



Biological Sciences

Experimental tests of feeding behaviour, dietary breadth and cooperative feeding in a predatory carabid invading sub-Antarctic regions

Ella Daly^{1,2}  and David Renault¹ 

¹UMR CNRS 6553 ECOBIO (Ecosystèmes, biodiversité, évolution), Université de Rennes, avenue du Général Leclerc, 35042 Rennes cedex, France and ²Amsterdam Institute for Life and Environment (A-LIFE), Section Systems Ecology, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081HV Amsterdam, the Netherlands

Abstract

In the sub-Antarctic, where food webs are relatively simple and species richness is low, the introduction of predators can be devastating, as native prey may lack sufficient defences and native predators may be less competitive. *Merizodus soledadinus* Guerin-Meneville, 1930 is a predatory carabid beetle that has been introduced to two sub-Antarctic islands. This ground beetle is known to threaten native insect populations; however, the full extent of its impacts in its introduced ranges is unknown because of its poorly described dietary breadth. As invasive predator impacts depend strongly on their dietary preferences and behaviour, we performed experiments to study the responses of this beetle to olfactory cues and sub-Antarctic diet. We studied the responses of *M. soledadinus* to olfactory cues to understand whether this species relies on odour to locate prey or different habitats, but we found no significantly different responses to different stimuli. We found that *M. soledadinus* attacked and consumed mostly juvenile forms of invertebrates from diverse phylogenetic lineages, indicating that many native species may be at risk from this predator and that attack by multiple individuals increased their success with hunting difficult prey. Our findings reveal that *M. soledadinus* has a wide dietary breadth, which has probably contributed to its successful establishment in multiple novel communities. We discuss the implications of our results for the ecology and conservation of terrestrial macroinvertebrate communities in its colonized range, where limited options exist to prevent further spread of this invader.

Keywords: Beetle; insect behaviour; invasion; predation; prey choice; Y-olfactometer

(Received 14 June 2024; revised 9 February 2025; accepted 10 February 2025)

Introduction

Island ecosystems are often more vulnerable to biological invasions than continental ecosystems (Chown & Lee 2009). This is particularly relevant in the sub-Antarctic, where the geographical isolation and cold oceanic climate have resulted in species-poor terrestrial biodiversity and detritus-based food webs lacking predators (Chown & Convey 2016). As a result, most sub-Antarctic (and Antarctic) communities are primarily structured by abiotic factors (Hogg *et al.* 2006) and have a relatively simple trophic structure. In a biological invasion context, this may leave native species more vulnerable to the emergence of invaders relative to species from more taxonomically diversified regions (Diamond & Case 1986, Carthey & Banks 2014). Additionally, the species-poor nature of sub-Antarctic ecosystems means that invaders outnumber native species in many taxonomic groups (Jones *et al.* 2003, Frenot *et al.* 2005). This can also mean that introduced species have adaptations or morphological differences allowing them to exploit unoccupied niches or to more effectively exploit resources, such as the morphologically unique invader *Porcellio*

scaber (Latreille, 1804) introduced to the sub-Antarctic (Martin *et al.* 2023). The effects of competition and predation may thus significantly threaten native sub-Antarctic biota, which lack sufficient defences against novel weapons and predators (Callaway & Ride-nour 2004, Daly *et al.* 2023b). This has been well illustrated with albatrosses, which evolved to breed on islands without predators and now lack effective behavioural responses to ward off predatory invasive mice, leading to significant chick and occasional adult mortality (Connan *et al.* 2024). Less obvious are the impacts of invasive predatory insects, which may have similar potential to decimate native populations of rare and endemic species (Lebouvier *et al.* 2020). However, the severity of these impacts remain poorly understood (Chown & Convey 2016).

Invasive generalist insect predators pose significant problems for invaded ecosystems because of their tendency to reach higher population densities than native predators, their frequent consumption of both native herbivores and predators and their potential competition with native predators (Crowder & Snyder 2010). Invasive predatory ground beetles can have wide-ranging effects in their novel ranges, probably owing to the plasticity and flexibility in their diets, habitats and behaviours (Evans *et al.* 2011). The presence of invasive carabids, such as *Trechus obtusus* Erichson, 1837 and *Pterostichus melanarius* Illiger, 1798, has been linked with declines in native carabids in their introduced

Corresponding author: Ella Daly; Email: e.m.daly@vu.nl

Cite this article: Daly, E. & Renault, D. 2025. Experimental tests of feeding behaviour, dietary breadth and cooperative feeding in a predatory carabid invading sub-Antarctic regions. *Antarctic Science*, 167–175. <https://doi.org/10.1017/S0954102025000082>

ranges, although in the case of *P. melanarius* these effects are habitat-specific (Liebherr & Krushelnycky 2007, Blubaugh *et al.* 2021, Busch *et al.* 2021).

As the effects of invasive predators can also interact with other processes to amplify or accelerate biodiversity declines, understanding their ecological interactions in their novel ranges is key to understanding their impacts. Doherty *et al.* (2015) identify three main pathways through which invasive predators synergize with disturbance to increase biodiversity declines. The first is that ecological disturbance can improve habitat quality or availability, increasing invasive predator abundance and decreasing the abundance of its native prey (Doherty *et al.* 2015). Second, disturbance can affect the per capita impact of the predator on its prey, leading to prey declines despite stable predator populations (Doherty *et al.* 2015). For example, habitat change following fire can reduce prey refuge availability, leading to a functional change in the predator-prey relationship and higher rates of predation (Conner *et al.* 2011, Doherty *et al.* 2015, 2022). Finally, the effects of invasive predators can also interact with disturbances that reduce prey abundance, leading to disproportionately negative impacts of the invasive predator that compound prey decline in a similar way to the Allee effect (Allee 1938, Doherty *et al.* 2015).

