

# *Syphacia obvelata* infections and reproduction of male domestic mice *Mus musculus domesticus* on a sub-Antarctic Island

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## Abstract

The reproductive activity of feral male mice on an island of the sub-Antarctic Kerguelen archipelago was influenced by biological factors depending on periods within the breeding season. After having controlled host reproductive activity indices for body size, i.e. age, and body condition effects, *Syphacia obvelata* prevalence did not vary with host reproductive status or age either during the beginning or the middle–end of the reproductive season. Considering the beginning of the breeding season, worm abundance was more pronounced in males the year following a strong winter crash of the population than in years when high overwintering survival occurred. During the middle–end of the breeding season, males with the highest reproductive status were more infected than males with a lower reproductive status in years when oldest individuals dominated the population. It is suggested that this situation was due to an endocrine related increased host susceptibility partly influenced by a change in the age structure of the population, and that an increase in worm transmission was not directly related to male activity concurrent with reproductive status, nor to population density.

## Introduction

Hormones influence sex differences in immune functions amongst vertebrates (Folstad & Karter, 1992; Klein, 2000). Numerous studies under experimental conditions have shown that relationships between the level of blood circulating steroid hormones and immune depression, and the consequences on micro-parasitic infections, are modulated by the social and physical environment of male house mice *Mus musculus* (Barnard *et al.*, 1993, 1994, 1996, 1997, 1998). Recently, small rodents showing endocrine activity, and recovered from natural populations, were found to be less immunocompetent (Klein

& Nelson, 1998) or more intensely parasitized (Barnard *et al.*, 2002). These processes, however, can be influenced by other factors in a natural host population, like territoriality, movement patterns, social interactions or diet that could influence the exposure of the host to parasite infective stages (Poulin, 1996).

The nematode *Syphacia obvelata* (Rudolphi, 1802) was the only helminth species found in the caecum of domestic mice on Guillou Island, sub-Antarctic Kerguelen archipelago (Pisanu *et al.*, 2001). An earlier study during the breeding season of the mouse population between 1995 and 2001 revealed that males were occasionally more intensely parasitized than females (Pisanu *et al.*, 2002). In the present work, the reproductive activity of male mice during the breeding seasons between 1995 and 2001 on Guillou Island was firstly characterized. Then variations in *S. obvelata* infection were investigated in relation to the

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age and reproductive status of male mice under various phase-specific changes of the population during the breeding season.

### Materials and methods

One of the most isolated oceanic islands in the southern Indian Ocean, the sub-Antarctic Kerguelen archipelago (48°25'–50°00'S, 68°25'–70°35'E) is formed by a main island (6500 km<sup>2</sup>), and about 60 other smaller islands (700 km<sup>2</sup>). Temperature ranges between a mean of 2.3°C in the coldest winter month of July and 7.8°C in the hottest month of February (Météo France, 1985–1997 records, Port-aux-Français).

The domestic mouse *Mus musculus domesticus* was involuntarily introduced on the sub-Antarctic Kerguelen archipelago at the end of the 19th century (Lésel & Derenne, 1975). It is the only mammal species that settles on Guillou Island (1.45 km<sup>2</sup>), inhabiting dense plant cover formed by closed communities of a Rosaceae, *Acaena magellanica* (Chapuis *et al.*, 2001). Mice were trapped using a standardized method (Spitz *et al.*, 1974) on a 10 ha area separated into six sectors presenting similar topography, soil and vegetation (Chapuis *et al.*, 2001; Le Roux *et al.*, 2002). Mice were removed from three lines, each formed by 34 baited live-traps, that were used for three consecutive nights on different sectors of the island, and the number of mice caught per 100 trap-nights was used as an indicator of mouse abundance (Pisanu *et al.*, 2002). The breeding season of mice on Guillou Island was defined from October until April, and split into two periods: the beginning, ranging from October until December, and the middle–end ranging from January until March, to avoid bias due to change in population density.

