

Morph-specific differences in life history traits between the winged and wingless morphs of the aphid, *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae)

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Life history traits were evaluated in the wing polyphenic aphid, *Sitobion avenae* (Fabricius), by rearing the winged and wingless morphs under the laboratory conditions. Winged morph with large thoraces exhibited a significantly greater morphological investment in flight apparatus than wingless morph with small thoraces. Compared to the winged morph, the wingless morph produced significantly more nymphs and exhibited significantly faster nymph development rates. In addition, the age at which reproduction first occurred for the winged morph was significantly delayed, and higher mortality was recorded. The results suggest that the fitness differences associated with wings may be related to nymph development, adult fecundity, and mortality. Based on these results, the trends and exceptions of life history traits for the wing polyphenic insects are discussed.

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1. Introduction

All organisms can flexibly alter their phenotypes depending on the environmental conditions they inhabit, which is termed “phenotypic plasticity” (West-Eberhard 2003). When multiple discrete phenotypes are formed, it is called “polyphenism” (Leimar 2009). Many insect species display polyphenism (Müller *et al.* 2001). Important examples include phase polyphenism in locusts,

caste polyphenism in social insects, seasonal polyphenism in butterflies, and wing polymorphism in a wide variety of insect groups (Zera 2004). Insects with wing polymorphism not only exhibit distinct differences in morphological characteristics, but also in life history traits and behavioral features (Walters & Dixon 1983, Roff 1986, Denno *et al.* 1989). A general observation, derived from many studies, is that wingless or short-winged phenotype shows earlier onset of

oviposition and enhanced reproductive output compared with long-winged phenotype (Roff 1984, Zera 1984, Denno *et al.* 1989, Braendle *et al.* 2006).

Aphids (Hemiptera: Aphididae) exhibit extreme polyphenic development, such as wing polyphenism (Müller *et al.* 2001). Due to the complexity of life cycles of aphids, a number of different winged forms exist. Environmentally induced dimorphic wing polyphenism occurs primarily among parthenogenetic females, while wing polymorphism is a genetically determined dimorphism found only in males (Braendle *et al.* 2006). Wing polyphenic aphids exhibit winged and wingless phenotypes and the morphological differences between winged and wingless phenotypes usually correlate with differences in the life history traits (Xu & Cheng 2005). In general, the winged phenotype differs from the wingless phenotype by showing lower offspring production (Dixon & Wratten 1971, Dixon 1972, MacKay & Wellington 1975, Campbell & Mackauer 1977, Wratten 1977), longer pre-reproductive adult period (Campbell & Mackauer 1977, Kobayashi & Ishikawa 1993), and longer nymphal development (Noda 1960).

However, in these studies, only main differences have been documented, and there is limited information related to systemic comparison of life history traits among wing morphs in species-specific aphids. Therefore, a comparison of life history traits between the winged and wingless morphs would add valuable information to the fitness differences of wing polyphenic aphids, and provide a foundation for future biochemical and physiological studies based on these differences.

The grain aphid *Sitobion avenae* is a major pest of cereals in China (Zhang *et al.* 1985) and other regions of the world (Powell & Bale 2004). It causes damage directly by sap feeding and indirectly as a vector of barley yellow dwarf virus (BYDV) which may result in significant yield losses (Zhang & Zhong 1983). *S. avenae* is a non-host-alternating species. It reproduces parthenogenetically as fast-growing clone during the spring and summer months, and overwinters on grasses and cereals as holocyclic (eggs) and anholocyclic (aphids) clones in the autumn (Williams & Wratten 1987). In the present study, we describe an experiment, which 1) investigates

systematically life history traits for virginoparous females of *S. avenae* raised in laboratory conditions, 2) assesses the fitness differences between the winged and wingless morphs, and 3) discusses the trends and exceptions of life history for the wing polyphenic insects.

2. Material and methods

2.1. Insects used

Green stock cultures of *S. avenae* were used in the experiments. This species was collected from wild populations at Yangling, Shaanxi, China (34°18'N, 108°5'E) in 2008 and was cultured continuously using a modified procedure described by Lu & Gao (2007). Aphids were kept in 6-cm-diameter Petri dishes, in which five wheat seedlings (*Triticum aestivum*) were put on wet absorbent paper and watered (20 ml) every day. When wheat seedlings were 5–7 cm high, the aphids were transferred onto the plants. Density conditions were manipulated to induce both winged and wingless virginoparous females.

