asia and America were initiated and have made considerable achievements in a broad range of traits, including growth, survival, and resistance to a specific pathogen (Hetzl et al., 2000; Argue et al., 2002; Gitterle et al., 2007; Luan et al., 2012, 2014; Sui et al., 2016). However, studies and breeding programs of *E. carinicauda* are scarce.

To improve the germplasm quality of cultured *E. carinicauda*, a breeding project aimed at increasing the tolerance to ammonia and survival rate was conducted in 2012–2016. Although complete pedigree of the prawn of five generations and their phenotypic data were available, information on the genetic parameters remained limited. In this study, the heritability of ammonia tolerance and survival of *E. carinicauda* was estimated in four statistical models. The predictive performance of these models was compared to determine the most optimal fitting model. The results obtained in this study provide valuable information for subsequent selection breeding.

## 2 MATERIAL AND METHOD

### 2.1 Material

The breeding program was performed at Nantong Juhao Company, Jiansu Province, China. The base generation (G0), including 57 full-sib families, was bred by collecting females carrying eggs from Laoba port near Hai'an County, Jiangsu Province in 2012. When the offspring were cultured to the stage of post-larvae, 500 individuals from each family were selected randomly and reared in 200-L white plastic tank separately based on a family-culturing unit. To ensure that the rearing conditions were kept as consistently as possible, all the plastic tanks were put in the same workshop. Eighty percent of the water was changed every 2 d, using disinfected seawater

**Table 1 Numbers of full-sib families and prawns tested**

Generation	Year	Numbers of full-sib families	Numbers of prawns involved in tolerance to ammonia test	Numbers of prawns involved in survival test
G0	2012	57	2 280	28 500
G1	2013	89	3 560	–
G2	2014	56	2 240	14 000
G3	2015	31	1 240	7 750
G4	2016	30	900	9 000
Total		263	10 220	59 250

Note: Survival test was not conducted in 2013. – means no data.

from the same reservoir. Water temperature was varied with air temperature (22–32 °C), at the salinity of 20±2, pH of 8.2–8.5. The light source was natural light. After 50 d, the survival rate of each family was calculated. Meanwhile, another 40 individuals from each family were selected randomly to test their tolerance to ammonia exposure. The testing ammonia concentrations were determined by preliminary experiments to ensure that about half of the prawns died within 96 h after ammonia exposure. The total ammonia nitrogen concentrations used for formal testing were 50 mg/L in G0 and G1; 55 mg/L in G2–G4. After the tolerance to ammonia nitrogen was tested for each family, the top 20 families for each trait were selected to produce G1 by mating among families in 2013. The subsequent generations (G2–G4) were established using similar approaches as G1. A total of 263 full-sib families in 5 generations were used for data analysis. In total, 10 220 prawns were involved in the ammonia tolerance test and 59 250 prawns in the survival test (Table 1). Phenotypes of alive and dead individuals after tolerance to ammonia nitrogen test and survival test were recorded as 1 and 0, respectively.

### 2.2 Genetic analysis

In this study, genetic parameters for two traits were analyzed using both linear mixed model and threshold generalized linear mixed model. Additionally, each type of model contained both animal model and sire-dam model. Four models were applied as follows:

**Model 1:** Binary linear animal model (BLA):

$$y_{ij} = \mu + \text{year}_j + cb_i + a_i + e_{ij}, \quad (1)$$

where,  $y_{ij}$  is the survival status of individual  $i$  (0 for dead, 1 for alive);  $\mu$  is the overall mean;  $\text{year}_j$  is the fixed effect of year  $j$  (five levels);  $c$  is the regression coefficient for the covariate for day-age of  $i^{\text{th}}$  offspring  $b_i$ ;  $a_i$  is the random additive genetic effect of animal  $i$ ,

with  $a \sim (0, A\sigma_a^2)$ , where  $A$  is the additive genetic relationship matrix among all individuals, and it was constructed using pedigree information in the current study;  $e_{ij}$  is the random error term, with  $e_{ij} \sim (0, I\sigma_e^2)$ , where  $I$  is  $n \times 1$  identity matrix,  $n$  is the number of individuals.

**Model 2:** Binary linear sire-dam model (BLSD):

$$y_{ijlm} = \mu + \text{year}_j + cb_i + \text{sire}_l + \text{dam}_m + e_{ij}, \quad (2)$$

where  $\text{sire}_l + \text{dam}_m$  are the random additive genetic effect of sire  $l$  and dam  $m$ , with  $\text{sire}_l$  or  $\text{dam}_m \sim (0, A\sigma_{sd}^2)$  ( $\sigma_{sd}^2 = \sigma_{\text{sire}}^2 = \sigma_{\text{dam}}^2$ ), where  $A$  is the additive genetic relationship matrix among all individuals; and the other parameters are as described in model 1.