The body of trapped mice was weighed to the nearest gram, and the head body length (nose to anus) measured to the nearest mm. Seminal vesicle maximal width was measured to the nearest mm to obtain a reproductive activity index (Lidicker, 1966). Exponential and simple linear regressions with groups (Scherrer, 1981) were used to fit seminal vesicle size and full body weight against body length in relation to year, to test for non-linearity in the relationships between these variables (Krebs & Singleton, 1993). New variables were obtained by calculating standardized residuals (Framstad *et al.*, 1985) from the linear fits. The first variable formed by the residuals calculated from the fit of the body weight against body length was named body condition, and the second one from the fit of the seminal vesicle size against body length was referred to as reproductive condition. Body and reproductive condition indices were correlated using a simple linear regression, and standardized residuals were again calculated to obtain a new variable called reproductive status. Then, individuals were included in two categories: males with negative values of the standardized residuals were defined as being of low reproductive status, and those with positive values were regarded as high reproductive status. In the laboratory, the caecum was dissected and mature worms were counted under the binocular microscope (Pisanu, 1999). Worm abundance was defined as the number of worms found in the caecum of a male mouse whether or not the host is infected, and mean abundance

was the total number of worms divided by the total number of male mice examined, including uninfected hosts (Bush *et al.*, 1997). Deviance analysis of generalized linear models using the binomial error and logit link function, and the negative binomial error and logarithm link function best fitting the observed data (Wilson & Grenfell, 1997), were respectively used to explore *S. obvelata* prevalence and abundance variation with year, body length and reproductive status. The negative exponent  $k$  was estimated using a maximum likelihood procedure provided by the Genstat software (Genstat 5 Committee, 1994). The deviance is a statistic assessing the goodness of fit of a model, and has approximately a  $\chi^2$  distribution. Models are built beginning with all possible interactions between factors, then excluding factors stepwise until only single factors remained. The significant contribution of a minimum sufficient model to the explanation of variation in the data is calculated by the change in deviance between two models, which have also a  $\chi^2_{df}$  distribution, where  $df$  is the change in number of degrees of freedom between both models.

### Results

#### *Beginning of the breeding season*

Using simple linear regression models, body weight was highly correlated with body length of male mice ( $n = 191$ ,  $F_{1,189} = 791.25$ ,  $P < 0.001$ ,  $R = 0.898$ , fig. 1a), with no interaction with the year effect ( $F_{5,179} = 0.88$ ,  $P = 0.499$ ). The model of exponential regression with the interactive effect of year and body length failed to reach convergence criteria in curve fitting. The exponential regression model with the single effect of body length ( $R^2 = 0.805$ ) did not improve the percentage explained by a simple linear model ( $R^2 = 0.807$ ). Also, the seminal vesicle size was correlated with the body length of male mice ( $F_{1,189} = 237.35$ ,  $P < 0.001$ ,  $R = 0.746$ , fig. 2a), with no interaction with the year effect ( $F_{5,179} = 1.48$ ,  $P = 0.186$ ). Again, the model of exponential regression with the interactive effect of year and body length did not fit the data. The exponential regression model with the single effect of body length ( $R^2 = 0.553$ ) did not improve upon the simple linear model ( $R^2 = 0.557$ ) in explaining the variation in the vesicle seminal size. Reproductive condition was significantly but poorly correlated with body condition ( $F_{1,189} = 22.79$ ,  $P < 0.001$ ,  $R = 0.328$ , fig. 3a).

The prevalence of *S. obvelata* in mice changed only between years (table 2), increasing from 18.4% up to 32.6% between 1995 and 1997, then maintaining at a high level from 63.6% up to 100.0% until 2001 (table 1). Overall, nematode burdens followed a negative binomial distribution ( $n = 191$ , mean = 7.0, variance = 360.0) with an estimated exponent  $k = 0.1221$ . Variation in the mean abundance of *S. obvelata* in male mice was only influenced by the year of the study periods, ranging from 20.8 to 36.4 worms per mouse in 1996, 1998 and 2000, and from 0.9 to 8.4 worms per mouse in 1995, 1997, and 1999 (table 2).

