Habitats, life histories, migration and dispersal by flight of two water-beetles Helophorus brevipalpis and H. strigifrons (Hydrophilidae)

Jan Landin

Populations of two Helophorus species from a Swedish lake were sampled during the ice-free periods of two years. Dispersing beetles were trapped in light-reflecting glass traps. Both species are univoltine and breed in the spring. The populations of adult H. brevipalpis are largest during the summer when great numbers emerge and migrate. Very few H. strigifrons adults emerge before spring. Its adult populations are largest in the spring, and small numbers of mature individuals fly with mature H. brevipalpis specimens. This is discussed in relation to their habitat utilization: H. strigifrons inhabits permanent waters only and is dimorphic for flight musculature; H. brevipalpis inhabits both permanent and ephemeral waters and is always equipped with a functioning flight apparatus. H. brevipalpis is an effective colonizer of ephemeral waters due to its large dispersal capacity and to the fact that the habitat of juveniles differs from that of adults.

Age, sexual maturation and feeding in flying and non-flying groups are compared. Food is seldom found in the gut of fliers of either species. In the spring flying H. brevipalpis females have larger oocytes than non-flying ones; flying H. strigifrons females have smaller oocytes than non-fliers. It is possible that the summer migrations of H. brevipalpis favour outbreeding since fliers are sexually immature; spring fliers, being sexually mature, are more efficient as colonizers.

1. Introduction

There are several characteristics which migrating insect species have in common (Dingle 1972, 1974). (a) Migrating individuals are usually young adults who have not yet reproduced or adults flying between successive reproductive occasions. Flying females usually have immature ovaries. (b) In migrating individuals, locomotory functions such as flight dominate over vegetative functions such as feeding and reproduction. (c) Migrating species live for the most part in temporary and ephemeral habitats. (d) These species are good colonizers; they are first or alone in invading and using new or temporary habitats.

Inland waters present numerous, more or less stable habitats, ranging from permanent lakes to ephemeral ponds and puddles. Many species disposed to migration by flight are found in ponds and puddles (Southwood 1962). Several of these species are widely distributed and common (Jackson 1952). Helophorus brevipalpis Bedel (Hydrophilidae) is one such species. It is an early colonizer of small and ephemeral ponds and puddles (Fernando 1958) but also inhabits permanent lakes (Landin and Stark 1973, Landin 1976a).

Helophorus strigifrons Thomson differs from H. brevipalpis in habitat utilization and flight habits (Landin 1976a). In small and temporary waters were H. brevipalpis is abundant, H. strigifrons does not occur (Bruce 1964, Angus pers. comm.).

I intend to describe the life histories and flight habits of these beetles. Some questions dealt with in this paper are: (1) What relationships exist between life histories, seasonal abundance and flight? (2) Can flying individuals be characterized by the statements in (a) and (b) above and do the sexes differ from each other in these
respects? (3) How are features of the life histories and flight habits adapted to the environment? These two closely related species seem to live together in permanent waters. Do they exploit the environment in different ways, thereby avoiding competition?

Migration by flight of female insects has been studied more than that of males. The reason for this is that a single mated or parthenogenetically reproducing female may suffice to colonize a habitat. Johnson’s concept “the oogenesis flight syndrome” (Johnson 1969, point (a) above) originally refers only to females. Dingle (1974) proposed the expression “reproduction flight syndrome” to include males, and I will use his expression. If, for example, males with immature testes migrate and mate with females from other populations, outbreeding will be promoted. Greater importance should therefore be attached to the role of males in the process of migration and colonization.

2. Study area

The field investigations were made at Lake Sågsjön which is located about 18 km NE of Stockholm. It is an eutrophic lake with large reed belts. Beetles were sampled in the open areas of the reed belt of an inlet, and flight traps were placed on the shores of the inlet. More detailed descriptions occur in Landin (1968, 1976a).

3. Materials and methods

Populations at Lake Sågsjön were studied throughout the ice-free seasons of 1966 and 1971. It was sometimes difficult to obtain samples large enough; therefore, I have also used material from 1964 and 1965 (Landin 1976a). Pooled samples from the same period in different years, and additional material from the water were also used.

All specimens collected in the field or extracted from bottom cores were preserved in 70% alcohol. The insects were dissected under a stereomicroscope at 25 or 50X magnification.

The ice-free season was divided into three periods (cf Landin 1976a): (1) spring and early summer, from the melting of ice and snow to 15 June (the time of melting varies between years, the period may or may not include late March and April); (2) summer, from 15 June to 31 August; (3) autumn, from 31 August until snow and ice appear again or almost all beetles have left the water’s edge to hibernate (this period usually ends at the beginning of November).

3.1. Seasonal variations in population size

In 1971 I used a relative method and sampled three stations. At each station beetles were collected along 13 m of the water’s edge during a period of 45 min, and the resulting number was regarded as an estimate of the population size (Landin 1976b).

