

# Variation of morphometric traits in populations of an invasive carabid predator (*Merizodus soledadinus*) within a sub-Antarctic island

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**Abstract** Invasive predators may change their own trophic conditions by progressively displacing or reducing diversity and abundance of native prey. As food quality and quantity are two main factors determining adult body size in arthropods, alteration of the available resources may thus affect predators' morphology. The flightless carabid beetle *Merizodus soledadinus* was accidentally introduced to Iles Kerguelen in a single site in 1913. Its successful spreading process has been monitored over the long term, providing an exceptional research opportunity with multiple snapshots of similar colonized sites mostly differing by the residence time of *M. soledadinus*. To test if *M. soledadinus*' morphology is correlated with its residence time in each habitat, we measured nine morphometric traits in five populations. We detected significant morphological differences: individuals from the first colonized site were the smallest, whereas individuals from the most recently colonized site were the largest. Our study also highlighted among-site variation in sexual dimorphism of the last abdominal sternite: its length

differed between sites for females, but not for males. We discuss this diminution of *M. soledadinus*' size in the light of both a priori (development under diet restriction, survival) and a posteriori (intrapopulation competition, cannibalism) effects on growth and development.

**Keywords** Trophic resources · Phenotypic plasticity · Morphometrics · Body size · Biological invasion · Insect · Predator · Gender · Sub-Antarctic islands

## Introduction

Several parameters, from physiological processes to environmental pressures, play a role in determining the body size and related morphological parameters in insects. Among a wide range of factors, ontogenesis, biomechanical constraints, sexual selection, fecundity, size-specific predation, resource quality and availability, overcrowding, competition and temperature have often been reported as the most prominent ones (Angilletta and Dunham 2003; Berven and Gill 1983; Juliano 1986; Wheeler 1996). Most of these factors may vary from one habitat to another and geographic variation in body size has thus been studied extensively (Boggs and Freeman 2005; Chown and Klok 2003; Schmidt-Nielsen 1984).

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At a large geographic scale, clinal variation of morphological parameters within species from different taxa has been found (Blanckenhorn and Demont 2004; Hallas et al. 2002). The nature of such variation has been addressed frequently along altitudinal and/or latitudinal climatic gradients (Arthur et al. 2008; Blanckenhorn et al. 2006). However, the mechanisms driving a differential expression of the genotype over a large range of thermal environments are not fully understood (Angilletta and Dunham 2003; Cabanita and Atkinson 2006). Fewer studies have examined divergence in the expression of morphological traits at local geographical scales, where trophic resources and trophic competition appear as prime determinants of adult size and morphology. When nutritional resources are limiting, metabolic trade-offs constrain the allocation of energy inputs to growth, somatic maintenance and reproduction [as shown for example in *Allomyrina dichotoma* (Coleoptera, Scarabaeidae) by Moczek (1998), and in *Onthophagus taurus* (Coleoptera, Scarabaeidae) by Karino et al. (2004)]. In holometabolous insects, restriction in the quality and quantity of the larval diet may result in altered adult morphology and fitness (Boggs and Freeman 2005), with imagos exhibiting specific allometric relationships among various body parts such as wings, flight muscles, ovaries and head.

Within insect species, the size of each organ, appendage or body region bears a specific relationship to overall body size (Shingleton et al. 2007). Positive correlations have been found between wings and body size (Stern and Emlen 1999), fore-femur length and body size (Stern et al. 1996), and body size and morphological traits associated with feeding (mandibles, head) (Thompson 1992). Besides these correlations, head width or mandible length can be related to an ability to consume larger food items (Pearson and Stemberger 1980). Such a positive relationship between feeding morphology and body size might also differ among populations because of distinct resource availability or foraging strategies. This is particularly significant in many predatory arthropods, often food-limited in natural situations (Bommarco 1998; Pearson and Knisley 1985), and for which food intake provides a major part of the resources used for reproduction (Juliano 1986; Sota 1985; Wise 1979).

Invasive predators appear even more affected by availability of resources. They often change their own trophic conditions by displacing or reducing diversity and abundance of native prey (Kenis et al. 2008; Snyder and Evans 2006), as found in the ground beetle *Merizodus soledadinus* Guérin-Ménéville 1832 (Coleoptera, Carabidae) (Chevrier 1996). This insect was introduced from the Falkland Islands to a single site (Port Couvreur) on Iles Kerguelen in 1913 (Jeannel 1940), where it has no efficient competitor [the only native predator species on Iles Kerguelen are one staphylinid, *Antarctophytosus atriceps* (Coleoptera, Staphylinidae) and two spiders, *Myro kerguelensis* (Araneae, Desidae) and *Neomaso antarcticus* (Araneae, Linyphiidae)]. During the past century, this flightless ground beetle has spread over the eastern part of the archipelago and colonized several habitats far from Port Couvreur. This spread has resulted in the formation of geographically distant populations characterized by distinct residence times in each habitat. Because the temporal evolution of the distribution of this alien predator was monitored, we have a set of snapshots ranging from formerly to recently colonized habitats. In addition, this insect can rapidly become a dominant species once established in a new site (Chevrier et al. 1997). The quality and quantity of available resources may be quickly altered and differ among colonized habitats according to the residence time of *M. soledadinus*, impacting individuals' development and morphometry. Also, most animals exhibit a sexual dimorphism mainly related to different exploitation of food resources by females for reserve storage (fat, proteins) for egg maturation, and to reduced longevity in males (Atchley 1971; Butler 1986; Fairbairn 1997). *M. soledadinus* exhibits a sexual size-related dimorphism (Chevrier 1996), hence its growth ability may be differentially affected in males and females by short-term variation in food abundance.

