

# The timing and departure rate of larvae of the warble fly *Hypoderma* (= *Oedemagena*) *tarandi* (L.) and the nose bot fly *Cephenemyia trompe* (Modeer) (Diptera: Oestridae) from reindeer

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**Abstract:** The emergence of larvae of the reindeer warble fly *Hypoderma* (= *Oedemagena*) *tarandi* (L.) (n = 2205) from 4, 9, 3, 6 and 5 Norwegian semi-domestic reindeer yearlings (*Rangifer tarandus tarandus* (L.)) was registered in 1988, 1989, 1990, 1991 and 1992, respectively. Larvae of the reindeer nose bot fly *Cephenemyia trompe* (Modeer) (n = 261) were recorded during the years 1990, 1991 and 1992 from the same reindeer. A collection cape technique (only *H. tarandi*) and a grating technique (both species) were used. In both species, dropping started around 20 Apr and ended 20 June. Peak emergence occurred from 10 May – 10 June, and was usually bimodal. The temperature during the larvae departure period had a slight effect (significant only in 1991) on the dropping rate of *H. tarandi* larvae, and temperature during infection in the preceding summer is therefore supposed to explain the uneven dropping rate. This appeared to be due to the occurrence of successive periods of infection caused by separate periods of weather that were favourable for mass attacks by the flies. As a result, the temporal pattern of maturation of larvae was divided into distinct pulses. Departure time of the larvae in relation to spring migration of the reindeer influences infection levels. Applied possibilities for biological control by separating the reindeer from the dropping sites are discussed.

**Key words:** Parasite, reindeer warble fly, reindeer nose bot fly, throat bot fly, review, larval departure rate, control, Norway, *Rangifer tarandus*.

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## Introduction

Larvae of the reindeer warble fly *Hypoderma* (= *Oedemagena*) *tarandi* (L.) and the reindeer nose bot fly *Cephenemyia trompe* (Modeer) are parasites that commonly infect reindeer and caribou *Rangifer tarandus* (L.) throughout most of the natural distribution of the host (Zumpt, 1965; Wood, 1987). The larvae of both species depart from the host in spring (Bergmann, 1917; Hadwen & Palmer, 1922; Sdobnikov, 1935; Breyev & Karazeeva, 1954; Paine, 1988; Solopov, 1989). Larval development of *C. trompe* has been investigated by Nilssen & Haugerud (accepted).

Most populations of *R. tarandus* migrate in spring from wintering grounds inland to coastal areas where the animals spend the summer (Kelsall, 1968; Skjenneberg & Slagsvold, 1968; Skoog, 1968; Syroechkovskii, 1984; Boertje, 1985). The migration of semi-domestic reindeer in northern Norway starts in late March or April and the reindeer reach their summer ranges between early May and the end of June. The distances covered may be as much as 300 km.

The dropping of the larvae of *H. tarandi* and *C. trompe* coincides with the spring migration and, consequently, the parasites become separated by consi-

derable distances from their host individuals (Winogradova, 1936). These parasites have an annual life cycle and, for a short period (from when the last larvae have dropped to when new infections start in July), the reindeer are almost free of these parasites. Thus, to continue their life cycle, the flies actively have to seek new host individuals in the summer.

The proportion of the larvae brought into the summer range, where they can infect their host, depends on the timing and speed of the migration of the reindeer in relation to the dropping of the larvae. The further the animals migrate, the further the larvae are left behind, and driving the reindeer greater distances between the time of larval departure and infection time has been recommended as a means of reducing infection by oestrid parasites (Hadwen, 1926; Palmer, 1934; Hearle, 1938; Saveljev, 1968; Washburn *et al.*, 1980). Folstad *et al.* (1991) found that distance of the post calving migration was negatively correlated with mean intensity of infection of *H. tarandi* in semi-domestic reindeer in northern Norway. Kelsall (1975) showed that sedentary populations of caribou have higher infections levels of *H. tarandi* than migratory ones.

The migratory habits of the reindeer during the

oestrids' free-living stages (dropped larvae, pupae and flies) influence the transmission rate of the parasites. Clearly, the fitness of the parasites would be increased by delaying their departure from their host until after the reindeer have reached their summer grazing areas. However, the potential for delaying eclosion is limited by the need for the flies to hatch early enough to reproduce before the short sub-Arctic summer is over.