3.2. Seasonal flight periodicity

Four light-reflecting glass traps (Fernando 1958) were placed on the shore at intervals of 60–80 m. A sheet of glass (66 × 102 cm) in a sloping wooden frame was placed on the ground, with a collecting trough under the lower, shorter side. The edges of the frame, with the exception of the part over the trough, were 2 cm high to reduce the chances of insects escaping. Light-reflections attracted flying water insects, and those landing on the glass moved downwards and usually fell into the trough. This contained a weak formalin solution and a little detergent. Landin (1968), Landin and Stark (1973), and Landin and Vepsäläinen (1977) have discussed the method in greater detail. The traps were placed in the field 30 April–14 November 1966, and 2 April–7 November 1971.

The correlation between Fernando’s (1958) catches of *H. brevipalpis* in artificial habitats and glass traps \( r = 0.684, df = 47, p < 0.025 \), calculated by me) indicates that glass trap catches are good estimates of numbers of beetles invading waters by flight.

3.3. The flight apparatus

I considered hind wings reaching beyond the abdomen as functioning flight wings and noted the presence or absence of the large flight muscles in the metathorax.

3.4. Cuticle hardness and colour

Cuticle hardness and colour was estimated according to an arbitrary scale and regarded as an index of age:

- Grade 1 Entire underside soft and light yellowish-brown – young beetles
- 2 Metasternum soft and dark, abdomen soft, light or dark brown
- 3 Metasternum hard and dark, abdomen hard and dark except at the rear end
- 4 Entire underside hard and black or blackish-brown – old beetles

I inspected the underside (metasternum and abdominal sternites) of the beetles under a stereomicroscope and pressed upon the sternites with hard, fine forceps to judge their hardness. In *H. stirigifrons* it was difficult to separate grade 2 and 3 so they are assigned to 2.5.

3.5. Sexual development and sex ratio

Fig. 1 shows the female reproductive systems of both species. I measured the length of the largest oocyte(s) with an eye-piece micrometer and used it as an estimate of the stage of development. Mature eggs were distinguished from immature ones. Mature eggs include eggs...
The female reproductive organs of *Helophorus brevipalpis* and *H. strigifrons*. The *H. brevipalpis* specimen was a young female with immature ovaries, collected in a pond at Olands Skogsby, on the Island of Oland, southern Sweden, 19 August 1976. The *H. strigifrons* specimen was an overwintered, mated female with large oocytes, from Lake Sågsjön, 6 May 1972. One of its accessory glands and the spinnerets have been removed, besides the right ovary.

Fresh specimens or specimens fixed in 80% ethanol for a period of 3 to 16 h were dissected to enable description of the reproductive systems of both sexes. In fresh specimens of mated females it is easy to see living sperm by making a squash preparation of the sp. in physiological NaCl-solution and examining it under the microscope. In this way sperm can also be detected in a sp. from a female preserved in alcohol.

If a female has mated her bursa copulatrix is distended, containing a whitish mass, and a small, often globular, spermatheca (sp.) is attached distally. This is valid for both species and even for specimens preserved in alcohol for years. Unmated females have a very thin-walled, empty bursa and the sp. is invisible.

The females are easily recognized by their spinnerets (Fig. 1). Upon squeezing the abdomen the spinnerets, or the penis if the specimen is a male, usually protrude.

The males are hibernating on the shore of a pond at Oland Skogsby, on the Island of Oland, southern Sweden. 20 September 1973. The *H. strigifrons* specimen was an overwintered male with sperm in the vesicula, Lake Sågsjön, 31 March 1974. One of its left accessory glands is removed.
3.6. Presence of food in the gut

I noted the presence (wholly or partly filled gut) or absence of food in the entire alimentary canal.

4. Results

4.1. Seasonal variation in population size

Adult *H. brevipalpis* individuals are most abundant in late July (Fig. 3), *H. strigifrons* adults in May (Fig. 4) (cf Landin 1976a). Compared with 1966 the population of *H. brevipalpis* seems to have been smaller in 1971. The population of *H. strigifrons* was considerably larger in 1971 than in 1966.

4.2. Seasonal flight periodicity

Large numbers of *H. brevipalpis* fly and invade waters during the summer (Fig. 3). The peaks in numbers trapped for 1966 and 1971 lasted from the latter part of June to the beginning of August. The species flew from the time the ice and snow melted until late September in both years. In late May and early June however, probably only few individuals flew.

*H. strigifrons* flies only during May–June and then in very small numbers compared with *H. brevipalpis* (Fig. 4). In 1966 only one specimen was trapped, a male on 18 May.

The peaks in numbers trapped of both *H. brevipalpis* and *strigifrons* coincided with the peaks in numbers of adults in the water. Comparisons between numbers flight-trapped and numbers in relative samples indicate that the numbers flying are directly related to the size of the population in the water.