Winged adults readily produced winged aphids without crowding after having been cultured continuously over fifteen generations under a high-density condition (more than 30 adult winged aphids in each dish). Only one wingless adult was kept individually to induce wingless aphids under a low-density condition. Wheat seedlings and aphids were raised under the same conditions (16 h light: 8 h dark photoperiod, 21°C, and 65% relative humidity), and wheat seedlings were replenished every 7 days. To prevent the aphids from escaping, each plant was covered with an air-permeable transparent plastic cylinder cage (6 cm in diameter, 20 cm in height).

2.2. Wing form comparisons

In order to compare the morphological investment in flight apparatus between the wing forms, we chose head width (mm) as a measure of the absolute size associated with flight and used thorax length (mm) as an index of thorax size and investment in flight (Denno *et al.* 1989). Thirty females of both wing forms were measured under a

stereomicroscope fitted with an ocular micrometer.

Two to four days after emergence, aphid adults were placed individually on wheat seedlings, and were removed after six hours. Newly born nymphs (i.e., the first instar nymphs), were maintained individually on one wheat seedling in each Petri dish and checked for development at 6:00, 12:00, 18:00 and 24:00 every day. After emergence, adult longevity, nymphal production, and mortality were recorded daily at 6:00 and 18:00 until the aphids died. Nymphal development was recorded by checking their instars and the eventual evidence of molting (i.e., presence of exuviae), and winged individuals were determined by the present of wings. Sample sizes of the winged and wingless morphs were 50 and 58, respectively.

The fourth instar apteriform and alatform nymphs were collected and placed individually on one wheat seedling in each dish. Adult emergence and age at first reproduction were inspected every 30 min. The interval between adult emergence and age at first reproduction was recorded as the pre-reproductive adult period. Sample sizes of the winged and wingless morphs were 108 and 71, respectively.

In order to compare the development and reproduction between winged and wingless morphs, data were used to calculate the following life table parameters: net reproductive rate (R_0), time interval between subsequent generations (T), intrinsic rate of population increase (r_m), and finite rate of increase (λ), with (x) the age intervals, (m_x) the age-specific fecundity, and (l_x) the age-specific survivorship (Xu & Cheng 2005).

$$R_0 = \sum m_x l_x \quad (1)$$

$$T = \sum m_x l_x x / \sum m_x l_x \quad (2)$$

$$r_m = \ln R_0 / T \quad (3)$$

$$\lambda = e^{r_m} \quad (4)$$

2.3. Data analysis

The relationship between thorax length and head width was analyzed by analysis of covariance

(ANCOVA) (Denno *et al.* 1989). Thorax length, head width, developmental durations of the nymph, total fecundity, potential total fecundity, longevity, reproductive period, and post-reproductive period were analyzed using the Student's *t* test. Pre-reproductive adult period and mean daily fecundity failed to meet the assumption of the Student's *t* test. Therefore, we used the nonparametric Kolmogorov-Smirnov method to test differences between the mean values. The survival curves for specific ages were fitted using the Weibull frequency distribution,

$$S(t) = \exp[-(t/b)^c] \quad (5)$$

with $S(t)$ corresponding to the age-specific mortality, (t) corresponding to the age intervals, and (b) and (c) corresponding to the scale and shape parameter of the Weibull frequency distribution, respectively (Pinder *et al.* 1978). Values of the shape parameter $c > 1$, $c = 1$ or $c < 1$ correspond to Deevey's type I, II or III survivorship curves, respectively (Pinder *et al.* 1978). The differences of survivorship for the both morphs were then analyzed using the Kolmogorov-Smirnov test (Guo *et al.* 2006). Mean values (\pm standard errors of the mean) were calculated and used in all graphical illustrations. All data were statistically analyzed using SPSS 13.0.

