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Effects of intraspecific hybridisation between the northern and the southern populations of the cabbage beetle, *Colaphellus bowringi* on life-history traits

Research Paper

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Abstract

Significant differences in life-history traits between the southern population (S) and northern (N) population of the cabbage beetle *Colaphellus bowringi* make it an excellent model for studying inheritance in this insect. In the present study, we observed the life-history traits of pure strains, F_1, reciprocal backcross and reciprocal F_2 progeny under a photoperiod of L:D 15:9 h at 22 °C. The S population had shorter larval development time, longer pupal time, higher body weight, growth rate and weight loss compared with the N population. In the F_1 testing, the larval development time and body weight in hybrid populations were intermediate between the parents, and the paternal parents played a greater role in determining the larval development time, while the maternal parents exhibited a greater role in determining the body weight. The pupal time of hybrid populations was significantly shorter than that of the parents. In the reciprocal backcross testing, both father and grandfather affected the larval development time, while both mother and grandmother affected the body weight. Consistently, in the reciprocal F_2 cross testing, the grandfather was more influential in determining the larval development time, and grandmother was more important in determining the body weight. In all tested populations, females had greater body weight, higher growth rate and weight loss than males. Hybridization pattern did not affect sex dimorphism and sex ratio. Overall, these findings suggest that different pathways (maternal or paternal effects) were involved in the inheritance of various life-history traits in *C. bowringi*.

Introduction

Geographic populations of insects along latitudinal gradients tend to exhibit biological gradients in terms of larval development time, body weight and growth rate (Masaki, 1967; Roff, 1980; Gotthard *et al.*, 1994; Bidau and Martía, 2007; Chown and Gaston, 2010; Barton *et al.*, 2014; Parsons and Joern, 2014; Kivelä *et al.*, 2016; Tang *et al.*, 2017; Chen *et al.*, 2019). Therefore, the variation of life history traits in insects caused by environmental selection pressure among different geographic populations serves us as an excellent material for understanding the underlying genetic mechanism for evolution. Most studies on the inheritance of life-history traits have been carried out through hybridisation between geographical lines (Tauber *et al.*, 1986; Danks, 1987; Nylin and Gotthard, 1998). However, the genetic basis of these life-history traits remains unclear, and the effect of hybridisation between different geographic populations on life-history traits has been only reported in a few insect species. For example, the developmental duration of the hybrid offspring of *Wyeomyia smithii* was significantly shorter than that of their parents (Istock, 1981). The hybridisation of the northern and southern populations of *Ostrinia furnacalis* showed that the offspring of the hybridisation produced a significantly longer developmental period than their parents (He *et al.*, 2019). Also, the offspring of *Psyttalia lounsburyi* from South Africa and Kenya tended to be interparental in fertility, with no obvious advantages or disadvantages (Benvenuto *et al.*, 2012a), while the hybridisation of seven different geographical populations of *Trichogramma chilonis* significantly promoted the fertility of female offspring (Benvenuto *et al.*, 2012b). Understanding the influence of hybridisation among different geographical populations on the life-history traits can not only reveal the genetic differences in the life history traits among different geographical populations, but also potentially promote the reproduction of natural enemies of pests by using the favourable traits or reduce the harm of pests by using the unfavourable traits obtained from hybridisation (Benvenuto *et al.*, 2012b; He *et al.*, 2019).

The cabbage beetle *Colaphellus bowringi* (Coleoptera: Chrysomelidae) is one of the major pests of cruciferous plants and is widely distributed from south to north in China (Zhang and Zhao, 1996: 168–169). Adult beetles spend summer and winter in the soil. The life-history traits of the southern and northern populations differ greatly. The southern population exhibits a short-day response, entering diapause under long day-length. However, high temperatures strongly weaken the diapause-inducing effects of long day-lengths. All adults enter diapause at $\leq$20 °C regardless of photoperiods (Xue *et al.*, 2002a). The northern population lacks a photoperiodic response with temperature-dependent diapause induction (Lai *et al.*, 2008; Chen *et al.*, 2014). The southern populations are multivoltine with one generation in spring and three generations in autumn with both summer and winter diapause (Xue *et al.*, 2002a, 2002b), whereas northern populations are usually univoltine, with only winter diapause (Hu *et al.*, 2008). Also, southern populations have significantly shorter larval development time and significantly larger body weight than the northern populations (Tang *et al.*, 2017). The egg production of southern population is significantly higher than that of northern populations (Liu *et al.*, 2014; He *et al.*, 2021). The significant differences of life history traits between northern and southern populations of *C. bowringi* make it an excellent model for studying the inheritance of life history traits.