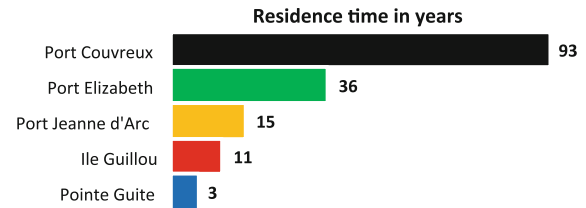
Using a morphometric analysis, we asked if long-term colonization process on Iles Kerguelen induced differences between *M. soledadinus* individuals. To address this question, we measured nine quantitative parameters in adults sampled in five distinct sites colonized at distinct periods. We hypothesized that (i) individuals of *M. soledadinus* are characterized by reduced sizes and morphological traits in habitats colonized early because this predator altered the amount of available trophic resources, (ii) food

limitation would lead to divergence in food-gathering characters and (iii) the selection pressure resulting from the availability of food resources affect males and females differentially.

## Materials and methods

### Collection sites and insect sampling

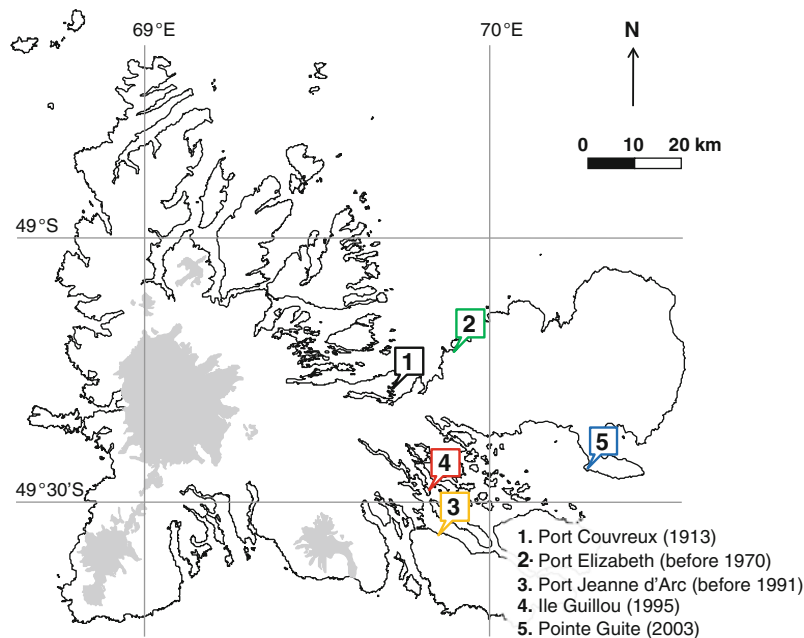
Wild specimens of *M. soledadinus* were sampled in December 2006 in five distinct sites (Fig. 1): (1) Port Couvreur (49°16'35.3''S, 69°41'5.1''E) where the species was first introduced to Iles Kerguelen in 1913 (Jeannel 1940), (2) Port Elizabeth (49°12'58.2''S, 69°51'57.6''E) (first individuals observed *ca.* 1970—Chevrier 1996), (3) Port Jeanne d'Arc (49°33'0.3''S, 69°48'18.2''E) (first observation in 1991—Chevrier 1996), (4) Ile Guillou (49°28'17.6''S, 69°48'23.4''E) (first observation in 1995—Lebouvier, unpublished data) and (5) Pointe Guite (49°25'22.5''S, 70°16'53.6''E) (first observation *ca.* 2003—Lebouvier, unpublished data). Literature and long-term monitoring schemes conducted on Iles Kerguelen since 1974 ensure the accuracy of these arrival dates, except for Port Elizabeth, where the estimated arrival date falls



**Fig. 2** Residence time in each habitat when the five populations of *Merizodus soledadinus* were sampled (2006)

between 1939 and 1970. Based on these data, we can determine the residence time of *M. soledadinus* in each site (Fig. 2). For the five sites, each batch of measured individuals will be considered as a “population.”

Imagos of *M. soledadinus* were all hand-collected from December 1st to 15th 2006 in coastal areas under tide drift lines, so there were strong similarities among sampled habitats. Because of the reduced geographical distance between the sites (less than 50 km) and the absence of major topographic barriers impacting temperature or rainfall, all collected individuals experienced similar meteorological conditions whatever the collection site (meteorological data—available for Port-aux-Français since 1950 and for Ile Guillou since 1997—confirmed this assumption). To ensure a



**Fig. 1** Localization of the five distinct sampled sites and their colonization dates by the ground beetle, *Merizodus soledadinus*

sufficient number of insects for each sex to conduct the study and the subsequent statistical analysis, 100 imago were randomly caught in each site and were immediately stored in vials filled with 70% ethanol before being measured in the lab.

### Traits measured

We measured nine morphometric traits (Fig. 3) in 30 males and 30 females for each one of the five sampled sites (except for Port Jeanne d'Arc, where only 26 males were in a preservation state that allowed reliable measurements of all the traits).

