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Assembly, mating, and energetics of *Hybomitra arpadi* (Diptera: Tabanidae) at Churchill, Manitoba.
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Abstract The mating system of *Hybomitra arpadi* was studied at a subarctic, treeline site near Churchill, Manitoba. Males aggregated in linear clearings on a hilltop in spruce-larch forest, hovering at a mean height of 13 ± 1.3 (SE) cm. Hovering occurred only on sunny days ($\geq 12°C$) for periods of up to 11 h. Males oriented parallel to the longitudinal axis of the aggregation site, independent of wind direction or solar azimuth. Few copulations were seen but there was a high frequency of aborted copulations involving nulliparous and parous, con- and heterospecific females. Males that intercepted females were morphometrically distinguishable from the remainder of the population on the basis of allometric relationships described by principal components. Aggregating males had highly variable quantities of carbohydrate in the crop, with early-hovering males tending to have the largest quantities; carbohydrate concentration was much less variable. Potential hovering durations estimated from crop energy varied from a few minutes to nearly 5 h, but no individual male had sufficient energy reserves to hover for the entire aggregation period on continuously sunny days. Hovering males maintained a mean thoracic temperature of $40.0°C$, as much as $23.5°$ above ambient. Thoracic temperatures were almost invariant across males and over a wide range of ambient temperatures, increasing only slightly with increasing ambient temperature.

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Introduction

The Tabanidae is a moderate-sized family of about 3000 species (Daniels 1989), occurring everywhere except in arctic locales. The females are well known as bloodsucking pests of large mammals, and as vectors of disease (Oldroyd 1964). The wide distribution and abundance, rich generic diversity (>100 genera), and stable and straightforward taxonomy, make tabanids excellent subjects for behavioral studies. Most studies of the family have dealt with aspects of the biology of the adult females, particularly geographical and seasonal distributions, host preferences, and disease transmission.

The adult males, as in all lower Diptera, feed only on carbohydrates (Downes 1958; Oldroyd 1964); because they are not bloodsucking, they are much less well known than the females. The mating strategies of fewer than 100 species are known (Wilkerson *et al.* 1985), mostly species from the temperate region. The family is characterized by lek-*like* (Taylor and Smith 1990) aggregations of males at species-specific sites and times, at which the males engage in a variety of activities as a prelude to mating, including intermittent or continuous hovering (Magnarelli 1985; Gaugler and Schutz 1989) or perching-and-pursuing (Taylor and Smith 1990).

Here we examine some features of the mating system of *Hybomitra arpadi* (Szilády), a moderate-sized member of the Holarctic *borealis* group (Chvála *et al.* 1972), a species of the northern forest and taiga, extending as far north as the tree line (Teskey 1990). In the north, it is one of the most common species and a serious pest (Miller 1951; Lutta and Bikova 1982). The study provided an opportunity to explore aspects of the mating behavior and biology of a tabanid at the northern limit of its range. The following features were examined: (1) behavior of males, including intra- and interspecific relationships with females and other aggregating males; (2) physiological state (energy and water stores) of males; (3) morphological correlates of mating success; and (4) thoracic temperature.

Materials and Methods

Study Site. Field research was carried out at Twin Lake Hill, south of Twin Lakes, Manitoba, Canada (UTM: 15VVQ532976; 58.62°N; 93.81°W), about 26 km southeast of Churchill and about 17 km south of the Hudson Bay coast. Twin Lake Hill is a tree-line site within the black-spruce larch forest community (Johnson 1987); from about 4 km north of the site to the Hudson Bay coast, the habitat is muskeg, bog and tundra. The Hudson Bay lowlands have low relief; Twin Lake Hill is a local, gentle promontory, about 35 m ASL. Studies were conducted from 19 July to 3 August 1988 and from 12–26 July 1989. Surveys for aggregating males were made on 11 of 14 days in 1988 and on 12 of 14 days in 1989. The 5 days on which observations were not made were days of cool and heavily overcast weather; experience with *Hy. arpadi* and related species of *Hybomitra* had shown that males will not aggregate under these conditions.

Times of local (i.e. CDT) sunrise and sunset and the temporal distributions of solar altitude and azimuth were computed by *The Floppy Almanac* (Carroll 1991). Corrections for local altitude, refraction and parallax were not made.

Dissection of Adult Flies. Male flies were stored in individually numbered 1.5-ml polypropylene micro-centrifuge tubes. Flies were placed on ice immediately after capture and dissected within 6–12 h of capture in a solution of physiological saline (Hagedorn *et al.* 1977) to which minute quantities of liquid detergent were added to facilitate wetting of hydrophobic surfaces. The abdomen was opened along the pleural membrane and the esophageal diverticulum ("crop") was removed by grasping its duct. The presence or absence of meconium in the gut was noted and the quantity of abdominal fat was assessed on an ordinal scale (rank 0 = emaciated; rank 3 = obese). Fresh (wet) weights of males and their crops were measured on a microbalance (accuracy ≈ ± 1 mg) (Unwin 1980). The crops were blotted on bibulous paper prior to weighing, to remove surface dissection fluids. It was assumed that the crop of *Hy. arpadi*, like that of mosquitoes (Denisova 1943), is impermeable to water and hence, no change in the weight or concentration of crop contents took place in the 1–2 min required to dissect the animal and extract and weigh the crop. Concentration of carbohydrates was assessed by collecting 0.2–0.5 µl of the crop contents into a 2-µl Microcap® (microcapillary tube) and diluting it with distilled water to fill the tube. The concentration of the resulting 2-µl solution was read in sucrose equivalents (°Brix: g sucrose per 100 g solution) on a Reichert model-10423 temperature-compensated refractometer. Concentrations of sucrose in °Brix were converted to molarity (Bolten *et al.* 1979) using a polynomial-regression model fitted to the conversion data in Table 88 of the *Handbook of Physics and Chemistry* (CRC 1978). Molar values were converted to energy equivalents using the heat of combustion of sucrose (16.49 J mg^{-1}). Errors associated with mixed-sugar compositions of the crop contents will be <6% — the heats of combustion of fructose and glucose are close to that of sucrose.

There are no data on the rates at which hovering male tabanids metabolize carbohydrates. Therefore, an estimate of the hovering time remaining to a male at the time he was captured was estimated in the following fashion. The respiration rate of males of *Eristalis* (Diptera: Syrphidae) is of the form:

$$\log(V_{O_2}) = 1.03 \times \log(\text{mass}_{\text{mg}}) - 1.30$$

and is independent of temperature over the range 12–30°C (C.P. Ellington, pers. comm.). *Eristalis* males are larger than males of *Hy. arpadi*, but the fresh-weight ranges overlap. The average male of *Hy. arpadi* weighed 93.5 mg ($n = 210$, CV = 0.10, range 72–118); using the *Eristalis* model, the mean respiration rate is predicted to be 5.4 ml O_2 h^{-1}. Ellington (1984) stated that about 20 J of chemical energy is needed for each ml of oxygen consumed. The predicted energy-consumption rate of a hovering male *Hy. arpadi* is therefore about 108 J h^{-1}. Given the error in this estimate, a value of 100 J h^{-1} was used; although this estimate is coarse, it was satisfactory for the examination of hypotheses relating to residence time of males at aggregation sites.

Female flies at aggregation sites, including those intercepted by a Malaise trap (set adjacent to aggregation sites used by males) or captured *in copula* with males, were examined for parity and insemination status (sperm-negative or -positive). Dissections were carried out as for males. Parity was assessed by noting the presence of dilatations on ovariolar stalks and/or the presence of yellow bodies; ovarian stages were scored according to the scheme in Watts and Smith (1978). Insemination was judged either by examining crushed spermathecae under phase-contrast microscopy at ×200 or by noting the lustrous blue color of sperm-positive spermathecae when viewed under a stereoscopic microscope (Tucker and Lancaster 1990). Apparently uninseminated females from male-female pairs were assiduously inspected for evidence of sperm in the reproductive tract.