#### *Middle–end of the breeding season*

From January to March between 1996 and 2001, body weight was highly correlated with body length of male

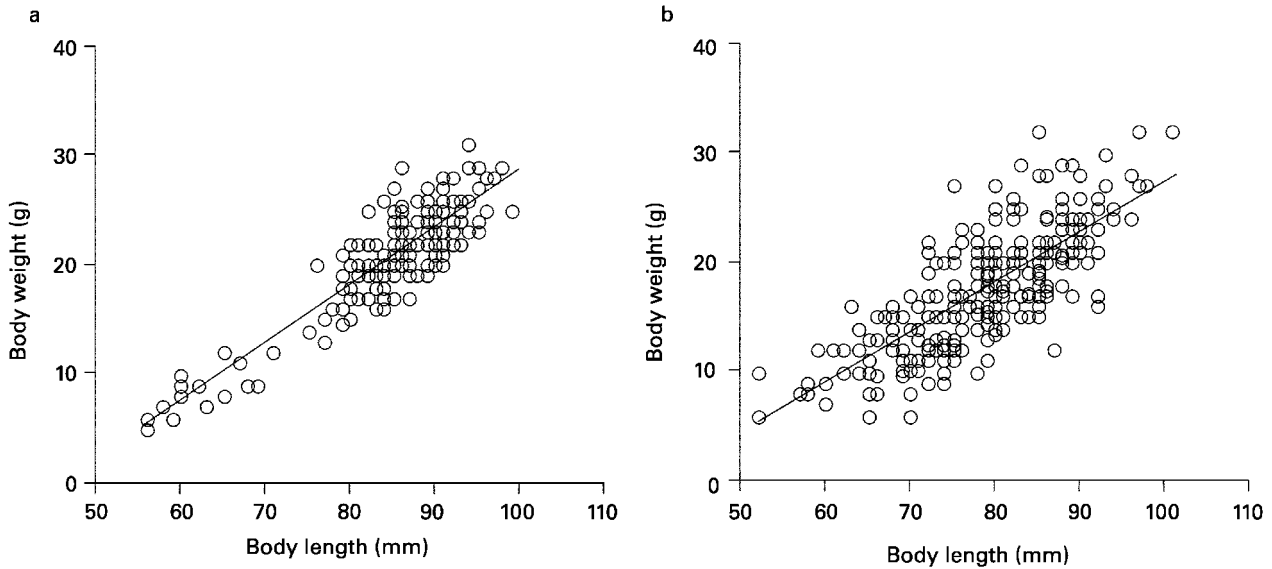


Fig. 1. The relationship between body weight and body length of male domestic mice during (a) the beginning and (b) the middle-end of the breeding season between 1996 and 2001 on Guillou Island, sub-Antarctic Kerguelen archipelago.

mice ( $n = 295$ ,  $F_{1,293} = 403.65$ ,  $P < 0.001$ ,  $R = 0.761$ , fig. 1b), with no interaction with the year effect ( $F_{5,283} = 1.51$ ,  $P = 0.186$ ). Neither did the model of exponential regression with the interactive effects of year and body length significantly improve the percentage of variation of body weight ( $R^2 = 0.671$ ) compared to the simple linear model ( $R^2 = 0.686$ ), nor the exponential regression model with the single effect of body length ( $R^2 = 0.579$ ) compared to the simple linear model ( $R^2 = 0.579$ ). Also, seminal vesicle size was correlated with body length of male mice ( $F_{1,293} = 268.20$ ,  $P < 0.001$ ,  $R = 0.691$ , fig. 2b), with no interaction with the year effect ( $F_{5,283} = 2.16$ ,

$P = 0.059$ ). Again, the model of exponential regression with interactive effects of year and body length did not significantly improve the percentage of variation of body weight ( $R^2 = 0.512$ ) compared to the simple linear model ( $R^2 = 0.533$ ), or the exponential regression model with the single effect of body length ( $R^2 = 0.473$ ) compared to the simple linear model ( $R^2 = 0.478$ ). Reproductive condition was well correlated with body condition ( $F_{1,294} = 155.15$ ,  $P < 0.001$ ,  $R = 0.588$ , fig. 3b).

