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ORIGINAL PAPER

New insights into the ecology of *Merizodus soledadinus*, a predatory carabid beetle invading the sub-Antarctic Kerguelen Islands

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Abstract Our knowledge of the main determinants of invasion success is still incomplete. Among these factors, the effects of biological traits, including fecundity, longevity and dispersal in newly colonised regions, are pivotal. However, while numerous studies have considered ecological and evolutionary impacts of non-native species, their biology often remains understudied. Despite the continuous geographic expansion of *Merizodus soledadinus* (Coleoptera: Carabidae) at the Kerguelen Islands over recent decades, the main life-history parameters of this species are unknown. We determined adult longevity under controlled conditions, monitored seasonal activity through pitfall trappings, and analysed temporal variations of egg load and body reserves in field-collected individuals. The median adult life span (LT_{50}) was 241 days, with maximum longevity of 710 days ($N = 500$). Females carried eggs throughout the year (8.94 ± 3.56 eggs per female), and it was not possible to pinpoint any clear egg-laying period. Year-round trappings demonstrated continuous activity of adults over seasons, with a peak during the austral summer that may arguably be associated with higher temperatures. Body stores (glycogen and proteins) did not vary significantly through the year, suggesting that adults feed continuously despite different prey availability between summer and winter, possibly via diet shifts. The amount of triglycerides increased at onset of summer, which may be associated with higher summer locomotor activity and/or more intense predation and reproduction.

Keywords Biological invasion · Body reserves · Egg load · Longevity · Seasonal activity

Introduction

Despite the prominent ecological and socio-economic impacts of non-native species (Pimentel et al. 2005; Vilà et al. 2010), our knowledge of the main determinants of invasion success is still incomplete (Pyšek and Richardson 2008; Gurevitch et al. 2011). Not all non-native species become invasive following their introduction into new geographical areas (terminology defined in Falk-Petersen et al. 2006), likely because of the diversity of interconnected biotic and abiotic parameters that drive invasion success (Williamson 2006). In parallel, several theories, including the evolution of increased competitive ability, the novel weapon hypothesis or the enemy release hypothesis, have been formulated over recent decades to try to explain how non-native species successfully overcome novel environmental filters (Callaway and Ridenour 2004; Colautti et al. 2004; Handley et al. 2008; van Kleunen et al. 2010). Invasiveness has also been suggested as a pivotal determinant of invasion rate (Williamson and Fitter

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1996; Kolar and Lodge 2001), and the plasticity of traits such as fecundity and longevity, together with dispersal capability and stress resistance, is of tremendous importance for the successful establishment and subsequent expansion of non-native organisms. However, there are often great shortcomings in our understanding of the biology and autecology of non-native species in introduced areas, thus impairing understanding of invasion processes.

At the sub-Antarctic Kerguelen Islands, located in the south Indian Ocean (48°30′–50°S, 68°27′–70°35′E) and subject to cold oceanic climate, multiple insect species have been accidentally introduced to the point that the archipelago now hosts more non-native than native species of arthropods (Frenot et al. 2005; Lebouvier et al. 2011). Among the introduced insects, several have spread significantly despite extremely limited human assistance, if any (Frenot et al. 2005; Lebouvier et al. 2011). The predatory carabid beetle *Merizodus soledadinus* (Coleoptera: Trechidae) was accidentally introduced from the Falkland Islands in 1913 at a single site at the Kerguelen Islands (Port Couvreux; 49°17′04.9″S, 69°41′41″E, Fig. 1), where the species was first observed in 1939 (Jeannel 1940). Historical data and long-term monitoring of the expansion of this flightless insect have shown that it first colonised localities near the introduction site, then spread along the north coast of the main island, and ultimately invaded several islands of the Golfe du Morbihan [likely via human- or bird-assisted introductions, or passive dispersal by flotation; see Renault (2011)]. When established, this predator becomes the dominant species in the colonised habitats and generates significant ecological impacts on native fauna, particularly endemic dipterans (Ottesen 1990; Ernsting 1993; Todd 1996, 1997; Chevrier et al. 1997; Lalouette et al. 2012).

