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Analyses of Relationships between the Abundance of Two Morphs of an Abomasal Nematode Species, *Spiculopteragia houdemeri*, in Sika Deer (*Cervus nippon*) from Hokkaido, Japan, and Some Relevant Factors using a Generalized Linear Model

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一般化線形モデルを用いた北海道産ニホンジカ（*Cervus nippon*）の第4胃内線虫 *Spiculopteragia houdemeri* 2型の寄生虫体数と各種因子の関連性の分析

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ABSTRACT. Relationships between the abundance of two morphs of an species of abomasal nematodes, *Spiculopteragia houdemeri*, in sika deer, *Cervus nippon*, from the Ashoro District, Hokkaido Island, Japan, and relevant factors such as individual host traits (sex, age, and body weight) were examined using a generalized linear model, with AIC (Akaike's Information Criterion) for selection of optimal models. Many main and interactive effects significantly affected "morph houdemeri" abundance. As one of the main effects, abundance of this morph was significantly lower in male hosts; this result was attributable to sexual differences in habitat use (habitat segregation) by the hosts. Yearling hosts were parasitized by significantly fewer "morph houdemeri" than other age groups, probably because of the lack of some increasing factors such as maternal infection in fawns and large body mass in adults (age, ≥ 2 yr-old). Host body weight and "morph andreevae" presence - absence showed other main effects that significantly affected "morph houdemeri" abundance. The abundance of *S. andreevae* was higher in hosts with more "morph houdemeri", and other than this tendency, only host age significantly affected "morph andreevae" abundance. Various factors including individual host characteristics affected the abundance of "morph houdemeri", the dominant species, whereas the abundance of the subdominant *S. andreevae* was affected by fewer factors, such as "morph houdemeri" abundance. Some interactive effects were difficult to interpret, and further studies that include additional factors such as the seasonal dynamics of nematode abundance are needed.

Key words：abomasal nematode, abundance, *Cervus nippon*, sika deer, *Spiculopteragia*

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INTRODUCTION

Two species of parasitic nematodes of the genus *Spiculopteragia* (Trichostrongylidae: Ostertagiinae), *S. houdemeri* and *S. andreevae* (=*Rinadia andreevae*), had been found at high prevalence and abundance in the abomasum of sika deer (*Cervus nippon*) from Japan [1-5]. The 2 species have been often treated as 1 species, *S. houdemeri* recently [4], and

Sultan et al. [5]. concluded that they are 2 different morphs of this species, “morph houdemeri” and “morph andreevae”, based on morphological and molecular comparisons. Females of these two morphs were not distinguishable at least morphologically, though there are three types with different vulval ornamentations among the females [5]. We investigated the metazoan parasite fauna in 50 sika deer from the Ashoro District on Hokkaido Island, northern Japan, and tried to analyze the abundance of males of these 2 morphs in relation to various individual host traits (e.g., age and sex) using a general linear model (GLM) [3]. However, the GLM required transformation of objective variables to approximate normal distribution. The “*S. houdemeri*” and “*S. andreevae*” showed Poisson's and negative binomial distribution patterns, respectively, among which the former was possible to approximate normal distribution pattern with fourth-root transformation, but the latter was impossible to do so with any transformation method (Tables 1 and 2). Hence in the preceding paper [3], we could not analyze the abundance of “*S. andreevae*”. Furthermore, such transformation of objective variables often makes analytical results difficult to interpret [6]. The preceding study [3] showed significant relationships only between “*S. houdemeri*” abundance and host age and sex, but the precise processes of these relationships were unknown at the time because of the problem with the analytical method [6] as well as the possible high complexity of physiological and ecological processes in cervid host-parasite relationships. The high complexity results from the highly developed sex- and age-related social systems found in cervids [6-11] and specialized resource use patterns with sexual differences [7,

Table 1 Principle statistical values of the males of 2 abomasal parasitic nematode “species”, “*Spiculopteragia houdemeri*” and “*S. andreevae*”, in sika deer from eastern Hokkaido, Japan, and analytical results of the relationships between “*S. houdemeri*” abundance and host traits using a general linear model (GLM) (Kitamura et al. [3])

