Interactions between invasive and native harvestmen

Søren Toft (✉️ soeren.toft@bio.au.dk)
Aarhus University, Department of Biology
https://orcid.org/0000-0002-2839-3921

Karen Eva Brodersen
Aarhus University, Department of Biology

Thomas Hagen Hansen
Aarhus University, Department of Biology

Tuyen Vo
Aarhus University, Department of Biology

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Interactions between invasive and native harvestmen (Opiliones)

Karen Eva Brodersen, Thomas Hagen Hansen, Tuyen Vo, Søren Toft

Aarhus University, Department of Biology, Ny Munkegade 116, DK-8000 Aarhus C, Denmark

Corresponding author:

Søren Toft

Aarhus University, Department of Biology, Ny Munkegade 116, DK-8000 Aarhus C, Denmark

soeren.toft@bio.au.dk

Orcid: 0000-0002-2839-3921

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Abstract

The harvestman Opilio canestrinii arrived in Denmark around 1980 and quickly became a dominant species in urban habitats. This was followed by nearly complete disappearance of the formerly co-dominant Leiobunum gracile. A second invasive species, Dicranopalpus ramosus, arrived in 2007 and is still under population increase. Old forests have been a refuge for L. gracile, but both invasive species are now invading this habitat. We investigated the possible presence of exploitative and interference competition in relation to limited food resources between the three species in the laboratory using pairs of individuals, either heterospecific (O. canestrinii/L. gracile; D. ramosus/L. gracile) or conspecific (L. gracile/L. gracile) and offered food resources that were insufficient for both individuals. O. canestrinii gained significantly more weight than other species. L. gracile exhibited less startle behaviour and a higher contact time with its partner in the conspecific than in the heterospecific treatment. Overall, O. canestrinii performed better than L. gracile, when faced with food scarcity and restricted space, whereas D. ramosus did not. Thus, competition (both exploitative and interference) is a possible mechanism for explaining the disappearance of L. gracile from urban habitats following the successful establishment of O. canestrinii in Denmark; additionally, O. canestrinii may be a potential future threat to L. gracile in forests.

Key words: behavioural interaction, food limitation, invasion success, Opiliones
Introduction

The north-European fauna of harvestmen is poor in species, but during the last c. 40 years several national species numbers have increased considerably due to spreading of species from southern Europe (Martens 2021). For example, since 1980 the known Danish species increased by 47%, from 17 to 25, and additional species are expected to arrive in the future (Enghoff et al. 2014).

Most of these new species are thought to have been transported from their native ranges by human traffic (Vestbo et al. 2018). They arrived first to urban situations, but several species have subsequently spread to other habitats, including forests, agricultural fields etc. The first species to arrive, *Opilio canestrinii*, was already at its discovery in Denmark in the mid-1980s among the two most dominant species in urban areas (Enghoff 1987), and has subsequently become the absolute dominant, making up c. 70% of all harvestmen in towns (Toft 2018) and 54% in forests (Vestbo et al. 2018). Already c. 20 years after the arrival of *O. canestrinii*, the formerly co-dominant species in urban habitats, *Leiobunum gracile*, as well as two other formerly common species, *Opilio parietinus* and *Mitopus morio*, had almost disappeared from the urban habitat (Toft 2004) and have remained very rare here (Toft 2018). The decrease of *O. parietinus* after the arrival of *O. canestrinii* has been recorded in other European countries as well (Austria: Komposch 1993, 2002; Germany: Martens 2021; The Netherlands: Wijnhoven et al. 2007; but see Muster et al. 2014 for Luxembourg). Thus, much of Europe experienced serious changes in the native harvestman fauna following the spread of *O. canestrinii*, which naturally have prompted the hypothesis that these changes might be directly affected by *O. canestrinii*.

Several mechanisms may account for negative effects of invasive species on native species of related taxa, including resource exploitation, interference competition, intraguild
predation, reproductive interference, etc. (Gao and Reitz 2017). We here focus on the hypotheses that interspecific resource competition and/or interference competition may be important interactions between the invasive *O. canestrinii* and native *L. gracile* and can possibly explain the decline of the latter species as the former became dominant. We include experiments on *Dicranopalpus ramosus* (a more recent invader) and *L. gracile*, though we have no evidence from which to expect significant interactions. *Dicranopalpus ramosus* has co-occurred with *L. gracile* (and other native harvestman species) for only a few years, which means that possible negative effects of its invasion have hardly had time to manifest themselves; in addition, its population numbers in forests are still quite low (Vestbo et al. 2018; own observations), and there is no evidence of effects on numbers of other harvestman species, including *O. canestrinii* (S. Toft, unpublished data).