Pictures of each measured parameter were taken for each specimen with a video camera (720 × 576 pixels) connected to a binocular microscope. Measurements were done by vectorial layouts with *JMicroVision 1.2.5* (Geneva, Switzerland). Theoretical precision was 8.8 μm at ×6.4 magnification (used for TOT and ELYT, see Fig. 3 for a detailed description of the traits measured), 3.3 μm at ×16 (used for INTOC, PRONO<sub>L</sub>, PRONO<sub>W</sub>, FEMU<sub>1</sub>, FEMU<sub>3</sub> and STER) and 0.9 μm at ×40 (used for PALP). Each appendage was placed perpendicularly to the video

camera axis to limit parallax problems. Right legs of the first and the third pairs of legs were detached for measurement of FEMU<sub>1</sub> and FEMU<sub>3</sub>.

After the measurements, each individual (with previously detached legs) was dried for 5 days at 60°C and then weighed with a Mettler H20 micro-balance ( $d = 10 \mu\text{g}$ ). Mass is strongly related to size in ground beetles (Hodar 1996; Jarosik 1989) and this mass measurement (MASS) allowed us to compare individuals between sites, but it does not strictly correspond to dry mass because of the solubilization of several compounds in ethanol (den Nijs et al. 1996). However, den Nijs et al. (1996) showed a significant correlation between alcohol mass and dry mass in adults of *Pterostichus cupreus* (Coleoptera, Carabidae).

### Statistical analysis

A bias was identified in measurements of the total length (TOT) of individuals: because of their articulations, the distance between tagms (head, thorax and abdomen) differed greatly among individuals. The bias was confirmed by the low repeatability of this measure on each specimen. In addition, ethanol storage may modify insect abdomen size by swelling or distension (Gruner 2003). Hence, TOT was not used for the multivariate analyses. High variation was also found for dry mass (MASS), but this measure was reliable and reflects individual variability.

Adequate normality of the distribution of residuals was checked for each variable, each sex and each site by Q–Q plots and Shapiro–Wilk tests; Levene tests were applied to test homoscedasticity of the variables. A two-way MANOVA was then performed to test the significance of the factors (sex and site) with respect to potential correlations among variables. This multivariate analysis was followed by a Factorial Discriminant Analysis (FDA) for each sex to determine how the individuals from the five sites were structured according to the measured variables. Between- and Within-Group analyses were also used for each sex to determine the proportion of inertia explained by the differences among sites (inter-site variability) on the one hand, and by heterogeneity within sites (intra-site variability) on the other. Separation and neighbourhood of the sites observed on both discriminant planes were fully confirmed using Hierarchical Ascendant Classifications (HAC)



**Fig. 3** Morphological traits measured in adults of *Merizodus soledadinus* (male shown). *TOT* Individual total length from the labrum to the end of the right elytra, *ELYT* Length of the right elytra, *INTOC* Fore interocular width, *PRONO<sub>L</sub>* Length of the pronotum, *PRONO<sub>W</sub>* Width of the pronotum, *STER* Length of the last abdominal sternite, *FEMU<sub>1</sub>* Metafemur length of the right foreleg, *FEMU<sub>3</sub>* Metafemur length of the right hind leg, *PALP* Width of the last article of the right maxillary palp

on measured variables, with a priori input of five groups (data not shown).

A univariate procedure was performed to explore further the sex  $\times$  site interaction. Interaction plots showed only an interaction for the STER parameter. A two-way ANOVA was therefore performed for STER to test (i) differences among sites for STER in each sex (site effect), (ii) sexual dimorphism for STER in each site (sex effect), and (iii) variation among sites in the expression of the sexual dimorphism for STER (sex  $\times$  site interaction). Pairwise comparisons were performed by the Tukey post hoc procedure.

All statistical tests were done with  $R^{TM}$  2.7.0 with an  $\alpha$  threshold = 0.05. Multivariate analyses were run with ADE4 plugin for  $R^{TM}$  2.7.0 (Thioulouse and Dray 2007).

**Results**

**Sexual dimorphism and morphological differences among sites**

Mean trait values for each sex and each site are shown in Table 1 with the MANOVA results. A strong and significant sexual dimorphism appeared, as well as significant morphometric differences among sites. Interaction plots showed the highest sex  $\times$  site effect for STER (Fig. 4). This suggests that sexual size dimorphism expression was more altered by the site effect for the last abdominal sternite than for the eight other parameters and for the mass. As shown in Fig. 4, STER sexual dimorphism was highest in Port Elizabeth—with females showing the highest values—whereas it was similar in the other sites.

STER sexual dimorphism was further examined using the Tukey post hoc procedure (Fig. 5). Sexual dimorphism for STER was significant only in Port Couvieux, Port Elizabeth and Ile Guillou. Sexual dimorphism was highest in Port Elizabeth and lowest in Port Jeanne d’Arc. Moreover, STER did not differ significantly among males, whereas differences appeared among females (Fig. 5).