Hence, to explore the mechanism of inheritance, the present study conducted reciprocal and backcross mating experiments using a southern population (S population) and a northern population (N population) of *C. bowringi* and their hybrid progeny. The life-history traits, such as the larval development time, body weight, the growth rate, sex ratio and sexual size dimorphism (SSD) were observed in the pure strains, F_1, reciprocal backcross and reciprocal F_2 progeny, and then used these traits to analyse their genetic characteristics. It was hypothesised that the inheritance of these life history traits is regulated separately by different pathways in *C. bowringi*, i.e. some traits are determined by the male parent while others are determined by the female parent. Through reciprocal and backcross mating experiments on different geographical populations, this study provides new insights into investigating the genetic mechanism of life-history traits in insects.

Materials and methods

Experimental populations

In 2018, more than 100 naturally diapausing adults were collected from vegetable gardens in Xiushui County (29°1′ N, 114°4′ E), Jiangxi Province, China (as S population) in late April and from Shenyang city (41°48′ N, 123°23′ E), Liaoning Province, China (as N population) in early June. Adults of the two populations were transferred separately to glass bottles (diameter 18 cm; height 32 cm) containing soil in which they could burrow inside and enter diapause. To mimic natural conditions, the bottles were placed outdoors at Jiangxi Agricultural University, Nanchang, Jiangxi Province (28°46′ N, 115°59′ E). In spring 2019, when the post-diapausing adults of the two populations emerged from the soil, we conducted a reciprocal mating experiment between the two populations and obtained diapausing adults of S × S, N × N, S × N and N × S populations (female shown on the left, male on the right, the same below). The diapausing adults of the four populations were transferred to glass bottles (diameter 18 cm; height 32 cm) containing soil in which they could burrow inside and enter diapause. The bottles were placed outdoors at Jiangxi Agricultural University, Nanchang, Jiangxi Province (28° 46′ N, 115°59′ E).

In spring 2020, when the post-diapausing adults of the four populations emerged from the soil, they were sexed immediately and males and females were placed in separate Petri dishes (height 2 cm; diameter 9 cm), lined with filter paper and provided with fresh leaves of the potherb mustard (*Brassica juncea* (L.) Czern. et Coss. var. multiceps Tsen et Lee). Females were allowed to mate with males from the same population or different populations. Petri dishes were cleaned and provided with potherb mustard leaves daily.

Crosses and measurement methods

In 2020, 16 populations were obtained from cross-mating experiments: two purebreds (S × S, N × N), two F_1 crosses (S × N, N × S), four S-backcrosses (S × (S × N), (S × N) × S, S × (N × S) and (N × S) × S), four N-backcrosses (N × (S × N), (S × N) × N, N × (N × S), (N × S) × N) and four F_2 crosses ((S × N) × (S × N), (N × S) × (N × S), (S × N) × (N × S) and (N × S) × (S × N)). Fifteen pairs of adults were used in each cross. Eggs laid within the first 3 days by individual pairs were used in the experiment. The progenies of these crosses were reared in clear transparent plastic boxes (17.5 × 12.5 × 6.5 cm) with fresh leaves of the potherb mustard under a photoperiod of L:D 15:9 h at 22°C until pupation. There were four to eight boxes for each cross experiment; there were about 50 progeny in each box. The boxes were cleaned daily and fresh food was provided as needed. The pupation time was recorded every morning, and new pupae were placed individually in cell culture plates with 12-well cell culture plates for adult eclosion (for each cell: diameter: 2.4 cm; height: 2 cm). Adult emergence time was observed every day morning. Under this combination of light (L:D 15:9 h) and temperature (22 °C), all progenies from 16 populations entered adult diapause.

The larval development time from hatching to pupation and pupal time from pupation to adult eclosion were recorded. Pupae were weighed on the day following pupation, and adults were weighed after the release of the meconium using an electric balance (AUY120, SHIMADZU Corporation, Japan). Growth rate was computed as ln pupal weight/larval development times (Gotthard *et al.*, 1994). Weight loss between pupation and adult eclosion was computed using the formula: proportion weight lost = 1 − (adult weight/pupal weight). Using the Lovich and Gibbons (1992) sexual dimorphism index, the SSD was estimated in each population, in which SSD = (size of the larger sex/size of the smaller sex) − 1.

All experiments were conducted in four illuminated incubators (LRH-250-GS, Guangdong Medical Appliances Plant, Guangdong, China). The light phase intensity was about 1.97 W m^{-2}, and the temperature fluctuation was ±1 °C.

