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Mating Behavior and Thermoregulation of the Reindeer Warble Fly, *Hypoderma tarandi* L. (Diptera: Oestridae)

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Hypoderma (= Oedemagena) tarandi *L. (Diptera: Oestridae) is characterized by a mating strategy in which both sexes meet and mate at two types of distinct topographical landmarks. In the expansive, treeless vidda (= tundra-like) biome, mating places are unique, rocky areas located along rivers and streams or in rocky areas of drying river and stream beds. In wooded valleys below the vidda, flies mated at certain topographical areas along dirt road tracks/paths. Thermoregulatory activities of males occupying perches at mating places included selection of substratum at perch site, orientation of body to sun's rays, crouching, stilting, and flights into upper cooler air. On warm sunny days males perched for just 1-2 min before flying up into cooler air to promote cooling. Laboratory and field studies revealed that flies could not metabolically cool down when held at 25-38°C. Time spent at mating places depended on temperature, duration of sunshine, and wind velocity. Males were very aggressive in pursuing all* Hypoderma-*sized objects that passed by them or that landed near them, but they did not defend specific perch sites. Males either pursued and caught females in flight, or they hopped onto females that landed near them. During 5 years, 74 males and 14 females were seen at mating places. Dissection of six females caught at mating places revealed them to be recently eclosed flies full of fat body and with all eggs intact; two not paired with males were non-inseminated. Three experimentally paired females remained* in copulo *for 10, 13, and 19.5 min.*

KEY WORDS: *Hypoderma tarandi*; reindeer warble fly; mating behavior; thermoregulatory behavior.

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INTRODUCTION

Warble flies in the genus *Hypoderma* (Diptera: Oestridae) are the most important oestrid parasites of vertebrates throughout much of the world. They are responsible for large economic losses to the beef and dairy cattle industry (Drummond *et al.*, 1981, 1988; Boulard and Thornberry, 1984; Williams *et al.*, 1985; Klein and Jetter, 1987) as well as to the northern regional reindeer industry (e.g., Nordkvist, 1967; Erne and Nordkvist, 1970; Washburn *et al.*, 1980). Considering the vast amount of research conducted on these economically important parasites of domesticated and semidomesticated livestock, accounts of their mating places and mating behavior are extremely rare. There are only two brief descriptions of the mating places and behavior of *H. lineatum* (DeVillers) (Gansser 1951, 1957; Catts *et al.*, 1965), and apparently none for other species of *Hypoderma*. During a 5-year period Gansser (1951, 1957) discovered two major and two minor mating places of *H. lineatum* in the Swiss Alps; in the next 20 years he found no new sites. In California, Catts *et al.* (1965) found three mating places of *H. lineatum* in 2 years. Although he did not mention mating of *H. tarandi* (as *Oedemagena tarandi*) or describe specific mating places, Bergman (1917) stated that, "The males on the contrary are generally rare, but I have seen them in the mountains sitting on stones, where the sun was shining. They are lively, watchful and hard to catch."

As part of a broad study of the biology of parasitic flies associated with reindeer in subarctic Norway, one objective was to locate the mating places of the two oestrid parasites of reindeer. This paper describes the mating places and the mating and thermoregulatory behavior of the reindeer warble fly, *H. tarandi* L. (=*Oedemagena tarandi* (L.), Wood 1987) and discusses how it is adapted to reproduce under sometimes severe climatic conditions. A brief abstract (Anderson *et al.*, 1988) previously summarized some results of this research.

METHODS

Description of the General Study Area and Time Spent at Actual and Potential Mating Places. Our studies were conducted in Finnmark and Troms Counties in northern Norway, 340 to 360 km north of the Arctic Circle. Here, at Suolovuopmi, 69°37′N, 23°31′E, and Vaddas, 69°50′N, 20°40′E, the typical mountainous reindeer habitat consists of an upper vidda biome (a treeless tundra-like biome with almost no permafrost) that is interspersed with numerous rivers, streams, and lakes and characterized by vegetation such as dwarf birch, bilberry, cloud berry, mosses, lichens, and sedge tussocks. Below about 500-m altitude there are wooded hillsides and valleys and, generally, larger streams and rivers.

The predominant trees are mountain birch and willows, with an underlayer of dwarf birch and juniper.

Our search for mating places was guided by previous general knowledge of the mating behavior of Diptera (Anderson, 1974), by the specific mating place descriptions by Gansser (1951, 1957) and Catts *et al.* (1965) for *H. lineatum*, and by visits (of J.R.A.) to California mating places described by Catts *et al.* (1965). Although it is generally known that all oestrids are active at mating places during bright, sunny periods, we searched for, and made observations at, mating sites during all types of weather.

From 1984 through 1988, on 18 full or partial days climatically favorable for flight (see descriptions of various climatically characterized days under Results), we spent 33 h observing flies at known mating places. On 10 of these days there were two observers present at all times, and on 8 days three observers participated (total observation h, 79.5). Additionally, on 8 climatically favorable days and on 2 other days with good to marginal climatic conditions for oestrid flight activity, we spent 23 h searching for the above (and other) *H. tarandi* mating places. On climatically unfavorable days we also spent 34 h (on 8 days) looking for flies at known mating places and 48 h (on 12 days) searching for other likely mating places that could be examined on favorable days. About half of our searching time (on both favorable and unfavorable days) was spent at rocky areas along rivers and streams. The remainder of our searching time was spent looking along lakeshores, well-worn reindeer trails, and various types of dirt roads and paths. Also, in other research involving the nasopharyngeal bot fly, *Cephenemyia trompe* (Modeer) (Diptera: Oestridae), we spent several hundred hours of study on many mountain tops (mostly during favorable conditions for oestrid flight activity).

Methods of Studying Flies. While we searched for mating places we usually concurrently operated a series of CO_2-baited insect flight traps (Anderson and Hoy, 1972; Anderson and Nilssen, 1986) that were used to capture host-seeking females. The activities of these large flies (circa 5 mm wide × 18 mm long) at mating places were observed (with and without binoculars) from distances of about 25 cm to 10 m. On several days, perching and flying activities were recorded with a 35-mm camera and a videocamera and later studied in the laboratory. Flies were occasionally captured with insect nets for use in various laboratory studies.

Three females caught at mating places were put into separate vials with males, and two females caught at a *Cephenemyia trompe* (Modeer) mating place each were paired with males in a laboratory cage. Other captured flies were flown on a laboratory flight mill (16 males and 22 females) or used in longevity and thermoregulatory experiments (3 males and 38 females). Most flies were dissected to assess their reproductive condition and nutrient reserves. In 1988, five males captured at one mating place were marked with a dot of white Liquid Paper on the thorax and then released to determine the recapture rate.