**Variation of morphological traits in males**

The MANOVA confirmed the significant differences among populations. FDA was performed to determine which traits act to separate the populations. In males,

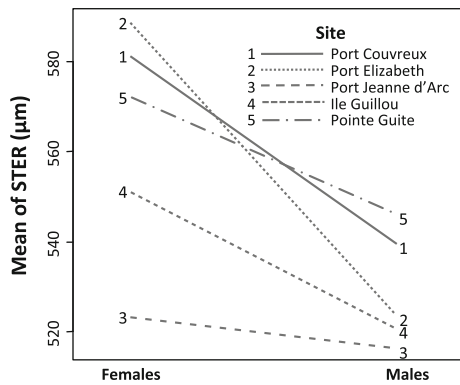
**Table 1** Values (mean  $\pm$  SD) of the traits measured in males and females sampled in the five sites on Iles Kerguelen

	1. Port Couvieux		2. Port Elizabeth		3. Port Jeanne d’Arc		4. Ile Guillou		5. Pointe Guite		MANOVA	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	Factor	P
TOT	5677 $\pm$ 320	5977 $\pm$ 371	5568 $\pm$ 229	5908 $\pm$ 248	5685 $\pm$ 181	5883 $\pm$ 227	5550 $\pm$ 215	5828 $\pm$ 280	5832 $\pm$ 219	5907 $\pm$ 283	Sex	35 <sub>9</sub> ***
ELYT	3168 $\pm$ 111	3336 $\pm$ 141	3202 $\pm$ 114	3411 $\pm$ 117	3236 $\pm$ 102	3371 $\pm$ 139	3227 $\pm$ 106	3397 $\pm$ 157	3288 $\pm$ 123	3423 $\pm$ 118	Site	8 <sub>36</sub> ***
INTOC	859 $\pm$ 36	872 $\pm$ 37	879 $\pm$ 34	912 $\pm$ 34	895 $\pm$ 34	907 $\pm$ 24	893 $\pm$ 32	919 $\pm$ 35	897 $\pm$ 35	906 $\pm$ 32	Sex $\times$ site	2 <sub>36</sub> ***
PRONO <sub>L</sub>	1103 $\pm$ 45	1137 $\pm$ 57	1111 $\pm$ 53	1175 $\pm$ 42	1117 $\pm$ 42	1161 $\pm$ 51	1121 $\pm$ 48	1176 $\pm$ 60	1139 $\pm$ 45	1158 $\pm$ 50		
PRONO <sub>W</sub>	1453 $\pm$ 55	1479 $\pm$ 85	1485 $\pm$ 58	1538 $\pm$ 68	1473 $\pm$ 78	1546 $\pm$ 69	1517 $\pm$ 59	1562 $\pm$ 76	1488 $\pm$ 78	1545 $\pm$ 54		
STER	540 $\pm$ 29	582 $\pm$ 36	522 $\pm$ 36	589 $\pm$ 36	517 $\pm$ 31	523 $\pm$ 37	520 $\pm$ 37	551 $\pm$ 49	546 $\pm$ 40	572 $\pm$ 36		
FEMU <sub>1</sub>	1068 $\pm$ 40	1073 $\pm$ 46	1063 $\pm$ 52	1092 $\pm$ 41	1046 $\pm$ 52	1080 $\pm$ 49	1062 $\pm$ 40	1085 $\pm$ 56	1094 $\pm$ 50	1100 $\pm$ 39		
FEMU <sub>3</sub>	1443 $\pm$ 54	1458 $\pm$ 67	1442 $\pm$ 68	1478 $\pm$ 53	1424 $\pm$ 60	1450 $\pm$ 62	1435 $\pm$ 66	1462 $\pm$ 79	1488 $\pm$ 58	1487 $\pm$ 64		
PALP	75 $\pm$ 5	78 $\pm$ 4	80 $\pm$ 5	81 $\pm$ 3	80 $\pm$ 4	83 $\pm$ 4	80 $\pm$ 3	83 $\pm$ 3	80 $\pm$ 4	82 $\pm$ 3		
MASS	2062 $\pm$ 381	2547 $\pm$ 463	2279 $\pm$ 280	2572 $\pm$ 454	2040 $\pm$ 258	2344 $\pm$ 342	2321 $\pm$ 353	2783 $\pm$ 558	2785 $\pm$ 397	3032 $\pm$ 574		

TOT Individual total length from the labrum to the end of the right elytra, ELYT Length of the right elytra, INTOC Fore interocular width, PRONO<sub>L</sub> Length of the pronotum, PRONO<sub>W</sub> Width of the pronotum, STER Length of the last abdominal sternite, FEMU<sub>1</sub> Metasternur length of the right foreleg, FEMU<sub>3</sub> Metasternur length of the right hind leg, PALP Width of the last article of the right maxillary palp, MASS Alcohol-dry mass of body + detached legs

Biometrics are expressed in  $\mu$ m and mass in  $\mu$ g. 30 males and 30 females were measured for each site, except in Port Jeanne d’Arc ( $N_{\text{males}} = 26$ )

\*\*\*  $P \leq 0.001$



**Fig. 4** Interaction plot (sex  $\times$  site) for STER (length of the last abdominal sternite). Sex effect appeared higher in Port Elizabeth than in the four other sites