One of the species that have declined after the invasion of *O. canestrinii* is from the same genus (*O. parietinus*), and another from the same family (Phalangiidae) (*M. morio*), but interestingly, the species that declined the most (*L. gracile*) is from a different family (Sclerosomatidae). But all five species (the two invasive and the three declining native species) show strong ecological similarities: they are all long-legged inhabitants of higher vegetation strata (Todd 1949; Adams 1984); have similar annual life cycles with adults occurring only during the autumn months (Meinertz 1964); their diets are probably also quite similar, indicated by high overlap in macronutritional niches, i.e. in the self-selected protein:lipid:carbohydrate ratios (Nielsen et al. 2022). All species were further found to be food limited in the natural habitat (Nielsen et al. 2022), which is one condition for the existence of food competition (Miller 1967). Thus, high similarities in morphology, seasonality, habitat selection and trophic niches all increase the possibility of competitive interactions, especially considering that coexistence of *L. gracile* with
*O. canestrinii* and *D. ramosus* is so recent (in Denmark c. 40 and 10 years, respectively), thus, limited adaptation to coexistence has had time to evolve.

Little is known about the potential for interference competition among different harvestman species. When disturbed, some harvestmen show a startle response, that may include “bobbing” (Gnaspini and Hara 2007) followed by fleeing if under threat. Intra-assemblage predation occurs, especially among juveniles (Todd 1950, Cokendolpher and Mitov 2007), but its frequency is probably low.

Blackburn et al. (2019) concluded that alien species were implicated in 33% of animal extinctions. In spite of this, earlier reviews have concluded that interspecific resource competition from invasive species is not a main driver of native species extinctions (Davis, 2003; Gurevitch and Padilla, 2004). Nevertheless, it may contribute to population declines of native species along with other factors. Thus, several (laboratory) studies on invasive/native species pairs have indicated the potential for this effect in a range of taxa: fish (e.g. Almela et al. 2021), lizards (Damas-Moreira et al. 2020), crustaceans (Pintor et al. 2008; Olsson et al. 2009; Hobbs et al. 2017), ants (Human and Gordon 1996). Ladybirds are a relatively well studied group in this respect; here, evidence is accumulating that competition or intraguild predation from invasive species (*Coccinella 7-punctata*, *Harmonia axyridis*) may have been implicated in the decline of native ladybird species in Europe and the Americas (Roy et al. 2012; Turnipseed et al. 2014; Tumminello et al. 2015; Zaviezo et al. 2019).

The hypothesis that invasive *O. canestrinii* was driving the disappearance of other native species from the urban habitat is difficult to test. Experimental field studies of competition are not feasible due to the large ranges of these very active animals. Laboratory studies may not
represent the conditions in the field, but we argue that if a laboratory study designed with limited
food and space available to the animals do not show any signs of competition, then competition in
the field is unlikely. If, on the contrary, they demonstrate competition in the laboratory setting,
the hypothesis cannot be dismissed.

We here test for potential resource and interference competition between two invasive harvestman species and a native species that allegedly have suffered seriously from the presence of the first arriving invasive species. We used laboratory tests in which heterospecific and conspecific pairs of individuals interact in a limited space, and were provided with limited food resources to satisfy both individuals. We recorded the changes in live body mass over four days, and observed behavioural interactions between the individuals. *O. canestrinii* is a larger species than *L. gracile* (Table 1) and its daily consumption rate is c. twice as large (Nielsen et al. 2022). Therefore, we expected to find evidence of competition for food and perhaps of interference between *O. canestrinii* and *L. gracile*. In contrast, *D. ramosus* is a smaller species than *L. gracile* (Table 1) and their consumption rates are similar (Nielsen et al. 2022); therefore, we were open towards competitive effects also among these species, but had no *a priori* evidence to expect them.

**Materials and methods**

*Harvestman collection*

The experiments were completed during four weeks of October 2021. Females of *O. canestrinii*, *D. ramosus* and *L. gracile* were collected on Sunday nights from tree trunks in a beech forest (Risskov) located at Aarhus, Denmark (56°10'46.3"N 10°13’23.4"E); the number of *D. ramosus*
were sometimes insufficient, and supplementary specimens were collected at other locations near Aarhus. The specimens were kept in individual plastic tubes (diameter 3.5 cm, height 8.2 cm) with the inclusion of pieces of damp leaves in order to maintain humidity; they were stored outdoors until the experiments were started the following morning. Males were not included in the study because of their lower consumption rate and lower level of food limitation in the field than females (Christensen et al. 2020; Nielsen et al. 2022). A few individuals that had lost 1-3 legs were included in the study, given that harvestman performance is mechanically robust to bodily injuries inflicted by leg loss (Escalante et al. 2020).