In the sub-Antarctic, there are appreciable numbers of invertebrate invaders, with numerous predators representing diverse guilds from flatworms (Houghton *et al.* 2022) to wasps (Lee & Chown 2016) to carabids (Ernsting *et al.* 1995, Brandjes *et al.* 1999, Ouisse *et al.* 2017). Worryingly, all of these predators have generally exhibited high dispersal abilities and have rapidly expanded beyond their initial introduction sites. However, their impacts are as diverse as their taxonomies and the communities they invade. For example, in its introduced range the invasive wasp *Aphidius matricariae* Haliday, 1834 is only known to prey on the invasive aphid *Rhopalosiphum padi* Linnaeus, 1758 (Lee & Chown 2016) and thus probably has a smaller impact on native invertebrates than more generalist predators such as carabids. Multiple sub-Antarctic islands have been colonized by predatory carabid beetles, such as *Merizodus soledadinus* Guerin-Meneville, 1930 (Convey *et al.* 2011, Ouisse *et al.* 2017) and *Trechisibus antarcticus* Dejean, 1831 (Ernsting *et al.* 1995, Brandjes *et al.* 1999, Ouisse *et al.* 2017). However, even generalist species can have feeding preferences that influence their trophic interactions and population dynamics and therefore their impacts as invaders. For example, in the South Georgia Islands (Ernsting *et al.* 1995), the introduction of *T. antarcticus* has led to dramatic reductions in the perimylopod beetle *Hydromedion sparsutum* Müller, 1884, while *M. soledadinus* has had a similar effect on the sphaerocerid wingless fly *Anatalanta aptera* Eaton, 1875 in the Kerguelen Archipelago (Chevrier *et al.* 1997, Ouisse *et al.* 2017).

As these invaders continue to expand and their favoured prey consequently decline in abundance, other species may become at risk. In the case of *M. soledadinus*, which was first observed in the Kerguelen Archipelago in 1939 (Jeannel 1940) at Port-Couvreux (49°16'50.0"S, 69°41'29.0"E), the species is now widely distributed and is actively expanding its range (Lebouvier *et al.* 2020). *M. soledadinus* is thought to have been introduced to the Kerguelen Archipelago from the Falkland Islands, where it is common, through the import of sheep and their fodder in 1912 (Lebouvier *et al.* 2020). Since then, this flightless predator has spread, mainly in coastal habitats, and colonized many other sites, leading to widespread declines in *A. aptera* (Chevrier *et al.* 1997, Lebouvier *et al.* 2020). Despite considerable study of the morphology and physiology of this species in its invasive range (Laparie & Renault

2016, Ouisse *et al.* 2017, 2020, Engell Dahl *et al.* 2019), published data regarding its diet and feeding behaviour are lacking. This has inhibited understanding of its current impacts, as well as predictions about its future range and impacts (Géron *et al.* 2023). In order to predict the future trajectories and impacts of invasive predators, it is crucial to understand their predatory behaviours and dietary breadth.

To address this gap, we conducted several experiments under controlled conditions aiming to characterize *M. soledadinus*' predatory nature and potential in the Kerguelen Archipelago. Specifically, we examined its density-dependent feeding behaviour, prey choices and responses to olfactory cues. We tested the role of predator density and prey identity on attack behaviour. As *M. soledadinus* has been observed in the field tackling larger larvae as a group, we hypothesized that greater predator density would decrease the time to attack and increase the diversity of prey attacked, as group dynamics may encourage predation. Additionally, we hypothesized that all dipteran larvae would be consumed by *M. soledadinus* because of its known predation on *A. aptera* larvae and because it is thought to be responsible for population declines in this species (Lebouvier *et al.* 2020). As little is known regarding the foraging behaviour of *M. soledadinus*, we also tested the role of olfactory cues characteristic of terrestrial and coastal habitats and potential prey to assess whether *M. soledadinus* uses odours to aid in orientating itself. In the case that this sensory input is important for this species, as it is known to be for other carabids (Tréfás *et al.* 2001, Kulkarni *et al.* 2017), we hypothesized that it would prefer odours from plants characteristic of habitats where it is frequently found in the Kerguelen Archipelago to unloaded arms (lacking scented material) of the experimental apparatus. Similarly, as a voracious predator, we also hypothesized that it would be attracted by prey odour in comparison to unscented arms.

Methods

Study species and native biodiversity

M. soledadinus (Coleoptera, Carabidae) is a year-round active species in the Kerguelen Archipelago. It can be found primarily under stones and tide drift lines in coastal areas. In the present work, adults were hand-collected in Port-aux-Français (70°12'59.76"E, 49°21'0.00"S) and then maintained under controlled conditions at 8 ± 1°C. Batches of 100 insects were held for 1 week in plastic boxes (11.5 × 8.5 × 5.0 cm, L × l × h) and were supplied with water but without food. A preliminary study determined that food deprivation periods as long as 6 weeks did not affect the activity patterns of the species, and similar conclusions were reported in previous investigations (Laparie *et al.* 2012, Renault *et al.* 2022).