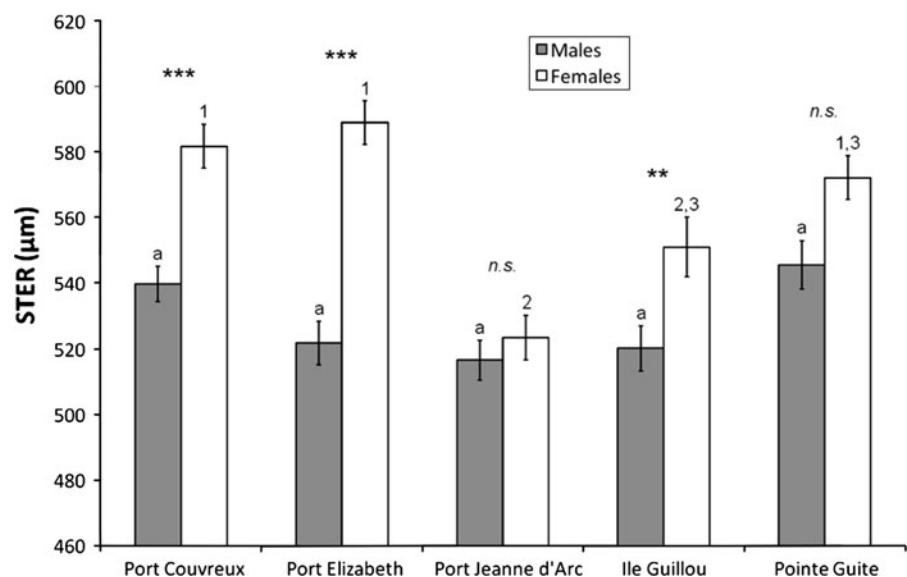
the first factorial plane (F1  $\times$  F2) accounted for 82.2% of the total inertia (Fig. 6). Groups were significantly separated by the first and second axes (Wilks  $\lambda \approx 0$ , Bartlett  $\chi^2$ ,  $P < 0.001$  for F1 and F2). The correlation circle and structure matrix (data not shown) indicated that F1 is a general body size axis (contributions from ELYT, FEMU<sub>1</sub>, FEMU<sub>3</sub>, PRONO<sub>L</sub> and MASS), with negligible contributions from STER, PALP, INTOC and PRONO<sub>w</sub>. The second axis (F2) mainly corresponded to a contrast between STER and PALP plus INTOC.

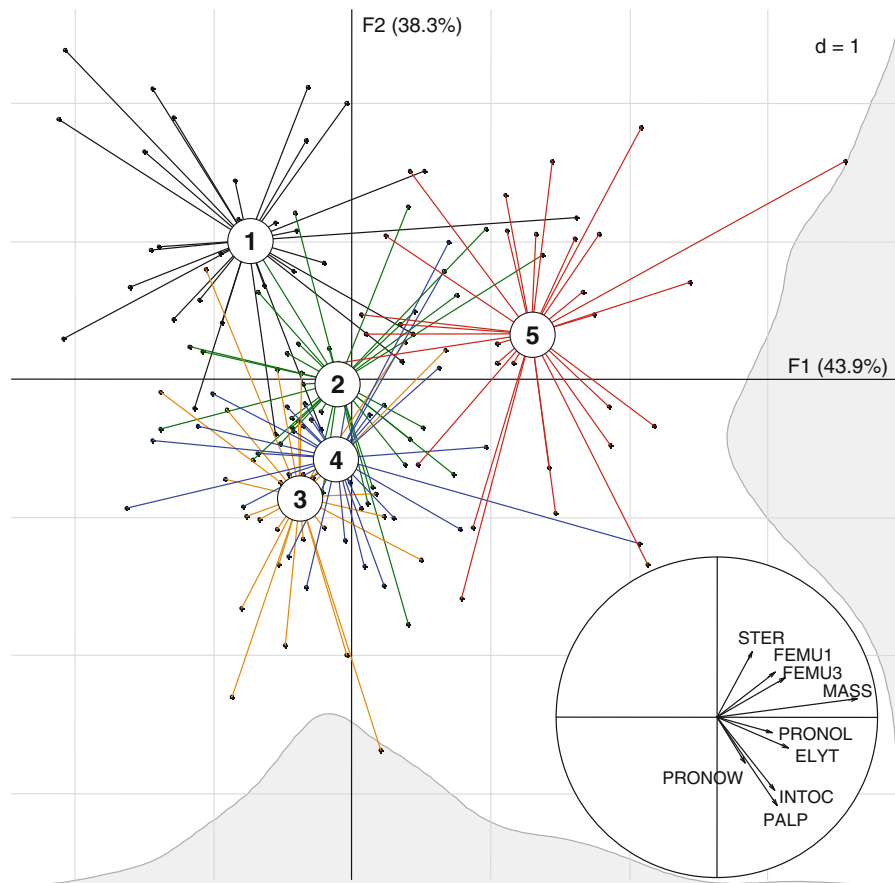
Individuals coming from the habitats with the longest (Port Couvreur) and shortest (Pointe Guite)

residence times were opposed on the first discriminant axis (Fig. 6): the smallest individuals were from Port Couvreur (1) and the largest from Pointe Guite (5). Individuals from populations 2, 3 and 4 had intermediate positions and were poorly discriminated on F1 axis. The F2 axis sorted populations as follows: 1; 5; 2; 4 and 3. Individuals from Port Couvreur (1) were well discriminated owing to the particularly low values of their PALP (see Table 1).