*Review of the known dropping time of the larvae of the reindeer oestrids*

Figure 1 gives a summary of the published dropping periods of *H. tarandi* and *C. trompe* from Fennoscandia, Russia and North-America. Most reports agree that the dropping of larvae of *H. tarandi* starts in the latter part of April and ends in the latter part of June or the beginning of July. The peak of the dropping generally takes place between mid May to mid June. Gomoyunova (1976) mentioned that mass departure of larvae of *H. tarandi* from young reindeer starts 15 Apr – 31 May, whereas in older reindeer this occurs between 10 and 20 May. Solopov (1989) also reported that the dropping time varies with age of host in that emergence from adult reindeer takes place 14 – 19 days later than

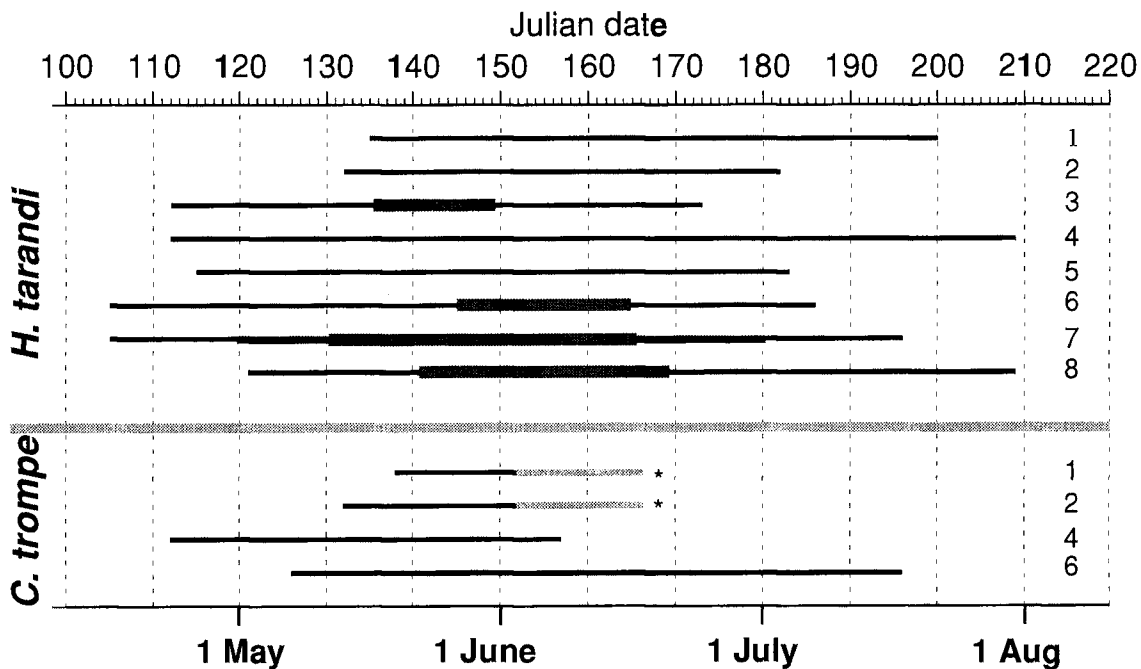


Fig. 1. Summary of published records of dropping periods of larvae of *H. tarandi* and *C. trompe*. Thicker portions of the lines denote mass departure of larvae. \*: End of dropping not given. The number after each line refers to: 1: Bergmann 1917 (Sweden). 2: Hadwen & Palmer 1922 (Alaska). 3: Palmer 1929 (Alaska). 4: Sdobnikov 1935 (Russia, Alaska). 5: Breyev & Karazeeva 1954 (NW Soviet Union). 6: Gomoyunova 1976 (Tsjuktsjer peninsula in Russia). 7: Solopov 1989 (various parts of northern Russia). 8: Nordkvist 1960 (Sweden).

Table 1. Host data and number of larvae of *H. tarandi* and *C. trompe* dropped from individual reindeer.