Morphometry. Morphometric measurements of aggregating males (wing length, width and area; leg length; total and thoracic dry weights (less 1 wing and 1 foreleg used for linear and areal measurements)) were used in a correlation-matrix-based principal-components analysis to derive synthetic, orthogonal variables as morphological descriptors of males. The right wing and the right foreleg were removed with microsurgical scissors and mounted on transparent tape affixed to a glass slide. Wing length and width (Fig. 1) were measured with an ocular micrometer on a stereoscopic microscope at ×60. Leg length did not include the coxa but did include one of the (subequal) tarsal claws; individual leg segments were measured and the total length derived by summation. Wing areas were obtained by digitizing xerographic enlargements (×11.25) of the wings; to avoid allometric distortion, repeated enlargements were done in the same orientation, and included a 1×1-cm scale that was later used for calibration. Wing area was computed from the digitized perimeter of the wing, truncated basally by a line parallel to the longitudinal body axis and running through the base of the anal vein (Fig. 1); truncation permitted standardization of areal measurements regardless of the precision with which the wing was removed from the body. Weights were obtained of specimens dried to constant weight (≃ 7 h) in a Savant rotary vacuum drier; specimens were split into head, thorax, abdomen, wing (1) and legs (5) prior to drying.
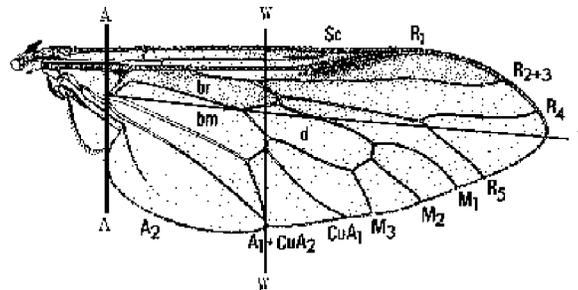

Fig. 1. Tabanid wing showing landmark vectors along which length (L) and width (W) were measured. The line A–A indicates where the wing was truncated for area measurement (after Pechuman and Teskey 1981).

Water content. Water content of flies was computed by the following equation:

$$\text{water content} = (\text{wet weight} - \text{crop weight} - \text{dry weight})$$

therefore estimating the water content of the tissues, and ignoring fluid present in the crop. The amount of body water as a proportion of body weight was computed as the ratio of water content to (wet weight – crop weight).

Thoracic temperature. Temperatures of aggregating males were measured by capturing hovering males with an insect net and rapidly inserting into the thorax an *Omega* model HYP-1 probe, a fast-response ($\simeq 0.2$ s) copper-constantan thermocouple, the sensory bead of which is embedded at the tip of a 30-gauge hypodermic needle (outside diameter 0.305 mm, length 15.1 mm). The probe was held by its insulated base to reduce heat transfer along the thermocouple wire. Temperatures were read by an *Omega* model HH-96T digital thermometer. The male was swept forcefully into the net and quickly immobilized in a fold; the insect was touched only momentarily and only through the net fabric, thereby avoiding heat transfer to or from the observer. In order to reduce errors attributable to post-flight cooling or warming, a 3-person team took temperatures, one worker sweeping, one manipulating the thermocouple, and the third timing the process with a digital stopwatch. Readings that required >7 s were discarded. Each time a thoracic temperature was taken, the ambient temperature at the same location was measured using a shaded hypodermic probe or a Taylor model-5351 thermistor. The thoracic temperature of a dead male *Hy. arpadi* was measured using the same apparatus used for aggregating flies. The impaled fly was exposed to the sun about 10 cm from the forest floor; temperatures were read frequently during 3 days of observations.

Observations of behavior. The low hovering height and the approachability of the aggregating males made special observational tools unnecessary; researchers could approach hovering males to within several cm, provided that the approach did not obstruct the animal's view of the overhead sky; such proximity made possible the real-time recording of hovering heights. In 1989, tape recorders were used to make near-continuous records of behavioral events (male-male interactions, male pursuits, copulations and other male-female encounters), the durations of which were timed with digital stopwatches.

The high speed and near-instantaneous acceleration that males could achieve in pursuit flights or in interactions with other males, and the rapidity with which some acts occurred, made it difficult to observe some behaviors. Although it was not possible to observe the details of pursuit flights, it was relatively easy to capture the resulting male-female pairs because of the tendency of the pair to remain relatively motionless for a few instants after contact had been made. It was not certain that all such pairs would proceed to copulation, so the term "encounter" has been used for a male-female pair resulting from a successful pursuit by a male.

Statistical analysis. Most parametric and multivariate analyses were carried out in *SYSTAT* (Wilkinson 1990); tests of outliers and eigenvalues in principal-components analysis were computed in *NTSYS* (Rohlf 1992). All hypotheses tested were 2-tailed. The maximal probability of a type-1 error in hypothesis testing was set at 0.05; probabilities of type-1 error are given as "P_α". For datasets involving disparate sample sizes, or in which there were violations of the assumptions of linear models (normality, homogeneity of variance, independence of residuals) results of parametric tests were confirmed by randomization tests (Simon and Bruce 1991), using a sample size of 5000, including the observed value; type-1-error probabilities resulting from randomization tests are given as "P_r". For hypotheses that were not rejected, probabilities of type-2 error were computed using *PASS* (Hintze 1991), with alternative hypotheses specified in terms of Cohen's (1988) definitions of "medium" and "large" effect sizes. The type-1-error rate for all power calculations was set at 0.05. Probabilities of type-2 error are given as "$P_{\beta m}$" and "$P_{\beta l}$" for medium and large effects, respectively. The maximal acceptable probability of type-2 error was set at 0.1; hypotheses that had type-2-error probabilities >0.1 for "large" effect sizes were regarded as uninformative and were not interpreted. Unless otherwise noted, error terms are standard errors.

Results

Mating Strategy. Males of *Hybomitra arpadi* aggregated in large numbers in both 1988 and 1989 at Twin Lake Hill. The 7.5-ha study site contained approximately 20 microsites (arenas) at which males aggregated. The aggregation strategy involved hovering, frequently pursuing other insects and then returning to hover; no perch-and-pursue behavior was observed.

Aggregation Sites. Aggregation sites used by male *Hy. arpadi* were small and linear, ranging from <1 to 2-3 m in width and from 2–3 to 5 m in length. Males aggregated without apparent regard to the plant species lining or covering the sites: arenas bordered spruce, birch or *Ledum*, or complex mosaics of these species, and flies were seen to hover over all ground-cover plants at the site. Some aggregation sites were simply bands or strips at the margins of shrubs or trees that abutted on more-open areas whereas other sites were narrow corridors within thick forest. Flies did not hover in open, relatively unstructured portions of the study site where distinct corridors or bands of vegetation were absent. Among all the sites the only features consistently apparent to us were that the sites were linear (longer than wide) and had a corresponding linear patch of sky overhead, the view of which was unobstructed by vegetation.

Aggregation and environmental conditions. Males were found hovering on 7 of 11 days in 1988 and 9 of 12 days in 1989. All days on which hovering was observed were days on which at least some sunshine occurred. Days on which hovering occurred for the longest time and on which males were present in large numbers were cloudless and of moderate temperature (>20°C).

The time at which hovering began is known precisely for 4 days (Table 1). There were insufficient data to test trends but it is clear that hovering began several hours after sunrise but not at the same time each day, and that early-morning cloud cover or low temperatures may have delayed its onset. The daily pattern of hovering activity on 6 representative days is shown in Fig. 2. When weather conditions permitted, males of *Hy. arpadi* aggregated for a substantial portion of the daylight hours (e.g. at least 11.3 h on 17 July). Dense stratus cloud cover interrupted or prevented hovering; heavy forest-fire smoke also may have inhibited activity. Low morning temperatures may have delayed the onset of swarming.

Table 1. Times of onset of hovering by males of *Hybomitra arpadi* and associated weather and solar conditions

Date (1989)	Time of onset		Sun position (deg)		Temperature (°C)	Sky conditions[a]
	CDT	h > sunrise	Elevation	Azimuth		
12 July	0857	4.52	30.95	98.5	17.7	Increasing stratus
13 July	0846	4.33	29.26	96.2	14.2	Clear
15 July	0930	4.98	34.70	106.4	12.4	Cirrus
21 July	1043	6.00	42.20	125.9	15.2	Smoke; stratus

