Cockbain, A. J. 1961. Viability and fecundity of alate alienicolae of Aphis fabae Scop. after flights to exhaustion. *Journal Of Experimental Biology.* 38, pp. 181-187.

J. Exp. Biol. (1961), 38, 181–187
With 2 text-figures
Printed in Great Britain

VIABILITY AND FECUNDITY OF ALATE ALIENICOLAE OF *APHIS FABAE* SCOP. AFTER FLIGHTS TO EXHAUSTION

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(*Received* 12 *August* 1960)

INTRODUCTION

I have studied the effects of exhaustive flight on *Aphis fabae* Scop. to see if a long migratory flight is likely to affect the subsequent life and reproductive potential of aphids.

MATERIALS AND METHODS

Alate alienicolae of approximately uniform size were obtained from healthy colonies of the same clone maintained in the laboratory at 18 ± 5° C. on broad beans (*Vicia faba* L., var. Claudia Aquadulce). They were collected within ¼ hr. of the final ecdysis and kept for 24 hr. on young beans in the dark at 20° C. to complete their teneral development and become ready for flight (Taylor, 1957).

The aphids were flown on pins (Cockbain, 1961) at 25–26° C., 21–84 % R.H., and in an air stream of 1 m.p.h.

Experiments 1–5. Within each experiment there were two experimental (*a* and *b*) and two control (*c* and *d*) batches, 7–8 aphids per batch. Test aphids were flown to exhaustion and control aphids were flown for 15 min. in order to induce settling (see B. Johnson, 1958; Kennedy, 1958). After flight the aphids were kept in darkness on young beans, one batch per plant, at 20° C. and 45 % R.H., and brought into light at the same temperature and humidity after 3 days, i.e. when they had lost the ability to fly because their flight muscles had autolysed (B. Johnson, 1957). Larvae produced by the aphids were counted and removed when the plants were changed every 2–3 days, or whenever an adult died.

Experiments 6–8. Test aphids were flown to exhaustion and then starved in glass tubes in darkness at 20° C. and 70 % R.H.; unflown controls were starved under the same conditions.

RESULTS

Flight durations and subsequent behaviour

Behaviour during prolonged tethered flight and determination of the point of exhaustion have been described elsewhere (Cockbain, 1961). Most aphids flew continuously for long periods, requiring only occasional stimulation, until they became fatigued. Further flight may have been possible after a period of rest as in *Drosophila* (Wigglesworth, 1949), but it is doubtful whether the duration of flight could have been increased significantly. Flight durations in different experiments were consistent enough to give confidence in the method.

Table 1 gives mean, minimum and maximum durations. Flights of 3–9 hr. are typical of tethered culture aphids in the temperatures and humidities stated above; variations are partly because the amounts of flight reserves differ (Cockbain, 1961). Expt. 8 was at a very low humidity (mean saturated deficit 23 mm. Hg), but the mean flight duration did not differ significantly from that of the other experiments; water loss by evaporation, related to the humidity of the air, is evidently not a limiting factor to flight under these conditions.

Table 1. *Flight durations at 25–26° C. of the 1-day-old aphids flown to exhaustion*

Expt. no.		1		2		3		4		5		6	7	8
R.H. (%)		70±3		67±4		67±3		71±3		67±4		67±4	79±5	24±3
Batch no.		*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	—	—	—
No. of aphids		8	8	8	7	8	8	7	7	8	8	14	16	10
Flight duration (hr.)	Mean	4·9	6·8	5·4	7·8	5·6	7·9	5·6	7·7	5·1	7·5	5·5	6·1	5·8
	Min.	3·3	5·5	3·8	6·9	4·4	7·3	4·7	6·5	4·5	6·3	2·5	2·6	3·6
	Max.	5·9	8·1	6·6	9·4	6·5	8·6	6·2	9·6	6·1	8·6	8·0	8·7	8·3

The exhausted aphids in Expts. 1–5 settled and began to feed within a few minutes of being placed on the plants. A few of the controls attempted to take-off after probing, but flight was prevented by placing the insects in darkness. None of the exhausted aphids was disturbed when exposed to light for 10–30 min. on the following day, but some controls immediately began to wander and flight had to be prevented again by darkness. An attempt was made to fly the exhausted aphids of two experiments (4–5) on the second day. Some would not fly and the others were difficult to start. Those which failed to fly could raise their wings but appeared unable to beat them; this is a sign of the beginning of flight-muscle autolysis and further flight may have been impossible. Table 2 shows mean, minimum and maximum durations of second flights, and the percentage of aphids which failed to fly. The corresponding controls, batches 4*c* and 4*d*, 5*c* and 5*d*, were flown with no difficulty for a further 15 min.