4.3. Flight apparatus

More than 130 *H. brevipalpis* specimens from the water were dissected. All of them had well developed flight muscles and hind-wings. Jackson (1956) reached the same result.

I have dissected more than 240 *H. strigifrons* specimens collected in the water. All had well developed hind-wings. However, during the spring of 1966 and 1971 only 15–21% of a total of 217 specimens had well

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Fig. 3. Numbers of adult *Helophorus brevipalpis* trapped flying during the ice-free seasons at Lake Ságjón, 1966 and 1971. The lower diagram shows numbers in relative samples, 1971. A dash above the time axis indicates a period when no beetles were trapped. In 1971, each bar represents the number trapped during one week. In 1966, the traps were not always emptied weekly, so the breadth of each bar represents the period the traps were left unemptied. The height of each bar and the accompanying number represent mean numbers trapped per week during the period. The total number trapped in 1966 was 2254. Catches on 6 and 25 July are excluded.

Fig. 4. Numbers of adult *Helophorus strigifrons* in relative samples and trapped flying during the ice-free seasons at Lake Ságjón, 1971. No individuals of this species occurred in the samples from station 2.
Tab. 1. Seasonal variation in the cuticle hardness and colour of Helophorus brevipalpis and H. strigifrons specimens from the water and H. brevipalpis specimens trapped flying. See Sect. 3.4, concerning the index of hardness and colour. The figures are means of the index ± standard deviation followed by numbers of beetles examined in parentheses. The asterisks refer to t-tests of the differences between the means (*: 0.01 < p < 0.05; **: 0.001 < p < 0.01; ***: p < 0.001; NS: no significant difference).

a) *H. brevipalpis* from the water, 1966 and 1971. No females and only two males were found during autumn. The males are not included in the table.

| Females | Apr–15 Jun | 16 Jun–31 Aug | 1 Sep–Nov |
|---------|------------|---------------|-----------|
| 1966    | 3.3±0.6 (3) | *             | 2.2±0.7 (21) |
| 1971    | 3.3±0.5 (4) | *             | 2.4±0.7 (26) |
| Males   |            |               |           |
| 1966    | 3.8±0.4 (5) | ***           | 2.4±0.7 (24) |
| 1971    | No males found |   | 2.6±0.5 (25) |
| Sum of the females and males | 3.6±0.5 (8) | *** | 2.3±0.7 (45) |
| 1971    | 3.3±0.5 (4) | *             | 2.5±0.5 (51) |

b) *H. brevipalpis* in pooled samples from the water, spring and autumn 1964–66 and 1971.

| Females | 1966 | 1971 |
|---------|------|------|
| 3.0±0.6 (14) | NS | 2.8±0.5 (4) |
| 3.1±0.8 (9) | NS | 3.0±0.5 (8) |
| 3.1±0.7 (23) | NS | 2.9±0.5 (12) |

| Males | 1966 | 1971 |
|------|------|------|
| 3.1±0.8 (9) | NS | 3.0±0.5 (8) |
| 3.1±0.7 (23) | NS | 2.9±0.5 (12) |

c) *H. brevipalpis* trapped flying, 1966 and 1971

| Females | Apr–15 Jun | 16 Jun–31 Aug | 1 Sep–Nov |
|---------|------------|---------------|-----------|
| 1966    | 3.4±0.5 (7) | ***           | 1.9±0.7 (100) |
| 1971    | 3.8±0.4 (24) | ***          | 1.9±0.7 (79) |
| Males   |            |               |           |
| 1966    | 3.5±0.5 (6) | ***           | 1.9±0.6 (112) |
| 1971    | 5 specimens, all graded 4 | *** | 1.9±0.6 (72) |
| Sum of females and males | 3.5±0.5 (13) | *** | 1.9±0.7 (212) |
| 1966    | 3.9±0.5 (11) | ***          | 2.5±0.5 (7) |
| 1971    | 3.5±0.9 (96) | ***         | 3.3±0.5 (4) |
| Males   |            |               |           |
| 1966    | 3.5±0.8 (90) | ***          | 3.8±0.4 (5) |
| 1971    | 3.4±0.4 (29) | ***          | 3.7±0.5 (9) |

d) *H. strigifrons* from the water spring 1966 and 1971, and from pooled samples from summer and autumn 1964–66 and 1971.

| Females | Apr–15 Jun | 16 Jun–31 Aug | 1 Sep–Nov |
|---------|------------|---------------|-----------|
| 1966    | 3.9±0.5 (11) |           |           |
| 1971    | 3.5±0.9 (96) |           |           |
| Males   |            |               |           |
| 1966    | 20 specimens, all graded 4 |           |           |
| 1971    | 3.5±0.8 (90) |           |           |
| Sum of females and males | 4.0±0.3 (31) |           |           |
| 1964–66 and 1971 | 3.5±0.8 (186) | 2.8±1.0 (9) | 2.6±1.2 (12) |

developed flight-muscles. I have not found any individuals with muscles I could consider to be degenerating or regenerating. The percent of individuals with flight-muscles did not differ between the sexes, and did not seem to change concomitantly with the changes in cuticle development during spring (Tab. 2). Wing size, taken into consideration also the wing breadth, did never seem to vary between individuals. This is valid for both species.