A range of recent studies on the Kerguelen Islands have described the autecology of *M. soledadinus* specimens exposed to a range of environmental factors. These works reported the physiological plasticity and tolerance of this insect to environmental variations, including temperature (Lalouette et al. 2012; Laparie and Renault 2016) and salinity (Hidalgo et al. 2013). Conversely, adults did not survive longer than two days when relative humidity decreased below 70 % (Ouisse et al. 2016), which is consistent with the main habitats where this species thrives (Renault et al. 2015). Meanwhile, data are still missing regarding several important key elements of its biology (e.g. longevity, fecundity and prey preferences). The few studies conducted on this species reported by Chevrier et al. (1997) mention continuous presence of adults throughout the year at the Kerguelen Islands, but no published empirical data are available for these observations. In South Georgia, another sub-Antarctic island invaded by

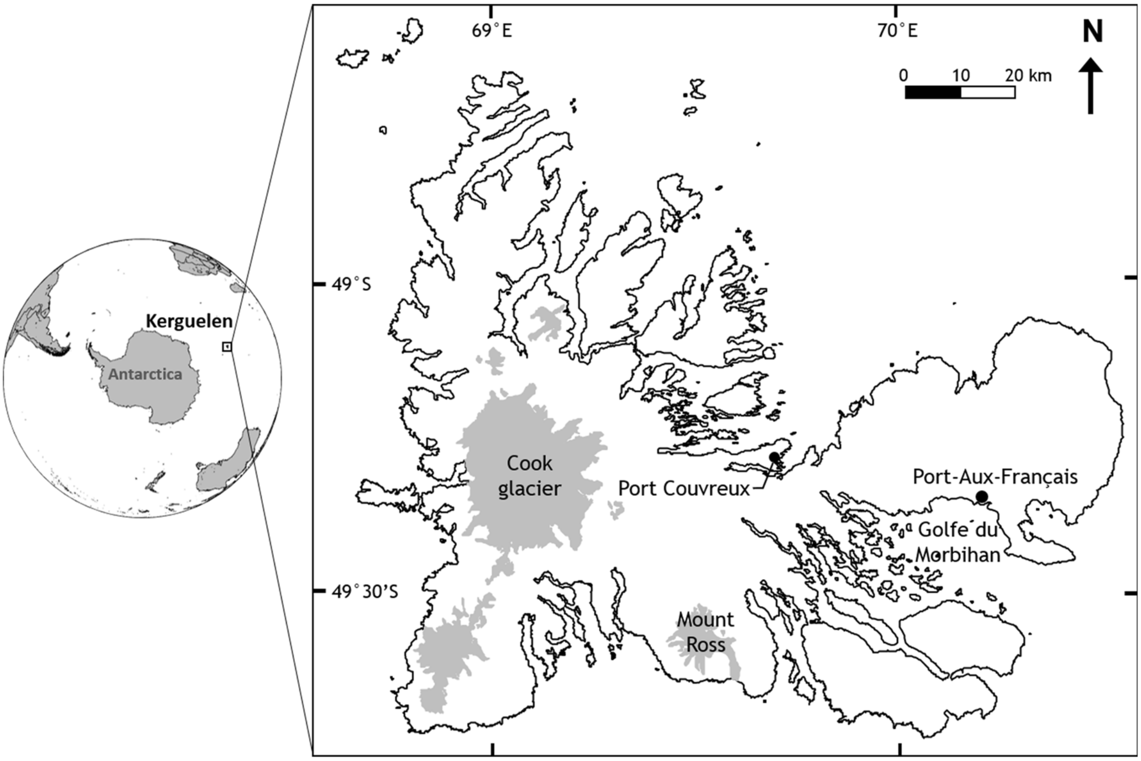

Fig. 1 Location of the sub-Antarctic Kerguelen Archipelago. *Merizodus soledadinus* was introduced only at Port Couvreux. All experiments were conducted at the research station at Port-aux-Français using beetles sampled in the vicinity of the research station

this insect (Ernsting 1993; Brandjes et al. 1999), egg load ranged from three to six eggs per female, and the absence of corpora lutea in females at the onset of summer periods (Ernsting 1993) suggested a single breeding period.