We recorded light intensity, wind direction and velocity, percentage cloud cover, air temperature, and perch site temperature. Light intensities were measured with a Gossen Panlux Luxmeter (0–120,000 lux) with the photosensor held 1 m aboveground, wind velocities with a handheld Elvometer AB Ventimeter, and temperatures with a Sensortek Model BAT-12 equipped with a 1-cm 29-gauge hypodermic needle microprobe with a time constant of 0.025 s. Temperatures of captured flies (held by forceps or glued to rock perches) were taken by inserting the thermoprobe into the thoracic muscles for about 1 s; temperatures of rock and vegetative perch sites were taken by touching them with the same probe. The microprobe was held in shade prior to these recordings. To determine how rapidly flies warmed and cooled under different conditions, the thoracic temperatures of flies glued to rocks and dead flies suspended on the probe were taken at 1 to 2-min intervals after they were moved back and forth between shade and sun and lifted from ground level to 1–2 m high. The thorax and abdomen of two flies glued to rocks were painted with white Liquid Paper and 10 thoracic and abdominal temperatures were taken per fly at periodic intervals and compared with like temperatures from two unpainted flies and areas of surrounding habitat. Twenty paired thoracic temperatures were taken from a male and female glued to rocks and intermittently exposed in sun and shade; 20 such comparisons also were made between a live and dead female. Wind chill temperatures were obtained by exposing the probe and probed flies to existing conditions of light (sunny or cloudy) and wind velocities for 1–2 min. At mating places we recorded the natural perching times of males exposed to different climatic conditions and when they were shaded by a person's shadows.

RESULTS

Description of Mating Places

We discovered two types of mating places where we observed and collected male or female *H. tarandi* or both. Both types of places are non-resource-based distinctive topographical landmarks that are attractive to both sexes (Anderson, 1974). The first type consisted of an expanse of large rocks located along one or both sides of a river or stream. Four such places were found above 500 m, and all were associated with the treeless, vidda biome. The V-I place shown in Figs. 1–3 typifies the topography of all four mating places found on the vidda, and it is where most of our observations were made. The rocky area on the left in Figs. 1 and 2 (bisected by the receding river) measures about 60 × 15 m. All flies here were seen only in the upper 40 × 15-m area and most were seen

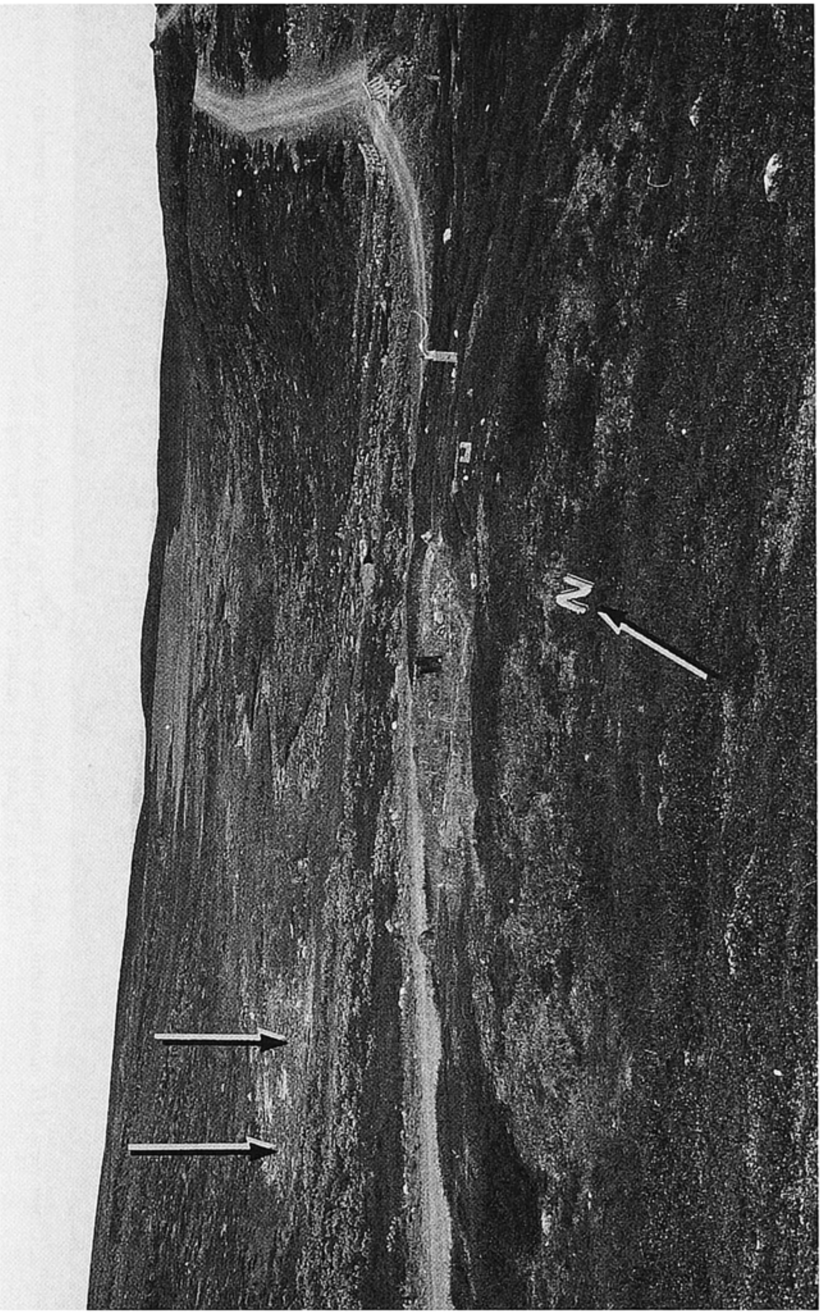

Fig. 1. General view of the topography associated with a typical vidda mating place (V-I) of *H. tarandi* (small arrows identify primary perching sites).