Sex	Sampling		<i>H. tarandi</i>		<i>C. trompe</i>
	Start	Stop	Larvae	Scars	Larvae
1988					
m	4 May	31 May	4	4	—
f	4 May	31 May	21	52	—
m	4 May	4 Aug	14	140	—
m	4 May	19 Sep	91	140	—
Sum 1988			130	336	—
1989					
m	18 Apr	20 July	14	24	—
f	18 Apr	20 July	43	73	—
m	18 Apr	7 July	34	80	—
m	18 Apr	21 June	7	23	—
f	18 Apr	7 July	19	30	—
m	18 Apr	7 July	70	154	—
m	18 Apr	21 June	151	151	—
f	18 Apr	20 July	16	27	—
m	18 Apr	21 June	30	41	—
Sum 1989			384	603	—
1990					
m	7 May	28 June	243	380	27*
f	7 May	26 June	16	31	1
f	7 May	28 June	77	170	0
Sum 1990			336	581	28
* In addition, 42 undropped larvae (alive L <sub>3</sub> ) were found at autopsy					
1991					
f	1 May	2 July	231	335	7
f	1 May	2 July	79	109	46
f	1 May	2 July	145	145	36
m	1 May	3 July	127	136	54
m	1 May	3 July	104	136	5
m	1 May	3 July	73	73	4
Sum 1991			759	934	152
1992					
f	5 May	26 June	42	55	1
f	5 May	26 June	137	228	7
m	5 May	26 June	78	78	27
f	5 May	26 June	82	91	12
m	5 May	26 June	257	286	34
Sum 1992			596	738	81

Sex: m = male; f = female. All reindeer were yearlings ( $\approx$  1 year old), naturally infected the preceding year when 2–3 months old. Start: Start of sampling. Stop: Slaughter of host. Scars: Scars after *H. tarandi* warbles under skin + undropped (dead or alive) larvae at slaughter of host. Origin of reindeer: 1988: District 17 (Tromsdalen, n=2) and 33 (Spalca, n=2); 1989: District 33 (Spalca); 1990, 1991, and 1992: District 37 (Skarfvaggi).

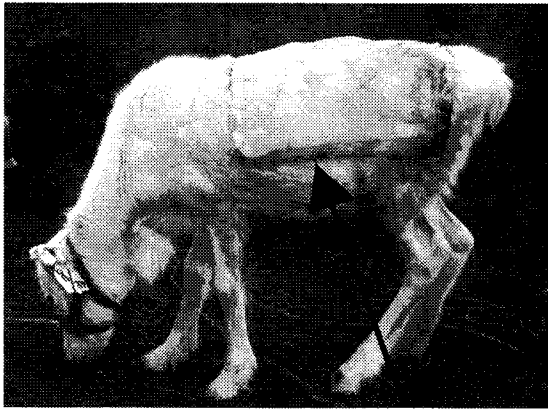


Fig. 2. The «collection cape technique» was used in 1988 and 1989 to collect *H. tarandi* larvae. The collection cape consisted of a nylon mesh fastened over the back of each animal. The mesh made a transparent bag into which the larvae collected when they emerged. The arrow points at one dropped larva.

those from young ones. The variability in dropping times also depends on climate, occurring latest in northern or more arctic climates.

The dropping periods of *C. trompe* have only been reported a few times (Figure 1). Generally, the departure time is similar to that of *H. tarandi*, lasting from end of April to the last part of June or beginning of July. Gomoyunova (1976) observed that the dropping of larvae of *C. trompe* (at Tsjuktsjer peninsula in Russia) was finished 10-15 July, somewhat earlier (15-20 days) in young reindeer. In her study, the dropping period lasted 63 and 71 days in 1968 and 1969, respectively.

Solopov (1989) showed that the emergence of *H. tarandi* larvae was not normally distributed but occurred in a series of pulses. He suggested two reasons for this:

1) The rate of dropping might be temperature dependent and warm weather during dropping might stimulate higher dropping rates.

2) The temporal pattern of infection might be temperature dependent, so that the dates of emergence of larvae might be controlled by the weather conditions in the previous summer.

In the present study, we have investigated the temporal pattern of emergence of larvae and compared this with temperature records to test these hypotheses.