Table 2. *Flight durations on the second day of aphids previously flown to exhaustion*

Expt. no.		4		5	
Batch no.		*a*	*b*	*a*	*b*
% unable to fly		0	57	38	0
Flight duration (hr.)	Mean	3·1	1·0	1·7	2·0
	Min.	1·9	0	0	0·6
	Max.	4·3	3·7	4·3	3·3

Of the exhausted aphids in Expts. 6–8 (starved after flight) twenty-eight per cent were able to take-off and fly when exposed to direct sunlight on the following day. Most of them flew upwards towards the light, as is characteristic of first flight. The remaining exhausted aphids could not take-off, some being moribund or dead. Of the unflown controls eighty-eight per cent were able to take-off and fly on the second day.

Longevity after flight

Tethered flight to exhaustion did not affect the longevity of aphids allowed to settle and feed on a host plant after flight (Expts. 1–5). The mean adult life of each batch ranged from 24 to 36 days for exhausted aphids and 28–37 days for controls (Table 3). A maximum life of 41 days for individual aphids occurred with both exhausted and control insects. Within the same experiment, one control batch (3*d*) lived significantly longer than an exhausted batch (3*b*) ($t = 2{\cdot}37$; $P = 0{\cdot}05$–$0{\cdot}02$), and one exhausted batch (5*a*) lived significantly longer than a control (5*d*) ($t = 2{\cdot}39$; $P = 0{\cdot}05$–$0{\cdot}02$). Mean adult lives of 31·1 and 32·4 days for combined data for exhausted and control aphids respectively showed no significant difference ($t = 1{\cdot}03$; $P > 0{\cdot}10$).

Table 3. *Mean adult longevities of aphids feeding on young bean plants (Expts.* 1–5)

Exhausted aphids			Control aphids		
Batch no.	Mean longevity (days)	S.D. (±)	Batch no.	Mean longevity (days)	S.D. (±)
1*a*	28·5*	8·9	1*c*	34·6*	1·5
1*b*	32·9	4·7	1*d*	30·0	5·4
2*a*	34·3	4·5	2*c*	37·0	3·1
2*b*	36·3	2·5	2*d*	31·7	9·8
3*a*	34·5	4·2	3*c*	32·0	9·2
3*b*	24·3†	11·8	3*d*	35·3†	3·4
4*a*	25·0**	11·0	4*c*	34·0**	1·6
4*b*	33·9	2·2	4*d*	30·0	9·1
5*a*	34·5††	1·3	5*c*	31·1	6·0
5*b*	26·9	8·2	5*d*	28·3††	6·9
Mean	31·09	8·29	Mean	32·36	6·75

*, ** Differences significant at 10 % level; †, †† differences significant at 5 % level.

Fig. 1 shows survival curves for exhausted and control aphids in Expts. 1–5. The curves deviate slightly when all aphids are considered (1 A) but are almost identical when the comparison is restricted to aphids of uniform size, i.e. hind tibia length 1·125–1·250 mm. (80 % of the exhausted and 75 % of the control aphids in Expts. 1–5) (Fig. 1 B).

Aphids starved after flight exhaustion lived for a significantly shorter time than aphids starved without flight (Table 4). Mean survival time of flown aphids in Expts. 6–8 was 30·3 hr., i.e. they lived for *ca.* 24·5 hr. after flight; mean survival time of unflown aphids was 55·2 hr.; these means were significantly different ($t = 7{\cdot}68$; $P < 0{\cdot}001$). The unflown controls in Expt. 6 lived significantly longer than those in Expts. 7 and 8 ($t = 3{\cdot}48$ and $3{\cdot}54$ respectively; $P = 0{\cdot}01$–$0{\cdot}001$); this was associated with their greater size, as indicated by hind tibia length. There was a positive correlation between survival time and hind tibia length in the control aphids ($r = +0{\cdot}346$; $P = 0{\cdot}05$–$0{\cdot}02$), such that a difference of 0·1 mm. tibia length was associated with a difference of 13 hr. in length of life during starvation; no correlation was found between survival time and hind tibia length in the exhausted aphids ($r = -0{\cdot}086$; $P > 0{\cdot}10$), nor between length of life after flight and flight duration in these aphids ($r = -0{\cdot}119$; $P > 0{\cdot}10$).

