

## Research Paper

\*These authors have contributed equally to this work.

**Cite this article:** Wu Y-T, Hu X-S, Wu M-C, Yao W-Y, Xu X-L (2023). Morph-specific fitness throughout the life cycle of the grain aphid, nonhost-alternating, holocyclic *Sitobion avenae* (Hemiptera: Aphididae). *Bulletin of Entomological Research* **113**, 658–664. <https://doi.org/10.1017/S0007485323000329>

Received: 23 November 2022

Revised: 29 June 2023

Accepted: 2 July 2023

First published online: 7 August 2023


### Keywords:

Aphid; development; fitness; morph; reproduction; reproductive switching; survival

### Corresponding author:

Xiang-Li Xu; Email: [xuxiangli@nwsuaf.edu.cn](mailto:xuxiangli@nwsuaf.edu.cn)

# Morph-specific fitness throughout the life cycle of the grain aphid, nonhost-alternating, holocyclic *Sitobion avenae* (Hemiptera: Aphididae)

Yu-Ting Wu\*, Xiang-Shun Hu\*, Meng-Chu Wu, Wen-Ying Yao and Xiang-Li Xu 

Key Laboratory of Northwestern Loess Plateau Crops Pest Management of Ministry of Agriculture, Key Laboratory of Plant Protection Resources and Pest Management of the Ministry of Education, College of Plant Protection, Northwest A&F University, No. 3 Taicheng Road, 712100, Yangling, Shaanxi, China

## Abstract

Aphids exhibit seasonally alternating asexual and sexual reproductive modes. Different morphs are produced throughout the life cycle. To evaluate morph-specific fitness during reproductive switching, holocyclic *Sitobion avenae* were induced continuously under short light conditions, and development and reproduction were compared in each morph. Seven morphs, including apterous and alate virginoparae, apterous and alate sexuparae, oviparae, males, and fundatrices, were produced during the life cycle. The greatest proportions of sexuparae, oviparae, males, and virginoparae were in the G1, G2, G3, and G4 generations, respectively. Regardless of asexual or sexual morphs, alate morphs exhibited a marked delay in age at maturity compared with that of apterous morphs. Among the alate morphs, males had the longest age at maturity, followed by sexuparae and virginoparae. Among the apterous morphs, sexuparae were older at maturity than the fundatrices, virginoparae, and oviparae. The nymphs of each morph had equal survival potentials. For the same wing morphs, apterous sexuparae and oviparae exhibited substantial delays in the pre-reproductive period and considerable reductions in fecundity, compared with those of apterous virginoparae and fundatrices, whereas alate sexuparae and alate virginoparae had similar fecundity. The seven morphs exhibited Deevey I survivorship throughout the life cycle. These results suggest that sexual production, particularly in males, has short-term development and reproduction costs. The coexistence of sexual and asexual morphs in sexuparae offspring may be regarded as an adaptive strategy for limiting the risk of low fitness in winter.

## Introduction

Aphids have a complex life cycle and are one of the few organisms capable of alternating parthenogenesis and sexual reproduction (Dixon, 1977; Huang and Qiao, 2014). Corresponding to different reproductive and overwintering strategies, their distinct life cycle variants have been subdivided into holocyclic, anholocyclic, intermediate, and androcyclic types (Dedryver *et al.*, 1998; Vereshchagina and Gandrabur, 2016). Holocyclic aphids undergo multiple generations of parthenogenetic reproduction during the growth season (Huang and Qiao, 2014). In autumn, virginoparae exposed to short light conditions produce sexuparae, which in turn produce oviparae and males. After mating, oviparae lay cold-resistant eggs during the winter (Dedryver *et al.*, 2013, 2019). In the following spring, the fertilized eggs hatch, and the fundatrix initiates another annual cycle (Williams and Dixon, 2006). The production of distinct morphs plays an important role in coping with seasonal changes (Moran, 1992; Dedryver *et al.*, 2001).

Throughout the aphid life cycle, alternating reproductive modes is viewed as an adaptive response to specific functions (Dedryver *et al.*, 2001; Le Trionnaire *et al.*, 2008). Asexual reproduction has the ability to rapidly develop populations, but deleterious mutations can accumulate easily (Normark and Moran, 2000; Simon *et al.*, 2002, 2010; Downie, 2003). In contrast, sexual reproduction can improve cold tolerance capacity by egg laying and produces new genotypic combinations to reduce the accumulation of deleterious mutations through mating behavior, which is often accompanied by the cost of sex (Rispe and Pierre, 1998; Helden and Dixon, 2002; Simon *et al.*, 2002, 2003, 2010; Artacho *et al.*, 2011; Carter *et al.*, 2012). The benefits and costs of asexual and sexual reproduction also differ (Dedryver *et al.*, 1998). Accordingly, a detailed study of the fitness of aphid morph life-history components is essential for determining phenotypic plasticity and effective control measures.

