Flight Activity in the Parasitoid Wasp <u>Nasonia vitripennis</u>
(Hymenoptera: Pteromalidae)

Bethia King[1]
[1]Department of Biological Sciences, Northern Illinois University,
DeKalb, Illinois 60115

Flight activity in females of the parasitoid wasp <u>Nasonia vitripennis</u> (Walker) was examined by measuring still-air tethered-flight. There was a large amount of variation among females in flight duration. The longest single flight (with no pauses of more than five seconds) was more than two hours long. Mating status had a significant and large effect on flight: mated females flew twice as long as virgin females. There also was a slight but significant effect of age on flight, with three-day old females being less likely to fly than one-day old females. Flight duration was not affected by prior exposure to other females, to honey, or to low or to high host density.

KEY WORDS: <u>Nasonia vitripennis</u>, flight, dispersal, parasitoid wasp

INTRODUCTION

Much of the research on factors influencing insect flight has focused on species of Hemiptera, Orthoptera, Coleoptera, Diptera, and Lepidoptera, especially migratory species (e.g., references in Johnson, 1969; Dingle, 1974, 1980; Kennedy, 1975). Aside from aphids, the species studied have tended to be relatively large. This study investigates flight activity in females of the parasitoid wasp <u>Nasonia vitripennis</u> (Walker).
    <u>N. vitripennis</u> is relatively small, a few millimeters long, and is nonmigratory (Whiting, 1967). It has been especially well-studied in relation to its offspring sex ratios (e.g., Werren, 1980, 1983) because its dispersal pattern appears to lead to the population structure assumed by local mate competition theory (a group of natural selection sex ratio models) (Hamilton, 1967). Females have full wings and fly, whereas males have reduced wings and do not fly. Thus, mating probably takes place primarily at the site of emergence, followed by female dispersal to new oviposition sites. Flight is important in females because oviposition sites may be well-dispersed. Females parasitize pupae of fly species associated with carrion. In addition to ovipositing on fly pupae, females feed on host fluids. Females in the laboratory also feed on honey and presumably feed on nectar in nature.
        Here I examine the effects of mating status, age, exposure

to other females, access to honey, and host experience on tethered flight duration in female $\underline{N}$. $\underline{vitripennis}$. Mating status may affect flight activity in $\underline{N}$. $\underline{vitripennis}$ because female dispersal from the emergence site prior to mating may decrease the chance of mating. Because parasitoid wasps are haplodiploid, unmated females can produce offspring, but only sons. Flight may also be triggered by poor environmental conditions, such as low food availability, lack of oviposition sites, or high numbers of competitors (e.g., Dingle, 1968; Caldwell, 1974; Rankin and Riddiford, 1977; Rankin and Rankin, 1980).

METHODS

Wasps were from a laboratory colony of CB[+] wildtype strain (Skinner, 1985) and were maintained on the host $\underline{Sarcophaga}$ $\underline{bullata}$ Parker. Experiments were done at room temperature (24-28°C). Unless specified otherwise, females were recently emerged (less than two days old) and had been allowed to mate in a mass mating situation.

Each female was anesthetized with CO_2 and then glued (Elmer's stixall R adhesive) by the dorsal side of the thorax to the tip of an insect pin. The pin had been bent 90° so that the female would be suspended horizontally when the pin was inserted horizontally into a cork. Females recovered from the CO_2 in less than a minute with no obvious ill effects; also, a study of another parasitoid wasp, $\underline{Biosteres\ longicaudatus}$, showed no effect of CO_2 anesthesia on subsequent survival or offspring production (Greany et al., 1976). Each wasp was observed for three consecutive trials. In each trial, if it did not fly voluntarily (within a minute after being glued to the pin for the first trial, within 30 s of the last flight for the second two trials), it was waved through the air in a figure-eight five times to stimulate flight. In each trial, flight was timed from onset until the wasp stopped for more than 5 s. Similar still-air tethered-flight duration measurements have been made with other insects (e.g., Dingle, 1965).

The method of measuring flight activity may influence flight parameters. For example, migratory locusts have lower wing-beat frequency and fly slower when tethered than when flying free (Baker et al., 1981; Kutsch and Stevenson, 1981). I used tethered flight for practical reasons; the small size of $\underline{N}$. $\underline{vitripennis}$ makes it difficult to follow in free flight. In addition, my interest is less in the absolute parameters of flight than in differences between treatments. The flight activity measured in this study is assumed to be related to tendency to disperse rather than to strength of escape response; in milkweed beetles still-air tethered-flight duration is related to dispersal tendencies in nature (Davis, 1981).