The aim of this work is to improve our knowledge of the ecology of *M. soledadinus* at the Kerguelen Islands. To estimate adult longevity, a survival experiment was designed under controlled conditions. Based on females' reproductive status at South Georgia (Ernsting 1993), we hypothesised an adult life span of 1–2 years. The number of eggs carried by females through the year was also investigated, since high reproductive investment can be a key characteristic in the rapid success and establishment of invasive species (Hayes and Barry 2008). Finally, we used long-term pitfall trapping to verify Jeannel's (1940) and later field observations that *M. soledadinus* is active throughout the year. We expected a decrease in activity during the austral winter due to harsher climatic conditions and/or reduced prey availability, which should result in seasonal variations of protein, glycogen and triglyceride amounts, i.e. the major components of body fat in insects (Arrese and Soulages 2010). Altogether, this knowledge will complement our understanding of the invasion success of this insect at the Kerguelen Islands and, in parallel, the biological limitations that may set the limits of its range.

Materials and methods

Estimation of adult longevity

Trapping and field observations of teneral adults (individuals whose cuticle is not yet fully melanised, see Online Resource Fig. ESM_1) at the Kerguelen Islands revealed that the main emergence peak occurs in late February to early March, as also observed by Ernsting (1993) at South Georgia. Therefore, adults of *M. soledadinus* were sampled in March 2013 under stones (ca. 5 m above sea level) around the research station (Port-aux-Français, Kerguelen Islands) to maximize the proportion of newly emerged individuals in the samples. A total of 500 beetles were hand-collected, and used for estimating life span under controlled conditions. Soon after collection (<2 h), all individuals were equally distributed into five plastic boxes [18 × 12 × 7 cm, $N = 100$ adults measuring 5–7 mm in body length (Laparie et al. 2010) per plastic box] lined with sterilised moist sand. Boxes were placed into a thermoregulated room (L:D 12:12 h) set to 8 ± 2 °C, corresponding to thermal conditions close to those during austral summer at this latitude (Lebouvier et al. 2011). Beetles were fed monthly with live prey, i.e. field-collected diptera maggots (*Fucellia maritima*, *Calliphora vicina*) and enchytraeids (annelids), both part of their natural diet (Laparie et al. 2012). The boxes were checked fortnightly, when dead beetles were counted and removed, and sand moisture adjusted as needed; the sand was changed every 2 months. The exact age of imagos cannot be ascertained without accurate knowledge of their emergence date. Since breeding this species under laboratory conditions has not been successful so far, the number of days elapsed since the collection date of the specimens had to be used as a proxy for life span. When present, larvae were removed from the boxes. The experiment continued until all beetles died.

Annual activity in natural environment

Sets of three pitfall traps filled with 75 % ethanol were installed in 2005 at two locations (Isthme Bas 1, IS_1: −49°36′48″S, 70°24′36.3″E; Isthme Bas 2, IS_2: −49°36′44″S, 70°24′61.1″E) in the vicinity of Port-aux-Français (Kerguelen Islands) to monitor densities of arthropods active at ground level. Over the duration of the experiment (2005–2015), all six traps were opened for five to seven days every month (twice monthly for the needs of another study in March and May 2006, December 2009, November and December 2012, February and May 2013 and October 2015).

Adults were counted in the laboratory. Since traps were not always opened for the same duration, data were standardised as number of individuals/days of operation. Additionally, due to high inter-annual variability in catches, annual activity was calculated as relative monthly abundance for that year.

Reproductive status of females through the year

From December 2010 to March 2012, adults of *M. soledadinus* were hand-collected every two weeks under stones (ca. 5 m above sea level) at Port-aux-Français. They were immediately stored in 80 % ethanol at −20 °C until further analysis. For each sampling date, 20 females (when possible) were randomly collected for measurements of interocular width, pronotum width and length, right elytra length, abdomen width and last abdominal sternite length (Fig. 2a). The measurements were carried out on images taken using a video camera (AxioCam ERc 5s, ZEISS, Germany) connected to a stereomicroscope, through vectorial layouts, with AxioVision software (ZEISS, Germany). The females were then dissected to count eggs, if any (see Online Resource Tab.ESM_1 for details). Larger eggs, located on the distal part of the abdomen, and smaller ones, up in the ovarioles, were distinguished (Fig. 2b, c).