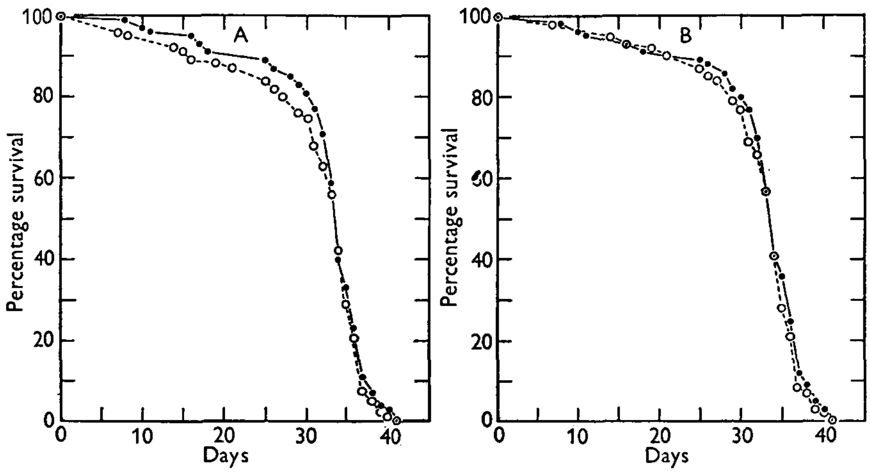

Fig. 1. Mean percentage survival of aphids feeding on young bean plants (Expts. 1–5). A, all aphids; B, aphids with hind tibia length 1·125–1·250 mm.; O- - - -, exhausted aphids; ●——, control aphids.

Reproduction after flight

Flight to exhaustion had no effect on rate of larviposition or on total number of larvae deposited by aphids allowed to feed after flight. The mean accumulative totals of larvae born to exhausted and control aphids in Expts. 1–5 were similar (Fig. 2A, B). The highest rate of larviposition was during the 24 hr. following flight in both exhausted and control aphids, with means of 11·4 and 11·0 larvae/aphid respectively. The rate then decreased to a mean of 2 larvae/aphid/day after 4 days and increased to 6 larvae/aphid/ day after about 12–14 days. A decrease occurred towards the end of the reproductive period which varied from 22 to 29 and 22 to 30 days in the exhausted and control batches respectively.

The reproductive capacities of aphids which completed their reproductive life were about the same in all batches, the combined data giving a mean of 84·2 larvae per adult for both exhausted and control insects (Table 4).

Table 4. *Mean survival times of aphids starved at* 20° C. *and* 70% R.H. (*Expts.* 6–8)

Exhausted aphids					Control aphids				
Expt. no.	Survival times* (hr.)	S.D. (±)	Hind tibia length (mm.)	S.D. (±)	Expt. no.	Survival time* (hr.)	S.D. (±)	Hind tibia length (mm.)	S.D. (±)
6	32·9	13·9	1·137	0·035	6	67·0	10·7	1·160	0·035
7	29·0	17·0	1·148	0·041	7	47·6	17·5	1·120	0·029
8	28·8	12·4	1·085	0·041	8	50·9	10·2	1·103	0·042
Mean	30·3	15·0	1·128	0·047	Mean	55·2	16·3	1·130	0·044

* Includes flight times.