Per site discriminations were not completely achieved, and overlapping between populations appeared. In Port Couvreur (1) and Pointe Guite (5), males were the best assigned to their group (respectively 78 and 70%). Individuals from Port Jeanne d'Arc (3) and Ile Guillou (4) were well separated too (respectively 65 and 63%), but most of the males from Port Elizabeth (2) were misclassified, with only 30% well assigned. This finding may be linked to the results of the Between- and Within-Group Analyses, which showed that inter-site differences accounted for only 15% of the total inertia, while intra-site heterogeneity accounted for most of the inertia (85%). These results point to the significant effect of the different sites as well as important intra-site variability caused by high inter-individual heterogeneity. The relative standard deviation (RSD) was used to quantify the variability between males within each population. For all variables, the RSD reached 6.0% in Port Couvreur, 5.6% in Port Elizabeth,

**Fig. 5** Mean STER (SE) in males and females sampled in the five distinct sites. Sites are sorted by colonization dates, from Port Couvreur (1913) to Pointe Guite (ca. 2003). Between sexes: \*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.005$ ; *n.s.* not significant. Between sites: different letters (males) and numbers (females) indicate significant differences between samples





**Fig. 6** Factorial Discriminant Analysis: projection of variables (*correlation circle*) and males of each population onto the first factorial plane. *Lines* link individuals to the centre of gravity of their group. *Gray curves* illustrate density

distribution of projected individuals on each axis. The amounts of inertia explained by axes F1 and F2 are expressed as percentages. 1 Port Couvreur, 2 Port Elizabeth, 3 Port Jeanne d'Arc, 4 Ile Guillou, 5 Pointe Guite

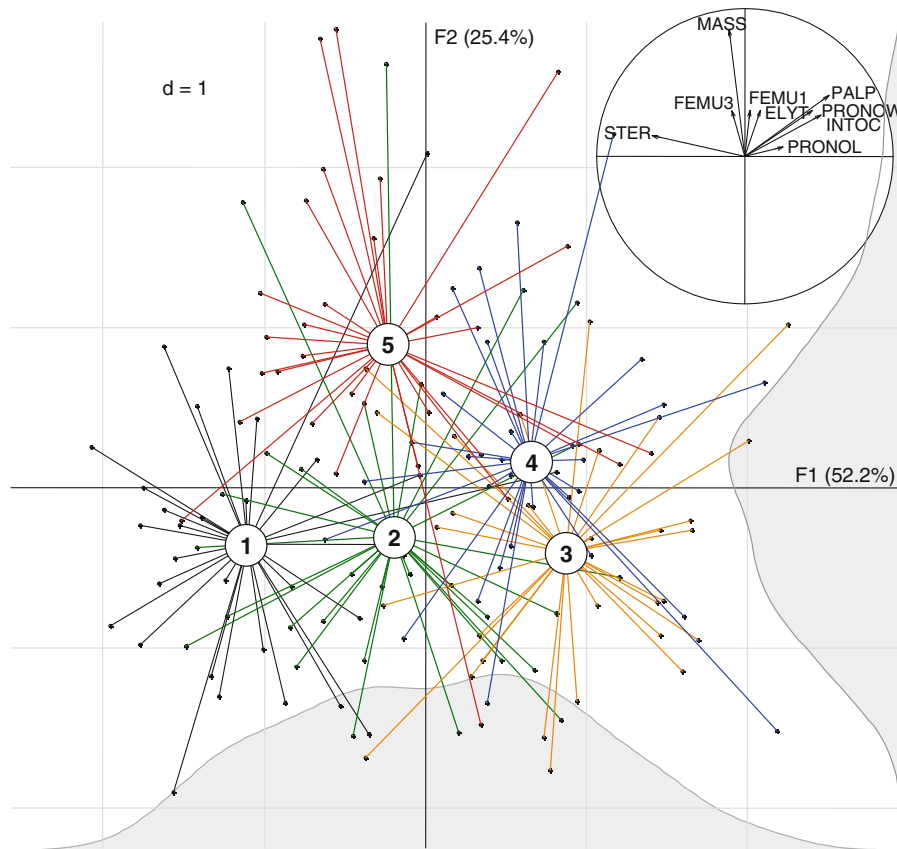
5.4% in Port Jeanne d'Arc, 5.4% in Ile Guillou, and 5.7% in Pointe Guite.

#### Variation of morphological traits in females

Overall, conclusions were similar for females except that the first factorial plane was rotated. The sign relationship of the F1 and F2 axes was inverted and did not account for the same amount of inertia as in males (Fig. 7). This first factorial plane accounted for 77.6% of the total inertia, with significant discrimination on the two-first axes (Wilks  $\lambda \approx 0$ , Bartlett  $\chi^2$ ,  $P < 0.001$  for F1 and F2). The F1 axis mainly discriminated populations by the contrast between STER and PALP plus INTOC (as for the males' F2 axis). F2 was an increasing general body size axis, mainly constructed by MASS, ELYT, FEMU<sub>1</sub> and

FEMU<sub>3</sub>. Port Couvreur (1) and Port Jeanne d'Arc (3) individuals were opposed on the F1 axis, and Pointe Guite (5) individuals were well separated on the F2 axis.

Misclassifications also appeared in females. In Port Couvreur (1), Port Jeanne d'Arc (3) and Pointe Guite (5), females were the best assigned to their groups (respectively 73, 70 and 67%), whereas only 50 and 40% of the individuals from Port Elizabeth (2) and Ile Guillou (4) were well assigned, respectively. As in males, Between- and Within-Group Analyses indicated high intra-site variability: inter-site and intra-site differences accounted for 13.7 and 86.3% of the total inertia, respectively. For the eight reliable measurements, the RSD were 6.4% in Port Couvreur, 5.6% in Port Elizabeth, 5.6% in Port Jeanne d'Arc, 6.9% in Ile Guillou, and 5.7% in Pointe Guite.