The ecological plasticity of aphid populations, except for their clonal diversity, is determined by a high degree of polymorphism within the population (Vereshchagina and Gandrabur, 2016). Production of each distinct morph is adapted to specific functions during

a particular part of its life cycle (Dixon, 1977; Nespolo *et al.*, 2009; Gilabert *et al.*, 2014). To the best of our knowledge, previous studies of adaptive traits throughout the aphids life cycle have focused on a few morph types under different environmental cues (Newton and Dixon, 1988; Lees, 1989; Nespolo *et al.*, 2009; Vereshchagina and Gandrabur, 2016; Peng *et al.*, 2017). However, little information is available regarding the costs and benefits of development and reproduction in holocyclic aphid species morph types under the same environmental conditions. The coexistence of sexual and asexual forms generally occurs within the same aphid species in nature (Dedryver *et al.*, 2001), which is beneficial for evaluating the adaptive characteristics of the different morphs.

The grain aphid *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae) is an agriculturally important cereal crop pest (Hansen, 2006; Han *et al.*, 2019). This species infests by ingesting plant sap and causes losses by transmitting viral diseases to crops (Liu *et al.*, 2014). *Sitobion avenae* has a typical nonhost-alternating holocyclic life cycle, and seven morphologically different morphs are produced during the alternating sexual and asexual reproductive modes, including virginoparae (alate and apterous), sexuparae (alate and apterous), males (alate), oviparae (apterous), and fundatrices (apterous) (Wu *et al.*, 2022).

In this study, we aimed to gain better insight into the costs and benefits of each morph throughout the life cycle of *S. avenae*. By investigating the proportions of different morphs in four generations under short light conditions, development and reproduction were compared among the morph types. The findings provide a basis for understanding the adaptive evolution of the holocyclic life cycle and serve as a reference for controlling aphids.

## Materials and methods

### Insect rearing

In May 2019, 10 *S. avenae* apterous virginoparae, were collected at least 20 m apart from each other in wheat fields located in Gulang County (102.97°E, 37.62°N), Gansu Province, China. Each aphid was maintained individually on wheat seedlings in cages (25 cm × 20 cm × 20 cm) according to methods described by Xu *et al.* (2019). The aphids and seedlings (*Triticum aestivum* L. CV. Xinong 979) were placed in a growth chamber (21 ± 1°C, 16 light:8 dark, and 65% ± 10% relative humidity). After three generations, aphids were used for the experiment.

### Induction under short light conditions and proportions of different morphs

According to Helden and Dixon (2002), *S. avenae* produce four generations under 14 ± 1°C and 8 light:16 dark conditions. Ten 4<sup>th</sup> instar virginoparae (G0) were placed individually onto one wheat seedling. When the virginoparae matured, two to three of the offspring produced (G1) were transferred individually to seedlings and raised to maturity. These adults produced offspring (G2) that were raised individually and continuously to maturity. This process was repeated twice, producing offspring (G3) and (G4) that were raised to maturity. Based on the morphological characteristics of the adults, offspring, and reproductive systems, the morph types were determined. The proportions of virginoparae (apterous and alate), sexuparae (apterous and alate), oviparae, and males in each generation were then calculated.

### Comparisons of development and reproduction of different morphs

*Sitobion avenae* were induced under short light conditions (8 light:16 dark) following the previous procedure used by Helden and Dixon (2002). Sexuparae (apterous and alate), oviparae and males, and virginoparae (apterous and alate) were picked up in the G1, G2 and G3, and G4 generations, respectively. The newly born nymphs of the different morphs were transferred individually to seedlings, and their molting and survival were recorded daily. After the sexuparae (apterous and alate) and virginoparae (apterous and alate) were raised to maturity, the offspring produced were recorded daily until death. The final molted males and oviparae were paired at a 1:1 ratio and raised continuously. The lifespans of the males, oviparae, and eggs laid by the oviparae were counted daily. After the eggs hatched, they were raised individually under short light conditions. The molting and survival of the fundatrices were recorded daily. After reaching maturity, the offspring produced were recorded daily until death. We used 30 apterous and alate sexuparae each, 50 oviparae, 50 males, 30 apterous and alate virginoparae each, and 30 fundatrices in the experiment.