Statistical analysis

SPSS 17.0 statistical software package (IBM, www.ibm.com) was used for statistical analysis. A mixed linear model was used to analyse the life-history traits, in which population and sex were treated as fixed main effects and rearing box was treated as a random effect. One-way analysis of variance (ANOVA) was used to determine whether there were significant differences in life-history traits among different populations. One-way ANOVA and Tukey's test were used to compare the differences in life-

Table 1. Results from a linear mixed-model analysis of fixed effects on life-history traits of *Colaphellus bowringi* in relation to population and sex

Life-history traits	Fixed factors	*df*	*F*-value	*P*-value
Larval time	Population	15	46.224	<0.001
	Sex	1	1.199	0.273
	Population × sex	15	2.613	<0.001
Pupal time	Population	15	14.401	<0.001
	Sex	1	22.514	<0.001
	Population × sex	15	1.681	0.048
Pupal weight	Population	15	372.398	<0.001
	Sex	1	8783.303	<0.001
	Population × sex	15	11.210	<0.001
Growth rate	Population	15	99.357	<0.001
	Sex	1	1314.524	<0.001
	Population × sex	15	2.142	0.006
Adult weight	Population	15	284.527	<0.001
	Sex	1	10,172.055	<0.001
	Population × sex	15	9.013	<0.001
Proportionate weight loss	Population	15	19.400	<0.001
	Sex	1	427.807	<0.001
	Population × sex	15	1.776	0.032

history traits between sexes in each population. The sex ratio was calculated by non-parametric test followed by binomial distribution test.

Results

Development time

The larval development time was significantly affected by population, but not by sex; there was a significant interaction between population and sex (table 1). In the purebred testing, the larval development time for both sexes was significantly shorter in the S population than in the N population ($P < 0.05$) (fig. 1A, table S1). In the F_1 testing, the larval development time in hybrid populations was intermediate between those of their parents with the hybrid S × N population being significantly longer than the N × S population ($P < 0.05$), indicating that males played a greater role in determining the larval development time. In the S-backcross testing, the larval development time in (N × S) × S (with grandparents of S population as males) was significantly shorter than those in (S × N) × S (with grandparents of N population as males) ($P < 0.05$), showing that grandfather also had significant influence on larval development time. In addition, the larval development time of female in S × (S × N) and (N × S) × S progeny was significantly shorter than that in S × S ($P < 0.05$) (fig. 1A), suggesting that the larval development time was shortened by hybridisation. In the N-backcross testing, the larval development time of all hybrids (N × (S × N), (S × N) × N, N ×(N × S), (N × S) × N) was longer than that of their S parents and significantly shorter than that of their N parents ($P < 0.05$). In the reciprocal F_2 cross testing, the larval development time in (S × N) × (S × N) progeny (with grandparents of N population as males) was significantly longer than those in (N × S) × (N × S) progeny (with grandparents of S population as males) ($P < 0.05$), indicating grandfather effect. There were significant differences in larval development time in S population and hybrid populations of N × S and N × (S × N) between the sexes, with the development time being significantly longer in females than males in S population ($t = 3.770$, $df = 321$, $P < 0.001$) and being significantly longer in males than females in N × S and N × (S × N) hybrid populations ($t = 2.149$, $df = 236.365$, $P = 0.033$; $t = 2.982$, $df = 274.719$, $P = 0.003$).

The pupal development time was significantly affected by population, sex and their interactions (population × sex) (table 1). The development time of pupae in S population was longest, significantly longer than that in N male population and all hybrid populations ($F = 14.083$, $df = 15$, $P < 0.001$) (fig. 1B, table S1). Also, the development time of female pupae in N population was also longest, significantly longer than that in all hybrid populations except for (N × S) × S, (S × N) × N, (N × S) × N, (N × S) × (N × S) and (N × S) × (S × N) ($F = 16.661$, $df = 10$, $P < 0.001$) (fig. 1B, table S1). These results showed that the development time of pupae was shortened by hybridisation. There were significant differences in the pupal time in S population and hybrid populations of (S × N) × S, (S × N) × N and N × (N × S) between the sexes, with the pupal time being significantly longer in males than females (S × S, $t = 2.545$, $df = 320.045$, $P = 0.011$; (S × N) × S, $t = 2.474$, $df = 231.259$, $P = 0.014$; (S × N) × N, $t = 2.296$, $df = 356$, $P = 0.022$; N × (N × S), $t = 3.438$, $df = 186.838$, $P = 0.001$) (fig. 1B, table S1).

Pupal weight and growth rate

Both pupal weight and growth rate were significantly affected by population, sex and their interactions (table 1). In the purebred testing, female and male pupae in S population were significantly heavier than that in N population ($P < 0.05$) (fig. 2A, table S1). In the F_1 testing, pupal weight was significantly higher in the S × N population than in the N × S population ($P < 0.05$), suggesting that the female parent played a greater role in determining pupal weight. The pupal weight of all hybrid populations was intermediate between both parents. In the S-backcross testing, the pupal weight of (S × N) × S hybrid (with grandparents of S population as females) was significantly greater than that of (N × S) × S hybrids (with grandparents of N population as females) ($P < 0.05$), showing grandmother effect on pupal weight. In the N-backcross testing, the pupal weight of N × (N × S) hybrid (with female having a N mother and male having a N grandmother) was lowest, followed by N × (S × N), (S × N) × N and (N × S) × N, showing the impact of grandmother on pupal weight. In the reciprocal F_2 cross testing, the pupal weight was significantly greater in (S × N) × (S × N) hybrid (with grandparents of S population as females) than in (N × S) × (N × S) hybrid (with grandparents of N population as females) ($P < 0.05$), also indicating grandmother effect. In all cross mating experiments, female pupae were significantly larger than male pupae (*T*-tests: $P < 0.05$) (fig. 2A, table S1), showing female-biased SSD.