[a] Stratus cloud and smoke from forest fires were low and sufficiently dense to reduce light intensity. Cirrus cloud was high and thin and did not noticeably affect light intensity.
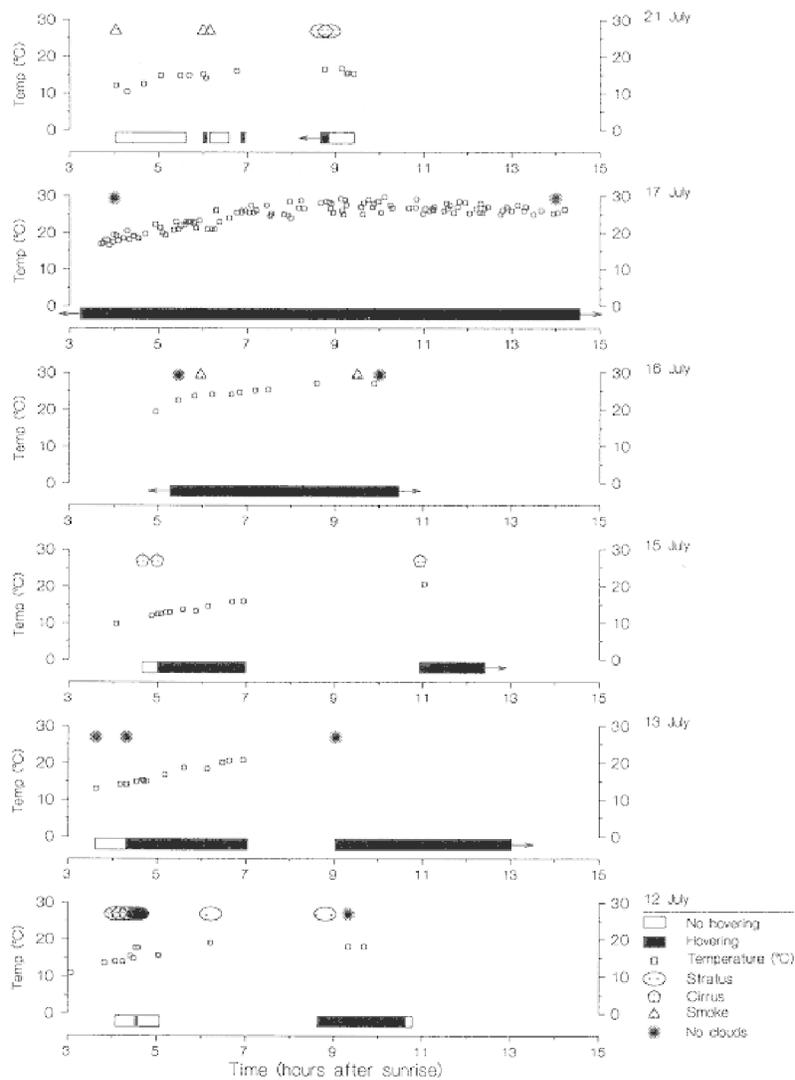
Fig. 2. Hovering times of male *Hybomitra arpadı* and weather conditions on 6 representative days in 1989. Terminal arrows indicate that times of onset and/or cessation of hovering are not known; gaps indicate no observations. Fill density in cloud and smoke symbols reflects density; a solid symbol represents complete cloud cover. Sky conditions over the time periods between identical symbols were unchanged.

Height and orientation of hovering males. Males of *Hy. arpadi* hovered close to the substrate (Fig. 3; $\bar{x} = 13.0 \pm 1.34$ cm; $n = 148$). The distribution of hovering height was right skew, owing to a few flies that hovered at heights >30 cm. In each case, these were individuals hovering over patches of *Ledum* or small birches; their mean height above the *Ledum* or birch stratum was indistinguishable from the mean height of flies over substrates such as *Empetrum*.
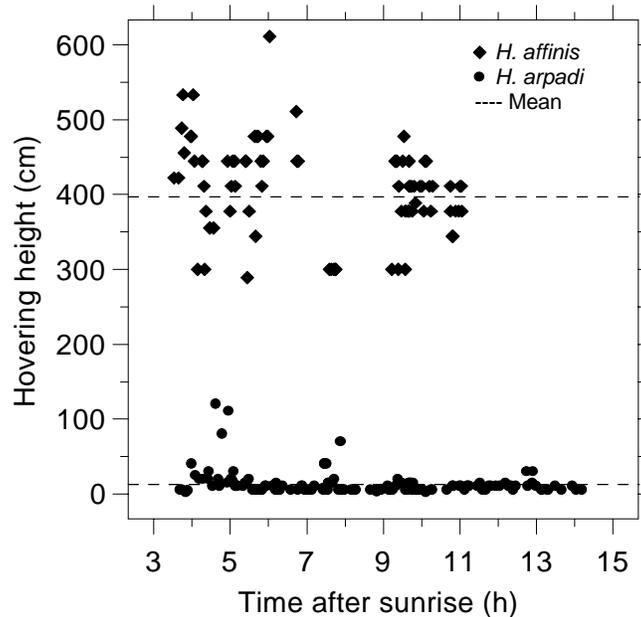

Fig. 3. Height above ground level of hovering males of *Hybomitra arpadi* and *Hy. affinis* at Twin Lake Hill throughout the aggregation periods.

Males of *Hy. arpadi* shared the Twin Lake Hill site with males of 3 other tabanid species, *Hy. affinis* (Kirby), *Hy. lurida* (Fallén) and *Hy. zonalis* (Kirby). The temporal overlap of hovering activity among the 4 species was extensive but there was a sharp division altitudinally and, in the case of *Hy. zonalis*, by microhabitat as well. The average male of *Hy. affinis* hovered nearly 4 m above the average male *Hy. arpadi* (Fig. 3). The sharp spatial segregation isolated the two species almost completely; interactions were rare. Males of *Hy. lurida* hovered at or above 6 m in forest-corridor aggregation sites used by males of *Hy. arpadi* and *Hy. affinis*; they did not occupy the vegetation-border arenas. The height at which the males of *Hy. lurida* hovered insured that they rarely came in contact with males of *Hy. arpadi*. Males of *Hy. zonalis* also hovered at or above 6 m but they did not occupy the same arenas used by males of *Hy. arpadi*. This species hovered in large (*ca.* 15–20 m), polygonal (i.e. non-linear) openings in the forest canopy.

Several hundred observations of hovering male *Hy. arpadi* showed that males invariably oriented to the longitudinal axis of the arena and not to wind (at least at the moderate levels observed), azimuth or elevation of the sun, or to conspicuous topographic features (e.g. large trees). We often saw males align themselves with the longitudinal axis of the arena and then abruptly alter their orientation by 180°; it was also common to see adjacent males facing in opposite directions. These observations provide strong evidence of the role of the topography and geometry of the arena in orientation.

Hovering. Males hovered, interrupting hovering only to pursue females or to interact with other con- and heterospecific males in the arena. At no time did we witness males adopting a "perch-and-pursue" strategy. Occasionally, males interrupted hovering to alight on the substrate or on vegetation bordering the arena. This behavior was most often associated with early-morning hovering at low temperatures. For example, at 0930 on 15 July 1989, at an ambient temperature of 12.4°C, a male *Hy. arpadi*, the first male observed hovering that day, hovered for 9 s and then landed on the substrate, where he remained, sometimes grooming, for 77 s, after which he resumed hovering. Instances of interrupted hovering at low ambient temperatures may represent cases in which males were encountering difficulty in maintaining adequate thoracic temperature (see below). Males sometimes ceased hovering even though weather conditions seemed permissive. For example, at 0945 on 21 July 1988, a male ceased hovering to rest on vegetation, even though it was warm (20°C), and, at 1537 on 15 July 1989, at 20.6°C, a hovering male landed on the substrate where it remained for 90 s, and then flew into the trees. These may be individuals that were nearly out of fuel (see below).

Males almost always hovered in the sun. Of 153 hovering males, 143 (93.5%) were in full sun, 4 in shade and 6 in dappled sunlight. Because the hovering arenas were situated in a complex forest mosaic, insolation of the arenas changed continuously throughout the day, and males dynamically altered hovering locations accordingly.

Intraspecific male-male interactions. An arena used by *Hy. arpadi* contained 1–7 males (Table 2). Males occupying the same arena sometimes hovered within 10–20 cm of each other (wider separations were common as well), often apparently "ignoring" one another. But because the arenas were small, the presence of more than one male in the same arena frequently led to persistent interactions between the resident males. These interactions were distinctively spiral in form, spatially constrained (diameter ≈ 15 cm), and readily distinguishable from the rapid, linear flights of males in pursuit of females, or of males in pursuit of a male pursuing a female. In cases in which the interacting pair were nearly at substrate level, the interaction was vertically restricted, leading to a series of circles rather than spirals. On arenas with more than 1 male, spiral interactions occurred frequently, at an average rate of about 1 per minute (Table 2). These spiral interactions were vigorous and rapid. They appeared to be the result of a male chasing another male, the pursued male becoming the pursuer, the original pursuer again pursuing, etc., the result being two males chasing each other in a compact swirl. Interactive spirals either drove the pair onto the substrate or to heights of 1 to 1.5 m, well above the usual hovering height (Fig. 3). On a few occasions a member of a pair left the arena following the interaction, so spiral interactions may rarely be agonistic rather than simply investigative.

Table 2. Number of male *Hybomitra arpadi* per arena during brief observation bouts on 16 July 1989 and the frequency of male-female encounters, male-male interactions (spirals) and pursuit flights by males

Time (CDT)	Duration of observations (min)	♂♂ in arena	♂–♀ encounters[a]	♂–♂ spirals[b]	♂ pursuits[c]	Comments
1008	5	3–7	1	6	15	
3012	5	2 or 3	—[d]	6	—	Usually 2 ♂♂
1017	5	4	—	—	31	Most by 1 ♂
1025	5	2–5	2	5	21	
1030	5	2 or 3	2	5	15	
1030	1	2	—	6	—	
1052	5	2	—	—	44	Most by 1 ♂
1057	0.5	2	—	4	—	1 ♂ departed
1100	5	5	4	—	23	
1111	5	1	—	—	23	
1120	5	5	4	6	15	
1201	5	5	5	5	>11	

[a] Instances of males capturing females. These pairs were not captured or observed following the male–female contact, so it is not known if these were true or aborted copulations.
[b] Interactions between two males of *H. arpadi*, involving spiral- or circle-shaped pursuits of one another.
[c] Instances of males pursuing females or other "likely" targets. Such pursuits were linear and up to several meters in length.
[d] Not enumerated.