There were six experiments, each with two treatments (Table I). 1) In the mating status experiment, virgin and mated females were compared. Females were separated from males at the pupal stage to ensure virginity. Mated females had been paired with, and observed to mate with, a virgin male immediately prior to testing. 2) In the age experiment, females were tested at 1-d or 3-d-old. 1-d versus 3-d old was chosen because casual observation in the laboratory suggested that there might be a difference. 3) In the female density experiment, isolated females were compared to females that had been in groups of ten. All females had been isolated singly in test tubes from the pupal stage until about 2 h before measuring flight; at that time females were put into clean test tubes singly or in groups of ten. Only one female was tested from each test tube. A two hour exposure period was chosen in an attempt to balance females

having sufficient time together to interact but not so long that they habituated to each other. 4) In the honey availability experiment, the day prior to testing, females were isolated and given a dab of honey about the size of themselves, or were given no honey. 5) In the low host density experiment, females were isolated and given honey and one host or honey and no host for the two days prior to testing. One host over two days is half the rate of hosts given to females for colony maintenance. 6) In the high host density experiment, females were isolated and given honey and two hosts or honey and no host for each of the two days prior to testing.

Comparisons were made only within, and not between, experiments. Within each experiment, to prevent effects of daily variation in the laboratory environment (e.g., temperature, humidity) from being confounded with treatment effects, equal numbers from each treatment were run on a given day.

The initial comparisons of treatments within experiments include females that did not fly and focus on two measures of flight, total flight duration, that is flight duration summed over the three trials for each wasp, and number of no-flights, that is number of trials in which a female did not fly even when waved through the air five times. I also repeated the analyses, first excluding females which did not fly and then using maximum flight time instead of total flight time to see how this affected the results.

Except in the mating status experiment and high host density experiment, flight duration was compared between treatments by t-tests, after being log-transformed when it improved normality (Sokal and Rohlf, 1981). The t-tests are based on pooled variances (Sokal and Rohlf, 1981). Number of no-flights was compared by the nonparametric Mann-Whitney U test. In the mating status experiment and high host density experiment, pairs of sisters were used; and therefore, treatments were compared using paired t-tests for flight duration and using sign tests for number of no-flights. Assumptions of normality were met for the paired t-tests without the use of transformations.

Two-tailed tests were used for the female age, honey availability, and host experiments because one could predict either that a given treatment would decrease flight time for motivational reasons or increase flight time for energetic reasons. One-tailed tests were used for the mating status and female density experiments: as explained in the introduction, virgin females may restrict flight to ensure mating; and females exposed to other females may fly to avoid competition. (For one-tailed tests, two-tailed P values are given if the direction of difference is opposite to that predicted).

RESULTS

Variation in Flight Duration. Females were quite variable in flight duration within and between experiments (Table I). Many females flew only for short periods or not at all. The longest flight was more than 2 h long. The same wasp flew for 2 h 59 min over three trials. There was generally a positive relationship between first and third flight within each treatment of each experiment (11 of 12 comparisons, 1-tailed sign test P = 0.003). First flights were significantly longer than third flights (11 of 12 comparisons, 1-tailed sign test P = 0.003).

Mating Status Experiment. Mated females flew significantly longer than virgin females (Table I). There was no difference between virgin and mated females in the number of no-flights

(Table I). When the analyses were restricted to pairs of females
in which both females flew, mated females approached having
significantly longer flights than virgin females (t = 1.64, df =
10, P = 0.07), and again there was no difference in number of no-
flights (sign test P = 0.50).

Female Age Experiment. 1-d-old females flew slightly but
significantly longer than 3-d-old females and had significantly
fewer no-flights (Table I). When the analyses were restricted to
females that flew, there was no significant difference in flight
duration between young and old females (t = 0.11, df = 39, P =
0.92); the difference in number of no-flights approached
significance (Mann-Whitney U = 158.0, P = 0.06).

Female Density Experiment. There was no evidence that
exposure to nine other females for 2 h increased a female's
flight time or number of no-flights (Table I). When the analyses
were restricted to females that flew, there were still no
differences between treatments (total flight duration: t = 0.15,
df = 58, P = 0.88; number of no flights: Mann-Whitney U = 442.0,
P = 0.90).