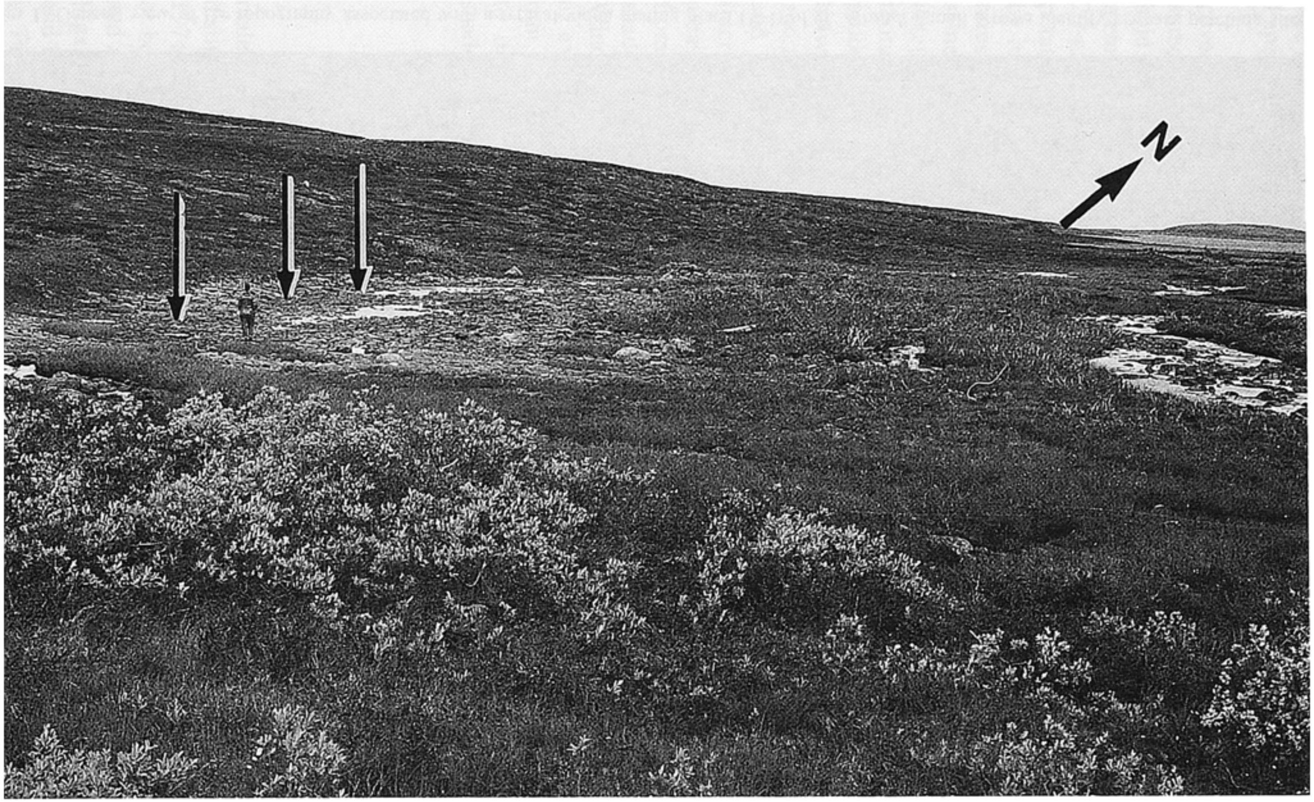

Fig. 2. Closer view of *H. tarandi* mating place V-I illustrating the large area of rocks curved along the base of a hillside that served as a windbreak. Human in Figure is 1.7 m tall; arrows identify perching sites.

Fig. 3. Closeup view of the *H. tarandi* mating place shown in Figs. 1 and 2, illustrating the variety of rock perches and the large sheltering hillside. Human in figure is 1.7 m tall; arrows identify perching sites.

perching on rocks on either side of the small left fork of the river (see arrows in front of the human). Most individual rock perches ranged in size from 20 to 40 cm in diameter, but males also occasionally perched on a few scattered larger rocks about 1 m long × 0.5 m wide (Fig. 3). As shown in Figs. 1 and 2, the place where flies aggregated was situated along the base of a sheltering hillside where the river made a sharp northward turn. At this place, flies perched on many different rocks. The maximum density of males seen at any one time in the 40 × 15-m area varied from 5 in 1987 to 10–12 on different days in 1986. Males usually perched about 5–10 m apart, but two sometimes perched less than 1 m apart.

The protective hillsides on three sides of the mating place (Fig. 1) formed a topographical bowl-like depression that was sheltered from the wind on most days. Wind velocities at the mating place nearly always were several meters per second less than at locations on the surrounding hillsides and much less than on the exposed ridgetops. Typical velocities on different days were 0–2 m/s at the mating place, 4–6 m/s on surrounding hillsides, and 8–10 m/s on exposed ridgetops.

On climatically favorable days (see next section), we located three other vidda mating places topographically similar to V-I, where we caught either male or female *H. tarandi* perched on rocks. All places were in areas largely sheltered from high wind velocities, and all were less than 30–40 m long. The spatial boundaries of each mating place where flies were seen on rocks appeared to be determined by fixed topographical features and the wind direction and velocity on given days. If the wind direction was such that the spatial boundaries of the mating place were exposed to high winds (i.e., 4 to 6 m/s), then few or no flies were seen.

The second type of *H. tarandi* mating place found was where males aggregated in or adjacent to dirt road tracks or pathways. Two such places (W-I and W-II) were located in wooded valleys below the vidda and one (W-III) was located on a dirt road along the base of a hillside adjacent to a lakeshore. Both wooded valleys were situated in a bowl-like area sheltered from wind and they were characterized by grassy hillsides with birch, willow, and juniper trees (Fig. 4). At study area W-II (Fig. 4) the seldom-used dirt road track resembled two parallel, well-worn paths separated by 1.5 m of short vegetation. In this study area males were found at the three different mating places identified in Fig. 4. The distance between place A and place B was about 360 m, and that between B and C was 100 m. Mating place C always had males present on climatically favorable days, and it always had the most males. It also was the place most sheltered from the wind.

At mating place C we found a maximum number of four or five males spaced out along the 30 m seen in the foreground of Fig. 5. Here individual males (Fig. 6) usually perched from 1 to 5 m apart (sometimes 1–10 m apart).

Fig. 4. General view of the topography associated with wooded valley mating places of *H. tarandi*. Mating place A extended from foreground of photo to standing observer. Arrows in background show location of mating places B and C.

Fig. 5. Closeup view of mating place C. Males perched in a zone from about 1 m beyond sitting observer to large rock at right margin of photo.

Fig. 6. Typical male posture while perched at mating place C.

The next-nearest male perches (place B) were located 100 m above place C. No *H. tarandi* males were ever seen below place C, although some other fly species and Lepidoptera frequently were seen perching along the first 50–100 m below and above place C.

W-II mating place A was located below the crest of a hill, where males usually were located in a 10-m zone beginning about 10–15 m below the crest of the hill. On several calm days males also were seen and caught at the crest, but none was ever seen beyond 25 m below the hilltop. The maximum number of males seen here at any one time was three. Mating place B was located in a broad, flat depression about 5 m below and parallel to the road. This specific place is hidden by the trees in Fig. 4. Here there were several large rocks situated in a zigzag row extending for about 10–15 m. The individual rocks varied in size from about 0.75 m long × 0.5 m wide × 0.25 m high to about one-half that size. On 2 days, a single male was seen or caught here while perching on one of the intermediate-sized rocks near the center of the row. Males usually were only seen at place A when there were up to four or five males at place C, and they were seen at place B only when other places had maximum numbers of males.