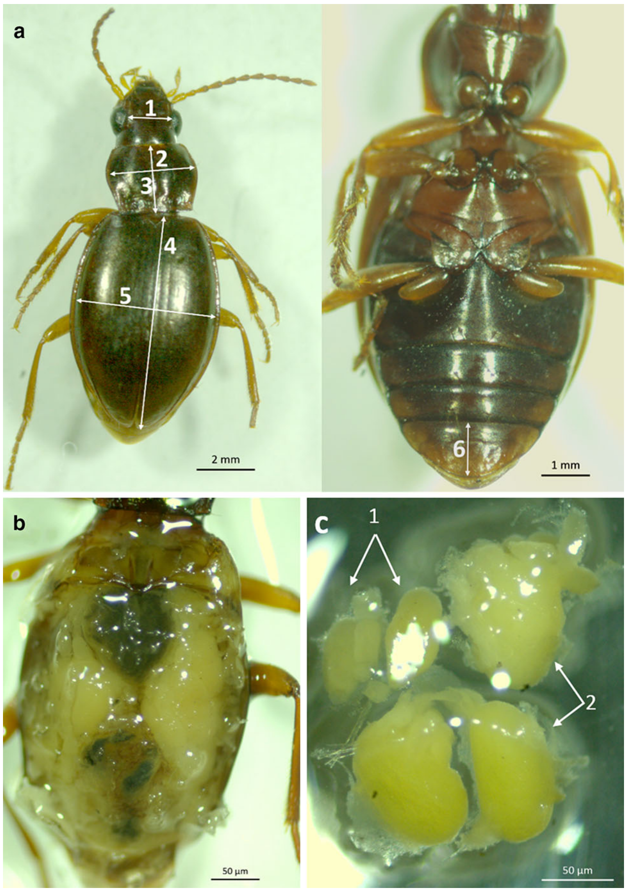

Fig. 2 Morphological trait measurements and dissection pictures of adult females of *Merizodus soledadinus*. **a** Five morphological traits were measured on each female prior to dissection: on dorsal side interocular width (1), pronotum width (2) and length (3), right elytra length (4) and width (5) as well as last abdominal sternite length (6) on ventral side. **b** Dissection picture of the abdomen after removal of elytra. One can see eggs in the ovaries on both sides of the abdomen. **c** Detail of the right ovary after uncoupling of the eggs. We distinguished 'small' eggs up in the ovaries (1) from 'large' eggs down in the ovaries (2)

Annual variation of body stores

From December 2012 to March 2014, adults of *M. soledadinus* were hand-collected under stones (ca. 5 m above sea level) at Port-aux-Français (Kerguelen Islands). As their physiological status may vary from one day to the next depending on temperature, precipitation or trophic status of the insect, each replicate was composed of three individuals caught on three consecutive days (one individual each day) to average environmentally induced noise. After collection, individuals were stored in 1.5 mL 80 % ethanol at −20 °C until analyses.

For each sampling period, six to eight replicates (each composing three individuals) were used to quantify total amount of proteins, glycogen and triglycerides via colorimetric assays [protocol adapted from Foray et al. (2012)]. Briefly, samples were first vacuum-dried (Speed Vac Concentrator, MiVac, Genevac Ltd., Ipswich, UK), and dry mass was measured (Balance XP2U Mettler Toledo, Columbus, OH, $d = 0.1$ µg). Then, samples were redissolved in 180 µL phosphate buffer and homogenised for 90 s at 25 Hz using a bead-beating device (Retsch^{TM} MM301, Retsch GbmH, Haan, Germany). After centrifugation, 10 µL supernatant was used for protein assays using Bradford's technique (total protein content of each sample). The remaining 170 µL of each sample was mixed with 60 µL 20 % Na_2SO_4 and 1200 µL methanol–chloroform [ratio 2:1, volume:volume], and centrifuged (4 °C, 180*g*) to separate (i) total lipids (dissolved in chloroform, lower phase), (ii) carbohydrates (dissolved in methanol, upper phase) and (iii) glycogen (precipitated in the pellet). Then, 300 µL chloroform phase was transferred into new microtubes for triglyceride assays, and stored at −20 °C overnight. Samples were eventually vacuum-dried and redissolved in 200 µL Triton-BSA buffer. The manufacturer's instructions were followed for the triglycerides colorimetric assay (kit reference CC02200, LTA srl, Italy). Glycogen was quantified through a reaction with 70 % anthrone.