## Material and methods

Naturally infected reindeer (age  $\approx$  11 months) were brought from their natural mountain pastures in

late April in 1988, 1989, 1990, 1991 and 1992 (Table 1). The animals were penned at Holt, Department of Arctic Biology, Tromsø, and given lichens and artificial fodder until slaughtering after the dropping period of the larvae. Two methods for collecting the larvae were used:

1. In 1988 and 1989, the reindeer yearlings were kept in a small outdoor corral. Pieces (1 x 1 m) of nylon mesh were fastened over the backs of the animals, so that all warbles of *H. tarandi* were covered. The mesh was fastened using Velcro strips, one of which was glued with Casco contact glue directly on to the fur while the other was sewn to the nylon mesh. When pressed together, these two strips adhere, and the mesh made a transparent bag into which the larvae collected when they emerged. The larvae were easily visible from the outside (Figure 2), and when present, could be collected by lifting the Velcro fastener. In this way, daily dropping from individual reindeer was registered. A similar technique has been used by Gregson (1958), Pfadt *et al.* (1975) and Barrett (1981) in collecting cattle grub larvae (*Hypoderma lineatum* and *H. bovis*). This technique will hereafter be denoted the «collection cape technique».

2. The «collection cape technique» did not catch *C. trompe* larvae because these are expelled via the nose or the mouth. There were also problems with the glue sticking to the hairs (especially when the shedding started). Consequently, in 1990, 1991 and 1992, larvae of both species were collected using the «grating technique». The reindeer were kept individually indoors in narrow (1 x 2 m) pens with slatted floors. They were not exposed to direct sunshine. Larvae fell through the slats and were collected on a wire mesh tray below, equal in size to each pen. Dropped larvae of both oestrid species were collected from each reindeer once a day.

The reindeer were slaughtered once dropping of larvae had stopped. Any remaining larvae of both species and scars from *H. tarandi* warbles under the skin were counted in each reindeer. In this way, a count of the total number of larvae (of *H. tarandi*) that had been present in the individual reindeer was obtained. There were no scars from previous infections, as might have been the case in adult animals, because the reindeer used here only had been infected one summer. Table 1 gives the sample size of the collected material and details about the host individuals.

In Figure 3, we have pooled the departure rate of *H. tarandi* from all reindeer for each of the five years

