No interspecific covariation in intensities of macroparasites of reindeer, *Rangifer tarandus* (L.)

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SUMMARY

The macroparasites *Cephenemyia trompe* (Modeer) and *Hypoderma* (= *Oedemagena*) *tarandi* (L.) (Diptera: Oestridae), *Linguatula arctica* Riley, Haugerud and Nilssen (Pentastomida: Linguatulidae), *Elaphostrongylus rangiferi* Mitskevich (Nematoda: Protostrongylidae), and abomasal nematodes (Nematoda: Trichostrongylidae) were sampled in semidomestic reindeer calves (*Rangifer tarandus* (L.)) (ca. 8 months of age) in northern Norway in 1988 ($n = 160$) and 1989 ($n = 191$). Each parasite showed an aggregated (clumped) distribution among the hosts and fitted the negative binomial distribution. Analyses of interspecific associations in intensities showed that there was no consistent covariation among the parasites apart from a weak correlation (Kendall's *tau* 0·104, $P = 0{\cdot}007$) between the 2 oestrids *C. trompe* and *H. tarandi*. This lack of covariation reveals that the parasites were distributed independently of each other, and suggests that innate host resistance is not a dominant factor that has a significant simultaneous effect on all parasites. The aggregated distribution of each parasite species is hypothesized to be caused by (1) random events and heterogeneities in host behaviour that create unequal transmission (exposure) rates, or (2) by heterogeneities in parasite specific immunocompetence among host individuals. Factors in hypothesis (1) are probably the most important at low transmission rates.

Key words: *Cephenemyia trompe, Hypoderma* (= *Oedemagena*) *tarandi, Linguatula arctica, Elaphostrongylus rangiferi, Rangifer tarandus*, interspecific covariation, multiple-species infections.

INTRODUCTION

Parasite burden in individual hosts is a function of transmission rates (i.e. exposure), establishment, and parasite mortality (Bundy & Medley, 1992). The frequency of parasites among individual hosts is often very aggregated (= clumped or overdispersed) and it is described empirically by the negative binomial distribution (e.g. Breyev, 1968*a*, *b*; Crofton, 1971; Anderson, 1982; Esch & Fernández, 1993; Shaw & Dobson, 1995). This implies that the parasites are not equally 'shared' among the host individuals: some harbour no, or a few, parasites, whereas a few have a very high burden of parasites, often called 'wormy hosts' (Croll & Ghadirian, 1981; Guyatt & Bundy, 1990). Whereas the general infection level (expressed as prevalence, mean intensity and abundance (Margolis *et al.* 1982)) is caused by a variety of factors and is well studied, the causes for the aggregated distribution are not well understood (e.g. Esch & Fernández, 1993; Tanguay & Scott, 1992; Shaw & Dobson, 1995).

At least 3 hypotheses have been proposed to explain why certain individual hosts carry excessive parasite burdens (Croll & Ghadirian, 1981). (1) All host individuals may be equally exposed to infection but some may have increased susceptibility. (2) Host individuals with excessive burdens may perform some behavioural traits that increase their rate of exposure (increased transmission). (3) Aggregation may result from the superimposition of several random events.

The first hypothesis implies that there is heterogeneity in resistance or immunocompetence among individual hosts by predisposition through genetic or physiological mechanisms causing a higher parasite establishment and survival in a few individuals (see Sorci, Møller & Boulinier, 1997). The second hypothesis indicates that certain individuals (for instance for behavioural reasons) come more easily in contact with the transmission stage of the parasite. There is no easy way to distinguish between these hypotheses as they may not be mutually exclusive. Besides, for some parasites the degree of aggregation has been shown to decrease with increased infection level (abundance or prevalence) (Nilssen & Haugerud (1995) and references therein).

If heterogeneity in *general* (non-specific) resistance/immunocompetence (hypothesis 1 above) is a dominant factor in explaining the variability in parasite burden, it can be expected that it has a similar effect on the whole assemblage of parasite

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species (the meta-population) in a given host population. In other words, if this factor is sufficiently strong, it may be predicted that the larval burdens (the infrapopulations) of the different parasite species show a tendency to positive covariation. Few studies of interspecific covariation in parasite intensities within a host population seem to have been reported, at least in large mammals. In humans, multiple-species infections have been investigated by Croll & Ghadirian (1981) (intensity data) and Booth & Bundy (1995) (prevalence data). Most studies have focused on 1 or a few of the parasite species, although free-living hosts are frequently challenged with multiple infections. In this study we have analysed the covariation and the pattern of frequency distributions of macroparasites of reindeer, *Rangifer tarandus* (L.). A review of the parasites of reindeer has been given by Halvorsen (1986).