**Fig. 7** Factorial Discriminant Analysis: projection of variables (*correlation circle*) and females of each population onto the first factorial plane. *Lines* link individuals to the centre of gravity of their group. *Gray curves* illustrate density

distribution of projected individuals on each axis. The amounts of inertia explained by axes F1 and F2 are expressed as percentages. 1 Port Couvreur, 2 Port Elizabeth, 3 Port Jeanne d'Arc, 4 Ile Guillou, 5 Pointe Guite

## Discussion

The importance of examining variation of morphological traits was recently re-emphasised because these traits (i) are used extensively for taxonomy, (ii) are partially under genetic control, (iii) are the target of selection, and (iv) reflect intraspecific clinal divergence (Garnier et al. 2005). Moreover, variation in morphology can exhibit clear patterns of differentiation that molecular markers may not detect (Nice and Shapiro 1999).

Imagos of *M. soledadinus* were collected at the same times on the Péninsule Courbet (Eastern part of Iles Kerguelen) in similar microhabitats (under tide drift lines and stones along the seashore). Climatic conditions differ greatly between the western and eastern part of Iles Kerguelen. The western region is mountainous and experiences Foehn winds. The

eastern region, and more particularly the Péninsule Courbet, is composed of large coastal plains, where climatic conditions at sea level are similar. This assumption is supported by our meteorological data collected on Ile Guillou and at Port-aux-Français at a depth of five centimetres below ground level. The size-trait divergence patterns observed among the five distinct sites on Iles Kerguelen can thus be related to the residence time of *M. soledadinus* in each location, i.e. to the distinct abundance and availability of the trophic resources as a result of predation pressure (Chevrier 1996; Chevrier et al. 1997; Laparie, Lebouvier and Renault, unpublished data), rather than to differential abiotic conditions in the microhabitats.

Variation in body size, either at the individual level or in the frequency distribution of individuals' body sizes within a population, may indicate different



types of environmental stress (McGeoch 1998). Nutrition is one of the best studied factors that affect morphometry and that can vary among habitats (Shingleton et al. 2007). In our study, in both sexes, morphometry of individuals from Port Couvreur (highest residence time) was always opposed to that one of individuals from Pointe Guite (shortest residence time), both being extremes in terms of general body size. As assumed by the “decreasing body size hypothesis” (Blake et al. 1994; Gray 1989; Szyszko 1983), highly disturbed habitats support smaller ground beetles more than less disturbed areas do (Magura et al. 2006). This probably results from their lowest energetic requirements for growth and their shortest durations of development (Peters 1983). Given the low arthropod diversity on Iles Kerguelen, the two native wingless flies *Anatalanta aptera* (Diptera, Sphaeroceridae) and *Calycopteryx moseleyi* (Diptera, Micropezidae) represent two of the most profitable prey for *M. soledadinus* in terms of energy (Vernon 1986) and handling time (including spotting, capture, eating and digesting—see Krebs and Davies 1993). Over the last 25 years, no *A. aptera* or *C. moseleyi* were observed at Port Couvreur and very few were observed near Port Elizabeth although they used to be abundant in both sites (Chevrier 1996; Lebouvier, unpublished data). These species disappeared from Port aux Français as soon as *M. soledadinus* arrived there (1995) and could still be observed some few kilometers away at Pointe Guite in 2006, where some adults of *M. soledadinus* were also observed for the first time. Populations of *M. soledadinus* were found to have a strong impact on invertebrate diversity and abundance (Chevrier 1996; Lalouette, Lebouvier and Renault, unpublished data). A potential predation switch to microinvertebrates such as springtails when the more profitable macroinvertebrate prey like the native flies become scarcer could explain the body size decrease. In addition, a morphometric differentiation also appeared in populations characterized by recent and close residence times, supporting earlier conclusions of Chevrier et al. (1997) that *M. soledadinus* quickly becomes the most abundant species in invaded habitats.

Besides the overall body size, shape and size of trophic appendages were found to vary between individuals supplied with distinct diets (Thompson 1992; Thompson 2001). Divergence in mouthparts may result in an asymmetry of the prey consumed

(Pearson and Stemberger 1980). The thinnest maxillary palps and smallest heads were found in individuals from Port Couvreur, but there were no significant differences among individuals from other sites for those variables. In light of the significant morphological differences among individuals from Port Elisabeth, Port Jeanne d’Arc, Ile Guillou and Pointe Guite, biometric evolution of both head and maxillary palps cannot be coupled to changes in size of the other morphological variables. The residence time in each habitat could be an influential variable in the morphology of *M. soledadinus*. We hypothesize that alteration of available resources, and the resulting prey-switching, act on the general morphology of the individuals and determine the evolution of the mouthparts parts’ size.

Body size of *M. soledadinus* can also be altered by intrapopulation competition. Lenski (1982) showed that body size was reduced when density and competition increased in *Carabus limbatus* (Coleoptera, Carabidae). During the survey of the geographic distribution and abundance of *M. soledadinus* in 2005–2006, we quantified population densities on Iles Kerguelen. We defined 4 abundance levels from 1 (no individual found after a 10 min search by one person) to 4 (very high densities, more than 250 individuals found in 10 min by one person). The five locations sampled in the present study were characterized by the highest abundance level (level 4, very high densities), thus suggesting intrapopulation competition. Despite significant discrimination of the five sampled populations, high variability occurred within each population. In the parasitic beetle *Brachinus lateralis* (Coleoptera, Carabidae), host size is of prime importance to individual size, but the limited opportunity for host choice may maintain size variation despite evidence of natural selection pressure on size (Juliano 1985). Intrapopulation competition may maintain size heterogeneity in *M. soledadinus* owing to different food intakes between individuals, regardless of the overall habitat resources. Developmental instability, i.e. intra-individual stochastic variation and phenotypic noise during growth (Nijhout and Davidowitz 2003; Dongen 2006), could also maintain variability within populations regardless of the factors studied here. In addition, the life cycle of *M. soledadinus* lasts about 1 year and its lifespan exceeds 1 year (Jeannel 1940; Ernsting 1993), suggesting that we should have more

than a single cohort within each population. Variation in adult body size may also result from different thermal conditions larval instars endured during their development (Angilletta 2009). Although there are no hints suggesting different population structure in different sites, we can therefore not rule out a possible effect on body size.