Statistical analysis

Median life span (LT_{50}) and 90 % of maximum life span (LT_{90}) values were extracted from the longevity dataset using parametric survival regression models [*Survival* package for R; Therneau (2013)]. The period of activity through the year was analysed using generalised linear models (negative binomial distribution), with months as explanatory variable (number of captures expressed as the proportion of adults caught per month cancelling the year effect), followed by post hoc comparisons to discriminate monthly differences. As there were no significant differences between the two sampling locations ($\chi^2 = 0.023$, $P = 0.88$), this factor was dropped.

Variation in the number of eggs carried through the year was tested using generalised linear models (Poisson distribution), with sampling date and body size index as explanatory variables. The body size index corresponds to individuals' coordinates on the first axis (accounting for 50.5 % of total variance) of a principal component analysis computed on the five morphological measurements [*FactoMineR* package for R; Lê et al. (2008)]. The ratio between females without eggs and gravid females for each sampling date was analysed using a generalised additive model [*mgcv* package; Wood (2004)].

Finally, linear models were applied for each of the three categories of body store (proteins, glycogen and triglycerides), with month and year as explanatory variables.

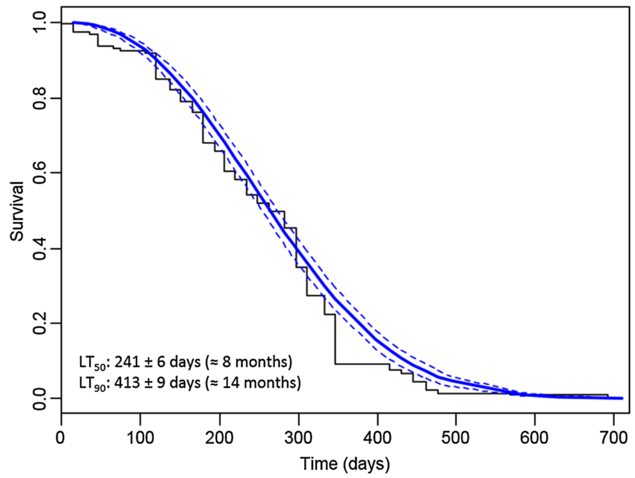

Fig. 3 Survival data of 500 adult *Merizodus soledadinus* reared in controlled conditions (8 °C, 12:12 photoperiod, regularly supplied with food and water) from March 2013 until the death of the last individual (*solid line*), and predicted probability of survival [*solid bold curve*; *dashed curves* 95 % confidence interval (CI)]

All statistics were computed using R 3.0.1 (R Development Core Team 2016).

Results

Estimation of adult longevity

The mean adult longevity under controlled conditions at 8 °C was 241 ± 6 days (about 8 months; LT_{50}), with 10 % of insects living 413 ± 9 days (LT_{90}) (Fig. 3). The last individual died after 710 days, almost two years after it was sampled from the field. The sex of each individual could not be determined a posteriori, because the fortnightly check caused substantial decay and scavenging of dead individuals, preventing reliable sex determination.

Annual activity in natural environment

From 2005 to 2015, a total of 7927 ground beetles were caught, with noticeable but non-significant inter-annual variability (from 367 specimens in 2009 to 1223 in 2014, $\chi^2 = 1.39$, $P = 0.24$). A seasonal pattern of activity was observed (Fig. 4, $\chi^2 = 114.95$, $P < 0.001$), with activity of adult *M. soledadinus* caught during austral summer [mean ± standard deviation (SD) total catches per month from October to March, $N = 12.74 \pm 9.93$ individuals] being about three times higher compared with austral winter (mean ± SD total catches per month from April to September, $N = 4.74 \pm 5.03$ individuals). The highest density was observed in December ($N = 20.27 \pm 13.69$ individuals) and January ($N = 15.44 \pm 7.86$ individuals) every year.