There was no significant difference in female growth rate among S population, S × (S × N), (S × N) × S and (N × S) × S hybrid populations ($P > 0.05$). This was probably because the

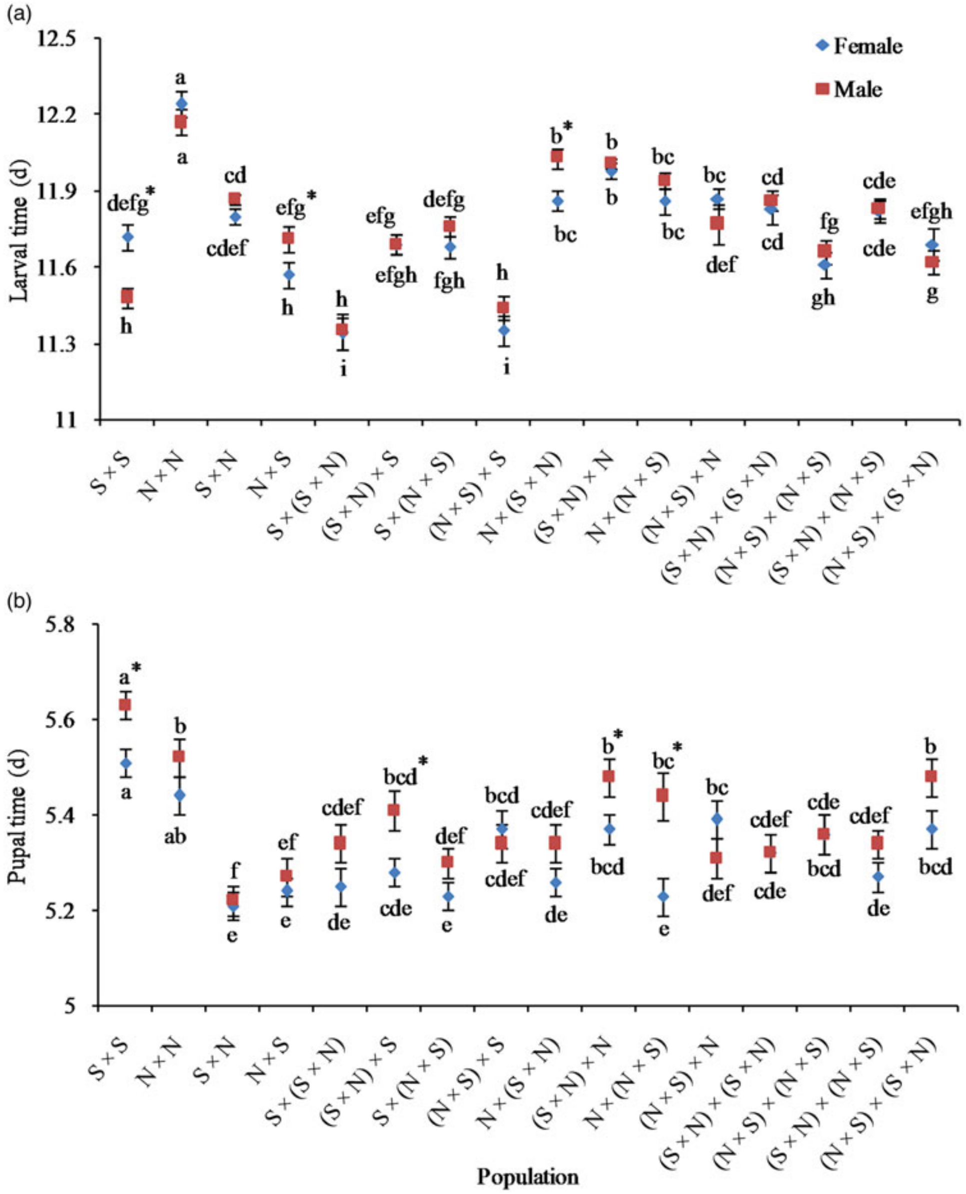

Figure 1. Larval and pupal development time of the pure populations (the southern S population and the northern N population), hybrid populations (the S♀ × N♂ and N♀ × S♂ populations), S-backcross and N-backcross populations and reciprocal F_2 cross populations in *Colaphellus bowringi*. Error bars indicate SEs. The values of different letters in a row differ significantly at the 0.05 level. The asterisk indicates a significant difference between the sexes (*t*-test, $P < 0.05$).

larval development time of the three hybrid populations was shorter than that of the S population. In other experiments, the growth rate was mainly related to pupal weight, i.e. the growth rate was higher for larger pupa. In all cross-mating experiments, except for (N × S) × N, the growth rates of females were significantly higher than that of males (*T*-tests: $P < 0.05$) (fig. 2B, table S1).