The occurrence of individuals with well developed flight muscles was larger during summer and autumn than during spring (samples from summer and autumn 1966 and 1971 pooled: N = 12, 75% with muscles, χ² = 10.19, df = 1, p < 0.005).
4.4. Cuticle hardness and colour

The hardness and colour of the integument did not seem to differ between the sexes, nor among beetles from the water or among flying beetles (Tab. 1). This applies to both species.

The difference in hardness and colour of individuals of H. brevipalpis during the spring and summer (Tab. 1a) shows that specimens living in the water are younger than those living in the spring. This indicates a generation shift during June.

Spring and autumn samples of H. brevipalpis from the water are at best small (Tab. 1b). I have therefore pooled samples from 1964–66 and 1971 (Tab. 1b). Testing the total autumn value in Tab. 1b against the total summer value (Tab. 1a, 1966 + 1971) yields a statistically significant difference but just at the 5% level (t = 2.76, df = 106, p < 0.05). Spring and autumn populations did not differ significantly (Tab. 1b). Evidently the maturation of the integument is nearly complete at the end of summer. At this time all beetles seem to have emerged from their pupae. No newly emerged specimens (graded 1) occurred during autumn or spring.

It is obvious (Tab. 1c) that the integument of an H. brevipalpis individual need not be fully hardened to allow flight. Many specimens graded 1 occurred in the flight catches of summer.

Cuticle hardness of flying females differed significantly from that of non-flying females during the summer of 1971 (t = 2.94, df = 103, p < 0.005) but not in 1966 (t = 1.79, df = 119, p > 0.05). In males the difference is significant in both years (1966: t = 3.13, df = 124, p < 0.005; 1971: t = 3.62, df = 95, p < 0.001). It is therefore evident that during summer, the principal dispersal period of H. brevipalpis, flying beetles tend to be younger than non-flying ones.

With the exception of the females from spring 1971 (t = 2.72, df = 26, p < 0.025) the differences between flying and non-flying groups during the springs and autumns are not statistically significant. This is possibly so because the samples are so small. Pooled samples differ for females (t = 4.14, df = 48, p < 0.001), but not for males (t = 1.53, df = 20, p > 0.05).

Tab. 1d shows the values for H. strigifrons sampled in the water. Only occasional specimens occurred in the samples from summer and autumn; therefore, summer and autumn samples from all four years, 1964–66 and 1971, are pooled. Because the mean values did not differ significantly from each other, I pooled all material from summer and autumn and tested the resulting mean against the means of spring 1966 and 1971. They differed significantly (t = 6.07, df = 50, p < 0.001; t = 3.33, df = 215, p < 0.005 respectively) which indicates a generation shift between spring and summer.

When the ice melted in the spring 1971 the population consisted of many young, newly emerged beetles (graded 1). They matured and bred in about two months (Tabs 2, 5) and then died.

Twelve of the fourteen flight-trapped H. strigifrons specimens are from spring 1966 and 1971 and two from 28 June 1971. The beetles trapped in the spring of 1971 had a mean of 3.3, SD = 1.0, which does not differ significantly from the mean of the non-flying individuals of the same year. Neither do flying females or males tested separately differ from non-flying females or males or from each other. Therefore this index does not indicate any age differences between flying and non-flying H. strigifrons.

4.5. Sex ratio

In both H. brevipalpis and H. strigifrons the sex ratio does not usually differ significantly from 1:1. This is valid for the groups in the water and for those flying. In neither of the species does the ratio seem to differ between seasons or between flying and non-flying groups. I therefore conclude that the males and females of both species are equally disposed to flight.

4.6. Sexual development of females

The female reproductive organs in both species are very similar (Fig. 1). The number of ovarioles per ovary can vary from 2 to 6 between individuals but 4 is most common, and it is very rare that an individual has 2 or 6 ovarioles. Numbers may differ between the ovaries in a single female. However, this is not common, and the difference never seems to be greater than one. The number of developing oocytes is always the same as the number of ovarioles. Mature eggs with chorion are about 0.6–0.7 mm long in H. strigifrons and about 0.5 mm in H. brevipalpis.