Climatic Factors Affecting the Activity of *H. tarandi* at Mating Places

Visits to known mating places and catches of females in CO_2-baited traps revealed that temperature, light intensity, and wind velocity all had a marked effect on the flight activities of *H. tarandi*. The most favorable days for both host seeking and mating flight activities were sunny, warm (15–22°C, with maximum temperature reached only on 1 day), and nearly windless, with light meter readings of 90,000 to 112,000 lux. A "good fly day" had cloud cover fluctuating from 0 to 50%, wind velocities (at the mating place) of 0–2 m/s, and temperatures between 15 and 20°C. A "marginal fly day" generally had a clear sky, wind velocities of 3–5 m/s, and temperatures between 12 and 15°C or 90–95% cloud cover, winds of 0–2 m/s, and moderate temperatures (15–17°C). The least favorable days for the appearance and activity of flies were either sunny, cold (10–14°C), and windy (4–8 m/s) or mostly cloudy and dark (about 20,000 lux) but moderately warm (15–17°C). The latter days usually had a dense cloud cover of 90–95%, but when brief intermittent periods of sunshine occurred between 0900 and 1500, one or two males might appear for 5–10 min and then disappear again when the sun became obscured by clouds. Flies were not seen at temperatures below 10°C, on dark, cloudy days (light intensities below 20,000 lux), at wind velocities above 6–8 m/s, or during periods of rain or snow. In all years of study, no flies were seen during 34 h of observation at known mating places on 8 days when unfavorable climatic conditions existed. Flies also were not seen at potential mating places during 48 h of searching on 12 climatically unfavorable days.

In the different years the weather was unfavorable for any kind of fly activity from 65 to 75% of the time. In 1985, for example, of the 40 days between 22 July and 30 August, there were 7 good days for *Hypoderma* flight associated with host seeking and mating activity, 4 moderately good days, 2 days that were moderately good for half the day, and 2 marginal days for flight activities. The 27 days of unfavorable weather had rain or any combination of dense cloud cover, high winds, or temperatures below 10°C. During 1987 field studies between 20 July and 15 August, the weather was unfavorable for *Hypoderma* flight activity on 21 of the 28 days (75%). Flies were observed at mating places on only 6 days and females were caught in CO_2-baited traps on only 7 days (unpublished data).

Seasonal Occurrence of *H. tarandi.*

Observations of flies at mating places and catches of host-seeking females in CO_2-baited traps revealed that *H. tarandi* was present from early to mid-July to about mid-August each year. In 1984 we saw (and caught) the first female on 10 July and saw the first male on 9 July. Prior to these dates there had been several favorable climatic days in late June and early July when we saw no *H. tarandi*, and none was caught in baited traps (unpubl. data). In 1984 the last male was caught on 31 July (last date site was visited), and the last female was trapped on 17 August. In 1985, the first and last females were trapped on 23 July and 18 August, respectively. That year we were able to visit a known mating site on only 1 day (July 21), when we observed and caught several males. In 1986, the first *H. tarandi* males were seen and caught on 8 July and the last on 18 July; studies terminated on 19 July that year. In 1987, flies were seen at study area W-II from 18 July through 9 August (the first and last days we visited this area). Both males and females were seen on 18 July. No females were observed attacking reindeer or caught in eight CO_2-baited traps operated on 18 and 19 July, but three were seen at mating place C. Females were caught in baited traps from 20 July through 10 August. In 1987, we saw from five to nine males at study area W-II on 18 and 19 July, but only three males on 10 August. At mating place V-I, we saw the last *H. tarandi* males (three) on 9 August; from four to six males had been observed there on several prior days in July and August. In 1988, males were seen and caught at study area W-II on 21 and 31 July (last date site was visited).

Total *H. tarandi* Seen and Caught at Mating Places

On the 18 days when flies were observed at mating places (from 1984 through 1988), we saw a total of 74 males and 14 females (Table I). Because males often undertook short flights to cool down or pursue other flies, it was difficult to precisely record how many were active at a mating place each day.

Table I. Total *Hypoderma tarandi* Caught or Seen at Mating Places on 18 Full or Partial Days Climatically Favorable for Fly Activity[a]

	No. seen/caught	
Year	Males	Females
1984	6/4	0.0
1985	7/2	0/0
1986	23/9 (2 released)	4/4 (2 released)
1987	29/13 (2 released)	10/5
1988	9/5 (5 released)	0/0
Total	74/33	14/9

[a] Two or three researchers spent 33 h observing on these days (79.5 total h). No flies were seen at known mating places during 34 h of observations when unfavorable climatic conditions existed.

The 74 males represent the total of the maximum numbers seen at one mating place at any one time on the different days. Because a male might leave a mating place after a few hours, our totals probably underrepresent the actual numbers that were active per mating place per day. Because we wished to observe individual males for as long as possible, we collected only 33 individuals, 9 of which were released again where collected. The increased number of flies for 1986 and 1987 is primarily a result of more time spent searching for mating places and in observing fly behavior at known places.

Activity and Behavior of Females at Mating Places

The few females we observed approached a mating place by flying upwind or cross wind, and they either flew through the zone of male perch sites or landed near a male. Females tended to land when they approached upwind. All of the nine females caught at mating places were caught at vidda study areas. One was netted while sitting on a rock *in copulo* with a male, one was caught immediately after a presumed copulation (when an unidentified *Hypoderma* was seen flying away and a female was netted from a rock), three females netted from rocks immediately copulated when paired with males in separate vials, two proved on dissection to be noninseminated, and two were of undetermined status (one was caught and released at the mating place and one that had been put in a ventilated vial was lost in the field). Based on its landing/perching behavior prior to capture, we believe that the released female was unmated. Females seen at vidda mating places either flew into the area being observed and landed on a large sun-exposed rock or already sitting (perching) on a rock when an investigator arrived. They did not seem to be attracted by movements of an observer (as those seeking a host are), and when they flew off spontaneously or were flushed by an observer, some females flew just a few meters and again landed on a sun-exposed rock. In addition to the females caught at mating place V-I, we observed two other females that landed on rocks at other vidda mating places but flew off before we could capture them.

At a wooded valley mating place (W-II, C) we saw males pursue and catch three presumed females. In all three cases, after the male had caught the presumed female, the two flies landed in vegetation several meters from the point of aerial contact. Although we searched the surrounding grasses and bushes, we did not find these flies. (Their coloration makes it very difficult to see a stationary fly when it rests in vegetative cover.) Our primary reason for believing that the three pursued/captured flies were females is that, while flying through the zone of male perching sites, these pursued flies were caught and carried beyond the border of the mating place. In contrast, the many male/male pursuits seen invariably terminated in the air at the mating place after only brief contact. On the few occasions when two males met in the air and fell to the ground, they separated after a few seconds of grappling, and one or both then flew off and again landed at a perching site.