Adult weight and weight loss

Adult weight and weight loss were significantly affected by population, sex and their interactions (table 1). Adult weight was positively related to pupal weight, i.e. large pupa produced large adult. In all cross-mating experiments, the body weight of females was significantly higher than that of males (*t*-tests: $P < 0.05$) (fig. 3A).

Weight loss was also directly related to pupal weight, i.e. large pupae lost more weight than small pupae (fig. 3B, table S1). For example, the weight loss from pupa to adult in S and (S × N) × S, S × (N × S) and S × (S × N) hybrid populations with larger pupal weight was greater than that in N and hybrid populations with smaller pupal weight. In all cross-mating experiment, male pupae lost significantly more weight during metamorphosis than female pupae (*t*-tests: $P < 0.05$).

Sexual size dimorphism

There was no significant difference in SSD among different populations for either pupae or adults (for pupae: $F = 0.715$, $df = 15$, $P = 0.715$; for adults: $F = 0.851$, $df = 15$, $P = 0.619$). However, the SSD index was higher at the adult stage (from 0.311 to 0.408) than at the beginning of the pupal stage (from 0.282 to 0.368) in all cross-mating experiments, with significant differences in SSD between pupa and adults in (S × N) × N and S × (N × S) hybrid populations ($t = -3.187$, $df = 6$, $P = 0.019$; $t = -3.150$, $df = 6$, $P = 0.020$) (fig. 4). The SSD