**Experimental protocol**

The experimental treatments comprised two heterospecific pairings (one *L. gracile* paired with one *O. canestrinii* or *D. ramosus*, respectively) and a conspecific control (two *L. gracile* together). The collected animals were assigned randomly to the treatments, which were run concurrently, and approximately equally distributed over the four weeks. The experiments took place at 20-23 °C and at a natural light regime.

The experimental units were plastic boxes (18.5*18.5*11 cm) covered by a translucent mesh cloth that allowed visual observations and video filming (see below). A food dish (⌀ 9 cm) was placed in the center of the box and two wetted foam sponges were placed in opposite corners to provide humidity and drinking water. The daily food ration for the two harvestmen of each replicate was 3 freeze-killed and oven-dried fruit flies (*Drosophila melanogaster*), since a preliminary test had indicated three fruit flies as daily consumption rate for one harvestman, thus securing food limitation in the experiment. Each trial lasted 4 days, starting on Mondays and ending Fridays. Individuals of the *O. canestrinii/L. gracile* and the *L. gracile/L.*
**gracile** treatments were marked with small dots of white or blue nail polish on the opisthosoma after being anaesthetized with CO₂; this allowed individual recognition in the video footage. In the conspecific treatment, the colours were allocated randomly to the two animals; in the heterospecific treatments, the colours were switched between *O. canestrinii* and *L. gracile* for each week in order to avoid potential colour bias. All animals were weighed (0.1 mg accuracy) before the experiments started and released on the wetted sponges in opposite corners of the experimental containers. At the start of each of the four days, three fruit flies were added to the food dishes and water was added to the sponges. After starting of the experiments, the heterospecific boxes were visually observed for 1 hour in order to see which animal came first to the food dish. When the experiments ended on Fridays, all harvestmen were weighed again and released back to the forest. Replicates where animals died or showed fatigue were excluded from data analysis (final sample sizes in Table 1).

As harvestmen are mainly night active (Santos 2007), video recordings were conducted during two nights (Tuesdays and Wednesdays, from 22:00 to 01:00) of each of the four weeks with two Sony HDRCX405 9.2MP HD Handycam Camcorders, placed above the experimental containers. Each camera covered two boxes of the same treatment, and different sets of boxes were filmed on Tuesdays and Wednesdays, i.e., a total of 16 heterospecific and 16 conspecific boxes were recorded (data from one replicate of each treatment were deleted from analysis due to low quality of the video recordings). A red light was mounted to illuminate the arenas for visibility during the night, which would not disturb the behaviour of the harvestmen. The information collected from the recordings comprised 1) total time of physical contact, i.e., touching legs or overlapping leg spans between the two harvestmen; 2) number of startle responses exhibited by *L. gracile*; in the conspecific treatment, we counted the startle responses...
of the white-marked individual. In the heterospecific treatment, we further noted which individual
initiated the contact that led to a startle response. A startle response is here defined as a sudden
jerking motion resulting in moving away from the other individual, sometimes followed by fleeing.
It is taken as a sign of interference between the two individuals. Bobbing was also part of the
startle response, but was difficult to see on the video recordings (taken from above) and thus
could not be quantified.

Statistical analysis

Because *L. gracile* was the smaller species in the *O.canestrinii/L.gracile* treatment, and the larger
species in the *D.ramosus/L.gracile* treatment, and because it could be assumed that relative body
size might influence relative competitive ability, we considered the smaller and the larger
individuals of the conspecific (*L.gracile/L.gracile*) pairs separately (Table 1). The absolute weight
change over the four days of experiment was calculated by subtracting the initial weight from the
final weight of each harvestman (one *L. gracile* laid eggs and was deleted from analysis).