The prevalence of *S. obvelata* in male mice on Guillou Island changed only in relation to year (table 3), as 16.7% were found infected in 1997, ranging from 49.3% and

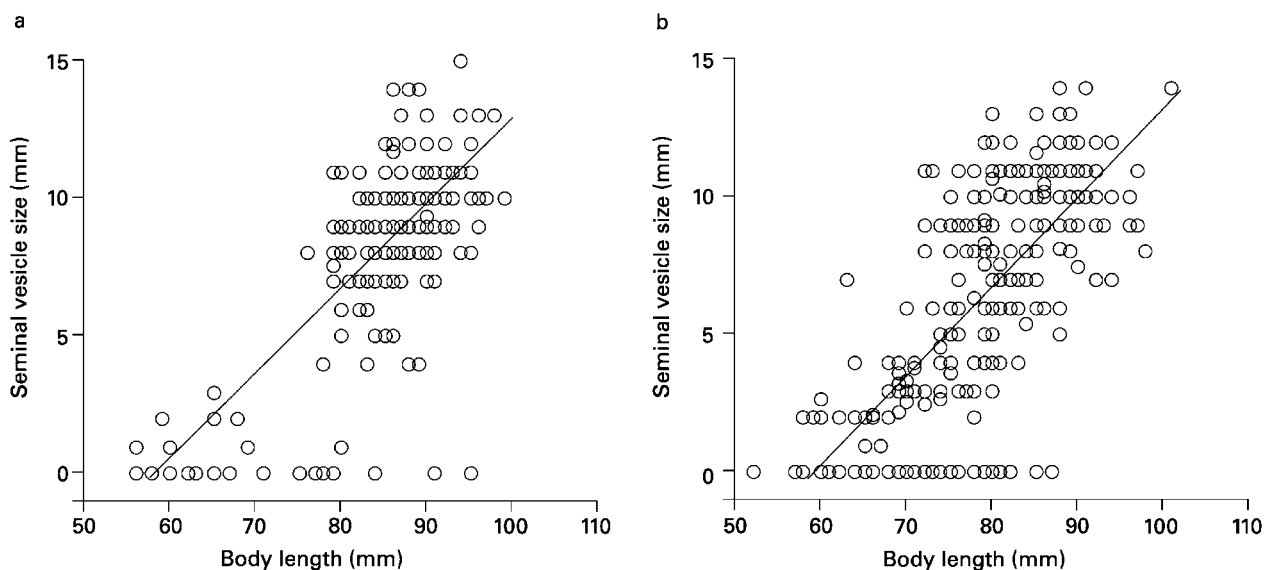


Fig. 2. The relationship between seminal vesicle size and body length of male domestic mice during (a) the beginning and (b) the middle-end of the breeding season between 1996 and 2001 on Guillou Island, sub-Antarctic Kerguelen archipelago.