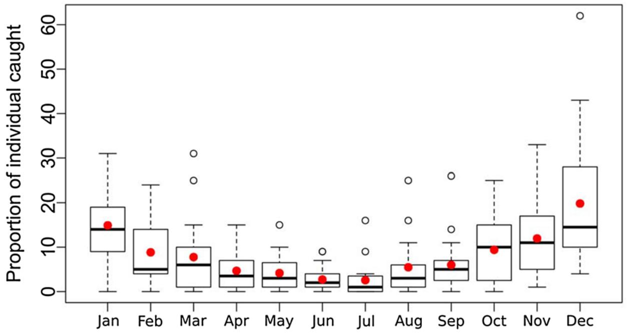

Fig. 4 Annual activity of adult *Merizodus soledadinus* measured as the proportion of individuals trapped each month to total catch of each year, over a 10-year period. *Boxes* represent median, upper and lower quartile of the monthly distribution. *Dots* correspond to the predicted values of the statistical model (GLM, negative binomial distribution)

Reproductive status of females through the year

Gravid females of *M. soledadinus* carried a mean of 8.94 eggs (SD = 3.56, $N = 367$), among which 6.73 (SD = 3.22) were mature, i.e. located in the distal part of the abdomen. Neither the total number of eggs per female ($z = 0.507$, $P = 0.612$; see Online Resource Fig. ESM_2) nor the number of larger eggs ($z = 0.127$, $P = 0.899$) varied by month. Larger females (with higher body size index) carried significantly more eggs ($z = 5.406$, $P < 0.01$). The ratio of females without eggs was marginally non-significant through the year (generalised additive model with sampling date as smoothed explanatory variable, $F_{8,02} = 2.2$, $P = 0.067$).

Annual variation of body stores

Amounts of proteins were remarkably stable through the year (months: $F_1 = 0.009$, $P = 0.927$; year: $F_1 = 0.333$, $P = 0.565$) (Fig. 5). Glycogen contents did not vary by month ($F_1 = 0.544$, $P = 0.85$) or year ($F_1 = 1.295$, $P = 0.26$). Finally, triglyceride contents progressively increased at onset of summer (from August to October), then decreased over the summer (from November to March), with significant differences between months ($F_1 = 11.08$, $P < 0.01$). This pattern tended to be consistent over the three studied years ($F_1 = 2.74$, $P = 0.1$).

Discussion

Our study found a median adult longevity of about 8 months. Adults were regularly fed and supplied with water over the duration of the experiment, and benefited from favourable thermal conditions. These experimental conditions may have elevated longevity as compared with the likely life span under natural conditions. On the other