	Prevalence	Intensity$^{1)}$	Abundance$^{1)}$	K-value of negative binomial distribution pattern	Results of GLM (F-value)						
					Sex	Age	BW$^{2)}$	Sex-Age	Sex-BW	Age-BW	Sex-Age-BW
“*S. houdemeri*”	48/48 (100.0%)	171.0 ± 19.5	171.0 ± 19.5	k →∞	4.18$^{3)}$	2.88$^{3)}$	0.07	1.14	3.30	2.69	0.70
“*S. andreevae*”	30/48 (63.0%)	33.4 ± 4.8	21.7 ± 4.5	0.21				―――			

1) Mean ± standard error, 2) Body weight, 3) Significant at P<0.05

Table 2 Abundance of males of 2 abomasal parasitic nematode “species”, “*Spiculopteragia houdemeri*” and “*S. andreevae*”, in sika deer from eastern Hokkaido, Japan, in different age and sex groups (Kitamura et al. [3])

Host sex	Host age (year)	Number sampled	Abundance$^{1)}$	
			“*S. houdemeri*”	“*S. andreevae*”
Male	0	5	84.0 ± 14.7	12.0 ± 4.9
	1	6	158.3 ± 40.4	3.3 ± 3.3
	2	6	166.7 ± 44.6	38.3 ± 16.8
	≥3	4	320.0 ± 132.1	62.5 ± 37.1
	Total	21	173.7 ± 32.8	26.7 ± 9.3
Female	0	6	153.3 ± 50.6	15.0 ± 6.2
	1	5	74.0 ± 22.5	4.0 ± 4.0
	2	4	210.0 ± 96.0	20.0 ± 7.1
	≥3	12	202.5 ± 33.3	24.2 ± 6.3
	Total	27	168.9 ± 24.1	17.7 ± 3.6

1) Mean ± standard error

13-19]. Therefore, more advanced analytical methods were needed.

In the present study, we re-examined and examined abundance data from male "morph houdemeri" and "morph andreevae" , respectively, in sika deer from the preceding study [3] using a generalized linear model (GZLM), which required no transformation of objective variables [6]. Our results clarified some of the ecological features of these 2 morphs, and we report the relationships between them and their hosts in this manuscript.

MATERIALS AND METHODS

Twenty-one male and 29 female sika deer were shot by hunters between 13 and 18 March 1991 in the Ashoro District, in the eastern part of Hokkaido, Japan (43° 15'N, 143° 30'E). Elevation varies from 80 to 1,636 m above sea level in this district. Most (84%) of the area is mountainous and covered with forests, mainly natural deciduous broad-leaved forests. Dominant plant species of the forests are shown in Kitamura et al. [3]. Reproductive characteristics and nutritional condition of the sika deer in this district are described in Suzuki and Ohtaishi [20] and Yokoyama et al. [21], respectively. Nutritional condition of the individual hosts was good, and no relationship between nutritional condition and abundance of the 2 morphs was observed [3]. We estimated the host age as fawn, yearling, 2-yr-old, or $\geq$3-yr-old according to Ohtaishi [22] and Koike and Ohtaishi [23].

The digestive tract from rumen to colon of each deer was isolated from other viscera by ligation, removed, and frozen for examination in the laboratory. In the laboratory, 5 or 10% of the contents of the 48 abomasa was used for the investigation. Two abomasa that were punctured when the deer were shot were excluded from the present analyses. Obtained nematodes were fixed in 10% formalin and cleared with glycerin alcohol for microscopic observation. Representative nematode specimens collected in this study were deposited in the collection of the Laboratory of Parasitology, Graduate School of Veterinary Medicine, Hokkaido University, Sapporo City, Hokkaido 930-0818, Japan.

The GZLM analyses were performed using R (Version i386 2. 15. 1; installed from http://www.okada.jp.org/RWiki/). The log-transformed abundances of both "morph houdemeri" and "morph andreevae" were used as objective variables; "morph houdemeri" was analyzed using the "glm" function (Case I) because it showed a Poisson's distribution pattern, and "morph andreevae" was analyzed using the "glm.nb" function (Case II) because it showed a negative binomial distribution pattern [3]. We used the following data as explanatory variables: (1) host sex (0-1 data), (2) host age (0-4 data), (3) host body weight in both cases, (4) fourth root-transformed abundance of "morph houdemeri" in Case II, and presence-absence of "morph andreevae" (0-1 data) in Case I. All main effects of the 4 explanatory variables and the interactive effects of all combinations of variables (1)-(4) were applied in Cases I and II. In both the cases, the optimal model was selected using the "step" function and Akaike's Information Criterion (AIC).