3. Results

3.1. Body size

Both the head and thorax were larger in winged morph (0.63 ± 0.007 mm and 1.09 ± 0.013 mm) than wingless morph (0.62 ± 0.008 mm and 0.97 ± 0.012 mm respectively) (Fig. 1). The difference was significant for thorax length ($t = 6.59$, *d.f.* = 58, $P < 0.001$) but not for head width ($t = 0.36$, *d.f.* = 58, $P = 0.72$). Thorax length was highly correlated with head width (Fig. 1). However, when head width was taken as a covariate, the difference in thorax length between wing forms remained significant (ANCOVA, $F = 72.5$, *d.f.* = 1, 57; $P < 0.001$). Thus, winged morph had proportionally larger thoraces and exhibited a greater investment in flight apparatus compared to wingless morph.

Table 1. Means ± S.E. of developmental durations of the nymph stage for the winged and wingless morphs of *S. avenae*.

Wing morph	Developmental duration (d)				
	1 st instar	2 nd instar	3 rd instar	4 th instar	Total nymph
Winged	2.0 ± 0.03	2.0 ± 0.04	2.1 ± 0.04	3.3 ± 0.06	9.3 ± 0.07
Wingless	1.9 ± 0.04	1.9 ± 0.05	1.9 ± 0.03	2.2 ± 0.05	7.9 ± 0.09
<i>t</i> -value	0.65	1.64	3.93*	13.88*	12.04*

* The difference is significant at $P < 0.05$, Student's *t* test.

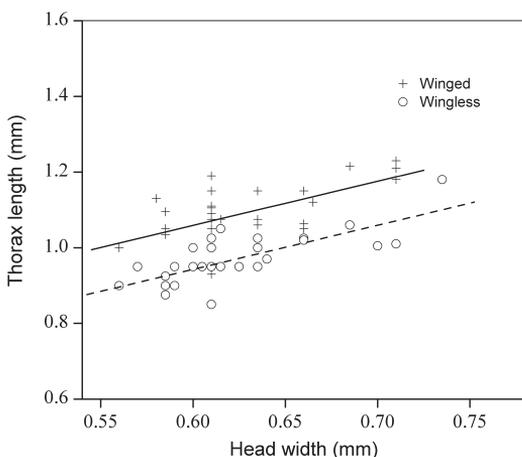


Fig. 1. Relationship between head width and thorax length for the winged and wingless female adults of *Sitobion avenae*. Winged: Thorax length = 0.360 + 1.165 (Head width). Wingless: Thorax length = 0.244 + 1.165 (Head width).

3.2. Developmental duration of nymph

The developmental durations of winged versus wingless morphs showed no differences for the 1st instar ($t = 0.65$, $d.f. = 106$, $P = 0.52$) and the 2nd instar development stages ($t = 1.64$, $d.f. = 106$, $P = 0.11$) (Table 1). However, significant morph-related differences were observed between the winged and wingless morphs in the developmental durations of the 3rd instar ($t = 3.93$, $d.f. = 106$, $P < 0.001$), the 4th instar ($t = 13.88$, $d.f. = 106$, $P < 0.001$), and for the total duration of the nymphal development ($t = 12.04$, $d.f. = 106$, $P < 0.001$). These results demonstrate that winged aphids need longer developmental time than wingless morph in general and the 3rd and 4th instars were the main stages which made the major difference between the two wing morphs.

3.3. Pre-reproductive adult period

The pre-reproductive adult period of wingless morph ranged from 1.0 to 10.0 h after emergence, with a dramatic peak occurring between 2.0 to 5.0 h (Fig. 2). The pre-reproductive adult period of winged morph exhibited a much longer duration, with the shortest being 14.0 h and the longest being 56.0 h. Thus, the wingless morph was characterized by a shorter and more regular pre-reproductive adult period compared with winged morph. Mean pre-reproductive adult periods for winged and wingless morphs were 33.2 ± 0.96 hours and 3.4 ± 0.24 hours, respectively, with the age at first reproduction for the winged morph being significantly delayed compared with wingless morph (Kolmogorov-Smirnov test, $n_1 = 71$, $n_2 = 108$, $Z = 6.55$, $P < 0.001$).