**Model 3:** Probit threshold animal model (PTA):

$$\lambda_{ij} = \mu + \text{year}_j + cb_i + a_i, \\ y_{ij} = \begin{cases} 0 & \text{if } \lambda_{ij} \leq 0 \\ 1 & \text{if } \lambda_{ij} > 0 \end{cases}, \quad (3)$$

where  $\lambda_{ij}$  is the underlying liability of  $y_{ij}$ , which is assumed to be a cumulative standard normal distribution and the residual variance of  $\lambda_{ij}(\sigma_e^2)$  is assumed to be 1; the other parameters are as described in model 1. The probit link function  $\eta = \Phi^{-1}(p_i)$  is used, with inverse link  $p_i = \Phi(\eta) = \int_{-\infty}^{\eta} \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx$ , where  $\Phi$  is the cumulative normal density function, and  $p_i$  is the probability of alive for individual  $i$ . The Bernoulli distribution for a binary trait for an individual prawn with  $y_i=1$  (alive) and  $y_i=0$  (dead) is the probability  $(y_i|p_i) = (p_i)^{y_i} (1-p_i)^{1-y_i}$ .

**Model 4:** Probit threshold sire-dam model (PTSD):

$$\lambda_{ijlm} = \mu + \text{year}_j + cb_i + \text{sire}_l + \text{dam}_m, \\ y_{ijlm} = \begin{cases} 0 & \text{if } \lambda_{ijlm} \leq 0 \\ 1 & \text{if } \lambda_{ijlm} > 0 \end{cases}. \quad (4)$$

Model 4 is a probit threshold sire-dam model. The parameters in model 4 are well described in model 2 and 3 and the probit link function was also applied. In particular,  $\sigma_e^2=1$  was also used in model 4.

When using animal models (models 1 and 3), the heritability of both traits was estimated from a single trait model. Phenotypic and genetic correlations were obtained using bivariate analyses, using the same statistical model. Phenotypic variance was the sum of additive genetic variance and residual variance as:  $\sigma_p^2 = \sigma_a^2 + \sigma_e^2$ . Heritability was calculated as the ratio between additive genetic variance and phenotypic variance:  $h = \sigma_a^2 / \sigma_p^2$ . Under sire-dam model (models 2 and 4), Heritability was calculated as:  $h = \frac{4\sigma_{sd}^2}{2\sigma_{sd}^2 + \sigma_e^2}$ .

Besides, the heritability would be overestimated in probit threshold model, so the estimates in models 3 and 4 were adjusted according to Robertson and Lerner (1949).

Genetic and phenotypic correlations between the two traits were calculated based on animal models (models 1 and 3) as follows:  $\gamma = C / \sqrt{\sigma_X^2 \cdot \sigma_Y^2}$  where  $C$  is the genetic or phenotypic covariance,  $\sigma_X^2$  and  $\sigma_Y^2$  are the additive genetic or phenotypic variance of trait  $X$  and trait  $Y$ , respectively. The Z-score, computed as the ratio between estimate of each parameter and its standard error (SE), was used for testing whether each parameter estimate was significantly different from zero.

The model solutions and genetic parameter estimations were processed in ASReml 4.0 (Gilmour et al., 2016).

### 2.3 Model comparison

To compare predictive abilities of four models in this study, we used phenotype dataset containing the first four generations (2012–2015) to calculate family estimated breeding value (EBVs) in 2016 from each model. Then, Spearman correlation coefficients between family EBVs and actual family average phenotype (survival rate) in 2016 were calculated. Since we paid more attention to the ranking difference of two sets of data, the Spearman correlation coefficient was adopted. The EBVs for families were estimated using ASReml and Spearman correlation coefficients were calculated using R (R Core Team, 2018).