Cannibalism may also impact body size when both quality and quantity of food are reduced. This phenomenon was described as prevalent when food resources are limiting because it reduces competition for these resources (Dong and Polis 1992; Currie et al. 1996). More cannibalistic interactions may occur in the first habitats colonized by *M. soledadinus*. When breeding *M. soledadinus* populations under controlled conditions, we observed predation only of imagos on larvae (no predation by larvae of one another). As smaller individuals develop faster than bigger ones under similar conditions (as shown by Blanckenhorn (1998) in *Scatophaga stercoraria* (Diptera, Scatophagidae)), small individuals of *M. soledadinus* may be less penalized by reaching the adult stage more quickly. Indeed, Chown and Nicholson (2004) reported that traits promoting large body size such as extended development time or increased growth rate (which depends on increased feeding rate) increase the risk of predation. In our study, the residence time could promote a body size diminution and a faster development owing to resource limitation and higher intrapopulation competition in the most altered sites. However, we also must keep in mind that larvae have a different space-approaching behaviour than adults, i.e. they bury themselves and are thus found in the soil, whereas adults are usually found at ground level.

As was previously demonstrated by Chevrier (1996), we found a significant sexual dimorphism in adults of *M. soledadinus*, with females larger than males. This result is consistent with the literature, since several insect species have already been characterized by marked sexual dimorphism in either mass, size, shape or even physiological capabilities (Day et al. 1994; Fairbairn 1997; Renault et al. 2003; Svensson 1977). Because of their different roles in reproduction, males and females are often under selection that favours their divergent morphological appearance (Badyaev 2002). Energetic allocation contributes greatly to explaining sexual size dimorphism, with females having a higher energy cost

associated with gamete production (Nylin and Gotthard 1998; Tammaru et al. 2002). On the other hand, male size may affect their dispersal and be important in sexual selection and competition for females (Nylin and Gotthard 1998).

The morphological traits covarying with reproductive and dispersal functions are of particular interest with respect to the invasive success of a species. They represent the level of developmental and morphological plasticity of the species to the environmental and ecological characteristics of the newly colonized habitat (Chown et al. 2007; Rosecchi et al. 2001). Reproductive traits and more particularly copulatory organs often exhibit reduced variation relative to body size within species of arthropods (Eberhard 1998). We found that STER variation was not paired with body size variation. STER values in males were similar in all sites regardless of body size variation. In females, STER values did not differ between the smallest individuals (Port Couvreur and Port Elizabeth) and the biggest ones (Pointe Guite). Energetic allocation during diet restriction thus involves differential developmental plasticity for STER. The target of sexual selection could be reproduction-related traits rather than body size, as was found previously by Preziosi and Fairbairn (1996). Because insects may have greater success with larger genitalia and not because they are bigger *per se*, the general body size-independent variation of STER is ecologically relevant. In addition, a stronger influence of reproduction on morphological traits in females than in males can be hypothesized. In Port Elizabeth, the sternites are short in males and long in females compared to the sternites of individuals from other populations. This may result from a greater difference in energetic allocation to reproduction between females and males in this population. Port Elizabeth could be a transitional stage in which reaction norms optimizing fecundity are expressed earlier in females. The relationship between STER and fecundity should be investigated further in *M. soledadinus* by measuring the number and size of ovarioles and eggs.

An integrative conjecture can be hypothesized to explain the relationship between morphometry and the invasion process in populations of *M. soledadinus*. In both sexes, differentiation occurred through body size (MASS, ELYT, FEMU<sub>1</sub>, FEMU<sub>3</sub>, PRONO<sub>L</sub>) and reproduction (STER) *versus* feeding strategy (PALP,

INTOC). Life histories promoting increased body size might be prominent when a species colonizes new sites, as was found in individuals from Pointe Guitte. Larger individuals may be characterized by higher dispersal ability (Thiele 1977) and may therefore be more efficient than smaller ones in colonizing and establishing populations in new sites. Subsequently, reproduction strategies and adjustments of the feeding behavior as a consequence of the available prey in the microhabitat may be important for the settlement of the populations, as suggested by the characteristics of Port Couvreur individuals.

Blanckenhorn (2000) highlighted the need for experimental and comprehensive studies that address the fitness costs at the ecological level of being larger. Selection of large body size occurs in most organisms and empirical evidence is needed to determine if sporadic selection in time and space suffices to counterbalance this major evolutionary force (Blanckenhorn 2000). In the present study, we demonstrated morphological differentiations at a local scale among several populations differing from both geographical and chronological standpoints. We suggest that the observed size diminution of *M. soledadinus* may reflect both a priori (development under diet restriction, survival) and a posteriori (intrapopulation competition, cannibalism) effects on development and selection. Our study indicates that being smaller might be advantageous in habitats where optimal trophic resources are altered by *M. soledadinus*, a view that supports some of the mechanisms proposed by Blanckenhorn (2000).

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