MATERIALS AND METHODS

The host material of semi-domesticated reindeer (*Rangifer tarandus tarandus* (L.)) was obtained at the slaughter house in Kautokeino in early January 1988 ($n = 160$) and 1989 ($n = 191$). The reindeer were 8-month-old calves and consisted mostly of males (83·8 % in 1988, 71·6 % in 1989). This age group was the largest homogeneous sample slaughtered and could be regarded as naïve with respect to previous infections of parasites. The reindeer originated from 8 different management districts (6 districts in 1988, 6 districts in 1989) in western Finnmark, northern Norway. The staff at the slaughter house provided each reindeer with individual numbers, which were recorded with age, sex, weight and origin (management district).

The reindeer were sampled to obtain individual intensities (= infrapopulations) of the following 5 parasites. (1) The reindeer warble fly *Hypoderma* (= *Oedemagena*) *tarandi* (L.) (Diptera: Oestridae). Second instar larvae were counted under the skin on raw hides at the slaughter house (for methods, see Folstad *et al*. (1989)). (2) The reindeer nose bot fly *Cephenemyia trompe* (Modeer) (Diptera: Oestridae). (3) The reindeer sinus worm *Linguatula arctica* Riley, Haugerud and Nilssen 1987 (Pentastomida: Linguatulidae). Heads of slaughtered animals were individually marked, frozen and sent to the laboratory. *L. arctica* was sampled by scrutinizing the sinuses (for methods, see Haugerud (1988)) and first instars *C. trompe* were sampled with a rinsing-sieving technique as described by Nilssen & Haugerud (1995). (4) The reindeer brain worm *Elaphostrongylus rangiferi* Mitskevich (Nematoda: Protostrongylidae). Faeces were taken from the rectum of recently slaughtered animals, frozen and then brought to the laboratory for sampling. The density of larvae (expressed as number per gramme faeces) was estimated using the extraction method described by Halvorsen & Wissler (1983). (5) Adult abomasal nematodes (Nematoda: Trichostrongylidae). Abomasa were taken from recently slaughtered animals, frozen and brought to the laboratory for sampling. Larval burdens (expressed as worms per reindeer) were estimated from subsampling nematodes in the abomasum with a technique described by Bye (1987). The nematodes were not identified to species, but previous studies (Bye, 1987) have shown that about 80 % of abomasal nematodes in Norwegian reindeer belong to *Ostertagia grühneri* Skrjabin.

Propagules of other macroparasites (e.g. intestinal nematodes *Nematodirus* spp.) were sampled from faeces, but their prevalences were either so low or the sampling technique so unreliable (own unpublished data) that these were not included in this study.

Covariation between intensities (infrapopulations) of different parasite species were analysed in pairwise correlation tests. Due to skewed distributions, many zeroes and tied ranks, Kendall's rank correlation test (Kendall's *tau*) was chosen (see Norman & Streiner, 1986), but Spearman's *rho* gave similar results. To test for covariation between 3 or more parasites, Friedman 2-way ANOVA followed by Kendall coefficient of concordance was used. Analyses were performed separately for each district within years, but also on all reindeer using standardized data. To do this, parasite numbers were first $\log_{10}(x+1)$-transformed and then standardized (z-scores: mean = zero, S.D. = 1) within each district/year. In this way, we could control for any district or year effect on the infection level which otherwise might give false correlations, and the complete material could be used in 1 test for each pair of parasites.

Frequency distribution and level of aggregation were also analysed. There seems to be some controversy about what index should be used in measuring degree of aggregation among hosts (e.g. Scott, 1987; Hurlbert, 1990), but we used the negative binomial parameter, κ, as also recently has been used by, for example, Quinnell, Grafen & Woolhouse (1995) and Grenfell *et al*. (1995).

All statistical tests and analyses were carried out using the statistical software SYSTAT 5.2 (SYSTAT, 1992). The pattern of parasite aggregation for each parasite species was compared with the negative binomial distribution using the maximum likelihood method described by Elliott (1977) and Krebs (1989). The model parameter κ and the U-statistic goodness-of-fit were calculated by means of a spreadsheet. Parasitological terminology used is that of Margolis *et al*. (1982).

RESULTS

The infection levels (prevalence and abundance) in each district and year for all parasites sampled is summarized in Table 1. The abundance did not

Table 1. Epizootiological data on the sampled reindeer macroparasites

(*n*, number of reindeer sampled for the parasite; Prev, prevalence (%); Abundance, mean infection (for definitions, see Margolis *et al.* 1982); Max, maximum intensity found in 1 reindeer; κ, coefficient in the negative binomial distribution. For *E. rangiferi*, intensity of larvae is expressed as number per gramme faeces; for the other parasites total numbers per reindeer are given (see Methods). District: 20: Kvaløy, 23: Seainnus, 24: Seiland, 26: Lakkonjarga, 27: Joahkonjarga, 28: Bergsfjord, 29: Frakfjord/Silda, 34: Aborassa (all in West-Finnmark management region).