Interactions with males of other tabanid species. Males of *Hy. affinis* exhibited the same type of spiral interactions as did males of *Hy. arpadi*. Commonly, these spirals were directed downward, taking the interacting pair of males much lower than the normal hovering height and occasionally even driving the pair to ground level, thereby intercepting the space used by hovering male *Hy. arpadi*. Spiral interactions involving male *Hy. affinis* and male *Hy. lurida* were also seen; these pairs often spiraled downward 6 m or more to the substrate. After breaking off the encounter, these males did not remain at substrate level and on only a few occasions, were hovering male *Hy. arpadi* seen to pursue or interact with males of these other species.

Male-female interactions. Judging by collections from a Malaise trap, females of *Hy. arpadi* and *Hy. affinis* were abundant at Twin Lake Hill (Table 3). Most females were already inseminated; only 6% ($^6/_{101}$; 95% confidence interval: 0.02–0.12) of the female *Hy. arpadi* and 9% ($^{10}/_{108}$; 95% confidence interval: 0.05–0.16) of the female *Hy. affinis* were uninseminated (Table 3). The inseminated females were probably intercepted during host-seeking flights — large numbers of host-seeking (presumably) females used the forest corridors as flyways, commonly flying at elevations of a meter or less. The uninseminated females were recently emerged (meconium present; abundant fat body; ovarian follicles <IIb) and may have been intercepted during mate-seeking flights. Clearly, males of *Hy. arpadi*, hovering low to the ground, might detect females of both species, most of which would have been already inseminated.

Table 3. Number of uninseminated and inseminated females of
Hybomitra arpadi and *Hy. affinis* intercepted by a Malaise trap

| Date (1989) | Time (CDT) | Inseminated? | | | | Total |
| | | *H. arpadi* | | *H. affinis* | | |
		No	Yes	No	Yes	
13 July	0830	0	5	0	5	10
	1035	0	5	0	5	10
	1130	0	3	0	5	8
	1330	1	8	3	8	20
	1448	1	3	1	1	6
	1550	0	6	1	2	9
	1647	0	0	0	6	6
15 July	1050	0	2	0	3	5
	1130	3	28	1	30	62
	1525	1	26	1	28	56
	1700	0	9	3	5	17

Male *Hy. arpadi* were frequently seen pursuing and capturing female tabanids. Pursuit flights were exceedingly common (Table 2) and involved linear flights of several meters. On "good" swarming days when males were active and large numbers of targets were moving through the arenas, individual males engaged in 5–7 pursuits per minute (Table 2). Commonly, pursuing males were themselves pursued by other males on the arena so that a single male initiating a pursuit could cause a radical but temporary shift in the activity within an arena. Many pursuits were unsuccessful and males usually returned to the arena to resume hovering, often at almost the same point from which the pursuit was initiated.

Often, however, pursuit flights were successful, and males captured females. On days on which considerable hovering activity was occurring, scores of such male-female interactions were seen. For example, on 13 July 1989, observers recorded at least 40 male-female encounters and on 15 July, 85 encounters. Encounters were detected throughout the entire aggregation period. We observed both encounters that progressed to copulations and encounters that were aborted soon after contact was made.

On only 2 occasions (1030 CDT on 15 July 1989 and 1053 CDT on 16 July 1989) were male-female encounters known to be true copulations. Interception of the female in flight was accompanied by a loud, distinctive "buzzing" sound, during which the pair hung almost motionless in space for a few seconds. Following the initial pursuit and contact, one pair flew upward to nearby vegetation, one member of the pair flying and the other suspended below, not flying. The pair alighted, continued to copulate, and were captured after 20 s. The second pair, uncharacteristically for *Hybomitra*, dropped to the forest floor where they were netted. Copulation continued in the net and lasted for 4.8 min, so, including the time required by the male to intercept and capture the female and the time required to net the pair and transfer the net to another observer, the copulation lasted about 5.5 min. Both females were recently emerged (nulliparous; fat-body rank 3; immature terminal ovarian follicles (stage Ib–IIa); considerable meconium).

A very high proportion (estimated >95%) of the approximately 200 male-female encounters that were witnessed were aborted; the pair would unite in flight as in a normal copulation, a behavior that was marked by the same buzzing sound and the apparent suspension of the pair in mid-air for a few moments, features that are characteristic of true copulation in *Hybomitra*. However, in most of the pair formations witnessed in the field, the pair separated quickly; on average, an aborted male-female encounter lasted only 2.2 s (SEM = 1.45, $n = 49$; Fig. 4).
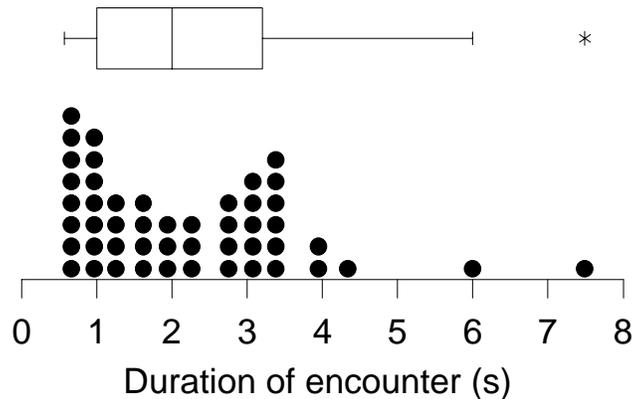
Fig. 4. Frequency of occurrence (dit plot) and Box plot of the duration of aborted male-female encounters in *Hybomitra arpadi*.
<redrawn in SYSTAT 8; not exactly as published>

In addition to the 2 pairs known to have been copulating, 39 male-female pairs (Table 4) were captured within a couple of seconds of detection. *Hy. arpadi* males intercepted both *Hy. arpadi* and *Hy. affinis* females, 74% of which ($^{23}/_{31}$; confidence interval: 55–88%) were already inseminated and 15% of which ($^{2}/_{13}$; 95% confidence interval: 2–45%) were parous (Table 4). (Although host-seeking *Hy. lurida* were abundant and the arenas were used (at about 6-m elevation) by hovering male *Hy. lurida*, none of the encounters involved that species.) The instances (8 of 31 — 26%; 95% confidence interval: 12–45%) in which the female was known to be uninseminated included 2 females of *Hy. arpadi*. It is conceivable that these were true copulations that were interrupted by the capture of the pair. Alternatively, a female may have rejected a male even if she were uninseminated, as might be expected to occur if a male *Hy. arpadi* captured an uninseminated female *Hy. affinis* (4 instances) (Table 4). However, in one encounter involving a male *Hy. arpadi* and a recently emerged (stage-IIa follicles; meconium) uninseminated female *Hy. affinis*, the pair flew to nearby vegetation, a behavior that is characteristic of copulation.

Table 4. Species, parity, and insemination status of females
involved in encounters with male *Hybomitra arpadi*

	Parity status						
	Nulliparous		Parous		Unknown[a]		
	Inseminated?		Inseminated?		Inseminated?		
Species	No	Yes	No	Yes	No	Yes	Unknown[b]
H. arpadi	1	4	0	2	1	5	6
H. affinis	3	3	0	0	1	6	2
Hybrid?	0	0	0	0	2	3	0

[a] Not scored for parity.
[b] Not scored for insemination.

Morphometrics. After listwise deletion of cases with missing values on the 6 morphometric variables (fly dry weight; thorax dry weight; wing length, width and area and leg length) and elimination of 2 obvious outliers, 185 cases were available for analysis. 90% of the variance of the 6 variables was explained by the first 3 principal components (70.8, 10.5 and 8.7%, respectively). As for most morphometric analyses, the first principal component reflected a general size component; all 6 original variables loaded heavily and coequally on this component (Fig. 5). The second component measured overall shape, contrasting wing variables with general- and thoracic-size variables, as did the third component, contrasting weight and wing dimensions with leg length (Fig. 5).
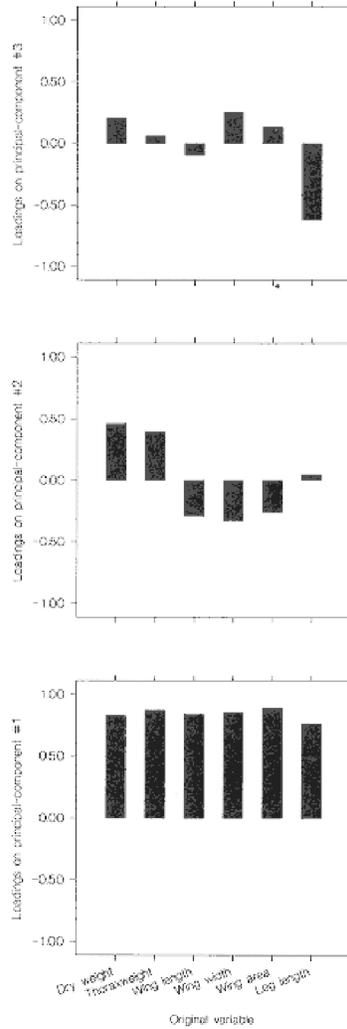
Fig. 5. Loadings of the first 3 principal components on the original 6 morphometric variables.