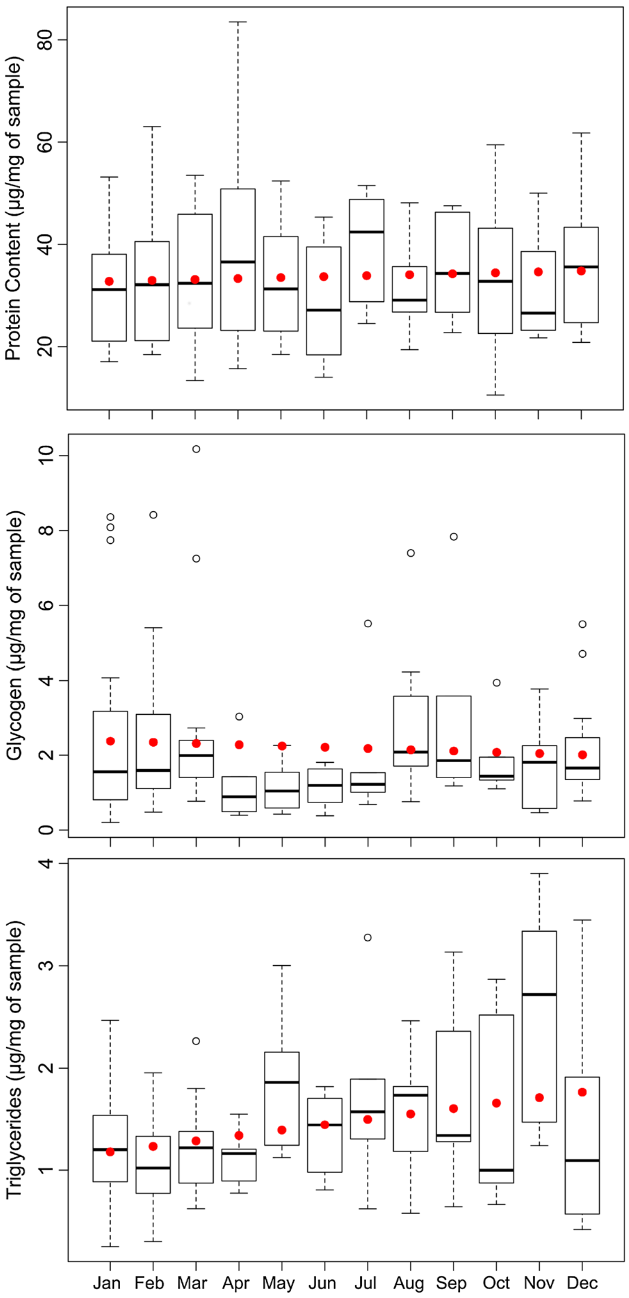

Fig. 5 Monthly variations in contents of three reserve compounds (proteins, glycogen and triglycerides) in adult *Merizodus soledadinus* sampled from December 2010 to March 2012. Colorimetric assays were performed on the same samples. *Boxes* represent median, upper and lower quartile of the monthly distribution. *Dots* correspond to the predicted values of the statistical model (GLM, negative binomial distribution)

hand, at the Kerguelen Islands, *M. soledadinus* can feed on abundant prey in most localities and only suffers from occasional mice predation in some invaded microhabitats (Le Roux et al. 2002) and cannibalism. Moreover, adults are also able to endure natural thermal conditions cooler than those applied in the present experimental setting (Lalouette et al. 2012; Laparie and Renault 2016), which may even slow down ageing processes and augment longevity.

Rearing trials of *M. soledadinus* were not successful, preventing exact estimation of the life span and total life cycle of this species. In the present work, the sampling period maximised the number of teneral individuals caught to allow more realistic estimations, and the calculated adult life span is more likely underestimated than overestimated. No peak of mortality was observed during the very first months of the experiment, and mortality largely increased one year after insect collection (between days 310 and 340, ca. 33 % of beetles died). Our measurement is consistent with life span estimations reported earlier by Ernsting (1993) based on egg load and assumptions regarding the life cycle of *M. soledadinus* at South Georgia. Data reporting carabid longevity are scarce, and range from one to seven years depending on species, with estimations based on mandibular or claw wear, reproductive status and number of overwintering periods (Thiele 1977; Lövei and McCambridge 2002). The adult life span of *M. soledadinus* is similar to native carabid beetles, including *Amblystogenium pacificum* and *A. minimum*, which belong to the same feeding guild at other sub-Antarctic islands (Davies 1987). The invasive *M. soledadinus* seems, however, to display lower seasonality in its life cycle as well as increased investment in reproduction (number of eggs in the ovaries) compared with this carabid beetle native to the Crozet Archipelago.

Our field observations at the Kerguelen Islands (Laparie, Lebouvier, Renault, unpublished data) correspond to Ernsting's (1993) reports from South Georgia, and likely suggest an emergence period ranging from September to April, with the main peak of tenerals around February–March. Gravid females were found throughout the year, and the number of eggs in the ovaries did not vary significantly over time. This finding suggests that egg-laying can theoretically occur at any time and result in high phenological variance, although higher summer activity may exacerbate reproduction. This result is in contrast to the semelparity of the ground beetle hypothesised by Ernsting (1993), i.e. one reproductive season per individual. Females of long-lived carabid species are usually capable of multiple cycles of egg maturation; for instance, *Abax parallelus* (Löser 1970), *Pterostichus chalcites* (Kirk 1975) and *A. pacificum* (Davies 1987) exhibit several consecutive egg-laying periods. Associated with a low periodicity of the life cycle, multiple egg-layings may conceal any inter-individual variance in seasonality of the egg load. In our work, the number of eggs per female was higher than reported at South Georgia by Ernsting (1993), although we examined fewer individuals. Climatic conditions are harsher at South Georgia than at the Kerguelen

Islands (Chown et al. 1998), and may thus be more restrictive and impair investment in reproduction.