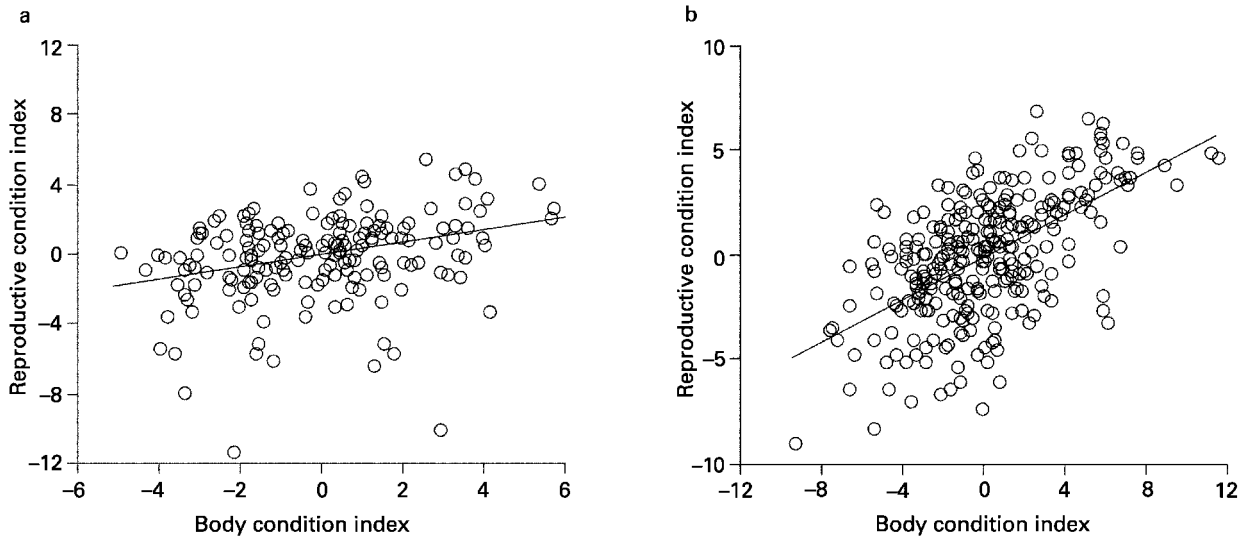


Fig. 3. The relationship between the reproductive condition and body condition indices of male domestic mice during (a) the beginning and (b) the middle–end of the breeding season between 1996 and 2001 on Guillou Island, sub-Antarctic Kerguelen archipelago.

65.6% during the remainder of the study periods (table 1). Overall, nematode burdens followed a negative binomial distribution ( $n = 295$ , mean = 10.0, variance = 1246.6) with an estimated exponent  $k = 0.1831$ . The model presenting an interaction between year and reproductive status better explained the variation in mean abundance of *S. obvelata* in male mice (table 3). Male mice presenting a high reproductive status were more heavily infected than those with low reproductive status in 1996 and 2000 (fig. 4). During these years, the mean body length of males were  $82.1 \pm 1.0$  mm and  $83.8 \pm 0.6$  mm respectively, whereas the mean body length ranged from  $72.7 \pm 1.5$  mm and  $77.5 \pm 1.3$  mm during the other periods (table 1).

## Discussion

No effect of the year on the relationships between body measurements in male mice on Guillou Island was observed from both breeding periods, indicating the absence of bias due to different observers. The relationship between body size and mass of Guillou mice can be explained by the growth of individuals, and variance about the regression must reflect body condition and inter-individual variability (Bailey, 1968; Krebs & Singleton, 1993; Viggers *et al.* 1998; Schulte-Hostedde *et al.*, 2001). The relationship between seminal vesicle and body size indicated an influence of the growth status of male mice on their sexual maturation on Guillou Island. These

Table 1. The mean body length, proportion of individuals with high reproductive status, and characteristics of *Syphacia obvelata* infections in male domestic mice during the middle–end of the breeding season between 1996 and 2001 on Guillou Island, Kerguelen archipelago.