		C. trompe					*L. arctica*					*H. tarandi*					*E. rangiferi*					Abomasal nematodes				
Year	District	*n*	Prev.	Abundance	Max.	κ	*n*	Prev.	Abundance	Max.	κ	*n*	Prev.	Abundance	Max.	κ	*n*	Prev.	Abundance	Max.	κ	*n*	Prev.	Abundance	Max.	κ
1988	20	38	60·5	6·66	57	0·30	38	73·7	5·53	23	0·67	42	95·2	26·95	96	0·85	41	7·32	3·31	70	0·01	—	—	—	—	—
1988	23	11	72·7	4·18	14	0·65	11	63·6	2·91	11	0·70	12	100·0	43·17	132	2·70	12	33·3	31·72	322	0·08	—	—	—	—	—
1988	24	40	50·0	2·65	55	0·26	40	77·5	9·78	34	0·61	49	100·0	46·78	222	1·32	34	26·5	11·86	120	0·06	—	—	—	—	—
1988	27	22	54·6	6·68	42	9·27	22	77·3	5·95	18	1·02	24	100·0	64·21	320	0·71	24	50	53·76	323	0·11	—	—	—	—	—
1988	28	10	30·0	3·90	19	0·11	10	80·0	6·90	26	0·64	10	100·0	66·10	142	2·17	3	33·3	0·73	2·2	0·45	—	—	—	—	—
1988	34	16	62·5	2·88	12	0·58	16	75·0	2·69	12	0·96	23	100·0	50·57	240	0·92	22	4·55	0·05	1·2	—	—	—	—	—	—
1989	23	4	100·0	25·50	79	0·58	4	100·0	7·25	14	1·65	4	100·0	116·50	340	1·33	0	—	—	—	—	—	—	—	—	—
1989	24	58	81·0	9·22	55	0·73	58	81·0	6·38	24	0·83	57	100·0	39·54	240	1·25	38	65·8	80·61	606	0·38	38	100	555·60	1121	3·70
1989	26	45	91·1	20·24	84	0·91	45	75·6	6·18	31	0·59	45	100·0	55·16	230	2·42	19	63·2	273·58	1172	0·01	16	100	122·70	197	5·15
1989	27	35	74·3	11·77	71	0·48	35	69·4	6·14	36	0·44	29	100·0	50·97	138	2·98	0	—	—	—	—	—	—	—	—	—
1989	28	21	81·0	12·48	48	0·65	21	81·0	15·10	46	0·73	18	100·0	89·67	212	3·68	0	—	—	—	—	—	—	—	—	—
1989	29	27	92·6	10·81	47	1·02	27	66·7	8·70	48	0·39	12	100·0	73·67	158	1·71	0	—	—	—	—	—	—	—	—	—
1988	All	137	55·5	4·65	57	0·28	137	75·2	6·39	34	0·62	160	98·8	45·67	320	0·99	136	22·1	16·27	323	0·10	—	—	—	—	—
1989	All	190	84·2	13·23	84	0·69	191	75·9	7·59	48	0·56	165	100·0	55·62	340	1·64	58	63·8	142·43	1172	0·32	54	100	427·30	1121	1·85

differ significantly between the sexes for any of the species ($P = 0{\cdot}10$–$0{\cdot}59$ in ANOVAs on $\log_{10}(x+1)$-transformed infrapopulations data with year or district as covariate), and the sexes were therefore pooled in the table and in all analyses.

The abundance differed significantly between years and between some districts within years for a majority of the sampled parasites, and to obtain homogeneous groups and to avoid false correlations caused by covariation in the *general* infection level, analyses were first performed for each district and year. This gave up to 12 separate tests for each pair (or set) of parasites with comparatively small sample sizes.

The correlation coefficients (Kendall's *tau*) for each pair of parasites for each district and year are shown in Table 2. The joint coefficients (based on standardized data, see Materials and Methods section) and also shown.

In general, the coefficients are distributed almost equally around zero, which indicate no covariation (Table 2). There are a few significant correlations in some districts for some of the pairs of parasites (Table 2), but the only coefficients consistently deviating from zero were those between the oestrid species *H. tarandi* and *C. trompe*. The correlation between these species was positive in 8 of 11 district-years (Fig. 1A), and the overall coefficient was positively significant (Kendall's *tau*: 0·104, $P = 0{\cdot}007$, Spearman's *rho*: 0·15, $P = 0{\cdot}009$). Scatter diagrams of infrapopulations ($\log_{10}(x+1)$-transformed) of *C. trompe* and *H. tarandi* are shown in Fig. 3. Coefficients of determination (r^2) of 0·004 and 0·08 for 1988 and 1989, respectively, imply that $\leqslant 8\,\%$ of the variability in one oestrid can be predicted by means of other oestrid species.