Tab. 2. Variation in the cuticle hardness and colour of Helophorus strigifrons specimens from the water, spring 1971. See Sect. 3.4. concerning the index of hardness and colour. The figures are means of the index ± standard deviation. The numbers of beetles examined are given in parentheses.

|                | 31 Mar       | 4 Apr | 15 Apr       | 29 Apr       | 15 May       | 29–30 May    |
|----------------|--------------|-------|--------------|--------------|--------------|--------------|
| Females        | 2.0±1.2 (6)  | 2.3±1.4 (9) | 2.9±1.1 (21) | 3.5±0.7 (20) | 4±0 (20)*   | 4±0 (20)*    |
| Males          | 2.7±0.9 (9)  | 2.5±0 (5)** | 3.3±0.8 (20) | 3.4±0.6 (20) | 4±0 (20)*   | 4±0 (16)*    |
| Sum of males and females | 2.4±1.1 (15) | 2.4±1.2 (14) | 3.1±1.0 (41) | 3.4±0.7 (40) | 4±0 (40)*   | 4±0 (36)*    |

* All graded 4.
** All graded 2.5.
Tab. 3. Seasonal variation in oocyte size of Helophorus brevipalpis and H. strigifrons females collected in the water and H. brevipalpis females trapped flying. Materials from different years were pooled. N: numbers examined. N.v: numbers with visible oocytes (≥ 0.1 mm) including individuals with mature eggs. X: mean length in mm of oocytes in all females SD: standard deviation in mm.

Female H. brevipalpis in samples from water

|                | Apr-15 Jun 1965, 1966, 1971 | 16 Jun–31 Aug 1966, 1971 | 1 Sep–Nov 1964 |
|----------------|-----------------------------|------------------------|----------------|
| N              | 14                          | 47                     | 4              |
| N.v.           | 5                           | 0                      | 0              |
| X              | <0.1                        | 0                      | 0              |
| SD             | <0.1                        | 0                      | 0              |

Female H. brevipalpis trapped flying

|                | Apr-15 Jun 1965, 1966, 1971 | 16 Jun–31 Aug 1966, 1971 | 1 Sep–Nov 1966, 1971 |
|----------------|-------------------------------|--------------------------|----------------------|
| N              | 35                           | 179                      | 11                   |
| N.v.           | 29                           | 4                        | Not calculated       |
| X              | 0.23                         | Not calculated           |                      |
| SD             | 0.14                         | Not calculated           |                      |

Female H. strigifrons in samples from water

|                | 31 Mar–15 Jun 1971          | 16 Jun–31 Aug 1965, 1966, 1971 | 1 Sep–Nov 1964, 1965, 1966, 1971 |
|----------------|------------------------------|---------------------------------|---------------------------------|
| N              | 96                           | 5                               | 6                               |
| N.v.           | 82                           | 1                               | 2                               |
| X              | 0.37                         | Not calculated                   |                                |
| SD             | 0.24                         | Not calculated                   |                                |

Tab. 3 shows that H. brevipalpis only lays eggs during the spring. During the summer and autumn the females of the new generation do not usually have developing eggs.

In the spring, oocytes of flying females are larger than those of non-flying females (Tab. 3). This difference is significant in the pooled material (t = 4.66, df = 47, p < 0.001). It is also significant in 1971 (t = 2.95, df = 25, p < 0.01) and in 1965 (t = 2.48, df = 10, p > 0.05), but not in 1966.

Mating takes place mainly in the spring (Tab. 4). Only a few beetles, all of which were fliers, were mated in the summer. The frequency of mated beetles was larger in autumn than in summer (p < 0.001, Fisher’s exact test). Mating frequencies for flying and non-flying parts of the population do not seem to differ (Tab. 4).

H. strigifrons also lays eggs only during spring (Tab. 3); most newly emerged females probably do not start developing eggs until after hibernation. In the spring of 1971 most of the females were not ready to lay eggs until May (Tab. 5).

Of the 13 flight-trapped individuals from 1971 (Fig. 4), eight were females, one of which was trapped after the spring period. Four specimens, including the late individual, had visible oocytes, none had mature eggs. The mean oocyte size, measurements from the “lagger” included, was 0.18 mm, SD = 0.21 mm. This differs significantly from the mean oocyte size of the females from the water. Comparing a random sample of 65 females collected in the water 15 April–30 May 1971 (mean = 0.43 mm, SD = 0.21 mm) with the eight flight-trapped females gives t = 3.75, df = 71, p < 0.001. Thus, flying H. strigifrons females seem to have less developed oocytes than non-flying ones.

All 11 females collected from the water in the spring of 1966 had mated. In spring, 1971 90% (n = 96) had...
I found only 11 females, four of which had mated. This frequency differs significantly from the frequency of mated females from the spring of 1966 and 1971 (p < 0.001, Fisher's exact test). Spring is therefore the main mating season of *H. strigifrons*.

Five of the eight flight-trapped females of *H. strigifrons* had mated. There is no significant difference between this fact and the fact that 90% of the females from the water in 1971 had mated.

### 4.7. Sexual development of males

In the summer only small numbers of *H. brevipalpis* males have sperm, and the vast majority of them seem to disperse without having mated (Tab. 6), just as the females usually do (Tab. 4). During spring and autumn almost all males have mature sperm, and it was in these periods that most of the mated females occurred, too. There seems to be no difference between the frequency of males with sperm in flying and non-flying groups (Tab. 6).