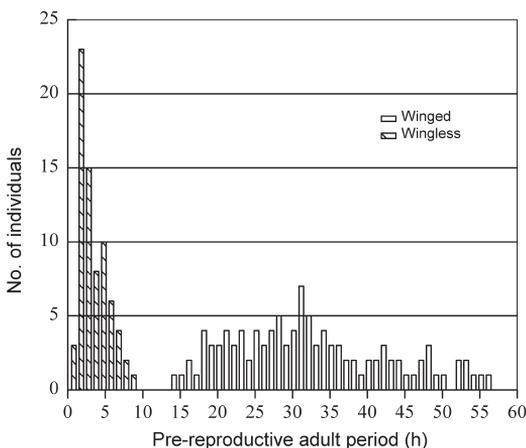


Fig. 2. Frequency distributions of the pre-reproductive adult periods for the winged and wingless females of *S. avenae*.

Table 2. Means \pm S.E. of total fecundity, potential total fecundity, longevity, reproductive period, and post-reproductive period for the winged and wingless female adults of *S. avenae*.

Wing morph	Total fecundity (n)	Potential total fecundity (n)**	Longevity (d)	Reproductive period (d)	Post-reproductive period (d)
Winged	29.0 \pm 2.03	31.4 \pm 2.13	19.2 \pm 1.16	17.3 \pm 1.03	2.1 \pm 0.22
Wingless	51.6 \pm 2.26	54.1 \pm 2.14	23.5 \pm 1.01	20.9 \pm 0.93	2.6 \pm 0.29
<i>t</i> -value	7.46*	7.45*	2.78*	2.55*	1.44

* The difference is significant at $P < 0.05$, Student's *t* test.

** Potential total fecundity means the sum of the total number of nymphs produced and pigmented embryos dissected in their abdomens after death. Number of nymphs produced was recorded on a daily basis.

3.4. Fecundity

Wingless individuals produced significantly more nymphs ($t = 7.46$, $d.f. = 106$, $P < 0.001$) and showed significantly longer lifespan ($t = 2.78$, $d.f. = 106$, $P = 0.006$) compared with winged individuals reared under the same conditions (Table 2). The potential total fecundity of wingless morph, 54.1 ± 2.1 nymphs and embryos per female, was significantly greater than that of winged morph, 31.4 ± 2.1 nymphs and embryos per female ($t = 7.45$, $d.f. = 106$, $P < 0.001$). These results indicate that the winged aphids with functional flight muscles are at a reproductive disadvantage compared with wingless aphids. There was a significant difference in reproductive period between the wing morphs ($t = 2.55$, $d.f. = 106$, $P = 0.012$), but no difference in post-reproductive period ($t = 1.44$, $d.f. = 106$, $P = 0.15$).

The mean daily reproductions recorded over the entire life spans of both winged and wingless morphs are shown in Fig. 3. Reproduction peaked in wingless morph between the 1st and the 10th day after adult emergence and in winged morph between the 3rd and the 10th day, and then gradually declined over the remainder of the birth sequence. The results indicate that the peak of reproduction was delayed for the winged morph. Wingless and winged females produced a maximum of 3.5 and 2.3 nymphs per female per day, respectively. The

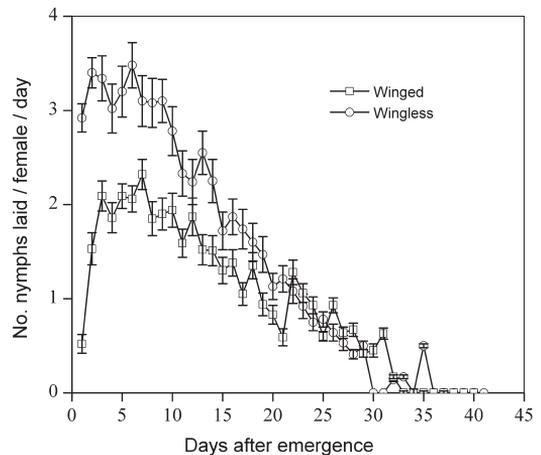


Fig. 3. Fecundity schedules for the winged and wingless female adults of *S. avenae*. The day of adult molt was considered as day 0, and the number of days past this day was used to indicate age. The average daily fecundity calculated for dead individuals assigned zero fecundity.

mean daily reproduction of winged morph was significantly less than that of wingless morph (Kolmogorov-Smirnov test, $n_1 = 50$; $n_2 = 58$, $Z = 1.42$, $P = 0.035$).