The few significant correlations observed in the other pairs of parasites are not part of a pattern, and would with a Bonferroni correction be insignificant. Besides, the 'overall' tests were far from significant with Kendall's *tau*'s close to zero.

The Friedman 2-way ANOVA and Kendall concordance tests, used to test the covariation between more than 2 parasites were insignificant apart from a significant concordance between *C. trompe*, *H. tarandi* and *L. arctica* in District 24 1989 ($W = 0{\cdot}45$; $n = 57$; $P = 0{\cdot}05$), and for all districts combined in 1989 ($W = 0{\cdot}41$; $n = 165$; $P = 0{\cdot}02$). This, however, is only caused by the positive covariation between *C. trompe* and *H. tarandi*, as shown earlier, because *L. arctica* did not exhibit any significant association with oestrid species (Table 2).

Table 1 shows interesting differences in abundance between years for some parasites. In *C. trompe*, the abundance was nearly 3 times higher in 1989 than in 1988 (Mann–Whitney U: 6767·5, $P < 0{\cdot}0001$). In *H. tarandi*, the abundance was slightly higher in 1989 than in 1988 (55·62 and 45·67, respectively), but significant (Mann–Whitney U:

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Table 2. Correlation coefficients (Kendall's *tau*) between pairs of parasites for each district within years

(The overall correlations for each year are based on standardized data to control for differences in general (mean) larval burdens; see text for further explanation.)

District-year	*n*	Kendall's *tau*	*P*
C. trompe versus *H. tarandi*			
20-88	38	−0·07	0·52
23-88	11	0·23	0·33
24-88	40	0·09	0·42
27-88	22	0·28	0·07
28-88	10	0·28	0·26
34-88	16	−0·41	0·03
26-89	45	0·05	0·62
27-89	29	−0·13	0·31
28-89	18	0·27	0·12
29-89	12	0·36	0·11
24-89	57	0·26	0·004
Overall	298	0·10	0·007
C. trompe versus *E. rangiferi*			
20-88	37	−0·07	0·57
23-88	11	−0·46	0·05
24-88	27	0·07	0·63
27-88	22	−0·05	0·74
34-88	16	−0·26	0·17
26-89	19	−0·04	0·79
24-89	38	0·03	0·80
Overall	170	−0·03	0·54
C. trompe versus *L. arctica*			
20-88	38	0·13	0·25
23-88	11	0·00	0·99
24-88	40	0·12	0·29
27-88	22	−0·14	0·38
28-88	10	0·09	0·70
34-88	16	−0·16	0·40
26-89	45	0·16	0·11
27-89	35	−0·17	0·15
28-89	21	−0·05	0·75
29-89	27	0·18	0·19
24-89	58	0·05	0·60
Overall	323	0·03	0·35
L. arctica versus *H. tarandi*			
20-88	38	−0·01	0·93
23-88	11	−0·06	0·80
24-88	40	0·10	0·36
27-88	22	−0·02	0·88
28-88	10	−0·09	0·70
34-88	16	0·40	0·03
26-89	45	0·09	0·40
27-89	29	0·05	0·70
28-89	18	−0·16	0·35
29-89	12	−0·19	0·38
24-89	57	0·05	0·60
Overall	298	0·05	0·23
L. arctica versus *E. rangiferi*			
20-88	37	−0·16	0·18
23-88	11	0·30	0·20
24-88	27	−0·11	0·41
27-88	22	−0·12	0·43
34-88	16	−0·10	0·58
26-89	19	−0·38	0·02
24-89	38	0·01	0·91
Overall	170	−0·06	0·22
E. rangiferi versus *H. tarandi*			
20-88	41	0·14	0·21
23-88	12	−0·16	0·50
24-88	34	−0·20	0·09
27-88	24	0·29	0·05
34-88	22	0·13	0·39
26-89	19	0·13	0·43
24-89	37	−0·02	0·83
Overall	189	0·04	0·43
Abomasal nematodes versus *C. trompe*			
26-89	16	−0·09	0·62
24-89	38	−0·03	0·79
Abomasal nematodes versus *H. tarandi*			
26-89	16	0·34	0·06
24-89	37	0·14	0·22
Abomasal nematodes versus *L. arctica*			
26-89	16	−0·04	0·85
24-89	38	−0·10	0·36
Abomasal nematodes versus *E. rangiferi*			
26-89	16	0·38	0·04
24-89	33	−0·07	0·58