RESULTS

Optimal models obtained for both cases are shown in Table 3. Almost all of the main and interactive effects involved, based on the factors of sex, age, and body weight of hosts and the presence-absence of "morph andreevae" , were significant in the optimal model for Case I (Table 3 (1)); compared with Table 1, the significant effects were much greater. Only the interactive effect of host sex and "morph andreevae" presence-absence was not adopted in the optimal model. Fig. 1 shows the relationships between "morph houdemeri" abundance and these factors. In the optimal model for Case II, only the main effects of age (yearling) and "morph houdemeri" fourth-root abundance (Table 3 (2)) were significant. The relationships between the abundances of the 2 morphs and the significant main and interactive effects of the factors are presented in detail in the Discussion.

DISCUSSION

Parasite abundance may be influenced by various factors including environmental variables (climate, geomorphology, vegetation, etc.), host population characteristics (density, reproduction, demography, etc.), and individual host traits (age, sex, body weight, social status, captive season, etc.) through degree of chance and duration of parasite infection. Among native North American cervid host species (genera *Alces, Cervus, Odocoileus*, and *Rangifer*), 8 genera and at least 23 species of abomasal nematodes have been identified [24]. Many studies have been conducted on these cervids and on introduced *Cervus* and *Dama* in North America [25-34], as well as on cervids in other areas (genera *Capreolus, Cervus, Dama*, and *Rangifer*) [3, 35-41]. These studies involve various factors, such as habitat type [36], habitat condition [40], host density [26, 40], host age [3, 28, 41] , host sex [3, 28] , host physical condition [27, 32-33], and captive season [25-26, 28, 33-34, 36, 41], and were on some other viewpoints, such as geographic differences in species richness [3] and comparison of infection and health status among multiple host populations [35] and host species [29-31, 34, 39-40].

In the present study, females of the 2 nematodes were not counted. The sex ratio of cervid abomasal nematodes can be affected by several factors, including season, population density, and abundance, and the sex ratio bias generated from these effects was suggested to be particularly important in cases of low abundance [42]. However, no effects of individual host traits treated as explanatory variables in this study (sex, age, and body weight) and the presence-absence of related other species on the sex ratio of abomasal nematodes have been identified so far, and the high abundance of the present 2 morphs was not relevant in this particular case.

In the present study, some individual host factors were shown to affect the abundance of the 2 morphs. These factors may act through various physiological, behavioral, and ecological processes; however, information about the physiological aspects of wild sika deer was inadequate for such a discussion. In many vertebrates, the association between testosterone and the immune system has been well documented, in which sexually mature vertebrates are often more susceptible to parasite infection and carry higher parasite burdens in the field [43] ; this point is discussed again below. On the other hand, various sexual differences associated with reproductive and social activities [8-9, 11-12] , age structure [10] , food habit [18-19], and space use pattern are well known in sika deer [11, 13, 16, 18] and in other cervids [7, 12, 14-15, 17] .

The optimal model for Case I showed a negative main effect of male host on "morph houdemeri" abundance (Table 3 (1)), which means a lower abundance in male hosts if other effects were excluded. This result is more attributable to habitat use

Table 3 Results of generalized linear model (GLM) analyses of the abundance of 2 morphs of an abomasal parasitic nematode species, *Spiculopteragia houdemeri*, in sika deer from eastern Hokkaido, Japan

(1) Case Ⅰ (objective variable: abundance of "morph houdemeri" ; AIC = 2058.6)