Breeding periods	Domestic mice		<i>Syphacia obvelata</i>	
	Sample size	Mean body length (mm)	Prevalence (%)	Mean abundance $\pm$ 1 SE
October–December 1995	49	$85.2 \pm 0.9$	18.4	$0.9 \pm 0.5$
January–March 1996	45	$82.1 \pm 1.0$	55.5	$28.6 \pm 11.0$
October–December 1996	4	$83.5 \pm 2.3$	25.0	$20.8 \pm 20.7$
January–March 1997	24	$73.9 \pm 1.4$	16.7	$0.4 \pm 0.2$
October–December 1997	86	$85.5 \pm 1.0$	32.6	$6.9 \pm 1.9$
January–March 1998	73	$76.3 \pm 1.2$	49.3	$4.0 \pm 1.0$
October–December 1998	5	$91.8 \pm 1.0$	100.0	$36.4 \pm 32.2$
January–March 1999	29	$72.7 \pm 1.5$	55.2	$8.0 \pm 3.2$
October–December 1999	44	$81.2 \pm 1.6$	63.6	$8.4 \pm 1.8$
January–March 2000	92	$83.8 \pm 0.6$	57.6	$9.4 \pm 3.1$
October–December 2000	3	$85.0 \pm 3.2$	100.0	$25.7 \pm 11.3$
January–March 2001	32	$77.5 \pm 1.3$	65.6	$8.0 \pm 3.2$

Table 2. Deviances of generalized linear models exploring the effect of year, body length and reproductive status on *Syphacia obvelata* prevalence (models with binomial errors) and abundance (models with negative binomial errors) in male domestic mice during the beginning of the breeding season between 1996 and 2001 on Guillou Island, Kerguelen archipelago.

Source of variation	df	Deviance
Models with binomial errors for prevalence		
Total	190	255.0
Reproductive status (RS)	1	2.9 <sup>NS</sup>
Body length (BL)	1	1.2 <sup>NS</sup>
Year	5	37.6 <sup>***</sup>
RS × BL	3	6.5 <sup>NS</sup>
RS × Year	10	42.3 <sup>***</sup>
BL × Year	11	42.9 <sup>***</sup>
RS × BL × Year	20	55.8 <sup>***</sup>
Models with negative binomial errors for abundance		
Total	190	141.6
Reproductive status (RS)	1	3.2*
Body length (BL)	1	0.1 <sup>NS</sup>
Year	5	17.8 <sup>***</sup>
RS × BL	3	5.2 <sup>NS</sup>
RS × Year	10	22.9 <sup>***</sup>
BL × Year	11	26.6 <sup>***</sup>
RS × BL × Year	20	34.2 <sup>***</sup>

NS, non-significant; \**P* < 0.05; \*\*\**P* < 0.001.

results are in accordance with other studies on reproductive activity in males of various small rodent species depending on the age of individuals (Raynaud, 1950a,b; Martinet, 1967). By analogy with the determination of body condition, variance about the regression must have reflected inter individual variability in the level of sexual maturation of male mice on Guillou Island.

Table 3. Deviances of generalized linear models exploring the effect of year, mouse body length and reproductive status on *Syphacia obvelata* prevalence (models with binomial errors) and abundance (models with negative binomial errors) in male domestic mice during the middle–end of the breeding season between 1996 and 2001 on Guillou Island, Kerguelen archipelago.

Source of variation	df	Deviance
Models with binomial errors for prevalence		
Total	294	408.2
Reproductive status (RS)	1	2.3 <sup>NS</sup>
Body length (BL)	1	1.5 <sup>NS</sup>
Year	5	17.1*
RS × BL	3	3.8 <sup>NS</sup>
RS × Year	11	23.9 <sup>NS</sup>
BL × Year	11	22.7 <sup>NS</sup>
RS × BL × Year	23	32.7 <sup>NS</sup>
Models with negative binomial errors for abundance		
Total	294	287.0
Reproductive status (RS)	1	17.9 <sup>***</sup>
Body length (BL)	1	2.6 <sup>NS</sup>
Year	5	39.8 <sup>***</sup>
RS × BL	3	20.6 <sup>***</sup>
RS × Year	11	57.0 <sup>***</sup>
BL × Year	11	53.0 <sup>***</sup>
RS × BL × Year	23	74.0 <sup>***</sup>

NS, non-significant; \**P* < 0.05; \*\*\**P* < 0.001.