10374·5, $P < 0·0009$). Also in *E. rangiferi* abundance was significantly higher in 1989 than in 1988 (Mann–Whitney U: 2077, $P < 0·0001$), but *L. arctica* seems to have very stable mean infection levels between years (Mann–Whitney U: 12594, $P = 0·56$) and between districts (Kruskal–Wallis test statistic = 17·8, D.F. = 11, $P = 0·085$). The summer 1987 was very cold (July mean at a representative weather station (Suolovuopmi in Finnmark county) was 9·5 °C) and rainy, whereas the summer of 1988 was unusually warm (July mean: 13·6 °C) (data from The Weather Bureau of northern Norway in Tromsø). Abomasal nematodes were only sampled in 1989 (2 districts, Table 1). The abundance in these 2 districts differed significantly Mann–Whitney U: 5·0, $P < 0·001$).

Table 1 includes the calculated parameter κ in the negative binomial distribution for each district and for each year pooled. The null hypotheses that the negative binomial fits the data could not be rejected at the $P < 0·05$ level (U-statistic goodness-of-fit test, Krebs, 1989) for any of the parasites apart from *C. trompe* in District 24 1988. A low value of κ means high aggregation. *E. rangiferi* was the most aggregated species with κ-values from 0·01 to 0·45 (Table 1). *H. tarandi* was less aggregated than *C. trompe* (compare the κ-values in Table 1). *L. arctica* had an intermediate aggregation (κ-values from 0·39 to 1·65), with prevalences around 75 % and a maximum burden of 48 worms/host. Most extreme numbers of the latter species are probably limited by space in the sinuses and the nasal cavity. The abomasal nematodes were present in all investigated animals and

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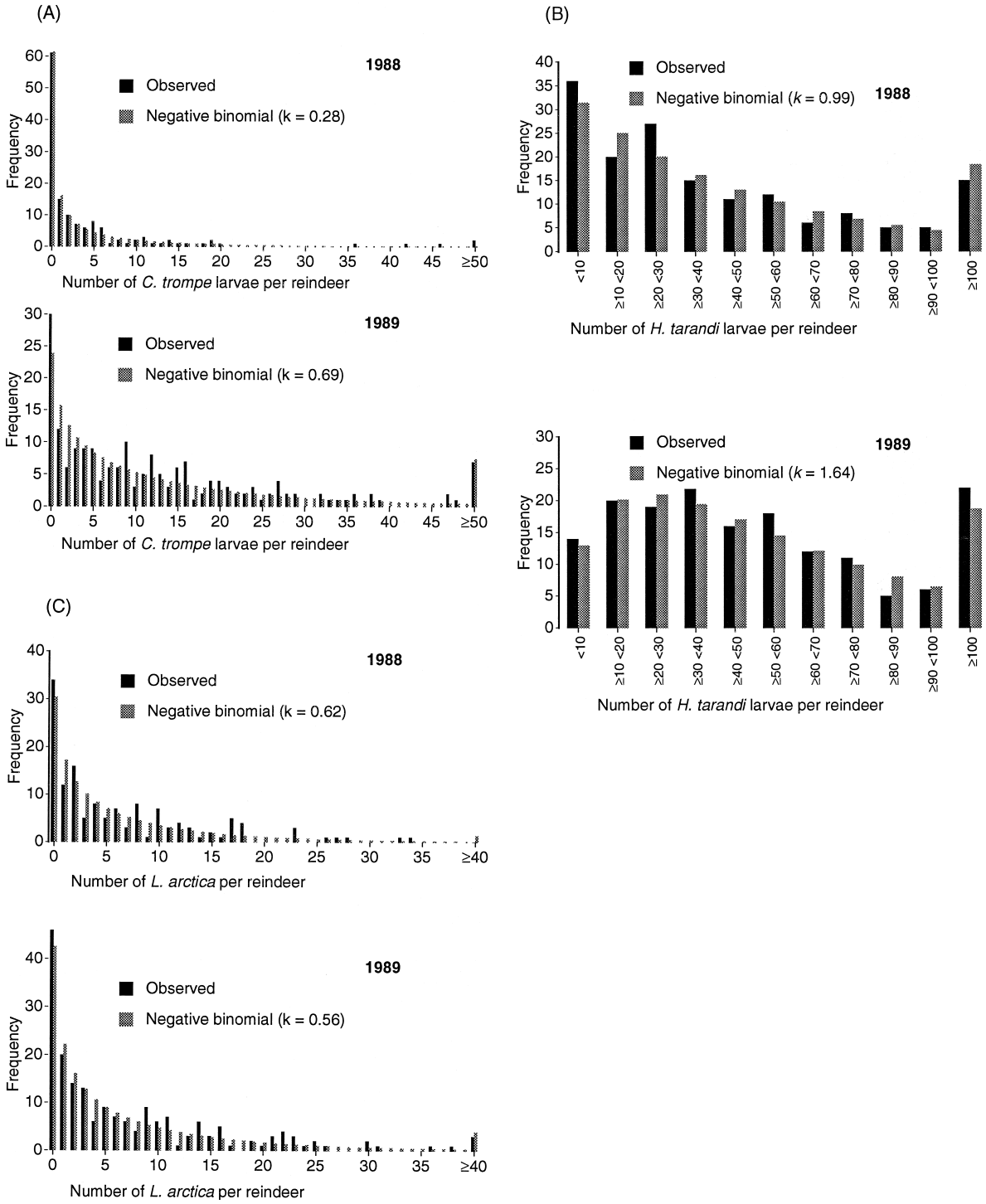