The terrestrial macroinvertebrate community in the Kerguelen Archipelago is species-poor, consisting of only 25 native species, 75% of which belong to the orders Coleoptera and Diptera (Hullé & Vernon 2021a,b). The 11 native Coleoptera are mostly represented by weevils, but they also include *Meropathus chuni* Enderlein, 1901 (Hydraenidae) and staphylinid *Leptusa atriceps* C.O. Waterhouse, 1875 (Hullé & Vernon 2021a,b). Native Diptera are less numerous and are outnumbered 11 to 7 by introduced congeners. Native Diptera are mostly flightless and belong to five different families. The remaining seven native macroinvertebrates consist of one earthworm (*Microcolex kerguelarum* Grube, 1877), two spiders (*Myro kerguelenensis kerguelenensis* Pickard-Cambridge, 1876 and *Neomaso antarcticus* Hickman, 1939), one flightless parasitoid

Table I. Different prey species (and corresponding life stages) presented to lone *Merizodus soledadinus* individuals or groups of 10 *M. soledadinus* individuals for feeding trials.

Prey order	Prey species (life stage)	Trials 1 predator	Trials 10 predators
Diptera	<i>Calycopteryx moseleyi</i> (L)	22	14
Lepidoptera	<i>Pringleophaga kerguelensis</i> (L)	8	8
Haplotaxida	<i>Microcolex kerguelarum</i> (A)	15	15

A = adult; L = larva.

wasp (*Kleidotoma icarus* Quinlan, 1964), two flightless moths (the larger *Pringleophaga kerguelensis* Enderlein, 1905 and the smaller *Embryonopsis halticella* Eaton, 1875) and one Psocoptera (*Antarctopsocus daviesi* Badonnel, 1970; Hullé & Vernon 2021a,b). Of the 31 established invasive species, the majority are composed of Araneae (5), Coleoptera (4), Diptera (11), Hemiptera (6) and Crassidellata (3), in addition to single members from the orders Psocoptera and Thysanoptera (Hullé & Vernon 2021a,b).

Merizodus soledadinus density experiment

In a first part of the study, we investigated the importance of density on the predatory behaviour of *M. soledadinus*, as lone individuals may not be capable of taking on all prey species effectively. To do this, we presented different prey types to single *M. soledadinus* individuals and groups of 10 individuals (see Table I for number of trials per species). The prey used were larval dipteran *Calycopteryx moseleyi* Eaton, 1875, annelid *M. kerguelarum* Grube, 1877 and larval lepidopteran *P. kerguelensis* Enderlein, 1905. As with the prey choice experiment, predators fasted for 1 week prior to the start of the experiment. The fasting period and experiments were conducted at 8°C by holding adult *M. soledadinus* individually in Petri dishes covered with filter paper on their bases and moistened with tap water.

The experiments were conducted in Petri dishes (diameter: 9 cm). For trials with a single *M. soledadinus* individual, the invertebrates were initially observed for a period of 1 h, with behavioural observations taken after 1, 30 and 60 min. The time of first contact, defined as the time at which the antennae or mandibles of one adult *M. soledadinus* first touched the prey, was also noted when it occurred within this first hour. Each Petri dish was then left for a period of 24 h, at which point a final observation of the remaining prey was taken. For trials with 10 *M. soledadinus* individuals, the invertebrates were observed for 1 h or until nothing remained of the prey, if that occurred before the hour had elapsed. We recorded the times of first contact between one, two, three and four or more *M. soledadinus* individuals and the prey.

To determine whether prey type or predator abundance influenced the initiation of predatory behaviour, we compared the time to first contact with prey across prey type and predator abundance as well as prey mortality after 5 h. For the time to first contact, we used a Kruskal-Wallis test as the data were not normally distributed ($W = 0.754$, $P < 0.05$). We were interested in determining whether the presence of other adult individuals reduced the decision time to attack, as has been shown in other species (Gamberale-Stille 2000). Similarly, we were interested in how decision time differed for *M. soledadinus* depending on prey type. We determined this using a Dunn's test to examine pairwise differences. To compare prey mortality across groups, we tested for significant differences using a two-sided Fisher's exact test.

Prey choice experiment

Adult *M. soledadinus* individuals were offered different potential prey species to assess their dietary breadth. The prey species used were a mix of native and introduced invertebrates from the orders Coleoptera, Diptera, Lepidoptera and Haplotaxida (Table II). These species were chosen because they are abundant and widely distributed within the Kerguelen Archipelago, and they represent the major non-predatory macroinvertebrate groups present in the same habitats as *M. soledadinus* (i.e. fellfield, tundra and coastal). The offered prey also included juvenile *M. soledadinus* because predation of larvae by adults has been observed in the field. All individuals used in these experiments - prey and *M. soledadinus* - were manually collected along the coast from the research stations Port-aux-Français (70°12'59.76"E, 49°21'0.00"S) and Baie de l'Aurore Australe (70°11'10.50"E, 49°20'56.51"S).

Trials were carried out in Petri dishes (diameter: 9 cm). The bottoms of the Petri dishes were covered with filter paper so that the insects were able to move more easily and to provide humid conditions through wetting of the paper with tap water. Predators fasted for 1 week prior to the start of the experiment. Prey individuals, alone or in combination with another of the same or different prey species, were placed in the Petri dishes prior to the introduction of the predators. We varied the number of *M. soledadinus* individuals to obtain different prey:predator ratios (1:1, 1:2, 1:5, 1:10 and 1:20) because this predator species is frequently found in high densities, especially under stones in fellfield areas at the Kerguelen Archipelago. In the Kerguelen Archipelago, the average monthly temperature ranges between 2°C in the winter and 8°C in the summer months (Frenot *et al.* 2001), although temperatures have been increasing recently (Daly *et al.* 2023a). We conducted this experiment under two different temperature conditions typical of the daytime in the sub-Antarctic Kerguelen Archipelago during winter and summer periods (4°C and 10°C) and one appreciably above such temperatures (15°C) to capture a range of temperatures, allowing for the estimation of potential changes in invertebrate predator behaviour as a function of environmental conditions (Table II). Due to constraints on the availability of prey individuals and limits on collecting wild individuals from the local natural reserve, not all conditions could be tested for all species. For summaries of conditions by species and number of replicates by combination, see Tables II & III, respectively.