Regression analysis of absolute weight change against initial body weight within each of the five
species groups (*L. gracile* in conspecific treatment (hereafter *L. gracile*<sub>con</sub>), *L. gracile* paired with *O.
canestrinii* (*L. gracile<sub>can</sub>); *L. gracile* paired with *D. ramosus* (*L. gracile<sub>ram</sub>); *O. canestrinii*; *D. ramosus*)
revealed consistent negative relationships (Fig. 1). To account for this relationship, we calculated
the residual weight change for each individual from an absolute weight change/initial body weight
regression that including all individuals from the three treatments. Subsequent ANOVAs were
performed on both the absolute and the residual weight change data, after checking for
parametric assumption using Shapiro-Wilk’s test and Levene’s test. We considered that under
conditions of limited food supply, the absolute rather than the relative weight change would be
the best indicator for comparing the ability to secure resources. As replicates were accumulated over four weeks, during which the reproductive status of the animals may have changed, their responses to interactions might also change. Therefore, in ANOVA we introduced “Week” as a factor with four levels, one for each week (coded ordinally). Additionally, we performed paired t-tests of absolute and residual weight change between species in heterospecific treatments and between the smaller and the larger individuals in the conspecific treatment; these paired analyses control for the block design.

Order of arrival to the food dish in the two heterospecific treatments was evaluated by counting the number of days (up to 4) each individual was the first to arrive. We performed Matched-pairs t-test on the data from each treatment; we further tested the frequencies of coming first among opponent groups (i.e. *O. canestrinii* vs *L. gracile*; *D. ramosus* vs *L. gracile*) by the Binomial Test (Siegel and Castellan 1988), discounting the days where no individual arrived within the observation time, and discounting the replicates where both individuals arrived first the same number of times. The behavioural data from the video recordings (startle response, contact time) violated parametric assumption. Number of startle responses were coded ordinally and analyzed with Ordinal logistic fit. Contact time was analyzed with Proportional hazards fit. A $\chi^2$ test was used to test whether *L. gracile* or *O. canestrinii* initiated the contacts. Statistical tests were performed in JMP v. 14 (SAS Institute Inc., 1989–2020).

**Results**

**Body weight changes**
In the heterospecific treatments, the initial average body weight of *O. canestrinii* was larger than that of *L. gracile* (Table 1; $t_{34} = -2.74$, $p = 0.0195$), while the weight of *D. ramosus* was considerably lower than that of *L. gracile* (Welch’s $t$-test, $t = 12.5$, $p < 0.0001$). There were no differences in *L. gracile* body weight from the three treatments (ANOVA, $F_{2,63} = 0.2853$, $p = 0.75$).

There were significant or near-significant negative relationships between initial body weight and absolute weight change for all species, including all treatments groups of *L. gracile* (Fig. 1). Thus, independently of species, large individuals increased less or lost more mass during the experiments than small individuals, indicating that small individuals cope with the experimental stresses (food limitation and possible interference) better than large individuals. Two-way ANOVA of absolute and residual weight change indicated that both Species and Week were significant factors (Table 2; their interaction was non-significant and therefore deleted). Mean residual weight change differed significantly between experimental groups (Fig. 2, Table 2). It was large and positive for *O. canestrinii*, negative for large *L. gracile*$_{con}$, and negative but close to zero for remaining groups (Fig. 2). There were no differences in residual weight change between *L. gracile* groups (ANOVA, $F_{2,63} = 0.9829$, $p = 0.3799$). Similar results were obtained when absolute body mass change was the dependent variable (Table 2). Paired $t$-tests of data from each treatment confirmed these patterns (Table 3): small *L. gracile* performed better than large *L. gracile* in the conspecific treatment; *O. canestrinii* performed better than *L. gracile*$_{can}$, and *D. ramosus* performed no better than *L. gracile*$_{ram}$; also here, similar results were obtained with absolute weight change as the dependent variable. From these results, we conclude that under the experimental conditions, *O. canestrinii* competed better than *L. gracile*, whereas *D. ramosus* did not, and that small *L. gracile* competed better than large *L. gracile*. 
Behavioural interactions

Of 19 pairs of the *O. canestrinii/L. gracile* treatment, *L. gracile* was the one that most often came first to the feeding dish in 13, while in 5 cases *O. canestrinii* was most often the first (Matched-pairs test $t = 2.023$, $p = 0.0387$; Binomial test, $p = 0.048$). Of 22 pairs of the *D. ramosus/L. gracile* treatment, *L. gracile* was the one that most often came first to the feeding dish in 17, while in 1 case *D. ramosus* was most often the first (Matched-pairs $t$-test $t = 5.10$, $p < 0.0001$; Binomial test, $p < 0.001$). Thus, in both treatments native *L. gracile* was faster to arrive at the food than its invasive opponent.