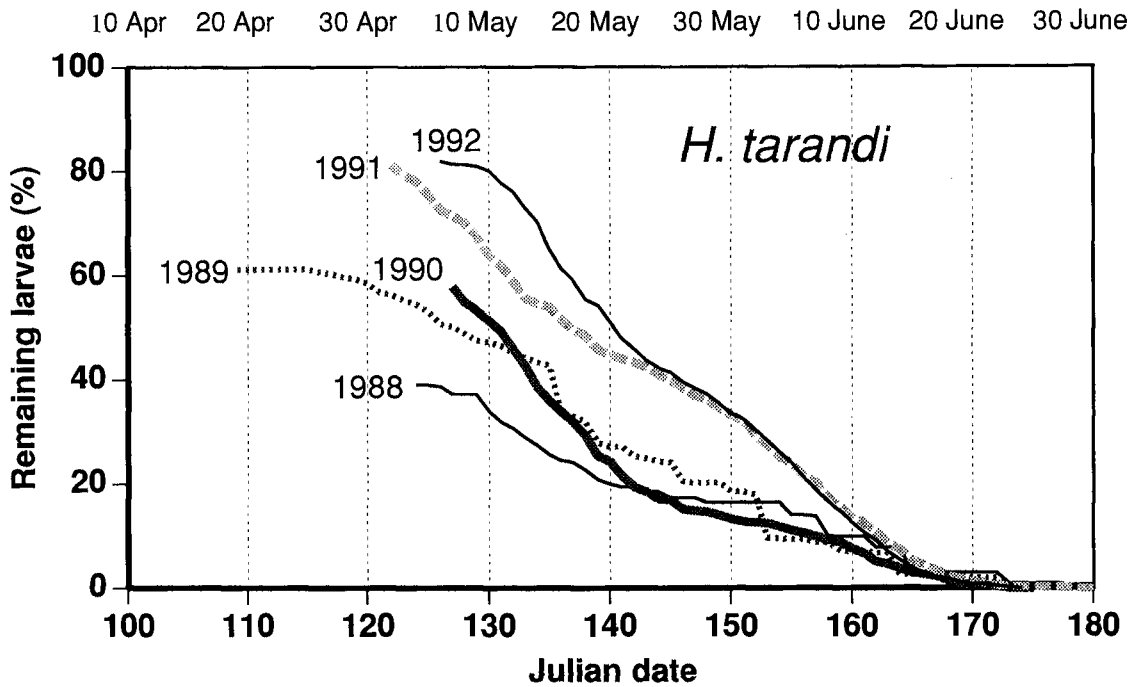


Fig. 3. Larvae of *H. tarandi* remaining in the host as a function of date from 5 years of investigation. (Sample sizes, see Table 1). 100 % is based on counting of larval scars at autopsy.

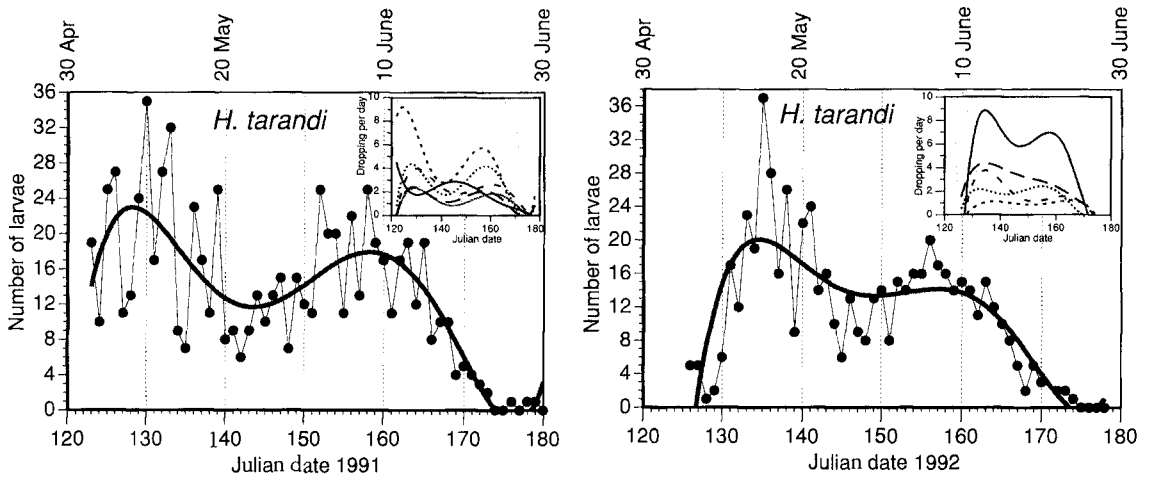


Fig. 4a and 4b. Daily departure of *H. tarandi* larvae from 6 reindeer yearlings in 1991 and 5 reindeer yearlings in 1992 as a function of date. The inserted graphs show the departure rates from individual reindeer. Curve fitting: Polynomial regression of degree 5.

of investigation. Percent remaining larvae are based on the number of scars. The curves in Figure 3 were calculated this way:

$$R\%_n = [(L - L_n) * 100] / S$$

where  $R\%_n$  is percent remaining larvae on day  $n$ ,  $L$  = the total number of larvae collected,  $L_n$  = the

cumulative sum of larvae found until day  $n$ , and  $S$  = number of scars. The calculated  $R\%_n$  values were plotted on the y-axis and the corresponding  $n$  (Julian dates) on the x-axis.

The effect of date and temperature during dropping on daily dropping rate of *H. tarandi* in 1991 and 1992 was examined by multiple regression where the number of larvae/day was the dependent

Table 2. Results from multiple regression of the influence of Julian date and mean temperature upon departure of *H. tarandi* larvae from host in 1991 and 1992.