Fig. 1. Observed frequencies compared with frequencies fitted to the negative binomial distribution for *Cephenemyia trompe* (A), *Hypoderma tarandi* (B) and *Linguatula arctica* (C), pooled within years.

was the least aggregated among the tested parasites (κ up to 5·15).

In Fig. 2A–C, observed frequencies are compared with the calculated negative binomial distributions in *C. trompe*, *H. tarandi* and *L. arctica* for the 2 sampling years. The overall fit is good. The values of κ for each district (Table 1) are plotted against prevalence (or abundance in *H. tarandi* since nearly all districts had 100% prevalence (Table 1)) in Fig. 2 to observe if aggregation decreased with (general) infection level. The value for κ increased (i.e. aggregation decreased) significantly with infection level for *C. trompe* and *L. arctica*, but not for *H. tarandi* and *E. rangiferi*.

DISCUSSION

The general lack of covariation in infrapopulations among the parasite species suggests that any innate

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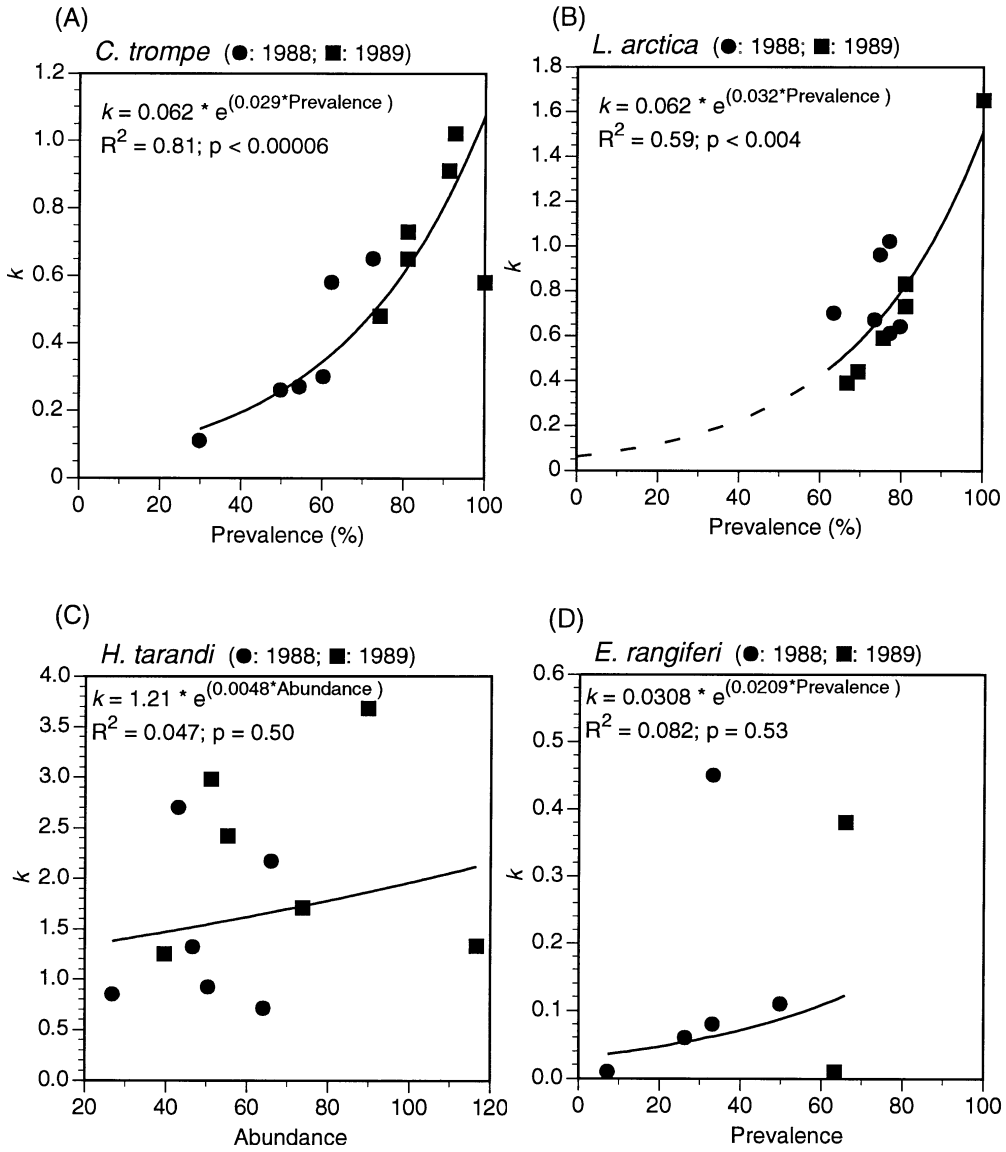