## 3 RESULT

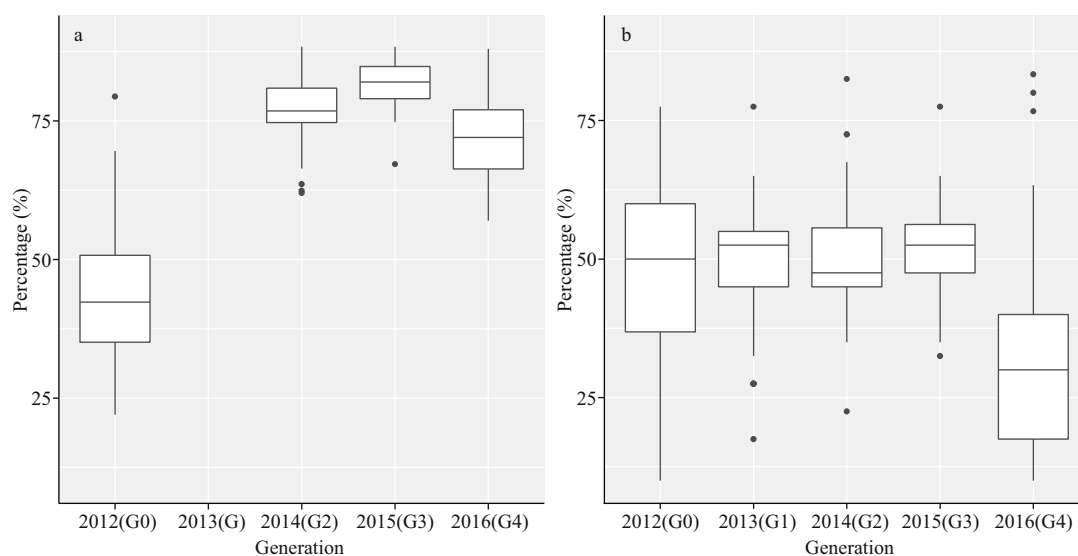
### 3.1 Descriptive statistics for phenotype data

The coefficient of variation of the survival rate in G0 was 27.21%, being higher than those of subsequent generations, ranging from 5.40% to 10.67%, and the data of cultured survival rate in 2013 were missing (Fig.1).

The coefficients of variation in family survival rate after 96-h acute ammonia stress test are relatively larger, ranging from 20.50% to 59.08% (Fig.1). And the overall survival rate after tolerance to ammonia test in 2012–2016 was 47.72%, 49.35%, 50.76%, 48.71%, and 44.22%, respectively.

### 3.2 Genetic analysis

Variance components, heritability for ammonia tolerance and survival calculated using different models are shown in Table 2. The heritability estimates



**Fig.1** Distribution of family survival rate after being raised for 50 d under normal conditions (a) and after 96-h acute ammonia stress (b) in each generation

The black dots are outliers.

**Table 2** Variance components, heritability of tolerance to ammonia and survival in four statistical models

Trait	Model	$\sigma_a^2 \pm SE$	$\sigma_{sd}^2 \pm SE$	$\sigma_e^2$	$h_2$	$h_2$ adjusted
Ammonia tolerance	1	0.034±0.005	—	0.220±0.004	0.13±0.02	—
	2	—	0.015±0.002	0.237±0.003	0.22±0.03	—
	3	0.155±0.021	—	1	0.13±0.02	0.09±0.01
	4	—	0.100±0.014	1	0.33±0.04	0.21±0.03
Survival	1	0.021±0.002	—	0.193±0.002	0.10±0.01	—
	2	—	0.088±0.001	0.203±0.001	0.16±0.02	—
	3	0.110±0.010	—	1	0.10±0.01	0.06±0.01
	4	—	0.075±0.009	1	0.26±0.03	0.16±0.02

— means no data.

**Table 3** Genetic correlation ( $\gamma_g$ ) and phenotypic correlation ( $\gamma_p$ ) between tolerance to ammonia and survival in models 1 and 3

Model	$\gamma_g$	$\gamma_p$
1	0.20±0.10	0.29±0.13
3	0.20±0.04	0.09±0.02

of tolerance to ammonia ranged from 0.09±0.01 to 0.22±0.03, and those of survival ranged from 0.06±0.01 to 0.16±0.02. Heritability for tolerance to ammonia was overall larger than that for survival. For both traits, estimates from sire-dam models (models 2 and 4) were close and they were higher than those from the other models. Estimated heritability using different models was highly significantly different from zero ( $P < 0.01$ ) through Z-score.

Genetic and phenotypic correlations between ammonia tolerance and survival calculated using

animal models are shown in Table 3. Genetic correlations were 0.20±0.10 and 0.20±0.04 based on model 1 and model 3, respectively. Phenotypic correlations were 0.29±0.13 and 0.09±0.02, respectively. All of them were low but significantly different from zero ( $P < 0.05$ ).

The family EBVs of two traits were also obtained from different models and their relationships are presented in Table 4. The Pearson correlation coefficients between EBVs calculated using different models were all greater than 0.9.

### 3.3 Comparisons among different models

Spearman correlation coefficients between family EBVs based on data of 2012–2015 and true family average phenotype (survival rate) in 2016 are presented in Table 5. For tolerance to ammonia, Spearman correlation coefficients under sire-dam

**Table 4 Pearson correlation coefficients among EBVs from different models**

	Model 1	Model 2	Model 3	Model 4
Model 1	—	0.958	0.999	0.953
Model 2	0.957	—	0.965	0.999
Model 3	0.995	0.963	—	0.961
Model 4	0.932	0.992	0.950	—

The upper triangular elements are the coefficients of tolerance to ammonia and lower triangular elements are the coefficients of survival.

models (models 2 and 4) were larger than those obtained from animal models (models 1 and 3), which reached a moderate correlation level. However, for survival, all models showed a low predictive ability (Table 5).