In *H. strigifrons* 110 males, out of a total of 120 from the water, had sperm. All six males trapped flying had sperm. Accordingly, almost all males seem to be physiologically ready to mate, irrespective of season.

Tab. 6. Frequencies of *Helophorus brevipalpis* males with sperm in the vesicula seminalis. Specimens were collected in the water, or trapped flying, during different seasons. Samples from different years were pooled. The numbers represent the percent of males with sperm; numbers of males examined are given in parentheses.

| Samples from the water: | Apr–15 Jun 1965, 1966, 1971 | 16 Jun–31 Aug 1966, 1971 | 1 Sep–Nov 1964–66, 1971 |
|-------------------------|-----------------------------|--------------------------|-------------------------|
| Males in samples from the water: | 100 (9) | 10 (49) | 88 (8) |
| Males trapped flying: | 100 (12) | 8 (184) | 94 (17) |

4.8. Presence of food in the gut

In *H. brevipalpis* the sexes do not seem to differ in regards to the presence of food in the gut within any of the groups in Tab. 7. The difference between flying and non-flying groups in summer is strongly significant ($x^2 = 114.3, df = 1, p < 0.001$, pooled samples). I found no significant difference between flying and non-flying groups in spring and autumn.

Food was found in the gut of 90% of *H. strigifrons* individuals (N = 218) collected from the water in the spring of 1966 and 1971, and in 56% of the 21 individuals collected during the summer and autumn of the same years. This seasonal difference is significant ($x^2 = 11.89, df = 1, p < 0.001$). The sexes do not differ from each other.

Of the 12 flight-trapped individuals from the spring of 1971, only one female and one male had ingested food. This is significantly different from the frequency of food in the guts of specimens collected from the water.
ter from 15 April to 30 May 1971 (p < 0.001, Fisher's exact test, females and males pooled).

5. Discussion

Observations of flight in *H. brevipalpis* have been made in three different geographical areas: (a) southern England (Fernando 1958), (b) southern Sweden (Landin and Stark 1973), and (c) central Sweden (this paper). These environments are very different, but in all three areas *H. brevipalpis* migrates during the summer, often in very large numbers, and invades very many different types of waters.

In England the flight period lasts from the end of March until the latter part of August. In central Sweden flight starts when ice and snow disappear, i.e. between two to seven weeks later than in England. In England flight seems to end during the latter part of August, but in central Sweden small numbers of individuals of this species still fly in late September. I do not know the cause of this difference. In southern Sweden (on the Island of Öland) we only followed flight during short periods and therefore cannot determine the exact length of the flight period, but *H. brevipalpis* does fly in September there, too.

The small catches during autumn could give a false picture of how many beetles were flying. Dispersing individuals could fly away from water in search of hibernation sites, as pond-skaters, *Gerris* spp., do (Landin and Vepsäläinen 1977). However, I do not know of any observations of *H. brevipalpis* or *H. strigifrons* specimens hibernating away from water. On the Island of Öland direct observations indicated that flight is much less common during autumn than during summer.

*H. orientalis* Motschulsky, in North America, is ecologically similar to *H. brevipalpis* (Angus 1970). It also colonizes small, ephemeral waters (Fernando and Galbraith 1973). Its flight period lasts from the latter part of April until October or sometimes even the beginning of November. The largest numbers of fliers occur during June and July. The fact that the flight period for *H. orientalis* is much longer than that for *H. brevipalpis* is probably due to the differences in climate between Waterloo, Canada and the Swedish regions. The mean annual temperature in Montreal (near Waterloo) is 6.7°C, in Stockholm, it is 6.6°C. However, September and October are, on the average, 2–3°C warmer in Montreal. On Öland the mean annual temperature is 7.5°C, but September and October temperatures are still 1–2°C lower than in Montreal (Liljequist 1970, and unpublished data from the Swedish Meteorological and Hydrological Institute). November temperature is about the same in the three places. The temperature thresholds for flight in *H. brevipalpis* and *H. orientalis* are similar, and even the periodicity of their flight during the 24-hour period is similar (Fernando and Galbraith 1973).

In central Sweden both *H. brevipalpis* and *H. strigifrons* are univoltine. The generation shift occurs in June with the appearance of beetles with soft and light-brown integument and the disappearance of older individuals. Corresponding to the shift there is also a minimum in the numbers of flying *H. brevipalpis* specimens during late May and the first part of June, both in England (Fernando 1958) and in Sweden.

In England *H. brevipalpis* individuals emerge from pupae during the summer (Fernando 1958). They also emerge at that time in Sweden, but females do not develop eggs until the next spring. In England, females already lay eggs in November and December (Fernando 1958), but Angus (1973) did not find egg-cases in the field during winter and concluded that few beetles breed at that time. So the difference is small, and, as the species develops slowly, there cannot be more than one generation per year; when spring arrives the winter breeders are in reality spring breeders, only a month earlier (Angus pers. comm.). In Sweden the colder climate certainly does not allow breeding late in the year. However, as in England, a small part of the population seems to sexually active in autumn: most males have mature sperm and some females have mated.