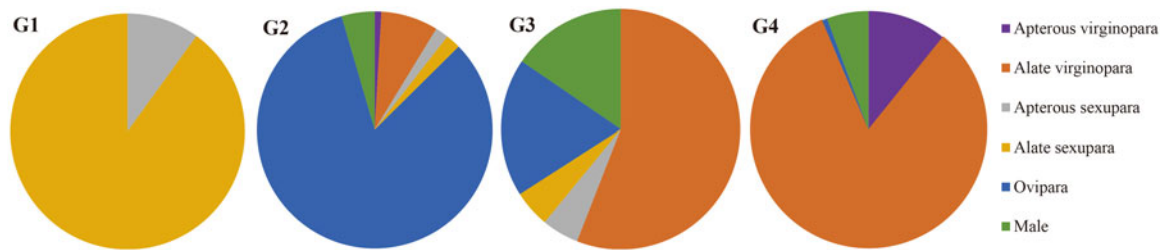
### Data analysis

Differences in development and reproduction among the morphs were analyzed using one-way analysis of variance (ANOVA) followed by Tukey's test, when the data could meet ANOVA assumptions by the Kolmogorov–Smirnov test. The proportions of different morphs and survival rates after arcsine transformation were also analyzed using ANOVA to test for differences among the morphs. Data collected throughout the lifespans of the aphid morphs were used to calculate the life table parameters: net reproductive rate ( $R_0 = \sum m_x l_x$ ); mean generation time ( $T = \sum m_x l_x x / \sum m_x l_x$ ); intrinsic rate of population increase ( $r_m = \ln R_0 / T$ ), which describes the rate of population growth; and finite rate of increase ( $\lambda = e^{r_m}$ ), which is a rate of increase per unit time per individual, with ( $x$ ) age intervals, ( $m_x$ ) age-specific fecundity, and ( $l_x$ ) age-specific survivorship (Xu and Cheng, 2005). The Weibull frequency distribution  $S(t) = \exp[-(t/b)^c]$  was used to fit the survival curve of a specific age, with ( $t$ ) representing age intervals,  $S(t)$  representing age-specific mortality, and ( $b$ ) and ( $c$ ) representing scale and shape parameters, respectively ( $c > 1$ , survival curves for Deevey I;  $c = 1$ , survival curves for Deevey II;  $c < 1$ , survival curves for Deevey III) (Pinder *et al.*, 1978). All data were analyzed using IBM SPSS 23.0 (IBM Corp., 2013).

## Results

### Proportions of different morphs

*Sitobion avenae* were induced continuously for four generations under short light conditions. G1 comprised both alate and apterous sexuparae, accounting for 90.0% and 10.0%, respectively. In G2, alate and apterous sexuparae dropped sharply to 2.1% and 1.8%, respectively. Oviparae and males accounted for 82.8% and 4.6%, respectively. In addition, small proportions of alate (7.8%) and apterous (0.9%) virginoparae were observed among the offspring of the sexuparae. In G3, a small number of sexuparae (10.0%) remained. Compared with G2, the proportion of oviparae decreased drastically to 18.6%, whereas that of males increased slightly to 15.5%, and the proportion of virginoparae reached 55.9%. In G4, small numbers of oviparae (0.7%) and males



**Figure 1.** Proportions of morphs of different generations under short light conditions in *Sitobion avenae*.

**Table 1.** Development times and survival rates of different morph nymphs under short light conditions in *Sitobion avenae*

Morphs	Development time (d)					Survival rate (%)
	1st instar	2nd instar	3rd instar	4th in star	Total nymph	
Apterous virginopara	2.70 ± 0.08c	2.48 ± 0.09c	3.34 ± 0.12de	3.97 ± 0.15d	12.52 ± 0.18e	96.7 ± 3.3a
Alate virginopara	2.79 ± 0.09bc	2.93 ± 0.07b	4.36 ± 0.12b	5.61 ± 0.13b	15.68 ± 0.26c	93.3 ± 3.3a
Apterous sexupura	2.63 ± 0.09c	2.96 ± 0.08b	3.74 ± 0.11cd	4.96 ± 0.17c	14.33 ± 0.24d	90.0 ± 0.0a
Alate sexupura	3.50 ± 0.10a	3.40 ± 0.09a	3.97 ± 0.15bc	5.73 ± 0.12ab	16.60 ± 0.20b	100.0 ± 0.0a
Ovipara	2.46 ± 0.08c	2.48 ± 0.08c	3.16 ± 0.05e	3.61 ± 0.08d	11.73 ± 0.18e	96.0 ± 2.5a
Male	3.14 ± 0.05ab	3.29 ± 0.07ab	4.91 ± 0.07a	6.18 ± 0.11a	17.55 ± 0.15a	90.0 ± 0.0a
Fundatrix	3.50 ± 0.10a	3.39 ± 0.09a	3.46 ± 0.10de	3.96 ± 0.10d	14.25 ± 0.19d	93.3 ± 3.3a

Data are mean ± SE. Different letters in a column denote significant differences at  $P < 0.05$ , according to Tukey's test.

(5.7%) were still observed, but many alate and apterous virginoparae appeared, accounting for 82.8% and 10.8%, respectively. Significant differences were observed among the morphs in each generation (G1,  $F_{5,54} = 39.20$ ,  $P < 0.001$ ; G2,  $F_{5,54} = 39.48$ ,  $P < 0.001$ ; G3,  $F_{5,17} = 4.25$ ,  $P = 0.01$ ; G4,  $F_{5,17} = 60.82$ ,  $P < 0.001$ ). The largest proportions of sexuparae, oviparae, males, and virginoparae occurred in the G1, G2, G3, and G4 generations, respectively. Asexual individuals remained among the offspring of the sexuparae, with a tendency for gradual increases in the virginoparae proportions from G2 to G4 (fig. 1).