The difference in life history traits between the two wing forms is summarized by the reproductive function (Table 3). Not only the net replacement rate was much greater for wingless

Table 3. Life table parameters for the winged and wingless females of *S. avenae*.

Wing morph	Net reproductive rate (R_0)	Mean generation time (T)	Intrinsic rate of increase (r_m)	Finite rate of increase (λ)
Winged	28.1	20.0	0.22	1.2
Wingless	51.9	17.7	0.17	1.3

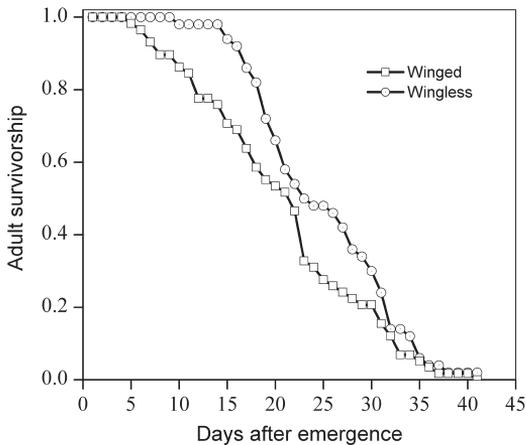


Fig. 4. Adult survivorship schedules for the winged and wingless females of *S. avenae*.

morph (51.9) than winged morph (28.1), but the peak of reproduction was delayed for winged morph (Fig. 2). Compared to winged morph, wingless morph had much greater intrinsic rate of increase and finite rate of increase, while there was shorter mean generation time. The results demonstrate that wingless morph exhibits faster development and greater fecundity than winged morph.

3.5. Survivorship

The survival curves of winged and wingless morphs are shown in Fig. 4. Adult survivorship exhibited similar trend in the winged and wingless morphs after adult emergence. Both the wing morphs showed higher survivorship in the earlier phase when compared to the later phase. The Weibull frequency distribution model fitted the survival curves of age-specific winged and wingless morphs, and the curve-fitting equations were $S(t) = \exp[-(t/22.29)^{2.32}]$ ($b = 22.29 \pm 0.26$, $c = 2.32 \pm 0.05$, $R^2 = 0.995$) and $S(t) = \exp[-(t/26.17)^{3.38}]$ ($b = 26.17 \pm 0.22$, $c = 3.38 \pm 0.17$, $R^2 = 0.991$), respectively. The results indicate that the death processes exhibits Deevy Type III survivorship in both wing morphs. Although wingless morph showed a higher adult survivorship than winged morph, this difference was not significant (Kolmogorov-Smirnov test, $n_1 = 50$; $n_2 = 58$, $Z = 0.96$, $P = 0.31$).

4. Discussion

4.1. Duration of the nymphal development

In the present study, the difference in size and morphology between winged and wingless morphs of *S. avenae* probably reflected changes due to the possession of functional wing muscles (Fig. 1). Winged morph exhibited a longer duration of nymphal development compared to wingless morph, especially in the fourth instar alatform nymphs (Table 1), indicating a possible 'developmental cost' to the possession of wings. Similar results have been reported for other aphid species, such as *Rhopalosiphum maidis* (Noda 1960) and *Acyrtosiphon pisum* (Kobayashi & Ishikawa 1993) as well as several wing polymorphic non-aphids, such as the waterstrider *Limnoporus canaliculatus* (Zera 1984).

However, previous studies have shown no significant differences in development time (time from hatching to the final molt) between wing morphs in either female or male crickets *Gryllus firmus* and *Allonemobius fasciatus* (Roff 1984). A summary by Denno *et al.* (1989) concludes that more than half of the 11 examined studies on 6 different planthopper species could not confirm the hypothesis that short-winged morph developed faster than long-winged morph. It further implies that no trend exists for differences in development duration from egg to adult between the two wing forms in planthoppers. Although the data are far from expansive, faster development rates may, in fact, be characteristic of wingless morph (compared to winged morph) in aphids and waterstriders, while no such trend exists between short- and long-winged cricket and planthopper morphs.