Explanatory variable	Estimate	SE$^{1)}$	z-value	Probability
Intercept	7.553	0.104	72.416	<0.001$^{3)}$
Sex (male/female)	−2.074	0.144	−14.452	<0.001$^{3)}$
Age (yearling/fawn)	−2.845	0.333	−8.545	<0.001$^{3)}$
Age (2-yr-old/fawn)	1.660	0.312	5.325	<0.001$^{3)}$
Age (≥3-yr-old/fawn)	0.775	0.208	3.724	<0.001$^{3)}$
Body weight	−0.090	0.004	−22.556	<0.001$^{3)}$
PAMA$^{2)}$ (absence/presence)	1.783	0.129	13.787	< 0.001$^{3)}$
Sex (male/female)*Age (yearling/fawn)	2.089	0.137	−7.105	<0.001$^{3)}$
Sex (male/female)*Age (2-yr-old/fawn)	−2.050	0.200	−10.246	<0.001$^{3)}$
Sex (male/female)*Age (≥3-yr-old/fawn)	−2.541	0.183	−13.841	<0.001$^{3)}$
Sex (male/female)*Body weight	0.062	0.003	18.098	<0.001$^{3)}$
Age (yearling/fawn)*Body weight	0.096	0.007	13.154	<0.001$^{3)}$
Age (2-yr-old/fawn)*Body weight	−0.030	0.006	4.911	<0.001$^{3)}$
Age (≥3-yr-old/fawn)*Body weight	0.068	0.005	14.928	<0.001$^{3)}$
Age (yearling/fawn)*PAMA$^{2)}$ (absence/presence)	−1.638	0.122	−13.374	<0.001$^{3)}$
Age (2-yr-old/fawn)*PAMA$^{2)}$ (absence/presence)	−0.368	0.176	−2.089	<0.001$^{3)}$
Age (≥3-yr-old/fawn)*PAMA$^{2)}$ (absence/presence)	−0.601	0.133	−4.509	<0.001$^{3)}$
Body weight*PAMA$^{2)}$ (absence/presence)	−0.022	0.003	−8.414	<0.001$^{3)}$

1)Standard error, 2)Presence – absence of "morph andreevae" , 3)P< 0.001

(2) Case Ⅱ (objective variable: abundance of "morph andreevae" ; AIC = 346.5)

Explanatory variable	Estimate	SE$^{1)}$	z-value	Probability
Intercept	−1.622	1.194	−1.358	0.174
Age (yearling/fawn)	−1.990	0.657	−3.031	0.002$^{2)}$
Age (2-yr-old/fawn)	0.224	0.640	0.350	0.727
Age (≥3-yr-old/fawn)	−0.040	0.597	−0.067	0.946
Fourth-root abundance of "morph houdemeri"	1.321	0.348	3.797	<0.001$^{2)}$

1)Standard error, 2)P<0.01

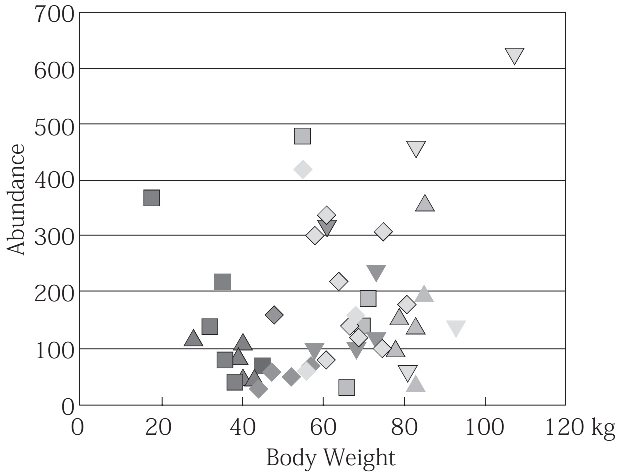

Fig.1 Relationships between host traits (sex, age, body weight) and abundance of "morph houdemeri" of *Spiculopteragia houdemeri* from sika deer in eastern Hokkaido, Japan, with presence-absence of "morph andreevae" (△▽ : male host; □ ◇ : female host; ▲■: fawn; ▼◆: yearling; ▲■: 2-yr-old; ▼◆: ≥3-yr-old; symbols with and without frames are with and without "morph andreevae" , respectively)

differences than food habit differences between both sexes, because infective larvae of trichostrongylid nematodes invade the host body by cutaneous infection. Habitat segregation of male and female sika deer has been reported [13, 16, 18], but its pattern is not adequately known in detail. However, adult males of some cervids use habitats of lower quality (with food containing a relatively low level of nutrients and less protein) and higher food supply than females (e.g., red deer, *C. elaphus*) [7], mule deer (*Odocoileus hemionus*) [14], and moose (*Alces alces*) [15]). Such habitats are often open and dry with lower host density, and trichostrongylid infection is probably more difficult. The interactive effects of sex and age were negative in adult male hosts (males*2-yr-old and males*≥3-yr-old) against male yearlings, in accordance with this view. Higher susceptibility to parasite infection because of the association between testosterone and the immune system, mentioned above [43], apparently is not involved.