Model:  $Number\ of\ larvae = Constant + Julian\ date + Daily\ mean\ temp.$

1991:

ANOVA:  $F_{2,55} = 24.64, p < 0.00001$

Regression:

	Standard coefficient	T	Multiple R <sup>2</sup>	p (2-tail)
Julian date	- 1.17	- 6.01	0.36	< 0.00001
Mean temp	0.65	3.35	0.13	0.00146

1992:

ANOVA:  $F_{2,41} = 13.93, p = 0.00002$

Regression:

	Standard coefficient	T	Multiple R <sup>2</sup>	p (2-tail)
Julian date	- 0.74	- 5.09	0.36	0.00001
Mean temp	0.25	1.73	0.03	0.09168

variable, and Julian date and daily mean temperature were independent variables. Daily mean temperatures in the infection period (July and August 1990 and 1991) for the larvae dropped in 1991 and 1992 were examined visually to determine whether any discrete and distinctly favourable periods for infection might have existed. All climate data were obtained from The Weather Bureau of Northern Norway, Tromsø. The statistical tests and analyses were performed using Systat (1992).

## Results

The pattern of dropping of *H. tarandi* in different years is shown in Figure 3. Evidently sampling started too late to detect the start of dropping, except in 1989. The dropping is finished around 20 June all years.

Larval departure was highly variable in both 1991 and 1992 (Figures 4a and 4b). In both years there appeared to be two separate peaks of dropping, the first around 10 – 20 May the second around 1 – 10 June. This bimodal pattern of dropping was synchronous among individual reindeer (inserted curves in Figures 4a and 4b). Pairwise comparison of daily dropping of larvae between individual reindeer gave the following Spearman's rank correlation coefficients ( $r_s$ ): 1991: mean  $0.28 \pm 0.13$  SD, range:  $-0.04 - 0.48$  (6 reindeer; 15 comparisons); 1992: mean  $0.35 \pm 0.16$  SD, range:  $0.09 - 0.55$  (5 reindeer; 10 comparisons).

The multiple regression analyses of possible effects of mean temperature (during the dropping

period) on daily dropping are given in Table 2. Temperature data from the infection area for July and August 1990 and 1991 (the infection period for the 1991 and 1992 sample, respectively) are depicted in Figure 6.

Figures 5a and 5b show the departure rate of *C. trompe* larvae for the years 1991 and 1992. A trend of bimodality in the departure rate may be traced as for *H. tarandi*. How many larvae were dropped before the sampling period is unknown because this species leaves no scars, but we assume that the sampling period covered the mass emergence. The first dropped larva were observed on 18th April, before the animals arrived at Tromsø. With one exception, no larvae remained at time of autopsy (Table 1).

## Discussion

There are three reasons for the difference between the number of scars and number of larvae of *H. tarandi* (Table 1). First, larvae were dropped before the sampling period. Second, some larvae were lost. This was a problem particularly in 1988 and 1989 when the «collection cape technique» was used. Third, some of the counted scars originated from dead larvae and thus, the number of larvae that were able to drop was overestimated.

In 1988, 1990, 1991 and 1992 we obtained the reindeer too late to observe the first larval departure. Inspection of the dropping curves for 1991 and 1992 shows that <20% of *H. tarandi* could have dropped before 1 and 5 May, respectively. In 1989, we obtained the reindeer 18 Apr, at a date when no