#### Development times and survival rates of different morph nymphs

Significant differences were observed among the seven morphs in the development times of the 1st instar ( $F_{6,240} = 25.21$ ,  $P < 0.001$ ), the 2nd instar ( $F_{6,234} = 23.04$ ,  $P < 0.001$ ), the 3rd instar ( $F_{6,229} = 47.80$ ,  $P < 0.001$ ), the 4th instar ( $F_{6,228} = 83.88$ ,  $P < 0.001$ ), and for the total duration of the nymphal development ( $F_{6,228} = 134.23$ ,  $P < 0.001$ ). For the same wing morphs, males had the longest age at maturity, followed by alate sexuparae and alate virginoparae. Apterous sexuparae had a longer development time than those of the fundatrices, apterous virginoparae, and oviparae. Alate virginoparae, alate sexuparae, and males had significantly longer nymphal development time than those of the apterous virginoparae, apterous sexuparae, oviparae, and fundatrices (table 1). Nymphs could survive to adulthood, and no significant differences were observed among the survival rates of the morphs ( $F_{6,18} = 1.86$ ,  $P = 0.14$ ).

#### Lifespans and fecundities of different morphs

Significant differences in fecundity were observed among the morphs ( $F_{5,185} = 28.78$ ,  $P < 0.001$ ) (table 2). The apterous

sexuparae and oviparae produced fewer offspring than the alate and apterous virginoparae, fundatrices, and alate sexuparae. For the same wing morphs, alate sexuparae and alate virginoparae had no significant differences in fecundity, whereas apterous sexuparae had a significant lower reproductive capacity than that of the apterous virginoparae. Apterous sexuparae and oviparae exhibited reproductive capacities that were three time lower than those of the apterous virginoparae and fundatrices. Apterous sexuparae and males possessed shorter adulthoods compared with those of other morphs ( $F_{6,227} = 5.27$ ,  $P < 0.001$ ). Significant differences in the pre-reproductive periods were observed among the morphs ( $F_{5,185} = 56.09$ ,  $P < 0.001$ ). Oviparae had a significant delay in reproduction compared with apterous virginoparae, apterous sexuparae, and fundatrices; alate virginoparae had significantly longer pre-reproductive periods than those of the alate sexuparae. Significant differences were observed among the reproductive and post-reproductive periods of the morphs (reproductive period,  $F_{5,185} = 12.19$ ,  $P < 0.001$ ; post-reproductive period,  $F_{5,185} = 10.95$ ,  $P < 0.001$ ).

Significant differences in average daily reproduction were observed among the morphs ( $F_{5,371} = 8.30$ ,  $P < 0.001$ ). Alate sexuparae had the highest rate (2.93 offspring per day), whereas oviparae had the highest (1.12 eggs per day). Significant differences in the survival rates were also observed among the morphs ( $F_{6,431} = 3.00$ ,  $P = 0.007$ ) (fig. 2). The Weibull equation was used to fit the survival curves of the seven morphs. All aphid morphs exhibited Devey I survivorship ( $c > 1$ ) (table 3).

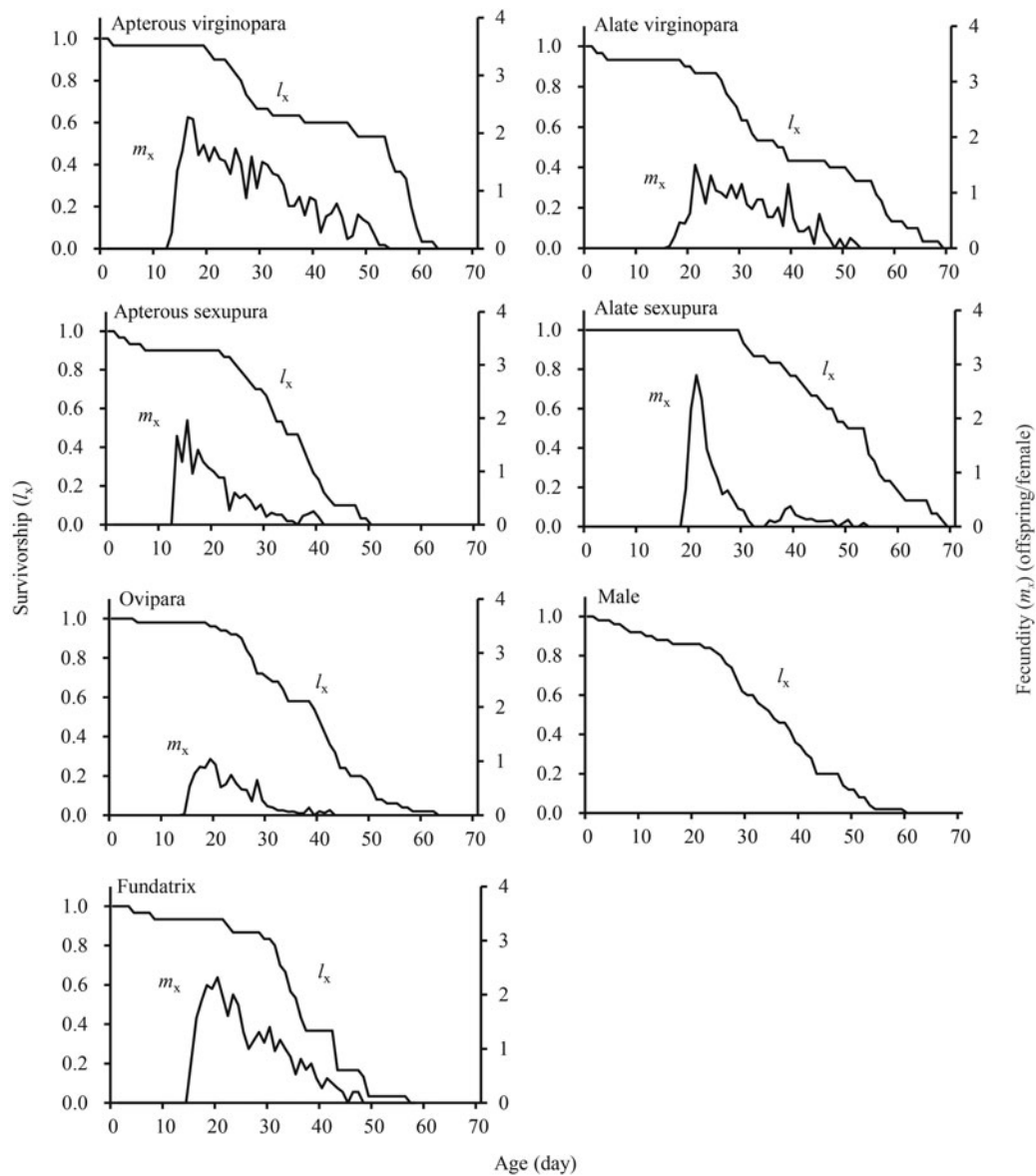
#### Life table parameters of different morphs