Reproductive State and Laboratory Pairing of Females Caught at Mating Places

Dissection of six females caught at mating places revealed that all were recently emerged individuals. The hemocoel of each was fully packed with nutrient reserves (fat bodies), and the rectum was filled with an off-white-colored fluid. The three females known to have mated, and the one involved in the presumed mating, had their spermathecae full of sperm. The number of eggs (608, 622, 642, and 720) in these females varied, but examination of the ovarioles revealed that no eggs had been laid. Two captured females (632 and 754 eggs) not experimentally paired with males also were found to have a full complement of eggs and to be noninseminated. All data associated with these six females indicate that they were newly eclosed flies that had been attracted to the mating place to mate.

The three females caught at the V-I mating place and placed with males in separate glass vials paired almost immediately and remained *in copulo* for 10, 13 and 19.5 min. The two females placed in cages quickly were mounted by their male partner and they remained paired for 40 and 67 min, respectively, during which several photographs were taken (Folstad, 1986).

Activity and Behavior of Males at Mating Places

Presence and Activity at Perching Sites. The presence and activity of males at known mating places were consistent from year to year. At W-II, for example, males were present at about the same densities, and at the same perching sites, from 1985 through 1988. In 1988, five marked males remained active throughout the day at the mating place where they were captured and released, but only one of five was resighted at the same place when visited 10 days later. On various days, males were present at mating places from 0930 to 1650 (Norwegian standard time), with peak numbers and flight activity usually occurring between 1100 and 1300. The presence and activity of males at mating places were influenced by temperature, cloud cover, and wind velocity (Tables II and III).

Within the boundaries of a mating place males always were found in the same perching sites, and they almost always were positioned facing away from the sun. At the woodland study area with smaller mating place boundaries, males were much more consistent in their selection of perching sites than males at the much larger, principal vidda biome mating place (V-I). Within the 30-m zone of male perch sites at the best woodland mating place (W-II, C) there were two preferred perching sites where *H. tarandi* males almost always were seen. If only one or two males were present, such as early or late in the day or during climatically marginal periods, they invariably would be sitting at these specific locations. The type of perch occupied by a male depended on its exposure to

Table II. Representative Temperatures (°C) of the Thoracic Muscles of *H. tarandi* and Their Perching Substrates in Relation to Cloud Cover, Sunlight, and Air Temperature[a]

	Air temp.		Wind speed 1 m aboveground (m/s)	Perch and muscle temp.		
Sky condition[b]	1 cm	15 cm		Green veg.	Dark rock of soil	Thoracic muscle
Cloudy	11	9–10	1-3	11	12-15	13-15
Cloudy	14.5	13-14	4-5	14.5	16	17
Cloudy	18-20	15-17	1-3	22	23-25	25
Sunny	8-10		4-5	—	13.5-17.0	23-24.0
Sunny	14	10	1-2	—	18	24
Sunny	19	16	1-3	22	24-26	28-29
Sunny	20	5-6	4-5	—	21-22	28-29.5
Sunny	21.5	19	1-2	—	33-34	37-38[d]
Sunny	18	—	2-3	—	27	38.7[d]

[a] Data associated with these nine flies are representative of temperatures associated with 15 females and 2 males glued to rock perches and taken at different times on 20 different days.

[b] Light intensities were 10,000 to 20,000 lux during cloudy periods and 80,000 to 110,000 lux on summy days.

[c] Multiple temperatures taken from perches and flies at about 1- to 10-min intervals often varied by 1-3°C, depending on changes in wind velocity and light intensity.

[d] After 2 min in sun, the thoracic temperature dropped a $\overline{X}$ of 10°C ± 0.802 (7-14°C) after the fly was placed in shade for 1-2 min or raised 1-2 m aboveground for 1-2 min. After a 1-min reexposure in direct sunlight, thoracic temperatures again rose to 37-38°C. (Each fly was raised four times and moved between sun and shade four times.) Rock temperatures declined only 2°C in 1 min and 4°C in 2 min.

Table III. The Relationship Between Perch Temperature and Spontaneous Flight of Male *Hypoderma tarandi* into Cooler Air at 1-2 m Above Perch Sites

Exposed perch temperature (°C)[a]	No. perching events timed	Perching time (min) to spontaneous flights	Air temperature (°C)	
			At 0.5 m	At 2.0 m
26-35[b]	32	1.67 ± 0.122 (0.5-3.9)	16-19	13-18
16-20[c]	9	16.6 ± 0.603 (15-20)	10-17	10-15
12-15[d]	4	>60	10-12	9-12

[a] These and air temperatures represent ambient "wind chill" temperatures obtained by exposing the probe to existing conditions of sunlight and wind velocity.

[b] For flies glued to or held on rocks in direct sunlight, thoracic temperatures on warm days were 2-11.7°C higher than perch temperatures (see Tables II and IV).

[c] Includes 5 mostly cloudy days when flies at perches were only briefly exposed to bright sunlight and 1 sunny, but cold day.

[d] Includes observations on 1 cold, sunny day and 1 partly cloudy day. All times terminated after 1 h with flies still present. Two flies observed continuously and two at about 15-min intervals.

the sun and the prevailing wind velocity. Thus, within an area of 100 cm^2 at the most preferred perching site, a male might perch on dark areas of bare ground, a small dark stone, or a clump of vegetation. Perching stones here varied from about 7 to 30 cm in diameter. At the V-I mating place, where there were thousands of individual rocks, males perched on many of the larger rocks, most frequently in the upper one-third of the perching area (the area immediately in front of the human in Fig. 1). At all mating places the closest observed spacing of males was about 1 m; most males occupied perches from 2 to 8 m apart.

Although some perches always were occupied by males, we did not see individual males defend specific perches. During male/male aerial pursuits, we saw other males land and occupy perches abandoned by the airborne pair, and on the one day males were marked, marked and unmarked males commonly interchanged perches. Thus, different males might periodically occupy several different perch sites while present at the mating site.

Pursuit Flights and Mating Behavior. On days generally favorable for mating, male activity alternated between perching and either spontaneous thermoregulatory flights or pursuit flights. During our 79.5 h at mating places we observed hundreds of these flights. From their perches, males would take flight and pursue almost any *Hypoderma*-sized object that approached from a lateral angle of between 60 and 110°. Objects pursued included *Hypoderma* males and females, large tachinids and butterflies, and even *Hypoderma*-sized pebbles tossed by investigators. Upon contact, males immediately released all except *H. tarandi* males and females. Males took off in pursuit of small pebbles tossed about a meter high in either a straight or an arched trajectory from positions lateral to a perched male. Perched males did not respond to pebbles tossed directly at them, from angles of about 45° from center, or from behind them.