M. soledadinus individuals were presented with either one or two prey individuals and were left with the prey for 24 h, after which we recorded the status of the prey as intact, partially consumed or totally consumed. Prey partially eaten but still alive within the observation period were considered partially consumed. We binary transformed our outcome (intact, partially consumed or totally consumed), with prey described as either consumed or intact. We used binary logistic regression to model predation by *M. soledadinus* during the first hour of the trial and at

Table II. Prey species offered to *Merizodus soledadinus* in feeding trials under different conditions (temperature, prey life stage and size, prey and predator abundance). Preys with abundances of 2 could be two of the same species or two different prey species.

Prey order	Prey species	Prey life stage (length)	Prey abundance	Temperature (°C)	Predator abundance
Coleoptera	<i>Merizodus soledadinus</i> ^a	Larva (9–10 mm)	2	10	2
	Unknown native weevil	Nymph (5–6 mm)	1	4	5
Diptera	<i>Anatalanta aptera</i>	Larva (2.5–8.0 mm) Adult (6.5–7.5 mm)	1, 2	4	2, 5
	<i>Calliphora vicina</i> ^a	Larva (14–15 mm) Adult (7–12 mm)	2	15	5, 10, 20
	<i>Calycopteryx moseleyi</i>	Larva (2.5–8.0 mm) Adult (5.5–6.5 mm)	1, 2	4, 10	1, 2, 5, 10
	<i>Fucellia maritima</i> ^a	Larva (1.0–5.5 mm) Adult (4.0–6.5 mm)	1, 2	4, 10, 15	1, 2, 5, 1
Lepidoptera	<i>Pringleophaga kerguelensis</i>	Larva (up to 50 mm)	1, 2	4, 10, 15	2, 5, 10, 20
Haplontaxida	<i>Microscolex kerguelarum</i>	Adult (> 10 mm)	1, 2	4, 10	1, 2, 5

^a Species not native to the Kerguelen Archipelago.

Table III. Proportion of prey consumed by *Merizodus soledadinus* in different prey choice feeding trials. Fractions show the number of prey consumed over the number of times each prey species was offered across trials with different predator abundances (1–20) in different temperatures (4°C, 10°C or 15°C).

Temperature	Prey species (life stage)	Predator abundance				
		n = 1	n = 2	n = 5	n = 10	n = 20
4°C	<i>Anatalanta aptera</i> (A)			0/1		
	<i>Anatalanta aptera</i> (L)		3/4	2/2		
	<i>Calycopteryx moseleyi</i> (A)	0/2		4/7	0/1	
	<i>Calycopteryx moseleyi</i> (L)	4/5	6/6	5/5	4/4	
	<i>Fucellia maritima</i> (A)			0/2		
	<i>Fucellia maritima</i> (P)		0/2	0/2		
	<i>Fucellia maritima</i> (L)	2/2	4/6	5/6	4/4	
	<i>Microscolex kerguelarum</i> (A)	1/1	4/4	2/2		
	<i>Pringleophaga kerguelensis</i> (L)		1/1	2/2	3/3	
		Unknown weevil (N)			2/2	
10°C	<i>Calycopteryx moseleyi</i> (A)			3/4	4/4	
	<i>Calycopteryx moseleyi</i> (L)		4/6	8/8	4/4	
	<i>Fucellia maritima</i> (A)			0/4		
	<i>Fucellia maritima</i> (L)	9/11	6/6	15/15	17/17	
	<i>Microscolex kerguelarum</i> (A)			1/1		
	<i>Pringleophaga kerguelensis</i> (L)			3/4	5/6	
	<i>Merizodus soledadinus</i> (L)		0/2			
15°C	<i>Fucellia maritima</i> (L)	4/4		12/12		
	<i>Calliphora vicina</i> (L)			3/4	3/9	1/6
	<i>Pringleophaga kerguelensis</i> (L)			3/4	10/12	1/1

A = adult; L = larva; N = nymph; P = pupa.

the end of 24 h with prey taxonomy, temperature (4°C, 10°C or 15°C), prey type (species), origin (i.e. native or non-native species), life stage (juveniles (larvae, nymph), pupae or adult) and predator density for the consumption of prey. Also included in the model was whether or not alternative prey were offered. We fitted several models using the 'drop1' function in the base R package *stats* (R Core Team 2023) and compared these to a simple model based on the life history traits of *M. soledadinus* in order to better understand what influences predatory behaviour in this species.