Males that successfully intercepted females ($n = 27$) were significantly different morphologically from other males ($n = 158$) at the arenas (MANOVA; $F_{3,181} = 4.19$, $P_{\alpha} = 0.007$), a difference that was due almost entirely to differences measured by the third component (PC_1: $F_{1,183} = 2.39$, $P_{\alpha} = 0.12$; PC_2: $F_{1,183} = 0.36$, $P_{\alpha} = 0.55$; $P_{\beta l} = 0.0003$; PC_3: $F_{1,183} = 9.66$, $P_{\alpha} = 0.002$); with only a few exceptions, males that successfully captured females occupied a subset of the ordination space (Fig. 6). In 6 univariate analyses, males that captured females were *statistically* indistinguishable from the rest of the males ($P \geq 0.09$) but, reflecting the difference detectable on the third principal component, males that captured females had shorter legs, were heavier and had larger wing areas than did the remainder of the population.
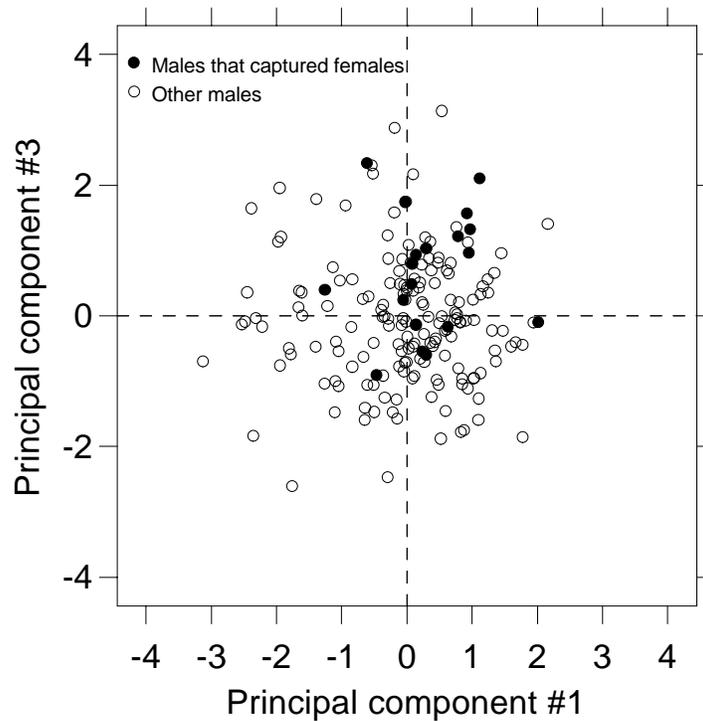
Fig. 6. Ordination of hovering males of *Hybomitra arpadi* in the shape-size space defined by principal-component axes 3 and 1.

Energy stores in the crop. The crop of every male examined contained at least a small amount of fluid; if the contents were ≥1 mg, the concentration and energy of the crop contents were assessed. On average, the crop contained 6.0 ± 0.36 mg of sugary solution ($n = 182$; range 0.25 (estimated) to 24.0), comprising about 7% (± 0.56) of the wet weight of a male; the proportion was as low as 0.005 in some males and as high as 0.21 in others (Fig. 7). The relatively largest crops were found in males hovering early in the hovering period (Fig. 7) and there was a tendency for relative crop weights to decline through the swarming period. The decline was slight, however, and the variance of relative crop weight was high (CV = 0.70) at all times (Fig. 7).
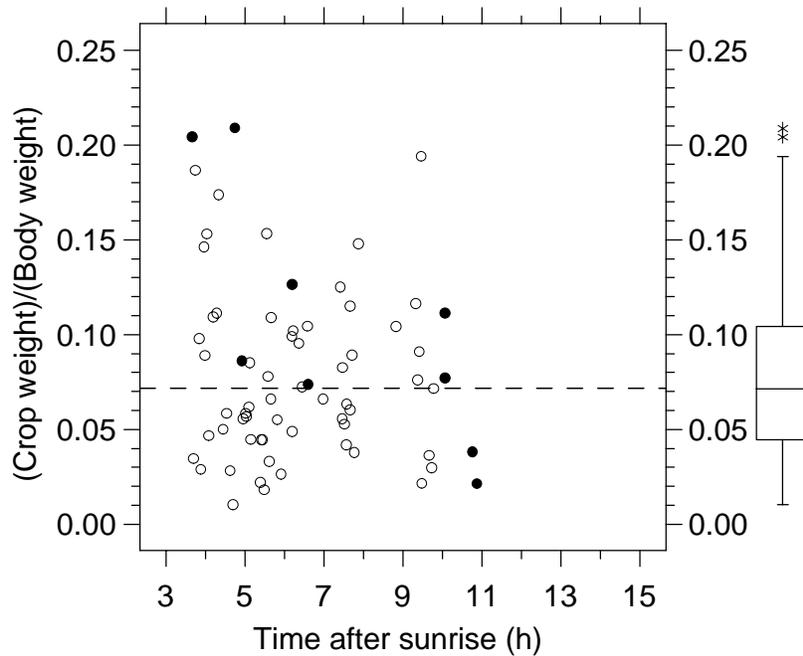
Fig. 7. Crop size relative to total wet weight of male *Hybomitra arpadi* throughout the hovering period. The dotted line is the arithmetic mean. Solid symbols are males that had captured females.

The crop contents were usually colorless and of high viscosity; the mean concentration, assuming the contents contained only sucrose, was 970 ± 21 g l^{-1} ($n = 162$; range 73–1460) (an average molarity of 2.8 and an average °Brix reading of $\simeq 71\%$). The variance of the concentration of the crop contents was low (CV $= 0.28$) and there was a weak tendency for the concentration to increase during the hovering period ($r = 0.155$, $n = 161$, $P = 0.05$; Fig. 8). The concentration of the crop contents was independent of crop weight ($r = 0.025$, $n = 161$, $P_\alpha = 0.76$, $P_{\beta m} = 0.026$) and unrelated to any of the 3 principal components used to measure the size and shape of males ($n = 150$; PC$_1$: $r = 0.147$; PC$_2$: $r = 0.047$; PC$_3$: $r = 0.120$; Bonferroni-adjusted type-1-error probabilities: 0.44, 1.00 and 0.87, respectively; $P_{\beta m} = 0.036$).
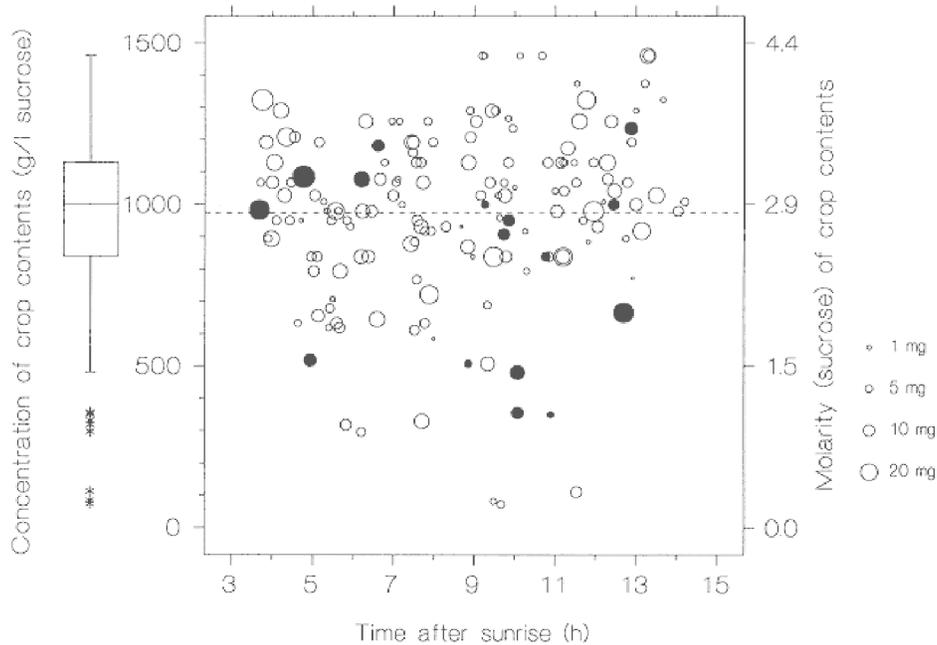
Fig. 8. Concentration of crop contents of male *Hybomitra arpadi* throughout the hovering period. Plotting-symbol area is proportional to crop weight. Filled symbols are males that had captured females.