Most naturally provoked flights involved other *H. tarandi* males; male/male pursuit flights were typically fast, brief flights of 2–10 m in length and about 1–2 m high. After 1–2 s, these flights often ended in brief in-flight contacts and separation. Males then returned to their perching sites in a slower, somewhat sinuous flight route to their landing site. Occasionally, three airborne males would fall to the ground and briefly struggle with one another before flying off to perch sites. When another *H. tarandi* or similarly sized insect landed within about 0.5 m of a perched *H. tarandi* male, the latter immediately fluttered its wings as it hopped towards the intruder. If the intruder did not fly away as the "resident" perched male approached it, the latter male would hop onto the newly landed fly and try to copulate with it. We observed the latter behavior four times, and following such behavior, we twice netted coupled pairs (a male and female *in copulo* on a rock and a pair of males grappling on the ground).

The responsiveness of males at perch sites varied with existing climatic conditions. When a person slowly approached a perched male, the fly typically would readjust its legs on the perch as it slowly turned its head and body to track a person's movements. After tracking a person through an angle of about 90° to either side, a male would then cease watching its observer and readjust to its original position. Quick movements, in contrast, would flush perched males into flight. On colder and partly overcast days when there were few males present at a mating site, males sat for more than an hour if not provoked into flight by another fly (Table III). Under these conditions males commonly crouched with their bodies lowered near or onto a pebble or a patch of bare, dark ground. The few males at mating places on such cold days were so docile that when slowly approached by a crawling investigator, a person could induce a male to perch on the tip of an extended finger. On sunny days having warm perch temperatures males frequently flew up into cooler air at 1–2 m above their perch sites (Table III). On cooler days having intermittent periods of sunshine (Table III; temperature, 16–20°C) males remained at perches for up to 10 to 15 min after clouds darkened the entire study area. When sunlight was obscured for longer periods males abandoned perches until after sunlight returned. However, during periods of sunshine on such days, when sun-exposed males at perch sites were shaded by the shadow of an investigator, they flew or hopped within 5 to 30 s to an adjacent sun-exposed perch a few centimeters away.

The two different mating behaviors (aerial pursuit versus hopping onto landed flies) appeared related to differences in prevailing wind velocities. During periods of mating activity at V-I, wind velocities commonly ranged from 2 to 6 m/s, but when velocities increased above 8 m/s, flies that had been present at lower velocities disappeared from the exposed rock perches. During *Hypoderma* activity at wooded valley mating places, wind velocities usually ranged from 0 to 2 m/s, and male/male pursuit flights were more frequent, lasted longer, and went higher aboveground. At the more wind-exposed vidda places, the higher wind velocities appeared to limit the height and duration of male/male pursuits. When wind velocities at the partially sheltered perching sites were 2 to 4 m/s, velocities over the exposed vidda landscape often were 8 or more m/s.

Behavioral Adaptations for Warming and Cooling

The behavioral adaptations used by the dark-colored males to regulate body temperature on colder days at mating sites consisted of using perches most exposed to the sun's rays and most sheltered from the wind. Such perches were either bare patches of blackish soil or dark rocks. On the colder marginal days for fly activity the few males present sat in a crouched position with the body pressed close to the warm surface, or they sat with the head and thorax pushed upward by the extended fore- and mid-legs and the abdomen slanted downward close to the substratum. These males faced away from the sun with their wings spread apart in the usual perching position, a posture that maximally exposed both the thorax and abdomen to the sun. Overall, only about 20% of the males were seen facing towards the sun, and all of these were seen during warm, cloudless, windless periods. During such conditions either males landed facing the sun, with the body positioned parallel to the sun's rays, or shortly after landing a male would take several small steps as it readjusted its body to face the sun. Moderate wind speeds did not seem to be a major factor affecting the perching position of males. On several occasions males were seen facing away from the sun and into wind gusts of 3–6 m/s.

When exposed to direct sunlight and on warm, calm days, males cooled down by selecting cooler perch sites, by engaging in postural movements, and by flying up into cooler air.

Perch sites selected on warm, sunny days were those that absorbed the least radiant heat and were maximally exposed to the wind. At the W-II mating place most perching sites during the warmest periods were on stems and leaves of vegetation elevated a few centimeters above the ground instead of on stones or bare areas of dark soil. In addition to avoiding warmed stones, this behavior allowed males to perch out of the superheated air layer at ground level and exposed them to any cooling wind movements. On warm, sunny days males typically perched on rocks or dark soil for less then 2 min, while those on more elevated vegetation perches often remained for 5 min before flying off.

Postural adaptations involved stilting and facing toward the sun. With the body parallel to the sun, the least area possible was exposed to the sun's rays. Stilting behavior raised the body higher above the substratum, and it often occurred just prior to flying from a perch. The long, thin legs of male *H. tarandi* also provide a high surface-to-volume ratio, which would minimize the conduction of heat from the ground or other perching surface to the body, as described for certain beetles (Peterman, 1973). In their maximum stilted posture *H. tarandi* males can raise the thorax about 10–15 mm above the perching surface. In only a slight breeze this could move the male into an atmospheric temperature several degrees lower than the perching surface.

The frequency of spontaneous flights up into cooler air (Table III) depended on the temperature at the perching site. In most cases males flew 1–2 m high on short flights of about 10–30 s. Then they usually circled back to the original perching site.

Thermoregulation of Males and Females Exposed to Experimental Conditions

All experimental exposures of flies to various thermal conditions revealed that they were dependent on behavioral thermoregulation. Experiments with both live and dead flies revealed that the thoracic muscles rapidly warmed when flies were exposed to sunlight, but that flies cooled down only when exposed to cooler air and increased wind velocities above ground level or when shaded. When live, wild-caught *H. tarandi* were glued to small rocks and held at various prevailing climatic conditions, the temperature of the thoracic muscles always was several degrees higher than their perch (Table II). Twenty paired thoracic temperatures from a male and female glued to rocks and exposed simultaneously revealed no differences when the flies were intermittently exposed in sun and shade. When sun-exposed flies were placed in shade or exposed to faster wind speeds and cooler temperatures at 1–2 m aboveground, their thoracic temperatures declined 7–14°C after 1–2 min (Table II, footnoted *d*). Experiments with dead flies glued to rocks and suspended by the probe inserted into the thoracic muscles revealed larger rapid declines in thoracic temperatures (Table IV). They also demonstrated that, when shaded cooled flies were reexposed to sunlight at perching sites, the thoracic muscle temperatures increased by 14–15°C in just a minute.

When the thorax and abdomen of a live fly were painted white and the fly glued to rocks at an air temperature of 9°C at fly level and a rock temperature of 14°C, the thoracic temperature of the fly after 2 min in sunlight was 13.5°C; the thoracic temperature of a paired, unpainted live fly was 23.5°C (neither varied over 0.2°C for 10 comparisons). At an air temperature of 19°C and a rock temperature of 24–25.7°C, the thoracic temperature of a white fly varied from 23 to 24.5°C and that of an unpainted live fly from 27 to 28.2°C (for 10 comparisons).