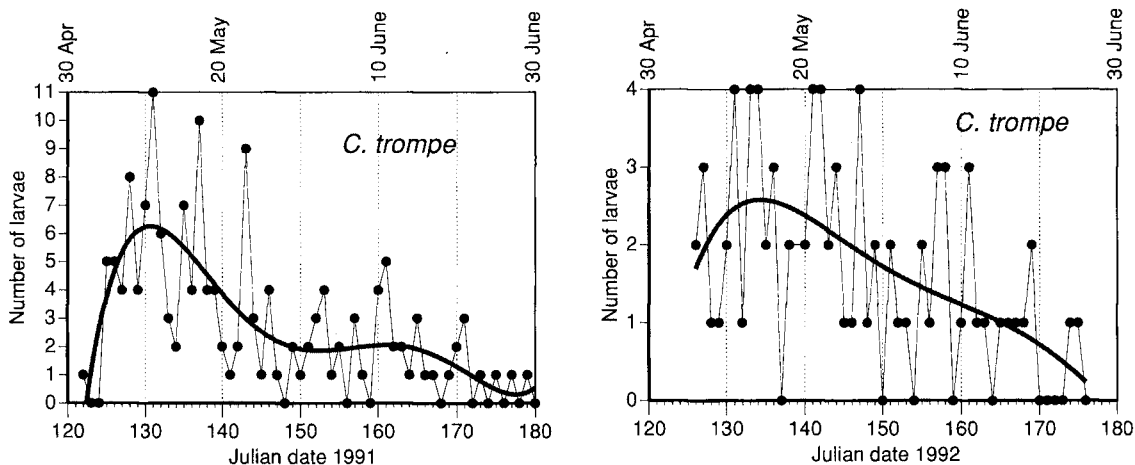


Fig. 5a and 5b. Daily departure of *C. trompe* larvae from 6 reindeer yearlings in 1991 and 5 reindeer yearlings in 1992 as a function of date. Curve fitting: Polynomial regression of degree 5.

emergence could be observed, see the horizontal start of the 1989-curve in Figure 3. First dropping occurred on 26 Apr. The highest dropping rate normally occurred from 10 to 20 May, but another high rate often took place later (around 10 June) (Figures 4a and 4b). In all years, the emergence is virtually completed around 20 June.

The observed departure rates of larvae of *H. tarandi* coincides well with results published by Solopov (1989) for reindeer calves (= yearlings) from the northern Taiga area of Russia, in which the dropping started around 20 Apr, with a mass departure from 10 May to 20 May. The end of departure in Russia (5 June) was, however, somewhat earlier than in our study (20 June).

The timing of the departure of *C. trompe* larvae coincides with the departure of *H. tarandi*, and dropping of *C. trompe* larvae is usually completed around 20 June (Figures 5a and 5b). Reindeer with high infection levels, may, however, continue to drop the larvae after this date. One reindeer harboured 42 third instar larvae as late as 28 June 1990 (Table 1). Some larvae may therefore drop during July. Larval development is density dependent (crowding effects) and influences the length of dropping period (Nilssen & Haugerud, accepted).

Solopov (1989) found that the departure of *H. tarandi* larvae was dependent on the climate, with a later departure in a colder climate. In a region called «sub-arctic tundra», the larval dropping started around 15 May and lasted until 10–15 July. He also found that calves (= yearlings) dropped earlier than did older animals. This was not tested in the present study, as we only used yearlings.

Like Solopov (1989), we observed two separate, synchronous mass droppings of *H. tarandi* larvae (Figures 4a and 4b). In hypothesis 1) cited in the introduction, the departure rate is a function of both the date and the temperature during dropping. The number of remaining larvae determines how many larvae can be dropped and therefore declines with date (Figure 3). Consequently, Julian date and remaining larvae are highly correlated ( $R = 0.99$ ), and date therefore equally well accounts for the decline due to decreasing number of larvae to drop. Date explained 36 % of the variance in the number of dropped larvae, whereas the mean temperature alone (when variance due to date has been accounted for) explains 13 % ( $p = 0.0015$ ) and 3 % ( $p = 0.09$ ) for the years 1991 and 1992, respectively

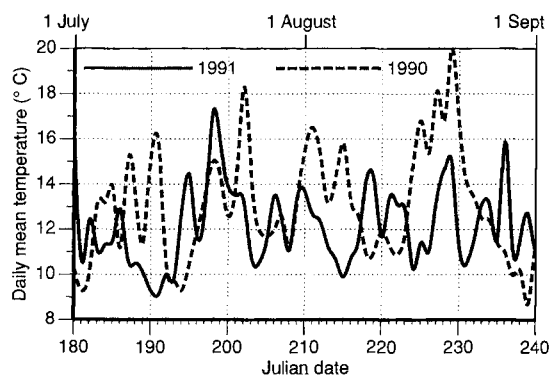


Fig. 6. Daily mean temperature fluctuations for July and August 1990 and 1991 near the infection area for the reindeer used in 1991 and 1992. The highest peaks between 10 July and 20 Aug are supposed to be the periods with mass attacks by the bot flies.