The net reproductive rate ( $R_0$ ) was significantly higher in the apterous virginoparae and fundatrices than in the alate virginoparae, alate and apterous sexuparae, and oviparae ( $F_{5,14} = 44.64$ ,

**Table 2.** Adult lifespans and fecundities of different morphs under short light conditions in *Sitobion avenae*

Morphs	Fecundity (n)	Adult lifespan (d)	Pre-reproductive period (d)	Reproductive period (d)	Post-reproductive period (d)
Apterous virginopara	34.03 ± 3.58a	32.44 ± 2.85a	1.17 ± 0.07c	23.17 ± 2.23a	8.10 ± 1.01bc
Alate virginopara	16.36 ± 1.82b	27.39 ± 2.89abc	3.82 ± 0.28a	16.46 ± 1.90b	7.11 ± 1.33c
Apterous sexupura	10.63 ± 0.85b	21.56 ± 1.49c	2.63 ± 0.21b	10.26 ± 1.06c	8.62 ± 0.91bc
Alate sexupura	15.73 ± 1.09b	31.47 ± 2.30ab	2.67 ± 0.13b	11.33 ± 1.38bc	17.47 ± 1.81a
Ovipara	9.76 ± 0.93b	26.55 ± 1.55abc	3.69 ± 0.11a	10.20 ± 1.02c	12.67 ± 1.19ab
Male	-	20.44 ± 1.52c	-	-	-
Fundatrix	30.00 ± 2.49a	23.61 ± 1.48bc	1.10 ± 0.06c	17.11 ± 0.12ab	5.39 ± 1.25c

Data are mean ± SE. Different letters in a column denote significant differences at  $P < 0.05$ , according to Tukey's test.



**Figure 2.** Survivorship ( $l_x$ ) and fecundities ( $m_x$ ) of the different *S. avenae* morphs under short light conditions.



**Table 3.** Weibull survival curve parameters of different morphs under short light conditions in *Sitobion avenae*

Morphs	Curve equation	<i>b</i>	<i>C</i>	<i>R</i> <sup>2</sup>
Apterous virginopara	$S(t) = \exp [ - (t/53.49)^{2.47} ]$	53.49 ± 1.09	2.47 ± 0.18	0.904
Alate virginopara	$S(t) = \exp [ - (t/47.49)^{2.34} ]$	47.49 ± 0.52	2.34 ± 0.09	0.973
Apterous sexupura	$S(t) = \exp [ - (t/37.65)^{3.99} ]$	37.65 ± 0.31	3.99 ± 0.18	0.979
Alate sexupura	$S(t) = \exp [ - (t/54.80)^{4.66} ]$	54.80 ± 0.20	4.66 ± 0.10	0.994
Ovipara	$S(t) = \exp [ - (t/42.69)^{3.88} ]$	42.69 ± 0.20	3.88 ± 0.10	0.994
Male	$S(t) = \exp [ - (t/39.55)^{3.04} ]$	39.55 ± 0.27	3.04 ± 0.09	0.990
Fundatrix	$S(t) = \exp [ - (t/40.52)^{4.54} ]$	40.52 ± 0.29	4.54 ± 0.19	0.984