Honey Availability Experiment. There was no evidence that
having been fed honey affected a female's flight time or number
of no-flights (Table I). When the analyses were restricted to
females that flew, there were still no differences between
treatments (total flight duration: t = 0.52, df = 60, P = 0.60;
number of no flights: Mann-Whitney U = 432.5, P = 0.35).

Host Experiments. There was no evidence that availability
of a single host for two days prior affected a female's flight
time or number of no-flights (Table I). When the analyses were
restricted to females that flew, there still were no differences
between treatments (total flight duration: t = 1.09, df = 32, P
= 0.28; number of no flights: Mann-Whitney U = 120.0, P = 0.17).

Likewise, availability of two hosts for each of two days did
not significantly affect flight time or number of no-flights
(Table I). When the analyses were restricted to females that
flew, again there were no differences between treatments (total
flight duration: t = 1.54, df = 24, P = 0.14; number of no
flights: sign test P = 0.77).

Maximum Flight Time. Reanalyzing the experiments with
maximum flight time instead of total flight time had little
effect on the comparisons. The difference in average flight time
between one-day old and three-day old females became marginally
nonsignificant (t = 1.94, P = 0.06).

DISCUSSION

Considerable variation in duration of tethered flight, such
as exhibited by N. vitripennis in this study, has also been found
in other insects (e.g., Johnson, 1976; Davis, 1980). Differences
among individual N. vitripennis females in flight duration were
consistent in that females that had long flights in their first
trials also tended to have long flights in their third trials,
and vice versa.
Mating status had a large effect on flight in this study.
Mated females flew twice as long as virgin females (Table I).
The greater flight activity of mated than of virgin females
suggests that, in this species, mating may occur primarily at the
site of emergence followed by dispersal to new oviposition sites,
as natural selection sex ratio theory has assumed (see, e.g.,
Hamilton, 1967; Werren 1980). Questions that remain include:

Does mating increase just flight activity, or overall activity level? How long does the greater flight activity of mated females persist? Is the lesser flight activity of virgin than of mated females related to lack of flight in males with consequent low potential for postdispersal mating? In contrast to N. vitripennis, two recently discovered congeners have winged males (Darling and Werren, 1990). Whether the flights of virgin females are still shorter than flights of mated females in these species where the potential for postdispersal mating may be greater has not been investigated.

The proximal mechanism for the greater flight activity of mated females may be related to effects of male pheromones or to effects of physical contact during mating. If the effect of mating on flight activity is through effects of increased contact, contact in other situations might be expected to increase flight activity. Exposure to other females did not increase flight activity; however, contact from other females may be less extensive than with mating. There is some evidence that contact increases activity levels of N. vitripennis females. In experiments with untethered females in an aquarium, repeatedly picking up N. vitripennis increases the amount of hopping, although not the number of flights (King, unpublished data). Because feeding on honey or hosts did not affect flight activity, it seems unlikely that the greater flight activity of mated than of virgin females was due to males transferring nutritional material to females along with their sperm, making more energy available for flight. Although it is not known if such transfer occurs in N. vitripennis, nutritional transfers with sperm apparently occur in some other insects (references in Thornhill and Alcock, 1983).

The effect of mating status on flight in other insects is in the direction opposite to that in N. vitripennis, perhaps because other species that have been studied are migratory. In Dysdercus intermedius, mating is followed by wing muscle histolysis (Edwards, 1969). Likewise, in Lygaeus kalmii and Helicoverpa armigera, mating decreases tethered flight duration (Caldwell, 1974; Armes and Cooter, 1991). Mating does not initially decrease duration of tethered flight in Oncopeltus fasciatus; however, it does decrease the probability of flying at older ages (Dingle, 1966).

The effect of age on total flight duration of N. vitripennis females in my experiment was slight but significant. The effect of age seems to result from older females being less likely to fly at all. Effects of age on flight have also been found in other insects, such as Oncopeltus fasciatus (Dingle, 1965), Tetraopes beetles (Davis, 1980), the Mexican bean beetle Epilachna varivestis (Saks et al., 1988), and the moths Helicoverpa armigera and Agrotis ipsilon (Armes and Cooter, 1991; Sappington and Showers, 1991). Female flight in these species initially increases but then decreases (see also references in Johnson, 1976). It might be worth testing the effect of age on flight in N. vitripennis over a greater range of ages.

Prior exposure to other females had no effect on flight in N. vitripennis. However, females were not simultaneously exposed to females and hosts. It would be interesting to test whether flight duration is affected when there has been competition for hosts. Crowding does affect flight levels in the milkweed bug Lygaeus kalmii, by increasing mating frequency, which increases flight (Caldwell, 1974).