4.2. Pre-reproductive adult period

In addition to morph-dependent differences in the developmental duration of the nymph stage, the short-winged or wingless morph has been shown to attain reproductive maturity faster than the fully-winged morph (Harrison 1980, Dingle 1982). In the current experiments, not only was the age at first reproduction significantly earlier for the wingless morph, but the duration of the

age at first reproduction was also shorter and more regular for the wingless morph (Fig. 2). These results agree with those obtained for the aphid *A. pisum* (Campbell & Mackauer 1977, Kobayashi & Ishikawa 1993).

We observed that wingless morph of *S. avenae* gave birth to their first nymph approximately two days earlier than winged morph. In addition, since in wingless morph the fourth instar was about one day shorter than in winged morph, the total delay of reproductive schedule in the winged morph summed up to about three days. It is probable that, in general, completion of the development of flight muscles occurs after the final molt (Roff 1984, Kobayashi & Ishikawa 1993). The delay in nymph production of the winged morph may thus be due to the diversion of energy into flight muscle development (Zera & Harshman 2001). However, further study is required to confirm this hypothesis in aphids.

The delayed age at first reproduction of the winged *S. avenae* was also consistent with several non-aphids. The long-winged females began reproduction later than short-winged females in the cricket *G. firmus* and *A. fasciatus* (Roff 1984), the pondskaters *Gerris lacustri* (Anderson 1973), milkweed bugs and *Dysdercus* bugs (reviewed in Dingle 1982) and the planthoppers, such as *Javesella pellucida*, *Laodelphax striatellus* and *Stenocranus minutus* (reviewed in Denno *et al.* 1989). In all instances reported, long-winged morph exhibited delayed age at first reproduction compared to wingless or short-winged morph. Therefore, the most consistent cost associated with the possession of wings appears to be a delay in reproduction.

4.3. Fecundity

Wingless *S. avenae* morph also exhibited substantially greater nymph production relative to winged morph. Similar findings have been reported for other aphid species, such as *Aphis fabae* Scop. (Dixon & Wratten 1971), *Drepanosiphum dixonii* H.R.L. (Dixon 1972), *S. avenae* and *Metopolophium dirhodum* Wlk. (Wratten 1977), and *A. pisum* (MacKay & Wellington 1975, Campbell & Mackauer 1977). Our fecundity results for wing morphs were also consistent

with the findings of Roff (1984) for the crickets *G. firmus* and *A. fasciatus*, Tanaka (1976) for *Pteronemobius taprobanensis*, Anderson (1973) for the waterstriders, *Gerris lacustri*, Kaitala (1991) for *Gerris thoracicus*, and Zera (1984) for *L. canalisculatus*.

Denno *et al.* (1989) examined 27 studies on 11 different planthopper species in order to determine if brachypters produced more nymphs than macropters. In these, brachypters demonstrated either higher fecundity than macropters, or there was no difference. Macropters have not been shown to be significantly more fecund than brachypters in any case where statistics have been performed. This suggests that increased fecundity is a general characteristic of the wingless morph, when compared to the winged morph in wing polyphenic insects.

Winged aphids possessed fewer embryos and exhibited slower growth rates of embryos than wingless aphids from the third instar onwards (Leather *et al.* 1988, Newton & Dixon 1990a, b). In addition, Tsitsipis & Mittler (1976) recorded the apparent cessation of embryogenesis in the fourth instar alatae of *A. fabae*, indicating that the development of wings had an effect on reproductive investment. Compared with the cricket *G. firmus* flying actively for a prolonged period of time, aphids engage in (active) short-distance flight but also exploit weather patterns mainly for (passive) long-distance migration (reviewed in Zhang *et al.* 2008). Differences of the development and reproduction for the wing polyphenic aphids are likely to result from the simple possession of wings rather than as a result of flying since winged individuals do not have to fly (Roff 1984).

4.4. Survivorship

Winged morph of *S. avenae* exhibited lower survivorship, but the difference in adult survival rate was not significant between wing morphs (Fig. 4). Differential survivorship between morphs observed in this experiment is similar to the results obtained for several other wing-poly-morphic species. Roff (1984) reported that morph-dependent survivorship was not significantly different in *G. firmus* and *A. fasciatus*.