**Table 4.** Life table parameters of different morphs under short light conditions in *Sitobion avenae*

Morphs	Net reproductive rate ( <i>R</i> <sub>0</sub> )	Intrinsic rate of increase ( <i>r</i> <sub>m</sub> )	Finite rate of increase ( <i>λ</i> )	Mean generation time ( <i>T</i> )
Apterous virginopara	33.400 ± 2.369a	0.137 ± 0.004a	1.147 ± 0.005a	25.616 ± 0.683b
Alate virginopara	15.267 ± 0.913b	0.093 ± 0.001c	1.098 ± 0.001c	29.166 ± 0.560a
Apterous sexupura	14.067 ± 1.247b	0.131 ± 0.002ab	1.139 ± 0.002ab	20.199 ± 0.625c
Alate sexupura	15.733 ± 1.770b	0.110 ± 0.008bc	1.117 ± 0.009bc	24.974 ± 0.745b
Ovipara	9.680 ± 0.915b	0.104 ± 0.006c	1.110 ± 0.007c	21.755 ± 0.435c
Fundatrix	28.133 ± 1.093a	0.138 ± 0.004a	1.148 ± 0.004a	24.179 ± 0.465bc

Data are mean ± SE. Different letters in a column denote significant differences at *P* < 0.05, according to Tukey's test.

*P* < 0.001) (table 4). The intrinsic (*r*<sub>m</sub>) and finite (*λ*) rate of increase in the apterous virginoparae and fundatrices were higher than those in the other morphs, while the lowest *r*<sub>m</sub> and *λ* were observed in the alate virginoparae. The mean generation time (*T*) was the shortest in the apterous sexuparae and the longest in the alate virginoparae.

## Discussion

Short light and low-temperature conditions are the main environmental factors that induce the production of sexual morphs in aphids (Williams and Dixon, 2006; Ogawa and Miura, 2014; Kwon and Kim, 2017; Oka *et al.*, 2018). We found that alate and apterous sexuparae produced virginoparae over the terminal reproductive series in *S. avenae* (fig. 1). The coexistence of asexual and sexual morphs in the sexuparae offspring was consistent with that of aphids in Aphididae, such as *Acyrtosiphon pisum* (Harris) (Lees, 1989; MacKay, 1989), *S. avenae* (Dedryver *et al.*, 1998), *Aphis fabae* Scopoli (Sandrock and Vorburger, 2011), and *Aphis glycines* Matsumura (Oka *et al.*, 2018). These data suggest that the production of virginoparae might be a general characteristic of switching to sexual reproduction in aphids. The coexistence of sexual and asexual morphs in the sexuparae offspring should therefore be regarded as a strategy for limiting the risk of low fitness, regardless of favorable or unfavorable climatic conditions in winter (Rispe *et al.*, 1998; Dedryver *et al.*, 2001; Helden and Dixon, 2002).

Insect development is affected not only by light, temperature, and food, but also by wing morphs (Braendle *et al.*, 2006; Peng *et al.*, 2017; Malinga *et al.*, 2022). Parthenogenetic aphids develop slower in alate than in apterous morphs under long light conditions (reviewed in Braendle *et al.*, 2006). Herein, we confirmed

that, regardless of sexual or asexual morphs, the development time of alate nymphs was noticeably longer than that of apterous nymphs under short light conditions (table 1). Longer nymphal duration for alate morphs could be due to wing development. Among the alate morphs, males had the longest age at maturity, further indicating that males exhibit a cost of development. Among the apterous morphs, sexuparae were older at maturity than fundatrices, virginoparae, and oviparae (table 1). We found that the ovaries of the apterous sexuparae contained a large proportion of male embryos. A delay in the development of apterous sexuparae accounted for the fact that the slow development of the male embryos (Newton and Dixon, 1987). Most nymphs survived to adulthood in each morph, and no significant differences were observed among morphs in *S. avenae* (table 1). We suggest that nymphs of each morph possess equal survival potentials, whereas males and apterous sexuparae bear the costs of developmental delays between asexual and sexual reproductive modes.

Many studies have indicated that, under long light conditions, parthenogenetic aphids have less fecundity and longer pre-reproductive periods in alate morphs than in apterous morphs (reviewed in Braendle *et al.*, 2006). In this study, the fecundities of the apterous sexuparae and oviparae were lower than those of the alate sexuparae, alate and apterous virginoparae, and fundatrices under short light conditions. Moreover, apterous sexuparae and oviparae had reproductive capacities three times lower than those of apterous virginoparae and fundatrices, and had longer pre-reproductive periods (table 2). These results indicate that sexual reproduction is accompanied by a marked reduction in reproductive capacity (Newton and Dixon, 1988; Nespolo *et al.*, 2009; Carter *et al.*, 2012; Peng *et al.*, 2017). The survival curves of the seven morphs throughout the aphid life cycle aligned with Deevey I (*c* > 1), but the lifespan of males was the lowest among

the morphs (fig. 2 and table 3), which was partly due to courtship and mating behaviors. These results indicate that oviparae and apterous sexuparae display the cost of a decrease in fecundity, whereas males display the cost of a shorter lifespan.