When flies with the thermoprobe inserted into the thoracic muscles were exposed on the surface of a laboratory bench warmed by sunlight passing through

Table IV. Thermoprobe and Thoracic Muscle Temperatures of Dead Flies Moved from Direct Sunlight to Shade or a Higher Elevation[a]

Condition[b]	$\bar{X}$ sun-exposed temp. (°C) after 1 min	$\bar{X}$ change after 1 min	
		In shade at 1 cm aboveground	At 1 m in direct sunlight[c]
Bare probe held 1 cm above patch of dark soil	33.0 ± 0.51 (31 to 36)	−9.7 ± 0.52 (−7 to −12)	−6.8± 0.33 (−5 to −8)
Two probed flies nested on green vegetation 1 cm above soil	36.7 ± 0.56 (34 to 39)	−14.4 ± 0.45 (−12 to −16)	−8.2 ± 0.47 (−12 to −16)
Two probed flies rested on gray rock 1 cm aboveground	40.2 ± 0.74 (36 to 44)	−14.7 ± 0.42 (−13 to −17)	−11.6 ± 0.58 (−9 to −14)
Two flies glued to rock 1 cm aboveground	40.6 ± 0.70 (38 to 44)	−10.5 ± 0.31 (−9 to −12)	−7.1 ± 0.31 (−6 to −9)

[a] Ambient shade temp. = 22°C during recordings. Sun-exposed temp. of dark brown patch of soil = 42.4 ± 0.26 (41–43); sun-exposed temp. of gray rock at 1 cm aboveground = 39.1 ± 0.40 (37–41).

[b] Eight to ten replicates per condition.

[c] Wind velocities at 1 m varied from 1 to 3 m/s.

a glass window, they quickly warmed to stressful temperatures. After four such flies were removed from a refrigerator at 5.5°C, the temperature of their thoracic muscles had warmed to 31.2–35.5°C after a 2- to 4-min exposure to sunlight (comparable temperatures for the surface of a white card and a piece of black plastic (styrene) were, respectively, 29.1 to 30.1 and 32.5 to 37.5°C). When probed flies were forcibly exposed to sunlight in still air for 5 min, their temperature increased to 41.5°C. As a fly exposed to direct sunlight warmed up, it began to make distress movements at about 22°C; the first signs of distress were rapid leg and head movements as it attempted to push itself upward and walk. As the thoracic temperature rose, the fly's abdomen rapidly pulsated and was swung from side to side as it continued to struggle in place while rapidly moving its legs. Two females placed into a glass doored laboratory oven at 35°C almost immediately exhibited the same stressful movements. During enforced heat stress the temperature of their thoracic muscles always was equal to that of the oven, or slightly higher. After 15 min the thoracic temperature was 36.4°C and at 20 min it was 36.8°C. Before dying (at about 20 min) the flies struggled vigorously at intermittent intervals between nearly motionless periods. Under these conditions death probably resulted from a combination of heat stress and dehydration.

DISCUSSION

In subarctic Norway where *H. tarandi* adults were present from 4 to 6 weeks/year, adverse climatic conditions (cloudy/rainy days, low temperatures, fast wind speeds) limit the mating activity of *H. tarandi* to only a few days in most years. However, asynchronous maturation and exit of larvae from the vertebrate host (Bergman, 1917; Breyev and Karazeeva, 1953; Zhigunov, 1968; Paine, 1988, unpublished data), plus variable microclimatic conditions affecting the rate of pupal maturation, result in a seasonally staggered distribution of newly eclosed flies. These phenomena, coupled with the seasonal migration and daily wide-ranging foraging activity of reindeer/caribou herds (Kelsall, 1968; Zhigunov, 1968; Boertje, 1985; Paine, 1988; Folstad *et al.*, 1991), appear to represent a bet hedging strategy in which some newly eclosed adults are present throughout the habitat at all times to mate, and for females to infect the vertebrate host.

The difficulty in locating *H. tarandi* mating places was associated with such factors as the limited number of climatically favorable or marginally favorable days for flight activity, the low density of flies at mating places (sometimes only one or two males present), the short season for adult activity and their brief periods of activity on marginally favorable days, and the vast area to be investigated for potential mating places. Results indicated that mating places were patchily distributed throughout our study areas and usually had only one–five males present at any one time. All vidda mating places appear to be much like the *H. lineatum* mating places in the Swiss Alps, where Gansser (1951, 1957) found males aggregated at particularly situated rocky areas, whereas the wooded valley mating places appear more similar to the mating places described by Catts *et al.* (1965) for *H. lineatum*. Although a few previous workers (e.g., Hadwen, 1926; Natvig, 1917) mentioned seeing male *H. tarandi* (as *Oedemagena tarandi*) on mountain summits, they may have confused *H. tarandi* males with females or with *Cephenemyia trompe* (Modeer). The latter is known to mate at such places (Downes *et al.*, 1985), and we found *C. trompe* males on 35 mountain summits and on many occasions (unpublished data). Although we often saw and caught host-seeking *H. tarandi* females on mountain tops, we never saw *H. tarandi* males at such sites.

Dissection of *H. tarandi* caught at mating places and females caught in traps (unpublished data) revealed that both sexes of the nonfeeding adults eclose with the abdomen packed with nutrient reserves and that females eclose with fully developed eggs. Under field conditions both sexes probably survive for about 1–3 weeks at most, depending on climatic conditions and their daily activities. Under laboratory conditions (unpublished data) the maximum survival of a laboratory-eclosed female was 23 days, and under field conditions one marked male was seen at the same mating place 10 days later. The maximum field longevity of marked *H. lineatum* males was 8 days (Catts *et al.*, 1965).

The mating behavior of *H. tarandi* is of a lek-like polygynous type (Thornhill and Alcock, 1983) in which males assemble at various distinct landmarks and engage in frequent pursuit flights, but do not defend individual perch sites (usually spaced a few meters apart) within the boundaries of the mating place. Certain perches within the mating arena are preferred, however, and always occupied, but they are not defended and always occupied by the same male. The behavior of *H. lineatum* is similar (Catts *et al.*, 1965). There appears to be no difference between the pursuit flight behavior of *H. tarandi* males that simply return to any unoccupied perch site after a pursuit flight and that of species whose males actively defend specific perch sites (Thornhill and Alcock, 1983).