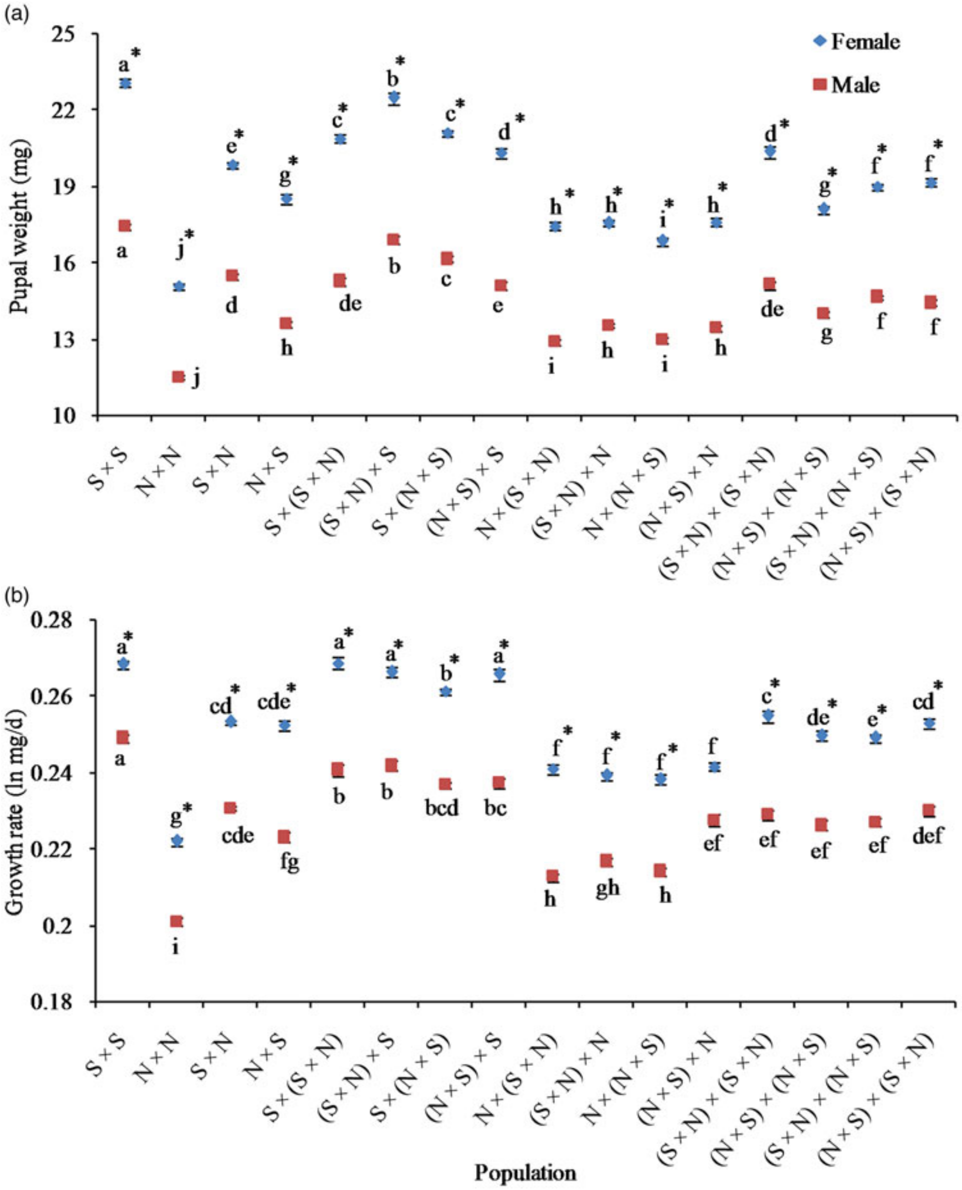

Figure 2. Pupal weight and larval growth rate of the pure populations (the southern S population and the northern N population), hybrid populations (the S♀ × N♂ and N♀ × S♂ populations), S-backcross and N-backcross populations and reciprocal F_2 cross populations in *Colaphellus bowringi*. Error bars indicate SEs. The values of different letters in a row differ significantly at the 0.05 level. The asterisk indicates a significant difference between the sexes (*t*-test, $P < 0.05$).

index of adults is higher than that of pupae, probably because male pupae lost more weight than female pupae during metamorphosis.

Sex ratio

In all cross-mating experiments, the sex ratios (female: male) were not significantly different among different populations, and all were close to 1:1 (table 2, $P > 0.05$).

Discussion

To our knowledge, the current study is the first revealing the differences of life history traits among the S and N populations, their F_1 hybrid population, S-backcross and N-backcross populations and reciprocal F_2 populations in insects. The findings supported the hypothesis that different pathways (paternal and maternal effects) were involved in the inheritance of various life-history traits in *C. bowringi*. This study further broadens our understanding of the effects of intraspecific hybridisation on life history traits.

In *C. bowringi*, the low-latitude S population showed a significantly shorter development time and a significantly higher body weight compared with the high-latitude N population. This is consistent with the previous research (Tang *et al.*, 2017; He *et al.*, 2021). It is generally assumed that the larval development time has positive correlation with body size, i.e. animals that take longer to develop should be larger at maturity (Nijhout *et al.*, 2010) or one has to take longer to grow bigger (Stearns, 1992; Roff, 2000). It seems that this assumption does not apply to comparisons between different geographic populations. Similarly, the diapausing individuals of the Asian corn borer, *O.*