There are large differences between the life histories of *H. brevipalpis* and *H. strigifrons*. Only small parts of the *H. strigifrons* populations emerge during summer and autumn. I believe that many individuals remain and hibernate in pupal chambers in shore soil and do not emerge until spring. In the beginning of spring there are large numbers of active specimens (Fig. 4 and Landin 1976a), many of which are newly emerged or young (Tab. 2) with soft, light-brown integuments.

The summer dispersal phase existing in *H. brevipalpis* is lacking in *H. strigifrons*. Both species fly during the spring, but only small parts of the *H. strigifrons* populations disperse by flight. This may be due, among other things to the fact that only about 20% of the specimens of *H. strigifrons* have a functioning flight apparatus.

To summarize, the different life histories of the two species are modifications of a common ground plan. *H. brevipalpis* has evolved an important dispersal phase during summer; large numbers of immature individuals emerge from pupae, migrate and leave their birth-places by flight during about one and a half months. *H. strigifrons* has not evolved such a phase; most of the specimens do not emerge until the next spring when it is time to breed. Consequently, the peak in abundance is shifted to spring.

The life history of *H. brevipalpis* on Öland probably is the same as at Sågsjön, as is indicated by more circumstantial observations (Landin and Stark 1973).

Angus (1973) classified *Helophorus* species into two groups according to their reproductive behaviour in the laboratory. Group 1 consisted of species who did not breed until four to six months after emergence. Group 2 started breeding two weeks after emergence. Two species were intermediate.
I think it may be concluded that group 1 species have an obligatory reproductive diapause, and those in group 2 do not. *H. strigifrons* belongs to group 1 (Angus 1973). Angus was unable to maintain a stock of *H. brevipalpis* in the laboratory. In England, in the field, *H. brevipalpis* needs at least three to four months after emergence before they are capable of producing eggs (Fernando 1958).

In the laboratory, newly emerged *H. orientalis* individuals start breeding after 10 d (Angus 1970). Consequently, this species lacks an obligatory diapause, which perhaps explains its second generation and the flight of gravid females during late summer and autumn (Fernando and Galbraith 1973). *H. brevipalpis* females are not gravid until after hibernation and therefore have longer time to disperse before reproducing. The species' migration is consequently neatly divided into two parts. Young specimens disperse before hibernation, and the few which survive until the breeding period in the spring (Fig. 3) fly as sexually mature individuals. This is the case on Öland, too (Landin and Stark 1973).

It may be questioned whether the flight of *H. strigifrons* actually is migratory; but see Kennedy (1975) and below. The young and immature individuals of *H. brevipalpis* flying in summer show a reproduction-flight syndrome (Johnson 1969). The large number of *H. orientalis* young flying during June and July (Fernando and Galbraith 1973) may likewise show this syndrome.

With one or two exceptions there are only small, and probably unimportant, differences between flying and non-flying *H. brevipalpis* groups in summer. Food was found in the guts of only 20% of the flying specimens but in 78% of non-fliers. Lack of food can induce flight (e.g. Dingle and Arora 1973, Solbrecq 1978), but adult water-beetles probably do not experience food shortage. They are sediment-surface-feeders (Cummins 1973) and are generalists in their food choice, eating plants and decomposing organic matter with its associated microflora and -fauna (Wesenberg-Lund 1943, Leech and Chandler 1956, Cummins 1973). Direct observations indicate that *H. brevipalpis* feed on the surface of and in the shore soil and in and on the sediment below the surface of the water (Landin unpubl.). Consequently, the lack of food in the guts of flying specimens should imply that they usually stop feeding when about to fly. This indicates that "locomotory" functions dominate over "vegetative", which is a characteristic of migrating insects (Kennedy 1961). This also seems to be the case during the spring, when 19% of the flying specimens and 43% of non-fliers were found to have ingested food.

The small difference in cuticle hardness and colour between fliers and non-fliers in the summer, indicates that fliers are a little younger. This is to be expected (Johnson 1969).

In the spring flying and non-flying groups also differed in the size of their oocytes and the occurrence of mature eggs. This indicates just the opposite of a reproduction flight syndrome, because it was, in this case, the flying females who had larger oocytes and mature eggs. Most of them had also mated. There are other exceptions to the general rule, and the syndrome is obviously labile (Johnson 1969, 1976).

*H. strigifrons* shows a more distinct reproduction flight syndrome. Although mated and gravid, the flying females have smaller oocytes than non-flying ones. Locomotory functions seem to dominate in fliers; only 17% of them had food in the gut, while nearly all individuals in the water had ingested food.