Male *Hy. arpadi* that had captured females had significantly less-concentrated crop contents ($\bar{x} = 810 \pm 70$ g l^{-1}) than did the remaining population of males in the arenas ($\bar{x} = 990 \pm 22$ g l^{-1}) ($t_{160} = 2.64$, $P_\alpha = 0.009$; $P_r = 0.012$). The sample sizes, however, were highly disparate (17 and 145, respectively) and this difference did not look convincing graphically (Fig. 8).

Although the variability of the concentration of the crop contents was low, the high variability of crop volumes determined that there was a correspondingly high variability (CV = 0.83) of the energy reserves available to males during the hovering period (Fig. 9). The energy content of the crop was independent of time ($n = 160$, $r = 0.061$, $P_\alpha = 0.44$, $P_{\beta m} = 0.027$) and the size or shape of the males ($n = 148$, PC$_1$: $r = 0.124$; PC$_2$: $r = -0.012$; PC$_3$: $r = 0.155$; Bonferroni-adjusted type-1-error probabilities: 0.80, 1.00, and 0.36, respectively; $P_{\beta m} = 0.04$).

Male *Hy. arpadi* that had captured females may have had slightly heavier crops ($\bar{x} = 8.1 \pm 1.53$ mg, $n = 19$) than did the remaining population of males ($\bar{x} = 5.8 \pm 0.35$ mg, $n = 163$) ($t_{180} = 2.023$, $P_\alpha = 0.045$, $P_r = 0.045$, $P_{\beta m} = 0.003$) (Fig. 7). However, the energy content of the crops did not differ between males that had captured females ($\bar{x} = 128 \pm 28$ J, $n = 17$) and the remaining population of males ($\bar{x} = 100 \pm 6.8$ J, $n = 144$) ($t_{159} = 1.33$, $P_a = 0.186$, $P_r = 0.019$, $P_{\beta m} = 0.007$) (Fig. 9).
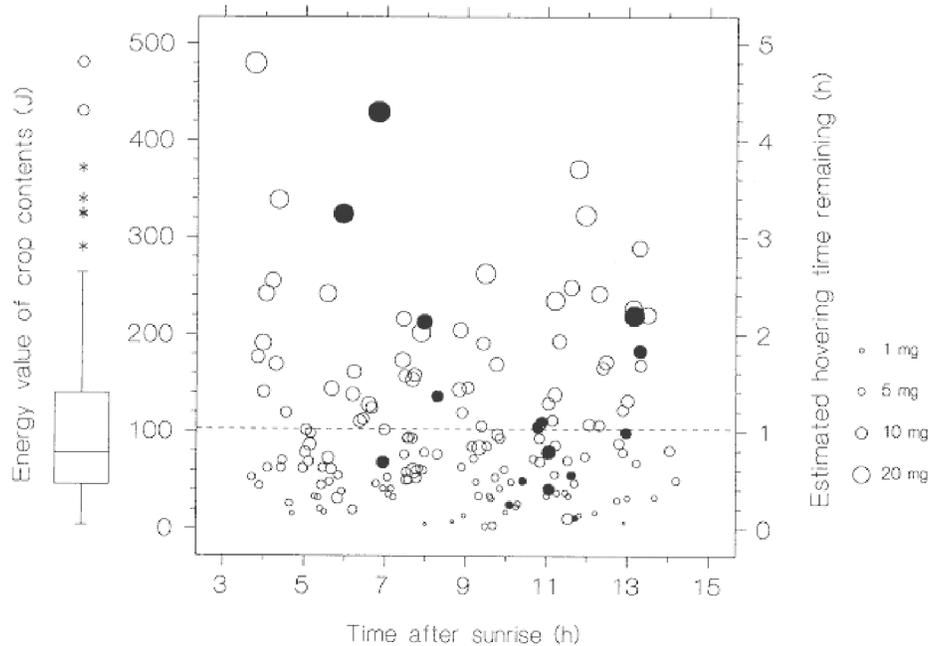
Fig. 9. Energy value of crop contents and estimated remaining hovering time of male *Hybomitra arpadi* throughout the hovering period. Plotting-symbol area is proportional to crop weight. Filled symbols are males that had captured females.

The estimated hovering time remaining to captured males based on the energy content of the crop was highly variable at all times during the aggregation period, and particularly near the times of onset and cessation of hovering (Fig. 9). Irrespective of the magnitude of the error in these estimates, it is clear that many males, including males hovering at the onset of the hovering period, had only very restricted flight times available, and it seems likely that no male had sufficient reserves to permit him to hover for the duration of the longest hovering period recorded (11.3 h).

Fat. The fat-body content of hovering males was ranked for males collected on 2 d in 1989. Fat was readily detectable in all males but most males were slim (rank 1), with only thin, translucent sheets of fat on the abdominal body wall and small quantities of omental fat. No males were devoid of fat (rank 0) and no males had fat stores that would be expected in recently emerged flies (rank 3).

Water. An average male *Hy. arpadi* weighing 93.5 ± 0.10 mg ($n = 88$, range 72–118) contained 61.2 ± 0.74 mg of water, so that on average, water constituted about 70% of the body weight, excluding the crop (Fig. 10). The proportion of the body comprised of water was remarkably invariant (CV = 0.024) but did show a small decline with time (Fig. 10; $n = 74$; $r = -0.246$, $P_a = 0.04$), a decline that should be interpreted cautiously, given the temporal distribution of the data.
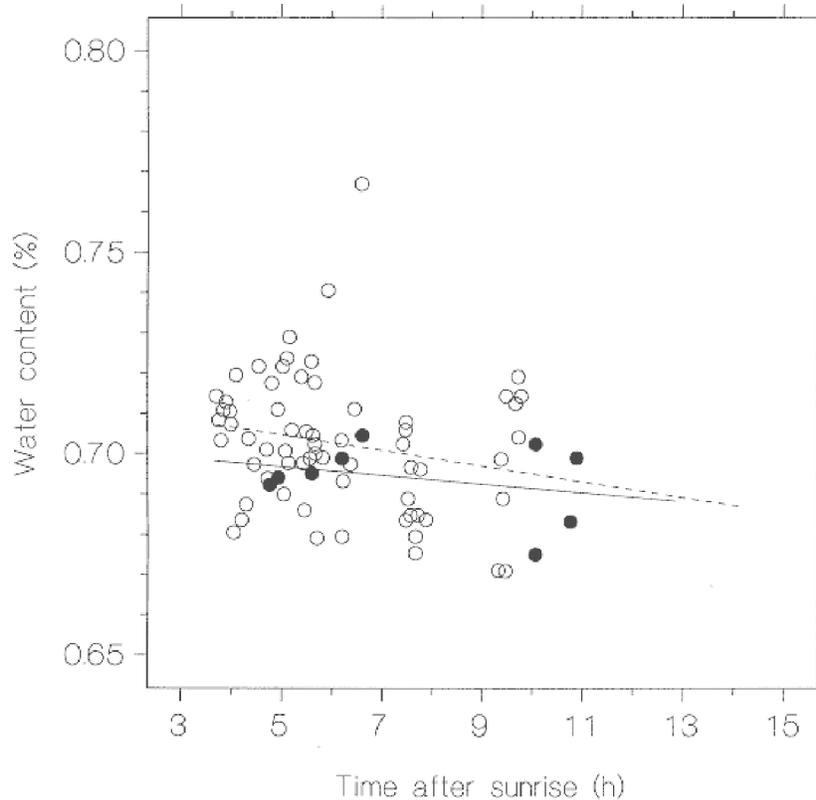
Fig. 10. Water as a proportion of wet weight (excluding the crop) in males of *Hy. arpadi* throughout the hovering period. FIlled symbols and solid line are for males that had captured females.

Males that had captured females had significantly lower water reserves than did the remaining population of males on the arenas ($F_{1,74} = 5.02$, $P_\alpha = 0.03$; this hypothesis was tested using an arcsine-transformation of the proportion-of-water data; water content could not be tested directly in an ANCOVA using wet weight as a covariate because the regressions for *in-copula* and other males were not parallel (Fig. 10; $F_{1,73} = 63.0$, $P_\alpha \ll 0.0001$)).