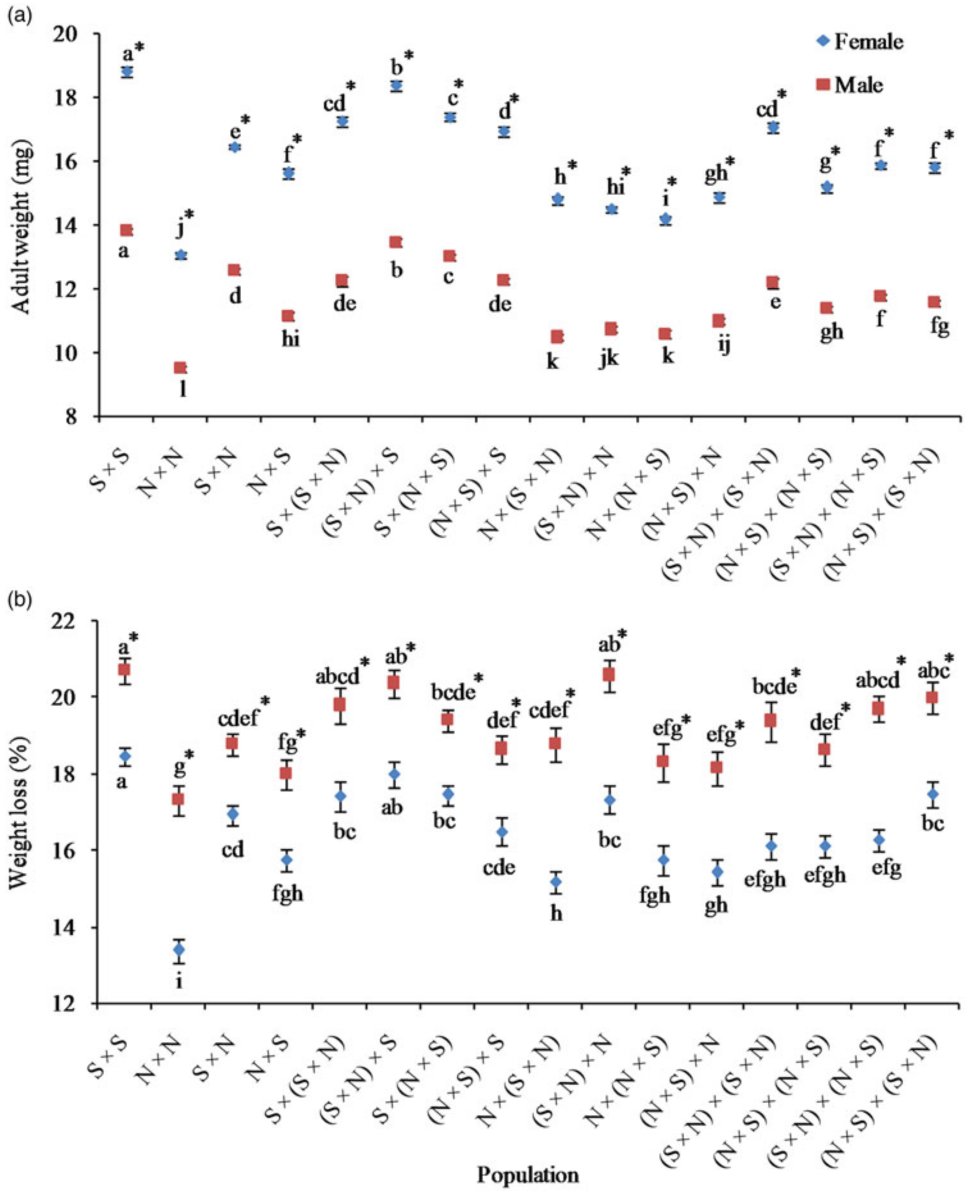

Figure 3. Adult weight and proportional weight loss of the pure populations (the southern S population and the northern N population), hybrid populations (the S♀ × N♂ and N♀ × S♂ populations), S-backcross and N-backcross populations and reciprocal F$_2$ cross populations in *Colaphellus bowringi*. Error bars indicate SEs. The values of different letters in a row differ significantly at the 0.05 level. The asterisk indicates a significant difference between the sexes (*t*-test, $P < 0.05$).

furnacalis (Guenée) had significantly longer larval development time and lower body weight in the high-latitude populations than in the low – latitude populations (Fu *et al.*, 2022). In addition, based on a compilation of published data, the study showed that voltinism is closely associated with body weight in arthropods, with larger species typically producing only one generation per year and smaller species producing multiple generations per year (Horne *et al.*, 2015). However, this rule does not apply to *C. bowringi*. The multivoltine S population showed significantly larger body weight compared with univoltine N population.

The highlight of this study is that the life-history traits of *C. bowringi* were affected by different hybridisation styles. In the F$_1$ testing, the results revealed that larval development time and body weight of hybrid populations were intermediate between those of both parents, showing that the two traits are controlled by both parents. Such an intermediate reaction in larval development time or body weight has also been found in the fruit fly *Drosophila melanogaster*, the ground beetle *Carabus tosanus* and the egg parasitoid *Trissolcus vassilievi* (Ghosh and Joshi, 2012; Tsuchiya *et al.*, 2012; Iranipour *et al.*, 2015). However, in the seed beetle *Callosobruchus maculates*, hybrid populations showed a faster developmental rate (Bieri and Kawecki, 2003). Furthermore, we found that the two traits were inherited in different ways. Males played a greater role in determining the larval development time and females played a greater role in determining the body weight. More interestingly, pupal development time of hybrids was significantly shortened by the hybridisation of the northern and southern populations. When the northern and southern parents backcrossed with their hybrid offspring (S-backcross and N-backcross tests), it showed that both father and grandfather had a significant influence on the larval development time while both mother and grandmother significantly

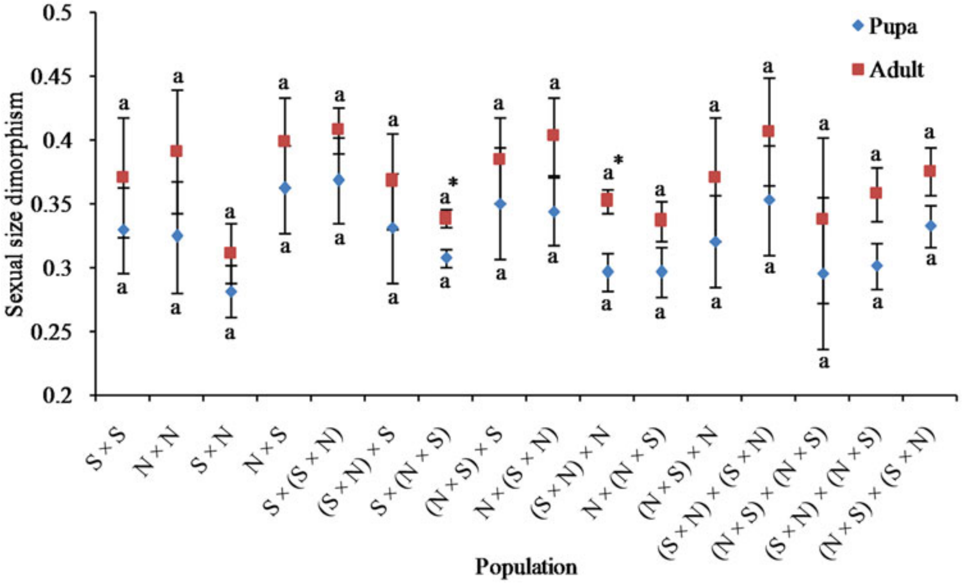

Figure 4. Sexual size dimorphism of the pure populations (the southern S population and the northern N population), hybrid populations (the S♀ × N♂ and N♀ × S♂ populations), S-backcross and N-backcross populations and reciprocal F_2 cross populations in *Colaphellus bowringi*. Error bars indicate SEs. The values of the same letter in a row do not differ significantly at the 0.05 level. The asterisk indicates a significant difference between the sexes (*t*-test, $P < 0.05$).