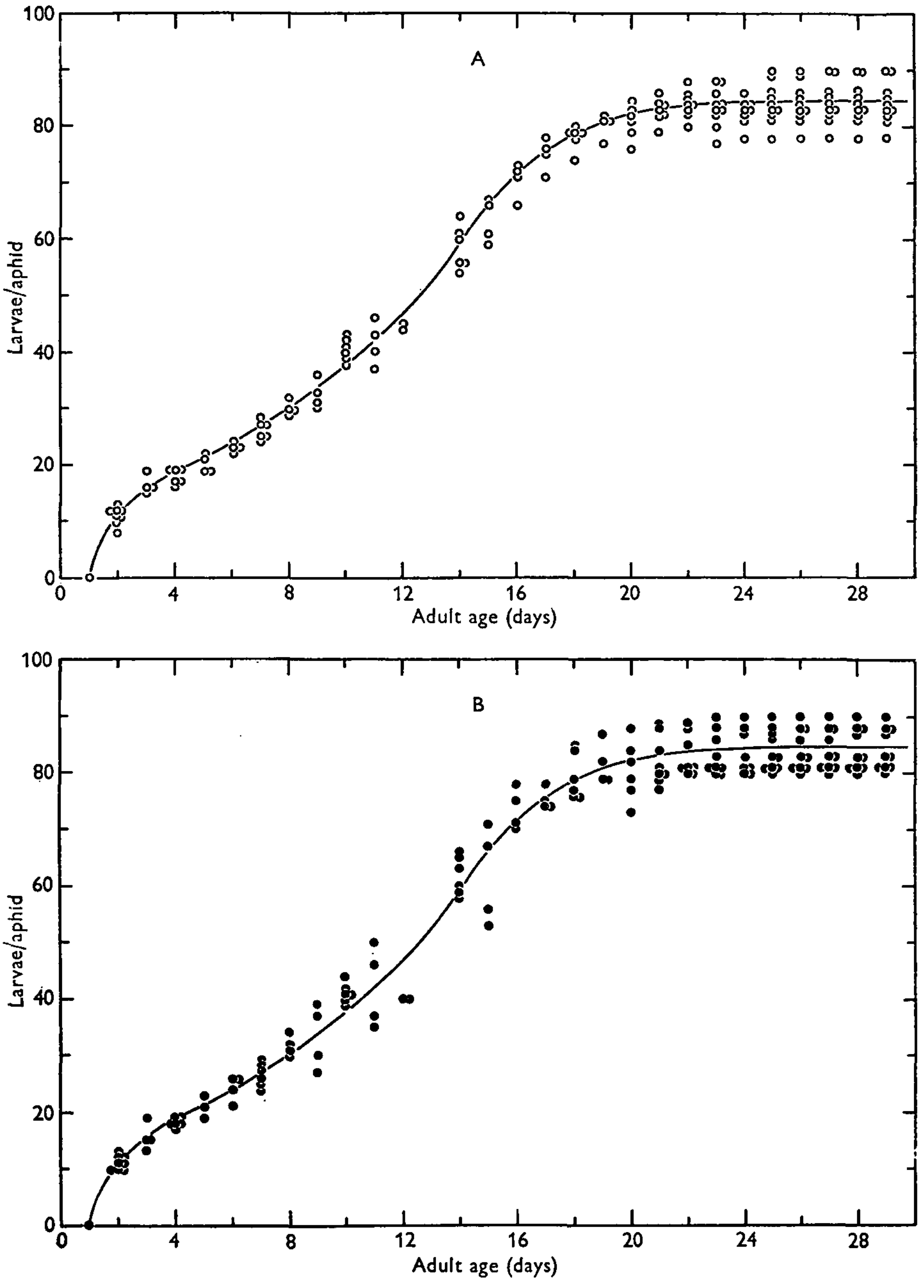

Fig. 2. Accumulative total number of larvae produced per aphid as a function of adult age; each point represents the mean of a batch. A, Exhausted aphids; B, control aphids.

Mortality of nymphs born of flight-exhausted aphids

Data in the preceding section show that exhaustive flight had no adverse effects on the development and birth of larvae carried during flight, or on further embryogenesis. Nor was the viability of these larvae affected, for pre-adult mortality of larvae born during the first week after flight in Expt. 1 was similar in both exhausted and control batches. Of 437 and 458 larvae born to the exhausted and control aphids respectively, 9 (2·1 %) and 8 (1·8 %) failed to complete development.

Table 5. *Number of larvae deposited by the exhausted and control aphids that survived the reproductive period (Expts. 1–5)*

Exhausted aphids				Control aphids			
Batch no.	Reproductive period (days)	% reaching post-reproductive period	Mean no. larvae/aphid	Batch no.	Reproductive period (days)	% reaching post-reproductive period	Mean no. larvae/aphid
1*a*	22	87·5	84·2	1*c*	24	100·0	89·9
1*b*	22	87·5	85·8	1*d*	22	87·5	80·6
2*a*	27	87·5	90·4	2*c*	30	100·0	87·7
2*b*	29	100·0	90·4	2*d*	24	83·3	83·2
3*a*	24	100·0	84·7	3*c*	23	87·5	81·4
3*b*	22	62·5	83·3	3*d*	22	100·0	80·7
4*a*	23	66·7	80·9	4*c*	22	100·0	88·4
4*b*	22	100·0	82·6	4*d*	26	71·4	87·9
5*a*	22	100·0	82·2	5*c*	23	87·5	82·7
5*b*	23	62·5	77·9	5*d*	22	75·0	79·7
Mean	23·6	85·4	84·2	Mean	23·8	89·2	84·2