## 4 DISCUSSION

### 4.1 Genetic parameter

Understanding the additive genetic variance existing in the target population was the foundation of initiating a selection-breeding program. One of the main objectives of this study was to estimate the heritability of tolerance to ammonia and survival in *E. carinicauda*. The results showed that heritability for tolerance to ammonia or survival based on four models was all highly significantly different from zero ( $P < 0.01$ ), which indicated that improvement on these two traits in *E. carinicauda* was theoretically feasible. Furthermore, heritability for tolerance to ammonia estimated in this study belonged to the medium, based on the following categorization: low (0.05–0.15), medium (0.20–0.40), high (0.45–0.60), and very high ( $> 0.65$ ) (Cardellino and Rovira, 1987), and that for survival was lower than tolerance to ammonia. Until present, knowledge about the heritability of ammonia tolerance or survival in crustaceans is still limited. The heritability for tolerance to ammonia in *Litopenaeus vannamei* juveniles was estimated to be 0.148–0.264 (Li et al., 2016; Lu et al., 2017), and it was reported as  $0.13 \pm 0.06$  in *Marsupenaeus japonicus* (Jiang et al., 2017). For the survival trait, the heritability was estimated to be 0.04–0.10 in *L. vannamei* (Gitterle et al., 2005, 2007) and 0.02–0.14 in *Macrobrachium rosenbergii* (Luan et al., 2014; Vu et al., 2017). Estimates in the present and previous studies were similar for both traits. What called for special attention was that we did our best to maintain the environmental conditions consistent among the families in the trait-testing process, but subtle differences were inevitable. Besides, the

**Table 5 Spearman correlation coefficients between family EBVs within G4 based on dataset consisting of G0–G3 and actual family average phenotype (survival rate) within G4 in different models**

Model	Tolerance to ammonia	Survival
Model 1	0.26	0.26
Model 2	0.47	0.19
Model 3	0.40	0.24
Model 4	0.48	0.16

absence of common environmental effects may lead to the bias of heritability estimates (Gallardo et al., 2010).

Analysis of the genetic correlation and phenotypic correlation between ammonia tolerance and survival showed a low but significant positive genetic correlation ( $0.20 \pm 0.10$  and  $0.20 \pm 0.04$ , respectively). This result suggested that selection on one trait would not cause a negative response to another one.

### 4.2 Model comparison

In previous quantitative genetics studies, the predictive abilities of statistic models were evaluated through model cross-validation (Gitterle et al., 2006; Saatchi et al., 2011; Rezende et al., 2012; Lever et al., 2016). In this study, we used a correlation between the actual family average phenotype in G4 and their family EBVs calculated from each model as the criteria for model predictive abilities to make the statistical model closer to practical application. Although the family EBVs calculated from different statistical models showed high correlations (Table 4), the predictive abilities were varied considerably among models (Table 5). For the tolerance to ammonia, the predictive abilities of threshold sire-dam model (model 4) were slightly higher than the linear sire-dam model (model 2), and clearly higher than animal models (models 1 and 3), suggesting that sire-dam models (both linear and threshold) are the optimal models. Previous studies indicated that animal threshold model was not suitable, because it tended to give a biased estimation of genetic parameters (Hoeschele and Tier, 1995; Luo et al., 2001; Stock et al., 2007). Therefore, threshold sire-dam model should be a preferred model for genetic evaluation on threshold traits in future selection breeding.

The predictive abilities of different models for survival traits were all unsatisfactory. There was no or weak correlation between predicted family EBVs and



actual phenotype values because survival is complicated and influenced by many factors. During aquaculture, the survival trait contains various traits, such as resistance to different pathogens, tolerance to different physical and chemical stresses and other lethal factors. Considering that the low predictive accuracies were obtained in survival trait, it is not an ideal breeding target. In fact, selective breeding aimed at increasing resistance to specific diseases, which is measured as survival under challenge testing with a specific pathogen, seemed to be a more targeted approach to improve the survival rate of aquaculture (Ødegård et al., 2011). Besides, as the accumulation of data and pedigree depth, selection based on EBVs instead of phenotypes is becoming increasingly urgent and effective to accelerate the progress of selective breeding.

## 5 CONCLUSION

Significant additive genetic variations for tolerance to ammonia and survival existed in *E. carinicauda*. Sire-dam models presented relatively high prediction accuracies for tolerance to ammonia of the prawn, which should be a preferred statistical model for genetic evaluation.

## 6 DATA AVAILABILITY STATEMENT

All data generated and/or analyzed during this study are included in the manuscript.

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