affected body weight. Being consistent in reciprocal F_2 cross testing, the larval development time was mostly affected by the grandfather, whereas the body weight was mainly determined by the grandmother. In the present cross-mating experiments, all populations of *C. bowringi* showed the sexually dimorphic growth rate, i.e. the growth rate of females was significantly higher than that of males. This probably explains why females were significantly heavier than males when their larvae developed at similar times.

Studies have shown that female lepidopteran insects generally lose less weight after emergence than their conspecific males (Fischer and Fiedler, 2000; Molleman *et al.*, 2011; Fu *et al.*, 2016; He *et al.*, 2019). In the current study, all 16 cross-mating populations of *C. bowringi* showed more weight loss in large pupae than small pupae in the same sex and male pupae lost significantly more weight during metamorphosis than female pupae. However, the physiological and adaptive background of sex-specific weight loss is unclear. According to Fischer *et al.* (2004), the weight loss of the adults is the cost of the high growth rate of larvae, while males lose more weight because they grow faster. This description clearly does not apply to *C. bowringi* because the male beetle had longer larval development time and lower growth rate compared with the female beetle. More likely, females were more efficient than males in converting metabolites into reproductive needs or there were differences in metabolic rates between females and males.

In the current 16 cross-mating experiments of *C. bowringi*, the SSD index for both pupa and adult showed a wavy change among different populations but there were no significant differences. Previously, the north–south hybridisation of *C. bowringi* also showed no significant deference in SSD index between populations at any temperature (He *et al.*, 2021). This suggests that the SSD index is a relatively stable characteristic. The SSD index was higher in adults than pupae in all populations of *C. bowringi*, because male pupae lost more weight than female pupae at metamorphosis.

In insect populations, sex ratios have important implications for the ecology and evolution of mating systems, reproductive strategies and genetics (Werren and Godfray, 1995). In general,

Table 2. Sex ratio of the cabbage beetle, *Colaphellus bowringi* in different populations at 22 °C

Population	Number	Sex ratio (♀:♂)	Population	Number	Sex ratio (♀:♂)
S × S	323	0.50:0.50^{ns}	N × (S × N)	277	0.50:0.50^{ns}
N × N	322	0.49:0.51^{ns}	(S × N) × N	358	0.49:0.51^{ns}
S × N	496	0.50:0.50^{ns}	N × (N × S)	198	0.51:0.49^{ns}
N × S	239	0.51:0.49^{ns}	(N × S) × N	256	0.49:0.51^{ns}
S × (S × N)	244	0.49:0.51^{ns}	(S × N) × (S × N)	199	0.51:0.49^{ns}
(S × N) × S	239	0.51:0.49^{ns}	(N × S) × (N × S)	235	0.49:0.51^{ns}
S × (N × S)	353	0.50:0.50^{ns}	(S × N) × (N × S)	370	0.50:0.50^{ns}
(N × S) × S	194	0.48:0.52^{ns}	(N × S) × (S × N)	217	0.51:0.49^{ns}

S for the southern population and N for the northern population.
^{ns}shows no significant difference.

in a randomly mating population the sex ratio varies around 1:1 due to the segregation of sex chromosomes during gametogenesis (Sheldon and West, 2002; Hoy, 2004) and this 1:1 sex ratio usually indicates a stable selection of females and males (Schowalter, 1996: 113–136). In the present study, the sex ratio of all populations of *C. bowringi* (2259 females: 2261 males) followed this rule with an equal ratio of female and male individuals (close to 1:1). Therefore, it is reasonable to infer that the intrinsic sex ratio of the species is 1:1.

Conclusions

The hybridisation of northern and southern populations of *C. bowringi* revealed some genetic characteristics of life-history traits. In the F_1 testing, the larval development time and pupal and adult weight of hybrid populations were intermediate between their parents. However, the pupal time was shortened by hybridisation. In the reciprocal backcross testing, both father and grandfather exhibited significant influence on the larval development time, while mother and grandmother exhibited significant influence on the body weight. Also in the reciprocal F_2 cross testing, the larval development time was mainly affected by the grandfather and the body weight was mainly affected by the grandmother. All these results suggest that the inheritance of the life-history traits is controlled by multiple genes. In all tested populations, the body weight, growth rate and weight loss were significantly higher in females than in males, regardless of mating style. The sex dimorphism and sex ratio were not affected by hybridisation pattern. These results provide new data for understanding the inheritance of life-history traits.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485324000865

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