Y-tube olfactometer bioassays

Behavioural responses of adult *M. soledadinus* to prey or plant odours were examined by conducting olfactometric tests. A Y-tube olfactometer that had two glass arms of 20 cm each in length, a stem of 12 cm and an inner diameter of 1 cm (Analytical Research Systems, Inc., Gainesville, FL, USA) was used. A two-channel air delivery system (Analytical Research Systems, Inc.) was used for filtering and humidifying the incoming air drawn into the two arms of the Y-olfactometer at a constant rate of 1.5 ml/min. The

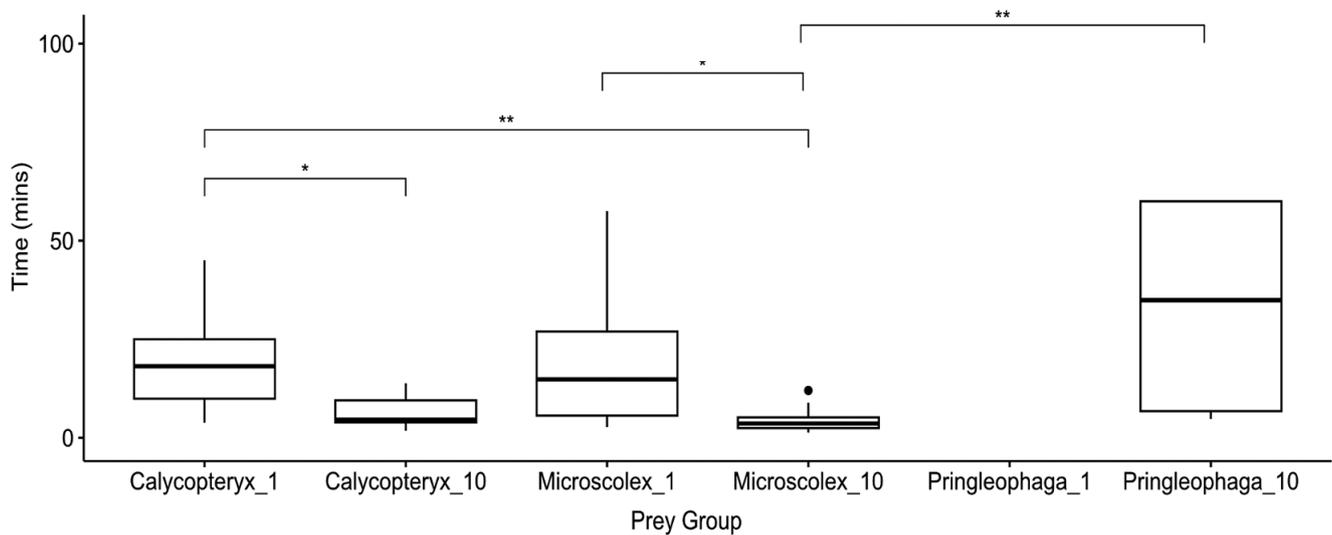


Figure 1. Boxplots showing time to attack by *Merizodus soledadinus* in experimental groups of three different prey species: *Calycopteryx moseleyi*, *Microscolex kerguelarum* and *Pringleophaga kerguelensis*. Trials were conducted with either 1 or 10 predators and always 1 prey individual. The number of replicates ranged from 8 to 22 and varied across condition due to prey availability (see Table 1 for details). Horizontal lines represent median time to attack, with upper and lower bounds of the boxes representing first and third quartiles. Maximum and minimum values are denoted by the whiskers, with dots denoting outlier values (data points 1.5 times smaller or larger than the interquartile range). Asterisks correspond to Bonferroni-adjusted significant differences between times to attack in different groups (* $P < 0.05$, ** $P < 0.01$) according to Dunn's test.

olfactometer was placed horizontally under a 60 W red lightbulb placed 70 cm above the experimental setup. The Y-tube experiment was realized at $8^{\circ}\text{C} \pm 1^{\circ}\text{C}$ and 70–80% relative humidity.

Scents were loaded from 1) one plant species, *Acaena magellanica* (Lam.) Vahl, 1771, and 2) decaying seaweed, representing terrestrial and coastal habitats, respectively. We also repeated this experiment with odours from potential prey species: the native fly *A. aptera* and the native caterpillar *P. kerguelensis*, which were either intact or injured. Lastly, we conducted another set of trials with starved and fed *M. soledadinus*. All bioassays were performed by presenting one stimulus vs one unbaited arm to individuals of *M. soledadinus* whose sex was not known. Bioassays were conducted by presenting the stimuli to 12 adult individuals (stimuli were placed six times in each arm of the Y-olfactometer) to *M. soledadinus* individuals used only once for each experimental condition. At the start of each experiment, one adult of *M. soledadinus* was placed in the stem of the Y-tube and allowed to acclimatize for 15 min. Then, the samples were introduced and the behaviour of the adult was monitored for 30 min; the choices made by each insect between one of the two arms were noted. For each assay, a choice was recorded when the adult *M. soledadinus* passed the intersection into one of the two arms and remained more than 15 s in that arm. Insects that made no choice were also counted. After every run, the Y-tube and the chambers were cleaned with ethanol and rinsed with water, and the connection of each chamber to the arm was reversed to take into account any potential position bias. To determine whether *M. soledadinus* responded to odour cues with increased activity in scented tubes, we again used a Kruskal-Wallis test, as the data were not normally distributed (plant data: $W = 0.768$, $P < 0.05$; prey data: $W = 0.881$, $P < 0.05$).

Results

Cooperative feeding by *Merizodus soledadinus*

We found significant differences ($P < 0.05$) in the time to first attack between single *M. soledadinus* individuals and groups of 10

individuals for all species examined (Fig. 1). When lone *M. soledadinus* individuals were presented with the caterpillar *P. kerguelensis*, none of the individuals attacked the caterpillars within the initial hour of observation, in contrast to all other treatment groups (Fig. 1). The groups of 10 predators presented with a caterpillar had the longest average time to attack of the remaining groups: 33 min 30 s (Fig. 1). The time to attack for single predators was similar for *C. moseleyi* and *M. kerguelarum*, taking ~20 min (Fig. 1). There was a shorter time to attack in treatment groups with 10 predators compared with the sole predator for all species (Fig. 1). The shortest times to first attack were observed for the groups with 10 predators and one larval dipteran (*C. moseleyi*) and one native worm (*M. kerguelarum*), with means of 6 min 36 s and 4 min 16 s, respectively.