This study revealed no effect of exposure to honey or hosts on flight in N. vitripennis. In contrast, nutritional state does affect flight in other insects. Females of the parasitoid wasp Trichogramma minutum are slightly more likely to fly in the presence than in the absence of honey (Forsse et al., 1992).

5

Three species of <u>Dysdercus</u> bug, the milkweed bug <u>Oncopeltus</u> <u>fasciatus</u>, and the convergent lady beetle <u>Hippodamia convergens</u> exhibit longer flights under food deprivation, at least initially (Dingle and Arora, 1973; Dingle, 1968; Rankin and Riddiford, 1977; Rankin and Rankin, 1980). Quality of food also affects flight in some insects, for example, <u>Lygaeus kalmii</u> (Caldwell, 1974), <u>Epilachna varivestis</u> (Saks et al., 1988), <u>Oncopeltus fasciatus</u> (Rankin and Riddiford, 1977), and honeybees (Skalicki et al., 1988).

The lack of an effect of exposure to hosts on flight in my study contrasts with reports of previous investigators. Davies and King (1975) suggested that <u>N</u>. <u>vitripennis</u> females that were exposed to hosts for the previous 24 h were less likely to fly than sucrose-fed females. The females that were given hosts exhibited a faster decline with age in the ultrastructure of their flight muscles (Davies and King, 1975). It is not known if the faster decline was caused by exposure to hosts or by lack of sucrose. Nagel and Pimentel (1963) have suggested that <u>N</u>. <u>vitripennis</u> disperses faster when not given hosts than when given hosts. However, the dispersal observed by Nagel and Pimentel (1963) was probably by walking, not flying; and unfortunately, their sample was unreplicated. The presence of hosts decreases the flight propensity of females of the parasitoid wasp <u>Trichogramma minutum</u> (Forsse et al., 1992).

Much remains to be learned about flight activity in <u>N</u>. <u>vitripennis</u> and other parasitoid wasps. Other investigations of factors influencing flight activity in parasitoid wasps have included studies of long range dispersal distance in the field (Antolin and Strong, 1987), studies looking at how environmental factors such as temperature and relative humidity affect number of individuals caught in the field (e.g., Juillet, 1960; Abraham, 1975, 1978), and studies on the effects of host pheromones on flight (e.g., Noldus et al., 1991). Further investigation of factors influencing flight activity in parasitoid wasps may be of practical value in planning releases for biocontrol of pest insects. Results with other insects suggest that interactions among factors influencing flight may be important. For example, the effect of age on flight in <u>Lygaeus kalmii</u> depends on food level: food deprived individuals fly at an earlier age (Caldwell, 1974). Walking would also be worth investigating in order to understand short range dispersal.

REFERENCES

Abraham, R. (1975). Uber die wirkung der temperatur auf die flugaktivitat parasitischer Hymenopteren. <u>Z</u>. <u>Angew</u>. <u>Entomologie</u> 79:113-123.

Abraham, R. (1978). On the flight activity of Pteromalidae (Hymenoptera: Chalcidoidea) depending on temperature and relative humidity. <u>Zool</u>. <u>Jahrb</u>. <u>Abt</u>. <u>Syst</u>. <u>Oekol</u>. <u>Geogr</u>. 105:489-501.

Antolin, M. F., and Strong, D. R. (1987). Long-distance dispersal by a parasitoid (<u>Anagrus delicatus</u>, Mymaridae) and its host. <u>Oecologia</u> 73:288-292.

Armes, N. J., and Cooter, R. J. (1991). Effects of age and mated

status on flight potential of <u>Helicoverpa</u> <u>armigera</u>
(Lepidoptera, Noctuidae). <u>Physiol</u>. <u>Entomol.</u> 16:131-144.

Baker, P. S., Gewecke, M., and Cooter, R. J. (1981). The natural
flight of the migratory locust, <u>Locusta migratoria</u> L. III.
Wing-beat frequency, flight speed and attitude. <u>J</u>. <u>Comp</u>.
<u>Physiol</u>. 141:233-237.

Caldwell, R. L. (1974). A comparison of the migratory strategies
of two milkweed bugs, <u>Oncopeltus fasciatus</u> and <u>Lygaeus kalmii</u>.
In Browne, L. B. (ed)., <u>Experimental Analysis of Insect</u>
<u>Behaviour</u>, Springer-Verlag, New York, pp. 304-316.