The spring and summer flights of *H. brevipalpis* may not serve the same functions. Both sexes migrate at the same time, and, as the large majority flying in the summer having not mated, it follows that the summer migrations throughly mix the populations and the gene pool. This is further promoted by the fact that, large numbers, after having invaded a body of water continue their migration (Fernando 1958). This is also true for *H. orientalis* (Fernando and Galbraith 1973). This reshuffling of the populations should make these species genetically and morphologically homogenous. However, the morphology of *H. brevipalpis* varies a great deal within the species (Angus pers. comm.).

The small numbers who survive until spring and then fly, usually have mated, and the females are gravid. Thus, they seem to be very effective colonizers (MacArthur and Wilson 1967). The summer fliers could perhaps be called "dispersers" and the spring fliers "colonizers", implying that the functions of their flights may differ.

It seems to me that the concept of a reproduction flight syndrome and the fact that a good colonizer should have a large reproductive value (Dingle 1972) might be interpreted as contradictory. This is because the syndrome emphasizes that migrants are immature. At the same time a maximal reproductive value and colonizing ability imply that migrating females should have eggs just about to mature and preferably have mated in order to utilize short-lived habitats. However, this contradiction is probably only apparent, as the function of migration may not only be to colonize but also to promote outbreeding. This may be more efficiently performed if migrants are immature. I think *H. brevipalpis* exemplifies a dichotomy in this case, summer fliers promoting outbreeding and spring fliers "the colonizing function". There is evidence concerning a bird, the Great Tit, that one function of dispersal is to reduce the possibility of inbreeding (Greenwood et al. 1978).

It is possible that many other water-beetles show such a dichotomy. Generally, in the Hydrophilidae, older, overwintered individuals fly in the spring and young ones during late summer and fall (Leech and Chandler 1956). However, the water beetle *Tropisternus ellipticus* LeConte behaves differently in some respects (Ryker 1975). At Lake Sågåsjön several species seem to follow the general pattern (Landin unpubl.), but *T. ellipticus*
young migrate in the spring, and older individuals in the fall (Ryker 1975). *H. brevipalpis* and *H. strigifrons* differing capabilities and tendencies for migration are to be expected when taking into consideration the differences in their habitats (Southwood 1962).

Gadgil (1971), on theoretical grounds, stated that a species’ environment which varies with time but in phase over the entire range of the species favours a low magnitude of dispersal. Individual littoral zones over large parts of northern Europe vary greatly throughout the year, but they do so simultaneously and in a predictable way along with the seasonal changes in precipitation, evaporation and other regularly varying factors. The low magnitude of dispersal for *H. strigifrons* is therefore to be expected.

In an environment which varies with time, but whose sites are out of phase with each other, an organism often gains by migrating. In this situation it should always be best to maintain a large magnitude of dispersal (Gadgil 1971). This is the situation that exists when a species inhabits many types of waters simultaneously (Price 1975), as does *H. brevipalpis*. Both ephemeral pools and lake littorals may change in a predictable way, but out of phase with each other due to the fact that the pools eventually completely disappear (cf. Landin 1976a). Consequently, *H. brevipalpis* constant large dispersal magnitude is to be expected.

Gadgil (1971) and others (refs. in Hamilton and May 1977) reached the same conclusion as Southwood (1962); thus, the idea that a positive relationship exists between habitat variability and migration has been arrived at in different ways.

Why does *H. strigifrons* not exploit small, temporary waters? Perhaps it utilizes littoral habitats more efficiently than *H. brevipalpis*. Adults of *H. strigifrons* are most numerous during the spring (Fig. 4) when the environment provides the most favourable conditions (strong insolation, high temperatures, plant remnants offering food and cover; Landin 1976a). *H. brevipalpis* adults are few in the spring and numerous in the summer (Fig. 3) when the littoral environment would be less favourable. Perhaps it avoids competition with *H. strigifrons*, and other water-beetles who are numerous as adults in the spring (Landin 1976a). *H. brevipalpis*, on the other hand, profits by exploiting ephemeral waters.

When reared in the laboratory at about 20°C *Helophorus* spp. usually need about five weeks to develop from egg to adult (Angus 1973). In their natural environment, in temperatures that are often lower, about two months may be a reasonable guess as to the time needed for development. Since the females lay their eggs above or just at the edge of the water, and the larvae are terrestrial (Fernando 1958, Angus 1973, superficially resembling carabid larvae) and pupate in the soil, the whole development takes place out of the water. If a female breeds in an ephemeral pond, that may well dry out, the site is still a suitable habitat for the young stages. In, for example, the steppe-like environment of Öland, large numbers should be capable of developing in ponds which have dried out. The bottoms of such ponds are often moist until late July. I think these large differences in habits and habitat between the young stages and the adult of *H. brevipalpis* along with its large dispersal power make this species the extremely efficient colonizer of ephemeral waters that it is. But this picture is a hypothesis, because the exact habitat of the larva is unknown (Landin 1976a).

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