In addition to differences in time to attack, there were also significant differences in mortality across prey type according to a two-tailed Fisher's exact test ($P < 0.05$). After 5 h, all of the caterpillars remained alive and intact in the sole predator group, but 75% were dead in the 10 predator group. *M. kerguelarum* demonstrated 100% mortality in both treatment groups, whereas *C. moseleyi* demonstrated 94% and 100% mortality rates in the lone and group predator treatments, respectively.

Dietary breadth and prey preferences of *Merizodus soledadinus*

The best model was selected based on significance of predictors and contained only prey stage and species (model 7, Table S1). Prey life stage ($z = 4.238$, $P < 0.05$) was the only significant predictor of predation within 24 h. Prey being in juvenile stages (larva or nymph) increased the odds of consumption by *M. soledadinus* by 46 times relative to adult life stages (95% confidence interval = 46.3 ± 1.77). Conversely, prey in pupal stages showed decreased odds of consumption by *M. soledadinus* relative to adult life stages; however, this was not significant, and there were very few pupal replicates, and so conclusions cannot be drawn regarding predation on pupa. Some prey species approached significance as predictors of consumption by *M. soledadinus*; however, none of the

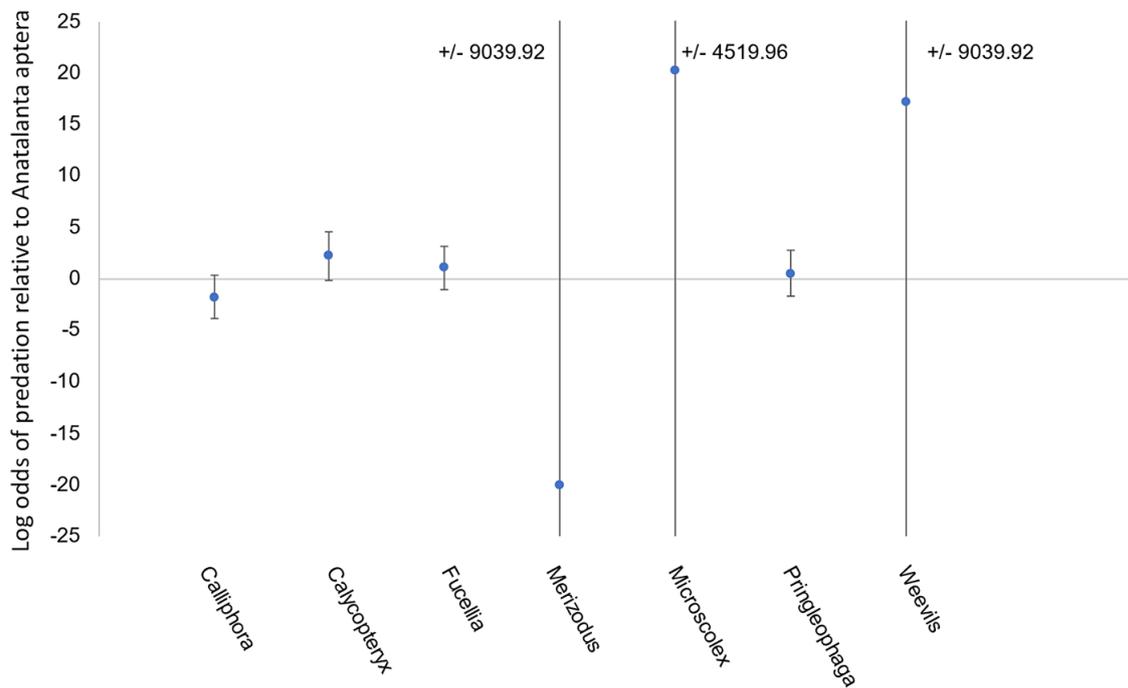


Figure 2. Model coefficients (average difference in log odds) for different species presented to *Merizodus soledadinus* in feeding trials. The odds of consuming *Anatalanta aptera* were used as the baseline in binary logistic regression, and points on this plot represent differences in consumption of other species relative to *A. aptera* from this regression. Plot margins are limited from -25 to 25, but error limits extending beyond this range are annotated on the plot. The number of replicates varied due to prey availability and can be found, along with the number of times each prey was consumed, in Table III.

individual species were significant predictors. *C. moseleyi*, *Fucellia maritima*, *M. kerguelarum* and weevils showed increased predation relative to *A. aptera*, whereas *Calliphora vicina*, *M. soledadinus* and *P. kerguelensis* showed decreased consumption (Fig. 2).

The juvenile forms (larvae and nymphs) of the prey presented were generally readily consumed across species. The main exceptions were *C. vicina* larvae, which were not consumed in the majority of the cases, and *M. soledadinus* larvae, which were never consumed (Table III). *F. maritima* pupa, which were the only pupa tested, were also left intact, despite *F. maritima* larvae being readily consumed (Table III). Adult *A. aptera* and *F. maritima* were not consumed when offered, nor was *C. moseleyi* when there was a low number of predators; however, *M. soledadinus* did consume *C. moseleyi* adults when there were five predators present (Table III). Adult earthworms (*M. kerguelarum*) were consistently consumed in feeding trials (Table III).