Mating activity was most intense on warm, sunny days, and under these conditions males launch into flight every few minutes to avoid heat stress or to pursue other males or other insects flying by them. As hypothesized by Alcock (1987) for some other insects, the numerous thermoregulatory flights of *H. tarandi*, plus the pursuit flights that may terminate in aggressive grappling interactions between males, probably select for the maximum presence and activity at mating places of males possessing superior flight speed, stamina, and endurance. Because such superior males would pursue every *H. tarandi*-sized insect that entered the mating arena, it seems likely that in the *H. tarandi* mating system most females would mate with such males. Slower fliers and males that tire easily (and periodically must seek shaded sites to avoid heat stress) will lose out in competing for receptive females arriving at a preferred mating place. Such less fit males probably were those observed at secondary mating sites such as WII-A and B (where males were seen only when the preferred site, WII-C, had four or five males present). Although other factors probably are involved in determining overall fitness, superior aerodynamic characteristics such as flight speed, stamina, and endurance would benefit both male and female progeny.

The overall mating strategy of *H. tarandi* is somewhat flexible in that, although both sexes independently select a particular mating place, females either may land near a male (behavior that seemed associated with particularly windy days) or may incite a male pursuit flight that likely sorts out the most fit male at the mating place. The latter behavior appears representative of the "passive choice" strategy (Thornhill and Alcock, 1983) or the "passive default strategy" of mate selection described by Beehler and Foster (1988) as a strategy, "in which the males sort out dominance among themselves and the visiting female simply selects an arena and mates with the dominant male." In any event, whether a female is pursued or lands near a male on a windy day, she probably is selecting a male that is a superior flier, and because *H. tarandi* females may have to fly hundreds of kilometers in search of their migratory host, individual flight ability may be very important for reproductive success.

The eight *H. tarandi* females caught at mating places, to our knowledge, are the only *Hypoderma* females that have been caught in association with mating. The 10- to 19.5-min *in copulo* times of the three *H. tarandi* females we held in vials with males were similar to the times reported by Weintraub (1961) for laboratory matings of reared *H. lineatum*. However, the coupling of the two males and females that remained "*in copulo*" for 40 and 67 min probably represent cases of pseudocopulation. Like the males we saw hop onto landed females at mating places, Weintraub (1961) reported that for four matings of reared, caged *H. lineatum*, "In each case copulation was preceded by a brief hovering flight of the male which alighted on or near the grounded female and moved into the copulatory position. . . ." Because males often held onto and momentarily grappled with other males at mating places but immediately released other insects, a contact recognition pheromone (Anderson, 1974) may be involved in mating.

This arctic/subarctic insect exhibited greatly reduced, but limited, mating activity of males even on climatically marginal days (10–14°C temperatures, low light intensities, and high wind velocities). However, males at mating places did not engage in many energy-draining pursuit flights on such days. As is common for many arctic insects (Downes, 1962, 1965; Kevin and Shorthouse, 1970), *H. tarandi* is a pilose, dark brown fly. Like other dark-colored insects known to absorb a maximum amount of radiant heat at low light intensities (Digby, 1955; Hamilton, 1973; Henwood, 1975; Schultz and Hadley, 1987), the thoracic muscles of *H. tarandi* always were warmer than surrounding objects at perching sites (Table II). Thus, *H. tarandi*, unlike many other insects (May, 1979), may not use much energy in endothermally warming the flight muscles on cold days. During cloudy periods the thoracic muscle temperatures of field-exposed flies remained only 1–2°C above perch temperatures, whereas they were 6–10°C higher on cool sunny days (Table II).

In contrast to their behavior on cold days, male *H. tarandi* may expend considerable energy on warm, favorable days when they make numerous short, rapid flights to cool down. On the warmest days a male would launch into a flight about every other minute, resulting in 30–40 short, rapid flights of about 30 s/h, or about 200 such flights/day (if they remained at the mating place for most of the male activity period). Such highly responsive males might be expected to best compete for available females, but this level of activity also probably would quickly deplete a male's energy reserves and shorten its life. Overheating and flight energy are major constraints for reproductively active males of other flies (Heinrich and Pantle, 1975; Toft, 1984).

Male *H. tarandi* at perching sites displayed the same types of thermoregulatory activities reported for other insects that also use similar types of relatively exposed mating sites (Casey, 1981; Peterman, 1973; May, 1979). Depending on air temperature, wind velocity and time exposed to direct sunlight, male *H. tarandi* regulated body temperature by selecting certain perch sites, orienting the body to the sun's rays, pressing the body to a warm substratum (crouching), extending the legs to elevate the body (stilting), or frequently flying up into the cooler atmosphere. The latter behavior would promote convective cooling, the primary method by which flying insects lose heat (Heinrich, 1974; 1981; Gilbert, 1984). Because flying may provide an insect with more water than it evaporates (Wheeler, 1989), the frequent brief flights may serve a double function on warm days. That is, in addition to heat loss by passive convection, the flights may provide the flies with metabolic water derived from the fat body reserves (to counteract the dehydrating effects of exposure to radiant heat) and, thus, promote cooling by evaporation (Wheeler, 1989).

Laboratory studies of the flight patterns of many *H. tarandi* (unpublished data) have revealed that the flying behavior and flight capacity of males and females are very different. The short, fast flights typical of males observed at field mating places were mimicked by males flown on a laboratory flight mill, and they are similar to laboratory flights of *H. lineatum* (Chamberlain *et al.*, 1986). Many mated females, in contrast, flew continuously for 6–8 h, and for 50–60% of the time when flown on the flight mill for 16–32 h.

The landmark mating places of *H. tarandi* in subarctic Norway appeared generally similar to those described for *H. lineatum* in Europe and North America (Catts *et al.*, 1965; Gansser, 1951). Of the many types of lek/lek-like mating systems described and postulated in recent years (Bradbury, 1985; Bradbury and Gibson, 1983; Bradbury *et al.*, 1986; Beehler and Foster, 1988; Queller, 1987), the mating system of *H. tarandi* appears to most fit the "hot spot" model (Bradbury and Gibson, 1983) in which male aggregations result from sequential settlement/activity of males along pathways or sites preferentially used by females. Our studies indicate that both male and female *H. tarandi* utilize either of two types of specific topographical landmarks as mating places; at these places either females land near a male that hops onto them and mates or they may be the object of a pursuit flight that terminates in copulation. The low male densities observed at each mating place probably minimize potential predatory mortality and make it unlikely that the purpose of male aggregations is to increase male attractiveness to females (on several days only one male was seen perching at a mating place).

The general mating strategy of *H. tarandi* thus appears to be one of low densities of males aggregated at distinct topographical mating places as numerous as several per square kilometer. This appears to be related to the very limited sustained flight capacity of males, but such a strategy also would be beneficial to females in that it would greatly increase an individual's chance of quickly finding a mating place (the time a receptive female spends searching for a mating place would be far less in a 250-km^2 area that had 250 mating places with 5 males each than in an area of similar size that had 25 mating places with 50 males per place). Such a mating strategy would result in a receptive *H. tarandi* female having to spend minimal time searching for a mate, thereby retaining a maximum amount of energy reserves for her search for a vertebrate host: an important factor for a parasitic fly that may have to fly hundreds of kilometers to find a host (Folstad *et al.*, 1991).

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