The year-round trapping of adult *M. soledadinus* is consistent with previous studies on this species (Kerguelen Islands: Chevrier et al. 1997; South Georgia: Ernsting 1993), and demonstrates continuous activity of adults. From our 10-year investigation, the peak of trapping occurred during summer, and is likely associated with a peak in the reproductive season of this insect [as demonstrated using similar methodology in *Pterostichus madinus* by Luff (1973)]. Importantly, Jeannel (1940) sampled all life stages of *M. soledadinus* at once in summer at the Kerguelen Islands, also suggesting a long-lasting developmental period of this species and the aforementioned phenological variance within populations. Lower pitfall catch rates during winter periods together with an average adult life span over one year suggest seasonal changes in adults' locomotor activity related to thermal conditions rather than a demographic decrease. This assumption is consistent with the results of Ottesen (1990), who found a positive correlation between daily activity of this insect and ground temperature.

The decreased activity of *M. soledadinus* during the austral winter, whether it is caused by, or consequential to, the colder environmental conditions, may contribute to sparing body reserves in a period when several native and introduced prey species are inactive or scarcer. Interestingly, amounts of glycogen and protein did not exhibit large variations through the year, whereas starving *M. soledadinus* were earlier characterised by declining amounts of sugars and lipids (Laparie et al. 2012). Our present data suggest that adults continuously feed during the supposedly less favourable winter season. *Merizodus soledadinus* has been described as an opportunistic predator fond of diptera maggots (Chevrier et al. 1997), implying the possibility of diet adjustments towards other available prey in winter periods; For instance, they have been shown to feed on the native beetle *Hydromedion sparsutum* at South Georgia (Convey et al. 2011). This idea is supported by variations of triglycerides, whose amounts did not vary much over the seasons. The only remarkable variation was observed at the onset of the summer period, with amounts of these stored lipids being augmented and more variable, likely revealing the return to maximal activity in parallel with increased food availability. Meanwhile, our samples were composed of whole body extracts and were not controlled for sex ratio. It is thus hard to determine the relative lipid part reflecting egg maturation, and the relative contribution of each gender to these lipid variations. Finally, resorption of unlaid eggs in females (Rosenheim et al. 2000), or cannibalism on laid eggs by males and females, cannot be excluded during extended periods of food deprivation.

This study provides additional insights into the life history of *M. soledadinus* at the Kerguelen Archipelago. Imagos of this generalist predator are long-lived. Gravid females are found during the whole year, and our data do not allow one to pinpoint restricted egg-laying phenologies or a clear age of reproduction. The life cycle appears to be marked by low seasonality, which concurs with the low climatic seasonality at the sub-Antarctic Kerguelen Islands. At present, the recruitment and mortality rates of new adults remain unknown (egg, larval and pupal mortality rates have not been assessed, nor adult mortality in natural conditions). However, knowing that adult abundances are substantial at most sites colonised by *M. soledadinus* (up to >200 individuals caught per person per 10 min of active search; Mathieu Laparie, Marc Lebouvier, David Renault, personal observation), and that larvae are also voracious predators, we can only glimpse the threat this carabid beetle poses to arthropod communities at the Kerguelen Islands (Lebouvier et al. 2011). Consistently, this species represents a major threat to native communities at South Georgia, threatening native populations of the beetle *Hydromedion sparsutum* (Convey et al. 2011). Transfer of this voracious predator to other islands must be avoided through extensive biosecurity measures (Laparie and Renault 2016).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical consent National and international laws concerning animal experimentation conditions were respected in this study.

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