Y-tube olfactometer bioassays

No significant differences were found in the time spent in the baited arm as compared with the fresh air sides for both *A. magellanica* ('terrestrial' stimuli) and seaweeds ('marine' stimuli; $P > 0.05$; Figs S1–S3). Similarly, no significant differences were found in the tube arms for the amount of time spent, distance travelled or number of visits between the terrestrial and marine stimuli trials ($P > 0.05$; Figs S1–S3). In trials with different prey (injured or intact), there were no significant differences in the amount of time, distance travelled or number of visits by *M. soledadinus* to loaded arms compared to arms containing fresh air ($P > 0.05$; Figs S4–S7).

Discussion

We modelled the choice of *M. soledadinus* to attack prey using binary logistic regression and found that predation was best

predicted by prey species and life stage (Fig. 2 & Table S1). We observed that *M. soledadinus* is able and willing to attack a variety of prey from diverse taxonomic groups (i.e. Diptera, Lepidoptera, Coleoptera and Haplotaenida), but that it prefers juvenile forms (larvae and nymphs). Depending on life stage, we showed that *M. soledadinus* predated on all species tested except for its own (Table III), despite cannibalism being observed in this species in the wild. Nonsexual cannibalism has been relatively well studied in beetles and can occur due to high density, size differences and starvation (Scharf 2016). Larval cannibalism occurs in some carabids such as *Pterostichus oblongopunctatus* Fabricius, 1787 and *Philonthus decorus* Gravenhorst, 1802, even when other food is available (Heessen & Brunsting 1980), while in ladybirds this is constrained to occurring under conditions of low food quality or availability (Michaud 2003). It is possible that cannibalism in *M. soledadinus* is constrained to specific stress responses that we did not produce in our trials.

Although the Kerguelen Archipelago has low macroinvertebrate diversity, we could not test every macroinvertebrate species in our trials. However, given the generalist nature of *M. soledadinus*, as observed in our prey choice trials (Fig. 2 & Table III), we posit that this species may opportunistically predate upon any larval coleopterans, dipterans and lepidopterans available locally. These include the moth *E. halticella* Eaton, 1875, along with native flies and weevils (see Hullé & Vernon 2021). Similarly, native and introduced worms are also probably at risk of predation. The wide dietary breadth of *M. soledadinus* probably contributes to its invasive success (Romanuk *et al.* 2009) and may exacerbate its impacts. Invasive generalist predators can be particularly impactful in their novel ranges as they can drive prey populations to lower levels than native predators (Crowder & Snyder 2010) and lead to top-down trophic cascades, where impacts propagate through multiple steps in a food web (David *et al.* 2017, Kehoe *et al.* 2021).

In this scenario, theory predicts a 'parity effect' whereby species connected by an odd number of links to the invasive predator, such as its prey, are negatively affected and species connected by an even number of links to the invasive predator, such as the prey of its prey, are positively affected (Gallardo *et al.* 2016, David *et al.* 2017). The impact of *M. soledadinus* may also be exacerbated due to the low species richness occurring at high trophic levels (Chown & Convey 2016), resulting in low competition and enemy release in its invasive range.

Despite our results indicating that the majority of native macroinvertebrates present in the Kerguelen Archipelago are theoretically suitable prey for *M. soledadinus*, not all of these species may match well in terms of habitat or phenology. A more in-depth analysis should be performed to identify species most at risk, especially endemic and rare species. Care should also be taken when extrapolating the results from laboratory tests of prey choice because field conditions can also significantly influence prey choice. For example, McKemey *et al.* (2003) showed that although the predatory carabid *P. melanarius* preferred smaller prey in experimental trials, they fed more often on larger prey in field trials, probably because smaller individuals were better able to find refuge in a heterogeneous field environment. Prey of different sizes and from different taxonomic orders probably experience differential success in evading *M. soledadinus* in a field setting. *M. soledadinus* may also have indirect impacts on native predators, such as the spiders *M. kerguelensis kerguelensis* and *N. antarcticus*, as invasive insect generalist predators can have asymmetrical impacts on other predators through a number of mechanisms (Crowder & Snyder 2010).

As insect life stage is an important determinant of predation by *M. soledadinus*, its impact probably depends on matching phenology, as demonstrated in other invasive insects (Russell & Louda 2004). For example, if one species reproduces such that there are many larvae available during *M. soledadinus*' activity or population peaks, there may be a much higher impact on that prey species than other similar prey, as has been demonstrated for the wingless Diptera *A. aptera* and *C. moseleyi* (Lebouvier *et al.* 2020). Phenological comparison of these two species should be carried out to determine whether this can explain the disproportionate impacts on *A. aptera* compared to similar native species. In the variable predator density and prey choice experiments, we showed that cooperative feeding between *M. soledadinus* individuals can improve predation success with difficult prey such as *P. kerguelensis* (Fig. 1 & Table S3), which could also have implications for prey choice depending on phenology and abundance along the invasion gradient. As this species expands its range, the prey it is able to successfully attack at the low population density range front may differ from that observed in established areas. In experimental trials with different densities of *M. soledadinus* predators and *F. maritima* prey, Géron *et al.* (2023) demonstrated that the proportion of attacked prey was positively related to predator density and negatively related to prey density, with a significant increase in attacks when five or more *M. soledadinus* individuals were present.