Denno *et al.* (1989) suggested that no trend existed for difference in adult survivorship between the two wing forms of planthoppers.

4.5. Conclusions

In summary, an earlier onset of reproduction and increased fecundity are general characteristics of wingless morph, when compared to winged morph in wing polyphenic insects. Other costs associated with the possession of wings may include delayed development, increased mortality, decreased mating success or reduced egg size (Roff 1984, Denno *et al.* 1989). The results reported in this study support the general concept that brachypterous or wingless morph has greater fecundity and earlier reproduction than macropterous or winged morph.

Wing form in aphids is determined by complicated environmental factors. Compared to laboratory conditions, many factors in nature have effects on the development and reproduction of aphids. Therefore, further studies are required to confirm whether the results of the present paper, based on the laboratory experiments, are consistent with field results. However, the results reported in this paper might be of interest to a wide variety of entomologists, add valuable information to the fitness differences, and provide a foundation for future biochemical and physiological studies of the differences between winged and wingless morphs.

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References

Anderson, N. M. 1973: Seasonal polymorphism and developmental changes in organs of flight and reproduction in bivoltine pondskaters (Hemiptera: Gemidae). — *Entomologica Scandinavica* 4: 1–20.

Braendle, C., Davis, G. K., Brisson, J. A. & Stern, D. L.

2006: Wing dimorphism in aphids. — *Heredity* 97: 192–199.

Campbell, A. & Mackauer, M. 1977: Reproduction and population growth of the pea aphid (Homoptera: Aphididae) under laboratory and field conditions. — *Canadian Entomologist* 109: 277–284.

Denno, R. F., Olmstead, K. L. & McCloud, E. S. 1989: Reproductive cost of flight capability: a comparison of life history traits in wing dimorphic planthoppers. — *Ecological Entomology* 14: 31–44.

Dingle, H. 1982: Function of migration in the seasonal synchronization of insects. — *Entomologia Experimentalis et Applicata* 31: 36–48.

Dixon, A. F. G. & Wratten, S. D. 1971: Laboratory studies on aggregation, size and fecundity in the black bean aphid, *Aphis fabae* Scop. — *Bulletin Entomological Research* 61: 97–111.

Dixon, A. F. G. 1972: Fecundity of brachypterous and macropterous alatae in *Drepanosiphum dixonii* (Callaphididae, Aphididae). — *Entomologia Experimentalis et Applicata* 15: 335–340.

Guo, J. Y., Gabor, L. L., Wan, F. H. & Han, Z. J. 2006: Survival and development of the wolf spider *Alopecosa pulverulenta* feeding on cotton aphid *Aphis gossypii* propagated on transgenic cotton. — *Acta Entomologica Sinica* 49: 792–799. [In Chinese.]

Harrison, R. G. 1980: Dispersal polymorphisms in insects. — *Annual Review of Ecology and Systematics* 11: 95–118.

Kaitala, A. 1991: Phenotypic plasticity in reproductive behavior of waterstriders: trade-offs between reproduction and longevity during food stress. — *Functional Ecology* 5: 12–18.

Kobayashi, M. & Ishikawa, H. 1993: Breakdown of indirect flight muscles of alate aphids (*Acyrtosiphon pisum*) in relation to their flight, feeding and reproductive behavior. — *Journal of Insect Physiology* 39: 549–554.

Leather, S. R., Wellings, P. W. & Walters, K. F. A. 1988: Variation in ovariole number within the Aphidoidea. — *Journal of Natural History* 22: 381–393.

Leimar, O. 2009: Environmental and genetic cues in the evolution of phenotypic polymorphism. — *Evolution Ecology* 23: 125–135.

Lu, Y. H. & Gao, X. W. 2007: A method for mass culture of wheat aphids. — *Chinese Bulletin of Entomology* 44: 289–290. [In Chinese.]

MacKay, P. A. & Wellington, W. G. 1975: A comparison of the reproductive patterns of apterous and alate virginoparous *Acyrtosiphon pisum* (Homoptera: Aphididae). — *Canadian Entomologist* 107: 1161–1166.

Müller, C. B., Iain, S. & Hardie, J. 2001: The role of nutrition, crowding and interspecific interactions in the development of winged aphids. — *Ecological Entomology* 26: 330–340.