Reproductive mode switches are the most noteworthy adaptation of aphids to deal with extremely low temperatures in winter (Moran, 1992; Gilabert *et al.*, 2014; Dedryver *et al.*, 2019). Under short light conditions, *S. avenae* required at least two generations to finish the switch from asexual to sexual reproduction, and the short-term cost of sex was observed. First, males had the longest age at maturity among the seven morphs. Second, compared with apterous virginoparae and fundatrices, the apterous sexuparae and oviparae had marked delays in the pre-reproductive period and substantial reductions in total fecundity. Third, the survival rates of males and apterous sexuparae were shorter than those of other morphs. These results suggest that aphid morph type affected the development time and fecundity. For the same wing morphs, alate sexuparae had a shorter pre-reproductive period than alate virginoparae, whereas no significant difference in total fecundity was observed between both morphs; apterous sexuparae had a longer pre-reproductive period and a reproductive capacity three times lower than that of apterous virginoparae. Thus, the phenomena of a high proportion of males over the apterous sexuparae reproductive series and a high proportion of oviparae over the alate sexuparae reproductive series, the short-term costs of sex in development and reproduction are largely associated with male production (Helden and Dixon, 2002).

## Conclusions

In this study, we clarified the costs and benefits of development and reproduction in seven morphs during reproductive mode switches of holocyclic *S. avenae*. Although aphids are associated with the cost of sex in development and reproduction, lower proportions of apterous sexuparae and males and the coexistence of sexual and asexual morphs in the sexuparae offspring might be regarded as a strategy for limiting the risk of low fitness. These findings are useful for understanding the adaptive evolution of the holocyclic life cycle in *S. avenae* and other aphid species and a reference for the controlling aphids.

**Acknowledgements.** This work was supported by the Fundamental Research Funds for the Central Universities (2452018108) and the National Natural Science Foundation of China (31101433).

**Competing interest.** The authors declare no conflict of interest.

## References

- Artacho P, Figueroa CC, Cortes PA, Simon JC and Nespolo RF (2011) Short-term consequences of reproductive mode variation on the genetic architecture of energy metabolism and life-history traits in the pea aphid. *Journal of Insect Physiology* 57, 986–994.
- Braendle C, Davis GK, Brisson JA and Stern DL (2006) Wing dimorphism in aphids. *Heredity* 97, 192–199.
- Carter MJ, Simon JC and Nespolo RF (2012) The effects of reproductive specialization on energy costs and fitness genetic variances in cyclical and obligate parthenogenetic aphids. *Ecology and Evolution* 2, 1414–1425.
- Dedryver CA, Le Gallic JF, Gauthier JP and Simon JC (1998) Life cycle of the cereal aphid *Sitobion avenae* F.: polymorphism and comparison of life history traits associated with sexuality. *Ecological Entomology* 23, 123–132.
- Dedryver CA, Hullé M, Le Gallic JF, Caillaud MC and Simon JC (2001) Coexistence in space and time of sexual and asexual population of the cereal aphid *Sitobion avenae*. *Oecologia* 128, 379–388.
- Dedryver CA, Le Gallic JF, Maheo F, Simon JC and Dedryver F (2013) The genetics of obligate parthenogenesis in an aphid species and its consequences for the maintenance of alternative reproductive modes. *Heredity* 110, 39–45.
- Dedryver CA, Bonhomme J, Le Gallic JF and Simon JC (2019) Differences in egg hatching time between cyclical and obligate parthenogenetic lineages of aphids. *Insect Science* 26, 135–141.
- Dixon AFG (1977) Aphid ecology: life cycles, polymorphism, and population regulation. *Annual Review of Ecology and Systematics* 8, 329–353.
- Downie DA (2003) Effects of short-term spontaneous mutation accumulation for life history traits in grape phylloxera, *Daktulosphaira vitifoliae*. *Genetica* 119, 237–251.
- Gilabert A, Simon JC, Dedryver CA and Plantegenest M (2014) Do ecological niches differ between sexual and asexual lineages of an aphid species? *Evolutionary Ecology* 28, 1095–1104.
- Han ZL, Tan XL, Fan J, Xu QX, Zhang Y, Harwood J and Chen JL (2019) Effects of simulated climate warming on population dynamic of *Sitobion avenae* (Fabricius) and its parasitoids in field. *Pest Management Science* 75, 3252–3259.
- Hansen LM (2006) Models for spring migration of two aphid species *Sitobion avenae* (F.) and *Rhopalosiphum padi* (L.) infesting cereals in areas where they are entirely holocyclic. *Agricultural and Forest Entomology* 8, 83–88.
- Helden AJ and Dixon AFG (2002) Life-cycle variation in the aphid *Sitobion avenae*: costs and benefits of male production. *Ecological Entomology* 27, 692–701.
- Huang XL and Qiao GX (2014) Aphids as models for ecological and evolutionary studies. *Insect Science* 21, 247–250.
- IBM Corp (2013) *IBM SPSS Statistics for Windows, version 23.0*. Armonk, NY: IBM Corp.
- Kwon SH and Kim D (2017) Effects of temperature and photoperiod on the production of sexual morphs of *aphis gossypii* (Hemiptera: Aphididae) in Jeju, Korea. *Journal of Asia-Pacific Entomology* 20, 53–56.
- Lees AD (1989) The photoperiodic responses and phenology of an English strain of the pea aphid *Acyrtosiphon pisum*. *Ecological Entomology* 14, 69–78.
- Le Trionnaire G, Hardie J, Jaubert-Possamai S, Simon JC and Tagu D (2008) Shifting from clonal to sexual reproduction in aphids: physiological and developmental aspects. *Biology of the Cell* 100, 441–451.
- Liu XF, Hu XS, Keller MA, Zhao HY, Wu YF and Liu TX (2014) Tripartite interactions of barley yellow dwarf virus, *Sitobion avenae* and wheat varieties. *PLoS One* 9, e106639.
- MacKay PA (1989) Clonal variation in sexual morph production in *Acyrtosiphon pisum* (Homoptera: Aphididae). *Environmental Entomology* 14, 558–562.
- Malinga GM, Acur A, Ocen P, Holm S, Rutaro K, Ochaya S, Kinyuru JN, Eilenberg J, Roos N, Valtonen A, Nyeko P and Roininen H (2022) Growth and reproductive performance of edible grasshopper (*Ruspolia differens*) on different artificial diets. *Journal of Economic Entomology* 115, 724–730.
- Moran NA (1992) The evolution of aphid life cycles. *Annual Review of Entomology* 37, 321–348.
- Nespolo RF, Halkett F, Figueroa CC, Plantegenest M and Simon JC (2009) Evolution of trade-offs between sexual and asexual phases and the role of reproductive plasticity in the genetic architecture of aphid life histories. *Evolution* 63-9, 2402–2412.
- Newton C and Dixon AFG (1987) Cost of sex in aphids: size of males at birth and the primary of sex ratio in *Sitobion avenae* (F.). *Functional Ecology* 1, 321–326.
- Newton C and Dixon AFG (1988) The cost of switching from asexual to sexual reproduction in an aphid. *Entomologia Experimentalis et Applicata* 47, 283–287.
- Normark BB and Moran NA (2000) Opinion-testing for the accumulation of deleterious mutations in asexual eukaryote genomes using molecular sequences. *Journal of Natural History* 34, 1719–1729.
- Ogawa K and Miura T (2014) Aphid polyphenisms: trans-generational developmental regulation through viviparity. *Frontiers in Physiology* 5, 1–10.
- Oka Y, Kagami-Yashima C, Kagawa K, Sonoda S and Murai T (2018) Clonal variation of sexual morph production in response to temperature and