The lack of coevolutionary history between invasive and native species often leads to asymmetrical interactions benefitting invaders, as in the case of albatrosses and invasive mice on islands (Connan *et al.* 2024), and sometimes this can even lead to extinction (Fritts & Rodda 1998). These imbalances (see Daly *et al.* 2023b for related hypotheses) can also create selective pressure on native species (David *et al.* 2017), as has been seen in the Italian agile frog's (*Rana latastei* Boulenger, 1879) homogenization over diverse landscapes following invasion by a crayfish predator

(Melotto *et al.* 2020). As the main native macroinvertebrate predators in the Kerguelen Archipelago are spiders, native prey may be evolutionarily unprepared to resist predation by a predatory beetle with different feeding habits, including a preference for low-mobility larvae. However, little is known about prey life stage preferences and prey acquisition in native predators, making this hypothesis difficult to evaluate (Hullé & Vernon 2021a,b). Whether this potentially functionally novel predator will cause enough pressure to lead to extinction of or selection in native species will depend on the adaptive capacity and life history traits of predator and prey, in addition to species-specific impacts of environmental change. Environmental change is likely to exacerbate these impacts, as warming in polar regions can favour invasive species relative to native ones, as with *M. soledadinus*, which is more tolerant to heat than many native sub-Antarctic species (Renault *et al.* 2022).

Despite the differential thermal stress tolerance of *M. soledadinus* relative to native prey (Renault *et al.* 2022), we found that the temperature at which the feeding trials were conducted was not included in the best predation models (Table S1). This was somewhat surprising, as thermal conditions are known to be important predictors of predator behaviour in ectothermic animals (Abram *et al.* 2017). This may be explained by the long timescale of observation (24 h), by the low number of replicates in different temperature regimes or potentially by the pre-adaptation hypothesis. This hypothesis states that successful invaders may be pre-adapted to conditions in their novel range because of conditions in their native range (Mack 2003, Daly *et al.* 2023b). As *M. soledadinus* is a native of the Falkland Islands and Patagonia (Johns 1974), which have similar temperature regimes to the Kerguelen Archipelago (Lebouvier *et al.* 2011), it may be pre-adapted to hunting in the low-temperature conditions of the Kerguelen Archipelago. Although the thermal regime of the Kerguelen Archipelago currently matches well with the native range and thermal requirements of *M. soledadinus* (Laparie & Renault 2016), climate change is rapidly increasing local temperatures (Lebouvier *et al.* 2011), which could eventually favour invaders from more moderate climates. This is especially true if conditions become drier, as *M. soledadinus* is sensitive to desiccation (Ouisse *et al.* 2017) and is thought to maintain a nocturnal lifestyle in the sub-Antarctic for this reason (Ottesen 1990).

The Y-tube olfactometer experiment showed no significant preference of *M. soledadinus* for apparatus arms loaded with stimuli from different environments (i.e. terrestrial and marine), nor for different prey species. This may suggest that *M. soledadinus* is an opportunist, as it is not strongly attracted to any of the specific odours tested, or that *M. soledadinus* relies on other methods to find food, as predatory ground beetles can rely on multiple sensory inputs to detect prey. Experimental tests of predatory and omnivorous ground beetles have demonstrated species-specific responses to odours in the detection of food resources (Kielty *et al.* 1996, Mundy *et al.* 2000, Ali *et al.* 2022), which we did not demonstrate in *M. soledadinus*. This species may instead rely on gustatory or tactile cues, as demonstrated in other Carabidae and Staphylinidae (Wheater 1989). Further testing is required to better understand the strategies used by this predator to detect prey.

Insect declines due to invasion are poorly studied compared to other major threats such as habitat loss, pollution, climate change and overexploitation (Sánchez-Bayo & Wyckhuys 2019), but the impacts of predation by introduced species can create transformative changes in invaded ecosystems (David *et al.* 2017). Despite

this, due to the potential for adverse consequences for native species there are currently no control methods for established invasive macroinvertebrates in the Kerguelen Archipelago and sub-Antarctic (Jones *et al.* 2003, Frenot *et al.* 2005, Lebouvier & Frenot 2007). The impacts of invasive generalist predators such as *M. soledadinus* and the limited management options for this species emphasize the need for strict biosecurity protocols to reduce further human-assisted dispersal of this species, as well as future introductions of non-native species. This is especially important in the context of global climate change, which is disproportionately affecting polar regions and could pave the way for the establishment of globally invasive species of concern in the Antarctic and sub-Antarctic (Duffy *et al.* 2017). Strict biosecurity controls and reduced access to the islands (relative to past farming and whaling eras) have successfully lowered the number of introduced species locally (Project 136-SUBANTECO from the French Polar Institute and long-term monitoring of the biota SEE-Life CNRS 'Ecologie & Environment'). However, this vigilance must be maintained as long as there is a human presence on these islands, as well as there being monitoring efforts to catch species that have already been introduced but have not yet had the opportunity to establish or spread widely.

Supplementary material. To view supplementary material for this article, please visit <http://doi.org/10.1017/S0954102025000082>.

Acknowledgements. The authors thank E. Fayel and M. Laparie for technical assistance when performing the experiments.

Financial support. The authors were funded by the French Polar Institute Paul-Emile Victor (Project 136-SUBANTECO), CNRS-Ecology & Environment (Zone Atelier Antarctique et Terres Australes) and ANR (ANR-20-EBI5-0004, BiodivERsA, BiodivClim call 2019–2020, ASICS project).

Competing interests. The authors declare none.

Author contributions. DR designed the project and oversaw the experiments. ED performed the data analyses. ED and DR both contributed to the writing and editing of the manuscript.

Data accessibility statement. All data discussed in this study have been made freely available on GitHub at the following link: https://github.com/davidrenault/Trophic_ecology_Merizodus_soledadinus.

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