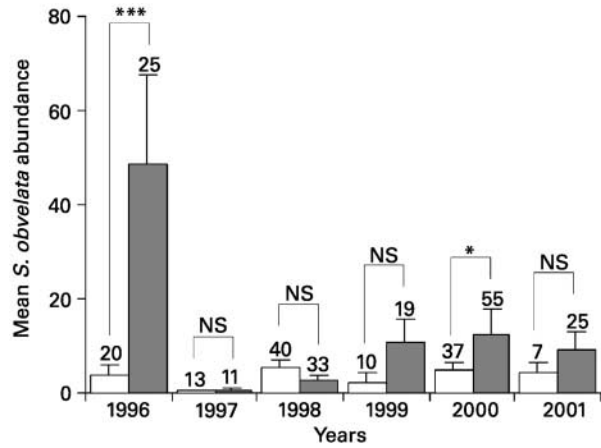


Fig. 4. Changes in the mean abundance of *Syphacia obvelata* ( $\pm 1$  SE) in male domestic mice with low (empty bars) and high (grey bars) reproductive status during the middle–end of the breeding season between 1996 and 2001 on Guillou Island, Kerguelen archipelago. Sample size, and significance in mean differences, are indicated above the histograms (NS, non-significant; \**P* < 0.05; \*\*\**P* < 0.001).

Sexual maturation was less influenced by biological factors at the beginning than at the middle–end of the breeding season. Such a pattern could have arisen by the loss of food availability or quality, which influence reproductive status in male mice (Bronson, 1979). However, it is commonly admitted that the reproductive condition of male mice is only affected under severe environmental conditions (Lidicker, 1966; Pryor & Bronson, 1981; Efford *et al.*, 1988), even on sub-Antarctic islands (Pye, 1993; Matthewson *et al.*, 1994). Hence, a critical evaluation of the role of food resources on sexual maturation in Guillou mice is needed.

The development of the seminal vesicle in male mice depends on the release of sex hormones (Bronson, 1979), and an increase in circulating levels of gonadal steroid hormones during reproductive activity can modify the immune responsiveness in laboratory mice (Grossman, 1985). Such patterns could partly explain why worm abundance in males on Guillou Island with high reproductive status, controlled for age and time effect, were significantly higher than in males with low reproductive status. Both years (1996 and 2000) when a change in the reproductive status of male mice was associated with more pronounced *S. obvelata* infections at the middle–end of the breeding season were characterized by an overall greatest mean body size in the samples. Clearly, age-related changes in the Guillou mouse population have influenced nematode infections relative to male reproductive status at different phase-specific periods of the breeding season.

When reproductively active, male mice increase their general activity patterns (Drickamer *et al.*, 1999; Chambers *et al.*, 2000). This could lead to an increase in worm transmission, as *S. obvelata* is mostly spread by contact between host individuals, where embryonated eggs which adhere to the fur (Grice & Procriv, 1993) are transferred from host to host. However, this hypothesis is

not supported for the Guillou mice as the prevalence, which mostly indicates patterns of pinworm transmission, was neither influenced by host age nor reproductive status. During the beginning of the breeding season, the highest nematode infections were only associated with the low-density phase of the mouse population, mainly formed by old individuals that survived strong preceding winter crashes (Pisanu *et al.*, 2002). Moreover, relative densities of mice during the middle-end of the breeding season in 1996 ranged between 14.2 and 11.1 mice trapped per 100 night traps, whereas relative densities were twice as high in 2000, ranging from 20.3 up to 27.4 mice trapped per 100 night traps (Pisanu *et al.*, 2002). Therefore, this high population density does not seem to directly influence patterns of infection in Guillou male mice.

A number of biological factors have influenced the reproductive status of male domestic mice in the sub-Antarctic Guillou Island. Variability in *S. obvelata* infections in male mice must have arisen from endocrine-related increased host susceptibility, and in turn was influenced by host age-related changes in the population, rather than from host density-related factors.

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