- photoperiod in soybean aphid *Aphis glycines* (Hemiptera: Aphididae). *Applied Entomology and Zoology* **53**, 509–517.
- Peng X, Qiao XF and Chen MH** (2017) Responses of holocyclic and anholocyclic *Rhopalosiphum padi* populations to low-temperature and short-photoperiod induction. *Ecology and Evolution* **7**, 1030–1042.
- Pinder JE, Wiener JG and Smith MH** (1978) The Weibull distribution: a new method of summarizing survivorship data. *Ecology* **59**, 175–179.
- Rispe C and Pierre SJ** (1998) Coexistence between cyclical parthenogens, obligate parthenogens and intermediates in a fluctuating environment. *Journal of Theoretical Biology* **195**, 97–110.
- Rispe C, Pierre JS, Simon JC and Gouyon PH** (1998) Models of sexual and asexual coexistence in aphids based on constraints. *Journal of Evolutionary Biology* **11**, 685–701.
- Sandrock C and Vorburger C** (2011) Climate effects on life cycle variation and population genetic architecture of the black bean aphid, *Aphis fabae*. *Molecular Ecology* **20**, 4165–4181.
- Simon JC, Rispe C and Sunnucks P** (2002) Ecology and evolution of sex in aphids. *Trends in Ecology and Evolution* **17**, 34–39.
- Simon JC, Delmotte F, Rispe C and Crease T** (2003) Phylogenetic relationships between parthenogens and their sexual relatives: the possible routes to parthenogenesis in animals. *Biological Journal of the Linnean Society* **79**, 151–163.
- Simon JC, Stoeckel S and Tagu D** (2010) Evolutionary and functional insights into reproductive strategies of aphids. *Comptes Rendus Biologies* **333**, 488–496.
- Vereshchagina AB and Gandrabur ES** (2016) Variability in the developmental parameters of bird cherry-oat aphid *Rhopalosiphum padi* (L.) (Homoptera, Aphididae) clones during the life cycle as a genotypic adaptation. *Entomological Review* **96**, 983–996.
- Williams IS and Dixon AFG** (2006) Life cycles and polymorphism. In van Emden HF and Harrington R (eds), *Aphids as Crop Pests*. Trowbridge, UK: Cromwell Press, pp. 69–81.
- Wu YT, Wu MC, Hui Z, Hu XS and Xu XL** (2022) Polyphenism in antennal sensilla among different adult morphs of nonhost-alternating, holocyclic *Sitobion avenae* (Hemiptera: Aphididae). *Journal of Insect Science* **22**, 1–9.
- Xu RM and Cheng XY** (2005) *Entomology Population Ecology*. Beijing, China: Science Press, pp. 54–67.
- Xu XL, Lv NN, Shi Q, Hu XS and Wu JX** (2019) Reproductive adaptation in alate adult morphs of the grain aphid *Sitobion avenae* under starvation stress. *Scientific Reports* **1**, 373–396.