Thoracic temperature. The thoracic temperature of hovering male *Hy. arpadi* was $40.0 \pm 0.1°C$ ($n = 108$; range 37.5–42.3) (Fig. 11) and almost invariant (CV = 0.025) over a wide range of ambient temperatures (Fig. 11). What little variance there was in thoracic temperatures of male flies was probably not attributable to the time required to obtain a reading (Fig. 11) ($r = 0.083$, $n = 55$, $P_\alpha = 0.55$, $P_{\beta l} = 0.02$). Thoracic temperatures were as much as 23.5° above ambient temperature during the early part of the hovering period, and at no time were they <10.2° above ambient. Males maintained steady thoracic temperatures during the morning period when ambient temperatures were rising rapidly, during mid-day when ambient temperatures were constant, and during the last part of the swarming period when ambient temperatures began to fall (Fig. 11). The thoracic temperature of hovering male *Hy. arpadi* was almost independent of ambient temperature (slope = 0.11 ± 0.028; 95% CL: 0.05–0.16). The low rate at which thoracic temperature increased with increasing ambient temperature was highly significantly <1 ($t_{105} = 31.95$, $P \ll 0.0001$), indicating impressive thermoregulation.
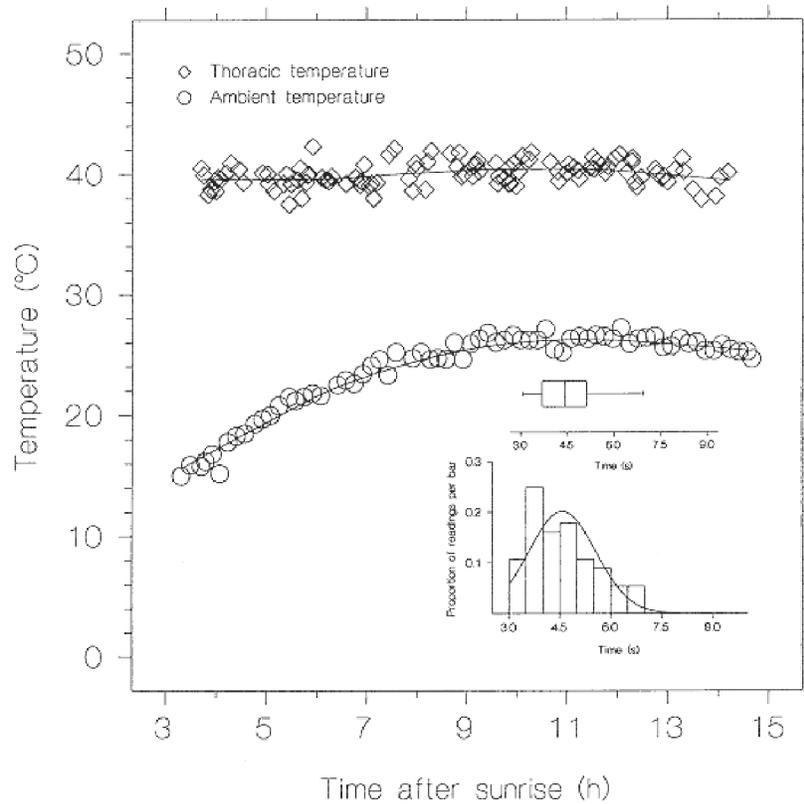
Fig. 11. Thoracic temperature of hovering male *Hy. arpadi* and ambient temperature. The fitted lines are locally weighted regressions. The insets illustrate the time required to obtain thoracic-temperature readings ($\bar{x} = 4.6 \pm 0.13$).

The thoracic temperature of a dead male *Hy. arpadi* exposed to the sun rose slightly more rapidly than ambient temperature, attaining a temperature similar to that of hovering males only after about 5 h of exposure (Fig. 12). The thoracic temperature of a dead male rose rapidly in the morning, as soon as the fly was illuminated by the sun; similarly, the thoracic temperature dropped precipitously, approaching ambient temperature, if the fly were shaded even briefly (Fig. 12). The sharp decline in the thoracic temperature after hour 13 (17:40 CDT) was associated with the sun reaching an elevation of about 30° and disappearing behind the spruce on the western edge of the site where the male was exposed.
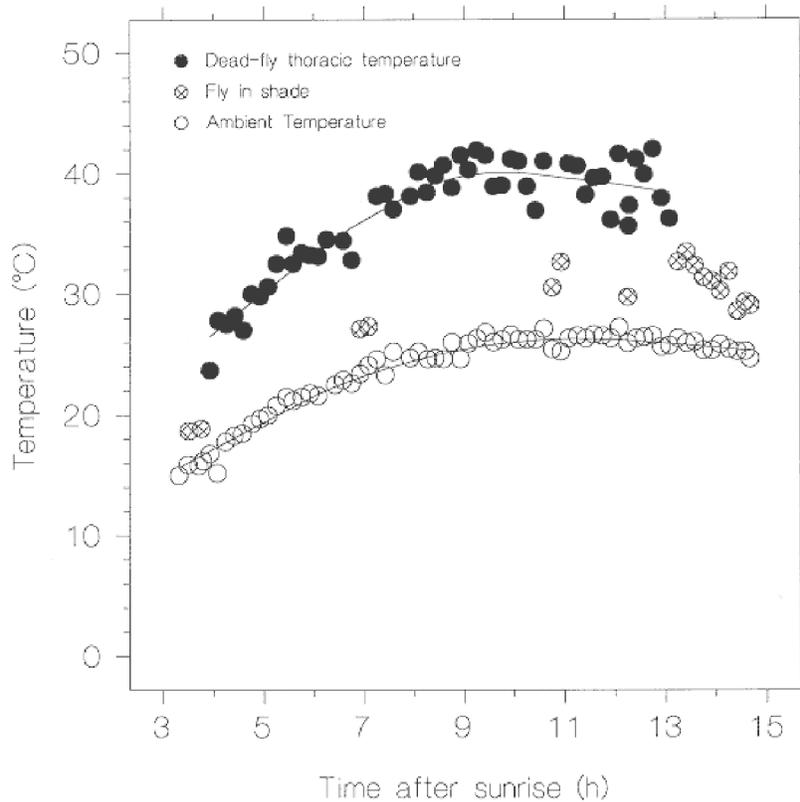
Fig. 12. Thoracic temperature of a dead male *Hy. arpadi* kept in the sun (for the most part) and simultaneous ambient temperature. The fitted lines are locally weighted regressions.

Discussion

The mating system. The mating system of *Hy. arpadi* is similar to that of many species of tabanids: males aggregate at a species-specific site and time, hover, and pursue and capture likely targets that traverse the arena (Wilkerson *et al.* 1985). However, in several interesting respects, the mating system of *Hy. arpadi* is unusual: hovering takes place (weather permitting) over an exceptionally long period of time; there is a high frequency of aborted copulations (mate refusal); the pattern of energy availability shows high variance at all times during the aggregation period; the thoracic temperature of hovering males is high and exhibits exceptionally low variance.

In some ways, the *Hy. arpadi* mating system *resembles* lekking in vertebrates, but the tabanid aggregation is not a lek. Although males of *Hy. arpadi* "kept station" while hovering and often returned to the same hovering spot following a pursuit, it is not clear that they defended territories within the aggregation sites. Many authors (e.g. Cookson 1967; Auroi 1986; Teskey *et al.* 1987) have concluded that hovering male tabanids defend territories, but there is little evidence that the behaviors exhibited by males are agonistic. Parsimoniously, the spiral interactions that are so common in *Hy. arpadi* and males of other Diptera (Wehrhahn 1985) and other insects (Rutowski and Alcock 1989; Cordero and Soberon 1990) are readily derived from the tracking system used by males to pursue females. As well, there is no evidence in tabanids of male display or female choice. However, Taylor and Smith (1990) speculated that the pursuit flight, involving as it often does, several males, may itself be a display. Whether a pursued female *Hy. arpadi* can choose among pursuing males is unknown, but the many observations of aborted copulation attempts observed in this study suggest that females may be capable of rejecting suitors. Males of *Hy. arpadi* that captured females were morphometrically and possibly physiologically distinct from the remaining population of males, providing at least some of the elements of a female-choice system.

The adult males of many insects, particularly Hymenoptera, Lepidoptera and Diptera, often aggregate on hilltops, which serve as mating sites for species that are rare or widely dispersed (Alcock 1987); the behavior is known in a number of Tabanidae (Chapman 1954; Cookson 1967; Leprince *et al.* 1983). Twin Lake Hill, where the present studies of *Hy. arpadi* were conducted, may constitute a hilltop. Although relief in the Churchill lowlands is slight, some insects are known to respond to very minor topographic features (Baughman and Murphy 1988). Twin Lake Hill, only 10–20 m above the surrounding terrain, was the most prominent elevation for many kilometers. Although *systematic* surveys of other potential aggregation sites were not made, forested sites to the north and south of Twin Lake Hill were visited several times per day; males of *Hy. arpadi* were not encountered at other sites. Even slight topographic features may be important in the biology of *Hy. arpadi*, a species that, although not rare, is exceptionally widely dispersed and in which the problems of the sexes encountering one another may be exacerbated by a brief flight season in subarctic locales such as Churchill.