Fig. 2. The binomial parameter κ plotted against prevalence (or abundance in *Hypoderma tarandi* because the prevalence was nearly always 100% in this species, see Table 1). An exponential function was fitted to the data as there seemed to be a non-linear relationship. (A) *Cephenemyia trompe*; (B) *Linguatula artica*; (C) *Hypoderma tarandi*; (D) *Elaphostrongylus rangiferi*.

(i.e. genetically based) resistance or immunocompetence does not have a significant simultaneous effect on all parasite species. Acquired immunity based on infections from previous years also can be ruled out in this study because the hosts had only experienced 1 summer, the season of transmission for most parasite species.

The observation that all parasites separately were overdispersed among the host individuals (κ-values in Table 1 and Fig. 2) may have 2 explanations: (1) that the heterogeneity in innate host resistance is parasite specific (i.e. that there are differences in parasite-specific predisposition among host individuals); (2) that the overdispersion was created by differences in exposure (transmission rate), but factors affecting the transmission of one species are independent of the transmission of the other species. The results cannot reveal any certain conclusion to distinguish between these 2 possibilities, which may work together.

The parasite species in this study are transmitted in various ways, but it is interesting that the only parasites that have a significant, though weak, covariation, were *C. trompe* and *H. tarandi*, which have a similar transmission. The adult flies are themselves 'active' transmitters in that both have a host-seeking flight. During warm days in July and August, both species may be observed attacking simultaneously (Anderson & Nilssen, 1996). If there are individual reindeer that for some reason are more easily located by the flies, these reindeer may suffer more heavy attacks of both species. Thus, heterogeneity in host behaviour may explain the aggregated parasite burden. The frequency distribution of oestrids has recently been analysed and reviewed by Nilssen & Haugerud (1995).

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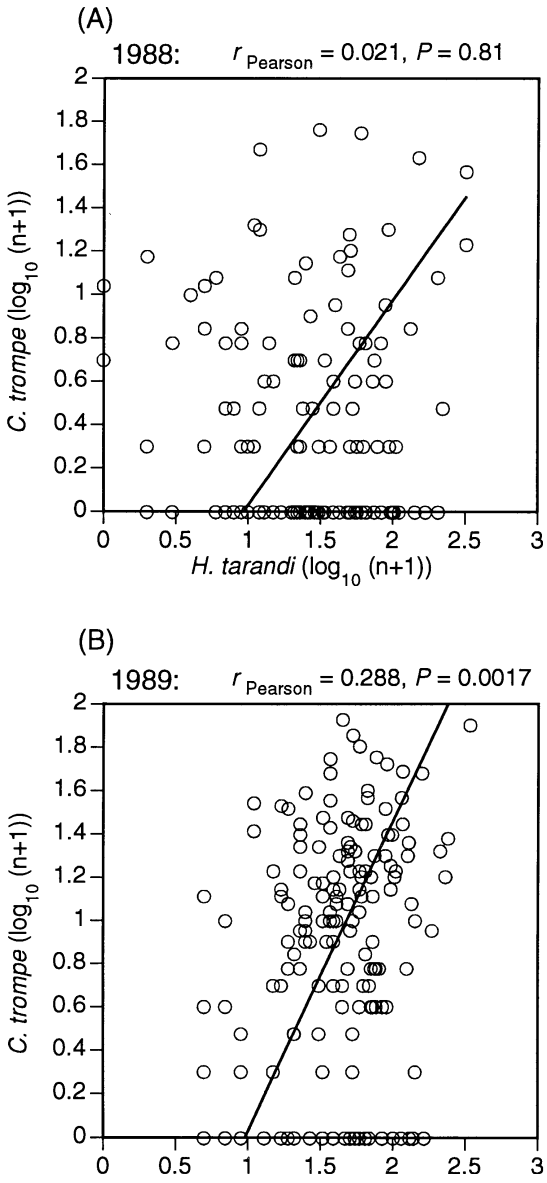