Darling, D. C., and Werren, J. H. (1990). Biosystematics of
<u>Nasonia</u> (Hymenoptera: Pteromalidae): two new species reared
from birds' nests in North America. <u>Ann</u>. <u>Entomol</u>. <u>Soc</u>. <u>Am</u>.
83:352-370.

Davies, I., and King, P. E. (1975). A morphometric and
cytochemical analysis of aging changes in the flight muscle of
<u>Nasonia vitripennis</u>. <u>Mech</u>. <u>Ageing Devt</u>. 4:459-468.

Davis, M. A. (1980). Variation in flight duration among
individual <u>Tetraopes</u> beetles: implications for studies of
insect flight. <u>J</u>. <u>Insect Physiol</u>. 26:403-406.

Davis, M. A. (1981). The flight capacity of dispersing milkweed
beetles, <u>Tetraopes tetraopthalmus</u>. <u>Ann</u>. <u>Entomol</u>. <u>Soc</u>. <u>Am</u>.
74:385-386.

Dingle, H. (1965). The relation between age and flight activity
in the milkweed bug, <u>Oncopeltus</u>. <u>J</u>. <u>Exp</u>. <u>Biol</u>. 42:269-283.

Dingle, H. (1966). Some factors affecting flight activity in
individual milkweed bugs (<u>Oncopeltus</u>). <u>J</u>. <u>Exp</u>. <u>Biol</u>. 44:335-
343.

Dingle, H. (1968). The influence of environment and heredity on
flight activity in the milkweed bug <u>Oncopeltus</u>. <u>J</u>. <u>Exp</u>. <u>Biol</u>.
48:175-184.

Dingle, H. (1974). The experimental analysis of migration and
life history strategies in insects. In Browne, L. B. (ed.),
<u>Experimental Analysis of Insect Behaviour</u>, Springer-Verlag,
New York, pp. 329-342.

Dingle, H. (1980). Ecology and evolution of migration. In
Gauthreaux, S.A., Jr. (ed.), <u>Animal Migration, Orientation,</u>
<u>and Navigation</u>, Academic Press, New York, pp. 2-101.

Dingle, H., and Arora, G. (1973). Experimental studies of
migration in bugs of the genus <u>Dysdercus</u>. <u>Oecologia</u> 12:119-
140.

Edwards, F. J. (1969). Environmental control of flight muscle
histolysis in the bug <u>Dysdercus intermedius</u>. <u>J</u>. <u>Insect</u>
<u>Physiol</u>. 15:2013-2020.

Forsse, E., Smith, S. M., and Bourchier, R. S. (1992). Flight
initiation in the egg parasitoid <u>Trichogramma minutum</u>: effects
of ambient temperature, mates, food, and host eggs. <u>Entomol</u>.
<u>Exp</u>. <u>Appl</u>. 62:147-154.

Greany, P. D., Ashley, T. R., Baranowski, R. M., and Chambers, D.
L. (1976). Rearing and life history studies on <u>Biosteres</u>
<u>longicaudatus</u> (Hym.: Braconidae). <u>Entomophaga</u> 21:207-215.

Hamilton, W. D. (1967). Extraordinary sex ratios. <u>Science</u>
156:477-488.

Johnson, C. G. (1969). <u>Migration and Dispersal of Insects by</u>
<u>Flight</u>. Methuen, London.

Johnson, C. G. (1976). Lability of the flight system: a context
for functional adaptation. <u>Symp</u>. <u>R</u>. <u>Entomol</u>. <u>Soc</u>. <u>Lond</u>. 7:217-
234.

Juillet, J. A. (1960). Some factors influencing the flight
activity of hymenopterous parasites. <u>Can</u>. <u>J</u>. <u>Zool</u>. 38:1057-
1061.

Kennedy, J. S. (1975). Insect dispersal. In Pimentel, D. (ed.),
<u>Insects, Science, and Society</u>, Academic Press, New York,
pp.103-119.

Kutsch, W., and Stevenson, P. (1981). Time-correlated flights of juvenile and mature locusts: a comparison between free and tethered animals. _J_. _Insect Physiol_. 27:455-459.

Nagel, W. P., and Pimentel, P. (1963). Some ecological attributes of a pteromalid parasite and its house fly host. _Can_. _Entomol_. 95:208-213.