Mating. Although many male-female encounters were seen, only two copulations were observed. In each case, copulation required several minutes, in agreement with the pattern observed in other tabanids. For example, Lavigne *et al.* (1968) reported a mean copulation time of 5.9 min (range 3.5–14.5) for 16 specimens of *Tabanus reinwardtii* Wiedemann, and Taylor and Smith (1990) observed *Hy. illota* (Osten Sacken) copulating for 2–5 minutes ($n = 24$). In some species, copulation times may be much longer: Gaugler and Schutz (1989) found the mean copulation time of 5 pairs of *Ta. nigrovittatus* Macquart to be 22.6 min (range 16–30). It is unlikely, therefore, that the many brief male-female encounters observed in *Hy. arpadi* were true copulations.

There are a number of hypotheses that could explain the small numbers of copulations seen: most mating occurred prior to the time when observations began; mating was taking place at sites other than aggregation sites; females are monogamous and refuse mates after they have been inseminated. Of these hypotheses, the last seems most plausible. If, as is generally believed, female tabanids do indeed mate only once, then their reproductive success will be proportional to the time spent seeking the resources needed for egg development and oviposition while minimizing the time needed for mating (Wiklund 1982); inseminated females should aggressively reject advances by males.

The high frequency of aborted copulation attempts seen in this study supports the view that female tabanids mate only once — certainly, most of the encounter pairs examined in this study involved already inseminated females. There are only two other observations of apparent mate refusal in the tabanid literature and, in both cases, the authors probably misinterpreted the observations as copulations. Miller (1951) observed encounters of *Hy. arpadi* at Churchill: "Mating took place on the wing over water in open woods. The individuals remained *in copula* for about five seconds while flying over the water from a low to a considerable height. They then parted and flew off separately." The CNC contains 3 pairs of tabanids collected at Churchill by Miller (12 July 1948; 13 and 19 July 1950). The males are *Hy. arpadi*; 2 of the females are definitely *Hy. arpadi* and the third is possibly *Hy. arpadi*. The significance of the "over water" observation is unclear, but otherwise the behavior described by Miller (1951) is identical to the behavior of *Hy. arpadi* pairs involved in aborted copulations. Teskey *et al.* (1987) observed what they thought was copulation in *Hy. agora* Teskey: "When flying females of *Hy. agora* entered the space above the hovering males, the male darted swiftly to the female grasping it and producing a very characteristic buzzing sound. The pair then flew upwards for about 3–4 m and separated after about 1 s of contact." It is noteworthy that in *Hy. arpadi* and *Hy. agora*, males hover close to the ground and continue to hover late in the day, in contrast to the pattern observed in many other species of tabanids in which the mating behaviors are known (Wilkerson *et al.* 1985). If males hover late in the day and if females host seek in the same habitats used by males, then temporal and spatial overlap of hovering males and inseminated host-seeking females is expected. For most other tabanids in which the mating system involves early-morning hovering, mating activity is probably either finished or at a low level when female host-seeking activity begins.

Males of *Hy. arpadi* not infrequently pursued and captured female *Hy. affinis* (Table 4). At least one of these encounters proceeded to what appeared to be a copulation, suggesting the possibility of hybrids between the two species. Certainly one encounters some females that cannot readily be assigned to one or other of these two species (Table 4).

Orientation of males and pursuit of females. Many authors have interpreted the orientation of hovering tabanids as a response to wind (Wilkerson *et al.* 1985). That hypothesis is strongly contradicted by observations of *Hy. arpadi*, the males of which invariably oriented to the longitudinal axis of the aggregation site. In the present study, however, wind speeds were always low to moderate in the forested aggregation sites used by *Hy. arpadi*; perhaps males respond to wind only when wind speeds are high. Taylor and Smith (1990) discussed the role of linear sky patches in the aggregation behavior of *Hy. illota* and speculated that the males oriented themselves in response to the direction of the sky patch in order to maximize their ability to detect and track females. The importance of skylight in male aggregation is affirmed by the common observation in this and other (Wilkerson *et al.* 1985) studies of the failure of tabanids to hover under overcast conditions. Resolution of the relative importance and mode of action of the environmental variables that are involved in the orientation responses of male tabanids will require experimental manipulation of features of the aggregation sites.

The eyes of male tabanids, in common with many male Diptera, are remarkably specialized for high-speed tracking and maneuvering (Land 1985); indeed, the male eye is uniquely specialized for that function in families such as the Tabanidae. In addition, the tabanid eye is sensitive to the plane of polarization of sky light (Smith and Butler 1991); such sensitivity may be important in male pursuit behavior.

The aggregation sites used by male *Hy. arpadi* were contemporaneously occupied by males of *Hy. affinis* and *Hy. lurida*, but at distinctly different elevations. The sensory inputs that regulate these species-specific hovering heights are unknown. Interactions among the species were rare; male *Hy. arpadi* did not pursue or investigate spiral interactions involving males of the other species, even when these spirals descended to near ground level, nor did they pursue males of *Hy. affinis* engaged in pursuit flights 3–4 m above them. Overhead targets to which male *Hy. arpadi* respond must therefore be <3 m away.

Energetics. In addition to the large energetic demands of hovering (Ellington 1984), aggregating male tabanids engage in high-speed pursuits of females, and intense interactions with conspecific and other males, all of which must also be energetically demanding. It is reasonable to hypothesize that energy, its availability and acquisition, will be an important contributor to both the dynamics of male aggregation sites and to male fitness. Tabanids are known to finance flight activities with stored carbohydrates, obtained from a variety of sources (Miller 1951; Roberts 1967; Magnarelli *et al.* 1979). The adult flies are capable of taking carbohydrates in both liquid and solid form (Mally 1983). Such nectar sources are abundant at Churchill (Hocking 1953) but the extent to which male *Hy. arpadi* uses any particular source or the rates at which the males can acquire energy are unknown. Among the species of tabanids that are known to hover, almost all species are either crepuscular or hover only in the morning, usually the very early morning (Wilkerson *et al.* 1985). Temporal constraints on the duration of hovering activity may result from depletion of energy reserves, but could also be an evolutionary response to predation pressures or female-activity profiles. That energy is a significant contributor to the duration of hovering is illustrated by a few studies that have shown declines in carbohydrate stores through the aggregation period (Magnarelli 1985; Taylor and Smith 1990).

The temporal pattern of energy reserves in *Hy. arpadi* departs strongly from the patterns in other species of *Hybomitra* (Magnarelli 1985; Taylor and Smith 1990). The variance in energy contents with time was invariably high, and some males, newly arrived at aggregation sites, must have been capable of hovering for only a few minutes; other males, simultaneously present on the sites, were capable of hovering for many hours (Fig. 9). In the absence of through-time observations of individual males and in the complete absence of information on the carbohydrate-feeding behavior of the males, it is impossible to speculate on what this dynamic picture means or its causes.

Although individual males may have been capable of hovering for only brief periods of time, on suitable days the aggregation sites were occupied by male *Hy. arpadi* for many hours — certainly for time periods that must exceed the duration of hovering time available to any one male. This pattern contrasts markedly with the usually brief hovering periods of most other species (Wilkerson *et al.* 1985); clearly rewards (i.e. uninseminated, receptive females) must be present for much of the daylight hours at Churchill. Perhaps uninseminated females are active throughout the day or females emerge over a wide temporal window, either of which could be an adaptation to the abbreviated flight season of subarctic locales.

Although energy availability showed high temporal variance in male *Hy. arpadi*, the uniformly high concentration of crop contents was much less variable. The mechanisms by which males regulate the concentration of the crop contents in the face of environmental sources that must be highly variable, are unknown. In some species of Diptera, adults can concentrate imbibed carbohydrates by evaporation of water in a behavior known as bubbling (Hendrichs *et al.* 1992). Similar behaviors have not been observed in tabanids.

Thoracic temperature and water content of hovering males. It is well known that aggregating male tabanids have high thoracic temperatures (Gaugler and Schutz 1989; Taylor and Smith 1990; Schutz and Gaugler 1992); these elevated thoracic temperatures account, in part, for the speed and agility of these insects. *Hy. arpadi* is remarkable for the unusually high thoracic temperature it maintained, with almost perfect regulation — thoracic temperatures were almost invariant. It is tempting to ascribe this precise thermoregulation to an adaptation to the subarctic environment, but the apparent uniqueness is probably spurious; the 3-person teams taking temperatures of *Hy. arpadi* assured a dataset of high quality.

In spite of probably lengthy hovering periods, the water content of males declined only slowly over the aggregation period. Nothing is known of the physiology of water balance in hovering male tabanids but it is possible that they make use not only of water of combustion but of the sometimes large stores of water in the crop.

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