(Table 2). We therefore conclude that the mean temperature has little effect on the departure rate. However, the reindeer in the experiment were not exposed directly to sunshine. Under natural conditions, there is still a possibility that the strong warming by sun radiation directly on the fur, and thereby the larvae beneath, accelerates the emergence of larvae. The statement of Skjenneberg & Slagsvold (1968) that the *H. tarandi* larvae preferably crawl out during warm, nice weather, may therefore be correct. In our study, the date (which was closely correlated with the number of remaining larvae) is the major determinant of departure rate. However, neither date nor the mean temperature during dropping explain the observed pattern of dropping peaks.

With the present data, it is not possible to test hypothesis 2) directly, where temperature during infection explains the separated peaks. Infection takes only place during warm days (above 12 – 14° C, with mass attacks at higher temperatures). Attacks seldom occur before 10 July, and normally end around 20 Aug (unpublished results). As there will be a positive correlation between ambient temperature and attack rate, we expect that certain days (or periods of days) will give higher infection. In Figure 6 the daily mean temperatures in July and August (the main infection period) 1990 and 1991 are plotted for a weather station (Nordstraum in Kvænangen) near the summer pastures of the reindeer used in 1991 and 1992. We observe that in 1990 there are three periods with high temperatures between 10 July and 20 Aug, namely around 20 July, 5 Aug and 17 Aug. These supposed periods of mass attacks may well be reflected in the uneven larval dropping observed in 1991 (Figure 4a). Similarly, in 1991 the supposed major attacks occurred around 16 July, and 1, 10 and 20 Aug (Figure 6), causing the separated peaks of dropping of larvae observed in 1992 (Figure 4b).

In our view hypothesis 2), with temperature during the infection period as the explanation for the uneven larval departure, is the most likely one. If there is a time difference of many weeks between the first and last infection, it is likely that the maturing time of the larvae will be different and consequently also the larval emergence. This is consistent with Saveljev (1968), who stated that time for removing the larvae in spring (for killing) should be postponed by approx. 2 weeks if the warble fly season was very late the previous year. Many other factors, such as density of larvae and condition of the

host, may however be involved. There may also be a selection for early or late larval emergence dependent on factors like local climate and migratory habits of host. Only experimental infection and otherwise controlled conditions can give conclusive evidence.

#### *Applied perspectives*

The reindeer oestrids are responsible for economic losses in the reindeer management (Saveljev, 1968; Nordkvist *et al.*, 1983), and different control measures have been applied. One «ecological» method is to separate the reindeer (in time and distance) from dropping sites of the larvae to infections sites (summer grazing areas).

We have established that the departure of both species of oestrids occurs between 20 Apr and 20 June. Thus, if the reindeer are moved to their summer pasture before 1 May, nearly all the larvae will be taken into the summer grazing land. The adult bot flies emerging in this area will consequently have short flying distances to find their host. Even if these flies are excellent fliers (Nilssen & Anderson, *in press*), distance *per se* is generally of importance for the infection levels (Folstad *et al.*, 1991; Nilssen & Haugerud, *accepted*).

In northern Norway, some herds of reindeer spend the summer grazing on islands. The reindeer are brought there by ship. In current practice, this takes mostly place during the last part of April. Consequently, nearly all larvae are brought to the summer pastures, with possibilities for high infection levels of oestrids. If, on the other hand, this transport of reindeer could be postponed until 20 June, most of the larvae would be dropped far away from the summer ranges. Postponement of the spring migration could also be tried on herds with summer grazing ranges on the mainland. However, the migratory pattern is highly traditional and difficult to change. The cost and trouble of changing the spring migration time will probably be greater than the harm caused by the oestrids. A very late spring migration will also be in conflict with the current management strategy to reduce grazing in the limited spring and autumn pastures. In the old, traditional husbandry system, the reindeer spent more time to reach the coast in spring, leading to more larval dropping along the migration route instead of the summer area. Therefore, the traditional migration system undoubtedly was a better anti-oestrid strategy than current practice. Today, the only antioestrid «strategy» used in management



is efficient medical treatment (e.g. ivermectin) (Nordkvist, 1984; Nordkvist *et al.*, 1984), being carried out to an ever increasing extent (Heggstad, 1988; Haugerud *et al.*, 1993). However, the need for treatment against oestrids can be reduced if the reindeer management make use of the «ecological» possibility to lower the infection levels of these two important parasites by altering the spring migration time.

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