Newton, C. & Dixon, A. F. G. 1990a: Embryonic growth rate and birth weight of the offspring of apterous and alate aphids: a cost of dispersal. — *Entomologia Experimentalis et Applicata* 55: 223–229.

Newton, C. & Dixon, A. F. G. 1990b: Pattern of growth in

- weight of alate and apterous nymphs of the English grain aphid, *Sitobion avenae*. — *Entomologia Experimentalis et Applicata* 55: 231–238.
- Noda, I. 1960: The emergence of winged viviparous female in aphids. VI. Difference in the rate of development between the winged and the unwinged forms. — *Japanese Journal of Ecology* 10: 97–102.
- Pinder, J. E., Wiener, J. G. & Smith, M. H. 1978: The Weibull distribution: a new method of summarizing survivorship data. — *Ecology* 59: 175–179.
- Powell, S. J. & Bale, J. S. 2004: Cold shock injury and ecological costs of rapid cold hardening in the grain aphid *Sitobion avenae* (Hemiptera: Aphididae). — *Journal of Insect Physiology* 50: 277–284.
- Roff, D. A. 1984: The cost of being able to fly: a study of wing polymorphism in two species of cricket. — *Oecologia* 63: 169–177.
- Roff, D. A. 1986: The evolution of wing dimorphism in insects. — *Evolution* 40: 1009–1020.
- SPSS 1998: SPSS User's Guide. — Chicago, IL, USA.
- Tanaka, S. 1976: Wing polymorphism, egg production and adult longevity in *Pteronemobius taprobanensis* Walker (Orthoptera, Gryllidae). — *Kontyu* 44: 327–333.
- Tsitsipis, J. A. & Mittler, T. E. 1976: Embryogenesis in parthenogenetic and sexual females of *Aphis fabae*. — *Entomologia Experimentalis et Applicata* 19: 263–270.
- Walters, K. F. A. & Dixon, A. F. G. 1983: Migratory urge and reproductive investment in aphids: Variation within clones. — *Oecologia* 58: 70–75.
- West-Eberhard, M. J. 2003: Developmental plasticity and evolution. — Oxford University Press, Oxford. 34–36 pp.
- Williams, C. T. & Wratten, S. D. 1987: The winter development, reproduction and life span of the viviparae of *Sitobion avenae* (F.) (Hemiptera: Aphididae) on wheat in England. — *Bulletin Entomological Research* 77: 19–34.
- Wratten, S. D. 1977: Reproductive strategy of winged and wingless morphs of the aphids *Sitobion avenae* and *Metopolophium dirhodum*. — *Annals of Applied Biology* 85: 319–331.
- Xu, R. M. & Cheng, X. Y. 2005: Entomology population ecology. — Science Press, Beijing. 54–67 pp. [In Chinese.]
- Zera, A. J. 1984: Differences in survivorship, development rate and fertility between the long-winged and wingless morphs of the waterstrider. — *Evolution* 38: 1023–1032.
- Zera, A. J. & Harshman, L. G. 2001: Physiology of life history trade-offs in animals. — *Annual Review of Entomology* 32: 95–126.
- Zera, A. J. 2004: The endocrine regulation of wing polymorphism in insects: state of the art, recent surprises, and future directions. — *Integrative and Comparative Biology* 43: 604–616.
- Zhang, Y., Wang, L. M., Wu, K. M., Wyckhuys, K. A. G. & Heimpel, G. E. 2008: Flight performance of the Soybean Aphid, *Aphis glycines* (Hemiptera: Aphididae) under different temperature and humidity regimens. — *Physiological Ecology* 37: 301–306.
- Zhang, X. C., Zhou, G. H., Shi, M., Fang, J. Z., Zhao, Z. P., Li, S. H., Dong, Q. Z. & Wei, K. 1985: Studies on the long-distance migration and virus transmission by the aphid *Sitobion avenae* (F.). — *Acta Phytophylacica Sinica* 12: 9–16. [In Chinese.]
- Zhong, G. X. & Zhong, T. S. 1983: Economic insect fauna of China (Homoptera: Aphididae). — Science Press, Beijing. 10–37 pp. [In Chinese.]