CONCLUSIONS

C. G. Johnson (1957) and Taylor (1958) showed that the average duration of flight of aphids in the field is probably of the order of 1–3 hr.; similar times for aphids flying freely in a flight chamber were recorded by Kennedy and Booth (1956). In the present study the aphids were flown tethered to pins for 3–9 hr., to apparent exhaustion of the available flight reserves; such flights, providing the aphids later settled and fed on a host plant, had no adverse effects on their subsequent life. The rate at which flight reserves are consumed may differ in free and tethered flight; 1 hr. of tethered flight may not be equivalent in terms of energy expenditure to 1 hr. of natural flight. Nevertheless, it appears unlikely that prolonged flight in the field lowers the viability (see also Taylor, 1960) or reproductive potential of aphids; provided that an aphid alights on a suitable host, length of life and fecundity are unlikely to be affected by flight duration.

Most natural migrants that experience prolonged flight and fail to alight on a host plant, or other plant from which they can derive some nourishment, probably live for only a short time. Results indicate that a few may be able to take-off on the following day; the first few seconds of flight is then similar in some respects to first flight, i.e. upwards towards light (C. G. Johnson, 1955); these aphids would have another chance to alight on a suitable host.

Those aphids that were flown to exhaustion and then allowed to settle and feed on young bean plants in darkness made no attempt to fly when exposed to light on the second day; some could not do so even when stimulated, possibly because of the early onset of flight-muscle autolysis. It is reasonable to infer that a natural migrant of *A. fabae*, alighting on a suitable host after an exhaustive flight, would not fly again.

SUMMARY

1. Laboratory-reared 24 hr.-old alate alienicolae of *A. fabae* were flown for variable periods, but all to apparent exhaustion; their subsequent longevity and fecundity on broad beans, or their survival times during starvation, were compared with controls.

2. Adult longevity, reproductive rate and capacity, and nymph viability were similar in exhausted and control aphids that settled on host plants after flight. Mean adult life was 31 days in exhausted aphids and 32 days in the controls. Both exhausted and control aphids produced an average of 84 larvae per adult.

3. The only major difference noted between exhausted and control aphids that fed after flight was a reluctance, or inability, of exhausted aphids to fly on the following day.

4. Exhausted aphids starved after flight lived for a significantly shorter time (mean of 30 hr.) than control aphids starved without flight (55 hr.). 28 % of the exhausted and 88 % of the control aphids could take-off on the next day.

5. The results indicate that long migratory flights are unlikely to affect the reproductive potential of aphids, and that alate alienicolae of *A. fabae*, having settled on a suitable host after an exhaustive flight, are unlikely to fly again.

I am most grafeful to Mr L. R. Taylor for his advice and encouragement during the course of the work, and to Dr C. G. Johnson and Dr K. Mellanby for reading and criticizing the manuscript.

REFERENCES

COCKBAIN, A. J. (1961). Fuel utilization and duration of tethered flight in *Aphis fabae* Scop. *J. Exp. Biol.* **38**, 163–74.

JOHNSON, B. (1957). Studies on the degeneration of the flight muscles of alate aphids. 1. A comparative study of the occurrence of muscle breakdown in relation to reproduction in several species. *J. Ins. Physiol.* **1**, 248–56.

JOHNSON, B. (1958). Factors affecting the locomotor and settling responses of alate aphids. *Anim. Behav.* **6**, 9–26.

JOHNSON, C. G. (1955). Ecological aspects of aphid flight and dispersal. *Ann. Rep. Roth. Exp. Sta.* pp. 191–201.

JOHNSON, C. G. (1957). The vertical distribution of aphids in the air and the temperature lapse rate. *Quart. J. R. Met. Soc.* **83**, 194–201.

KENNEDY, J. S. (1958). The experimental analysis of aphid behaviour and its bearing on current theories of instinct. *Proc. Xth Int. Congr. Ent., Montreal*, **2**, 397–404.

KENNEDY, J. S. & BOOTH, C. O. (1956). Reflex and Instinct. *Discovery*, **17**, 311–12.

TAYLOR, L. R. (1957). Temperature relations of teneral development and behaviour in *Aphis fabae* Scop. *J. Exp. Biol.* **34**, 189–208.

TAYLOR, L. R. (1958). Aphid dispersal and diurnal periodicity. *Proc. Linn. Soc. Lond.* **169**, 67–73.

TAYLOR, L. R. (1960). Mortality and viability of insect migrants high in the air. *Nature, Lond.*, **186**, 410.

WIGGLESWORTH, V. B. (1949). The utilization of reserve substances in Drosophila during flight. *J. Exp. Biol.* **26**, 150–63.