Fig. 3. Scatter diagrams of intensities (= infrapopulations) ($\log_{10}(x+1)$-transformed data) of *Cephenemyia trompe* and *Hypoderma tarandi* for (A) 1988 and (B) 1989. Central trend lines (= geometric mean or functional regressions; see Krebs (1989)) are also shown. The correlation was only significant ($P = 0{\cdot}0017$) in 1989, with a $r_{Pearson}$ of 0·288 and a coefficient of determination (r^2) of 0·08.

The marked difference in abundance between years and between districts is most likely explained by differences in transmission rates. The summer weather (temperature) has been shown to have a major impact on transmission and the resulting parasite burden in *C. trompe* (Nilssen & Haugerud, 1995). By coincidence, the summer weather prior to the 2 samplings was very different (1987 unusually cold and 1988 unusually warm), giving an abundance of 4·65 and 13·23, respectively for *C. trompe*. The abundance of *H. tarandi* was influenced more slightly, suggesting that *H. tarandi* is better capable to cope with cold summers than does *C. trompe*. Both oestrids are, however, directly dependent on the summer weather, both for mating (Anderson, Nilssen & Folstad, 1994; Nilssen & Anderson, 1995) and host seeking behaviour (Anderson & Nilssen, 1996) for successful reproduction. *E. rangiferi* showed a much higher prevalence and abundance in 1989 than in 1988, whereas there was no significant difference between the 2 years for *L. arctica*.

The observed differences in infection levels between districts within years for most parasites are probably caused by combined effects of local climate, density of reindeer in the herds, and management practice (for oestrids, such factors have been discussed by Folstad *et al*. (1991) and Nilssen & Haugerud (1995).

Thus, weather and other factors during transmission of the parasites obviously have the potential to greatly affect the general infection level (prevalence and abundance). The crucial question is, whether transmission factors also are responsible for the aggregated distribution. All parasite species investigated in this study were aggregated among the hosts, and the distributions fitted the negative binomial model.

Previous studies have shown that both transmission and susceptibility may create an aggregated distribution. The continuing question regarding cause of aggregation of parasites has been approached by a variety of methods (e.g. Wakelin, 1985, 1994; Scott, 1988; Haswell-Elkins *et al*. 1992; Tanguay & Scott, 1992; Haukisalmi & Henttonen, 1993; Poulin, 1996), but there seem to be no simple answers (see review by Esch & Fernàndez, 1993).

We have found only 1 study that used an approach similar to the present study. Croll & Ghadirian (1981) compared the distribution of several helminth species in a human population and found, analogous to our results, that persons who carried excessive burdens of one helminth were not necessarily predisposed to concurrent higher infections by other helminths, or to re-infection of the same species. They concluded that random events were important in creating larval burden (see also Poulin, 1996).

The present study reveals, as several previous studies also have shown for other hosts (e.g. Croll & Ghadirian, 1981; Haukisalmi & Henttonen, 1993) that reindeer parasites are distributed independently of each other. There are 'wormy reindeer', but absence of heavy infections occurring concurrently in a few reindeer argues against 'wormy reindeer' having increased susceptibility to infections of several parasite species. Transmission rates (exposure) and random events are therefore likely candidates for creating the aggregated distributions of the investigated parasites.

Host resistance may, under certain circumstances, play an important role in regulating the parasite burden. However, Wakelin (1984, 1985) and Gregory (1992) have advanced the argument that

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immunity may be unimportant in regulating parasites in natural host populations, since transmission rates are usually too low to elicit host responses. Host immune responses (probably also other resistance mechanisms) are therefore density dependent, and the effect will be a decreased aggregation. As shown for *C. trompe* (Nilssen & Haugerud, 1995), the aggregation decreased with increased transmission rate. This was interpreted to be a 'negative feedback' that started to function only at high intensities, a situation also found for *Hypoderma* spp. in cattle (Breyev & Minár, 1979).

A large number of factors can produce changes in aggregation of parasite burdens (Quinnell *et al.* 1995), and the relative importance of innate resistance, acquired resistance and behaviour in generating variable parasite burdens are likely to vary both spatially and temporally (Tanguay & Scott, 1992). However, for parasites in which aggregation decreases with infection level, the relative contribution of density-dependent factors (innate and acquired resistance) and transmission factors may vary. Thus, at low and moderate transmission rates, individual larval burdens and the frequency distribution may largely be determined by factors affecting transmission of the parasites.

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