Noldus, L. P. J. J., van Lenteren, J. C., and Lewis, W. J. (1991). How _Trichogramma_ parasitoids use moth sex pheromones as kairomones: orientation behaviour in a wind tunnel. _Physiol_. _Entomol_. 16:313-327.

Rankin, M. A., and Rankin, S. (1980). Some factors affecting presumed migratory flight activity of the convergent ladybeetle, _Hippodamia convergens_ (Coccinellidae: Coleoptera). _Biol_. _Rev_. 158:356-369.

Rankin, M. A., and Riddiford, L. M. (1977). Hormonal control of migratory flight in _Oncopeltus fasciatus_: the effects of the corpus cardiacum, corpus allatum, and starvation on migration and reproduction. _Gen_. _Comp_. _Endocrinol_. 33:309-321.

Saks, M. E., Rankin, M. A., and Stinner, R. E. (1988). Sexually differentiated flight responses of the Mexican bean beetle to larval and adult nutrition. _Oecologia_ 75:296-302.

Sappington, T. W., and Showers, W. B. (1991). Implications for migration of age-related variation in flight behavior of _Agrotis ipsilon_ (Lepidoptera: Noctuidae). _Ann_. _Entomol_. _Soc_. _Am_. 84:560-565.

Skalicki, N., Heran, H. and Crailsheim, K. (1988). Water budget of the honeybee during rest and flight. In Nachtigall, W. (ed.), Biona report 6. _The Flying Honeybee- Aspects of Energetics_, Gustav Fischer, Stuttgart, New York, pp. 103-118.

Skinner, S. W. (1985). Son-killer--a third chromosomal factor affecting the sex ratio in the parasitoid wasp _Nasonia_ (_Mormoniella_) _vitripennis_. _Genetics_ 109:745-759.

Sokal, R. R., and Rohlf, F. J. (1981). _Biometry_, Freeman, New York.

Thornhill, R., and Alcock, J. (1983). _The Evolution of Insect Mating Systems_, Harvard University Press, Cambridge, Massachusetts.

Werren, J. H. (1980). Sex ratio adaptations to local mate competition in a parasitic wasp. _Science_ 208:1157-1159.

Werren, J. H. (1983). Sex ratio evolution under local mate competition in a parasitic wasp. _Evolution_ 37:116-124.

Whiting, A. R. (1967). The biology of the parasitic wasp _Mormoniella vitripennis_ (=_Nasonia brevicornis_) (Walker). _Q_. _Rev_. _Biol_. 42:333-406.

Table I. Total Flight Time (s) and Number of Times a Female
Did Not Fly Out of Three Flight Trials per Female

Experiment Treatment	n	Flight Time Mean ± s.e.	# No-flights Mean ± s.e.
Mating Status Experiment[a]			
Virgin	19	170.9 ± 61.4	1.11 ± 0.31
Mated	19	346.4 ± 77.3	0.63 ± 0.27
Age Experiment[b*]			
One-day-old	27	389.7 ± 113.7	0.41 ± 0.19
Three-day-old	27	371.3 ± 126.9	1.22 ± 0.27
Female Density Experiment[c*]			
Solitary	36	320.0 ± 63.2	0.97 ± 0.20
Grouped	36	332.4 ± 49.3	0.86 ± 0.18
Honey Availability Experiment[d*]			
No honey	37	450.7 ± 160.5	0.84 ± 0.21
Honey	37	538.3 ± 120.3	0.65 ± 0.17
Low Host Density Experiment[e*]			
No host	19	459.5 ± 90.9	0.42 ± 0.23
0.5 host/day	19	323.8 ± 64.8	0.63 ± 0.24
High Host Density Experiment[f]			
No host	28	754.0 ± 381.7	0.57 ± 0.15
2 hosts/day	28	667.5 ± 156.8	0.57 ± 0.17

Table I cont.
[a]Flight Time: t = 2.06, P = 0.03; # No-flights; sign test, P = 0.27
[b]Flight Time: t = 2.09, P = 0.04; # No-flights; U = 251.5, P = 0.02
[c]Flight Time: t = 0.61, P = 0.27; # No-flights; U = 619.5, P = 0.36
[d]Flight Time: t = 1.28, P = 0.20; # No-flights; U = 656.5, P = 0.71
[e]Flight Time: t = 0.60, P = 0.56; # No-flights; U= 156.0, P = 0.34
[f]Flight Time: t = 0.80, P = 0.43; # No-flights; sign test, P = 1.00
[*]: t-test based on log-transformed data