The main effect of host body weight on "morph houdemeri" abundance was negative (Table 3 (1)). This result is attributable to emaciation of the hosts from heavy worm burden, and the effect of trichostrongylid nematodes on hosts is well known among various ungulates [24]. However, the interactive effect of sex and body weight was positive in males (Table 3 (1)). In cervids, body mass is heavier and its variation is more obvious in males than in females, and this phenomenon is remarkably combined with male social status [7-9]. Such large variation might make the carrying capacity of parasitic nematodes in the host body more variable in male deer.

The relationships between "morph houdemeri" abundance and host age were not simple. Female yearling hosts showed lower abundance than fawn and 2- and ≥3-year-old adult hosts (Tables 2 and 3 (1); Fig. 1), possibly because of the lack of some increasing factors of abundance affecting fawns (such as maternal infection) and adults (such as large body mass) in yearlings. The interactive effects of host age and body weight showed a different tendency among different age groups, i.e., positive in yearlings and ≥3-yr-olds and negative in 2-yr-olds. The reason for this discrepancy is not clear, but the complex relationships among "morph houdemeri" abundance and age (decreasing abundance in yearling females) and host body weight (emaciation and carrying capacity) may have affected the results.

Results of the analysis of "morph andreevae" abundance (Case II) were very different from those of "morph houdemeri" (Case I). Only 2 factors were significant, host age (decreasing abundance in yearlings) and "morph houdemeri" abundance (increasing abundance with higher "morph houdemeri" abundance) (Table 3 (2)). The factor of host age acted as same as that for Case I. The factor of "morph houdemeri" abundance was recognized in the preceding study [3], in which a positive rank correlation was observed between both abundances. On the other hand, the absence of "morph andreevae" showed some negative interactive effects with age (yearlings and older) and host body weight on the abundance of "morph houdemeri" . These results are difficult to interpret, but in general, interspecific competition among parasitic organisms is often affected by other potential factors, such as immunity and carrying capacity of individual hosts, discussed above.

"Morph andreevae" abundance apparently depends on the abundance of the more dominant nematode, "morph houdemeri" . However, this tendency is not seen in "morph houdemeri" , in which abundance was under the positive main effect of the absence of "morph andreevae" (Table 3 (1)). Therefore, this may be an irreversible phenomenon between the dominant and subdominant forms.

The complex social system and habitat segregation of male and female sika deer affected "morph houdemeri" abundance through various processes. Interpretation of the processes on the main effects of factors used in this study was easy, based on the present ethological and ecological knowledge of sika deer but was difficult for some interactive effects. A comprehensive study involving factors that are lacking in this study, such as seasonal dynamics, will contribute to a better understanding of the relationships between these abomasal nematodes and their cervid hosts. The factors affecting "morph andreevae" abundance were much simpler than those affecting "morph houdemeri" abundance. What causes this difference will be an interesting subject for future study.

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要約

北海道足寄町産ニホンジカ *Cervus nippon* の第４胃内に寄生する線虫，*Spiculopteragia houdemeri* の雄における２型，“morph houdemeri” および “morph andreevae” の寄生虫体数と，宿主個体の因子（性，齢，体重）などとの関連を一般化線形モデルで分析し，AIC（赤池情報量基準）により最適モデルを選択した。morph houdemeri” の虫体数に対して多くの因子の主効果，交互作用効果が有意に作用していた。主効果において，この線虫の虫体数は雄宿主で有意に少なく，宿主の生息地選択の性差が関係している可能性があるとともに，有意な齢差がみられ，1歳子の宿主で他の齢群よりも少なく，当歳子での母子感染や，2歳以上の成獣での体サイズの増大のような増加要因を欠くためと考えられた。他には宿主の体重，“morph andreevae” の寄生の有無の主効果が有意に影響していた。“morph andreevae” の虫体数は “morph houdemeri” の虫体数が多いほど多く，他には宿主の齢のみが有意に作用していた。優占している“morph houdemeri” の虫体数には宿主個体などの多様な因子が作用し，劣位な “morph andreevae” の虫体数には作用する因子が少なく，“morph houdemeri” の虫体数などが作用していた。いくつかの交互作用効果は解釈が難しく，今後は虫体数の季節的動態などに関する新たな因子を加えた分析が望まれる。

キーワード：寄生虫体数，第４胃内線虫，*Cervus nippon*，ニホンジカ，*Spiculopteragia*

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