In the heterospecific *O. canestrinii/L. gracile* treatment, *L. gracile* exhibited a significantly higher number of startle responses (due to contact with *O. canestrinii*) than *L. gracile* in the conspecific treatments (Ordinal logistic fit, Wald $\chi^2_1 = 7.92$, $n = 30$, $p = 0.0035$; Fig. 3a). In contrast, the amount of time that *L. gracile* stayed in physical contact with its opponent was significantly higher when the opponent was a conspecific than when it was *O. canestrinii* (Proportional hazards fit, L-R $\chi^2_1 = 12.79$, $n = 30$, $p = 0.0003$; Fig. 3b). This indicates that *L. gracile* was more comfortable in the conspecific than in the heterospecific treatment. Lastly, out of a total of 98 startle events, 38 were initiated by *L. gracile*, while 47 were initiated by *O. canestrinii*. This indicates that both species approached each other equally frequently (Pearson’s $\chi^2$ test, $\chi^2 = 0.95$, $n = 30$, $p = 0.329$), i.e. none of the species were more likely to initiate the contact.

Discussion

The negative relationships between weight change and initial weight that was common to all experimental groups, indicate a general advantage of small size under limited food conditions. This
is further strengthened by the finding from the conspecific control treatment in which the smaller
of the opponents performed better than the larger one; this was the case even when the size
effect was controlled for by analyzing residual weight change. These relationships would have
predicted that *O. canestrinii* as the larger species should be inferior to *L. gracile*, but we found the
opposite, i.e. *O. canestrinii* gained more weight than *L. gracile* both absolutely and when analyzing
the residual weight change. Thus, *O. canestrinii* was superior to *L. gracile* in handling the stressful
situation created by the limiting experimental conditions. In contrast, we found no evidence from
the weight change data that *D. ramosus* was neither a stronger nor a weaker competitor than *L.
*canestrinii*.  

In contrast to all other species groups, *O. canestrinii* was able to increase in weight
even though all had the same amount of food resources available. This may reflect the notion that
invasive species are more efficient in securing and utilizing food resources (Sakai et al. 2001; Gao
and Reitz 2017). The positive weight change of *O. canestrinii* was seen even though *L. gracile* was
most often the first to come to the food dish. It is possible that *L. gracile*, in contrast to most
harvestmen which are strictly nocturnal (Santos 2007), is a more active species during daytime
when food was renewed and these observations were made. In fact, Edgar and Yuan (1968, cited
from Santos 2007) concluded that species of shaded habitats are less strictly nocturnal than
species from more open habitats. If *L. gracile* has higher overall energetic expenses due to a wider
daily activity period, this may explain why this species did not increase as much in weight as *O.
canestrinii*, not even in the conspecific treatment. Alternatively, *L. gracile* may be more fearful
during the day (Segovia et al. 2019); if so, it may explain why *L. gracile* did not benefit from
arriving first to the food dish.
We conclude that *L. gracile* may be under pressure from both intra- and interspecific food competition in food limited situations. Interspecific competition may come from *O. canestrinii* (but not from *D. ramosus*) and seems to be stronger than intraspecific competition.

**Behavioural interactions**

Individuals of *L. gracile* engaged in more prolonged physical contact with their opponents when these were conspecific than when they were heterospecific (*O. canestrinii*). In contrast, they showed many more startle responses when paired with *O. canestrinii* than when paired with a conspecific. This strongly indicates a form of interference competition between the two species. However, the two species initiated equally often the meetings, which may indicate that these occurred accidentally. *L. gracile* was not chased away, even if the animals met at the food dish, but responded to encounters by startling and fleeing. Several species of the genus *Leiobunum* are known to aggregate during daytime resting, sometimes in large numbers (Machado and Macías-Odóñes 2007), but they are not observed in *O. canestrinii*. For *L. gracile*, only smaller aggregations have been observed (<10 individuals) (S. Toft, own observations). As the two species occupy the same microhabitats of the forests, physical meetings may occur also here. If an *L. gracile* meets a conspecific, they may stay in social contact for an extended time, while if it meets an *O. canestrinii* it will startle and flee. Thus, the dominance of *O. canestrinii* seems not to be due to aggressiveness; therefore, it is tempting to speculate that the habit of resting socially in *L. gracile* may become a disadvantage against a non-social, probably bolder species that has come to co-occupy its habitat. This is reminiscent of the situation in an invasive/native pair of gecko species (Petren et al. 1993).
In principle, exploitative and interference competition may be connected; i.e. interference may be the driver of the weight change results, if the disturbance of *L. gracile* induced by *O. canestrinii* inhibits its foraging. Against this speaks the observation, however, that the two species could meet at the food dish without releasing a startle, and seemingly with no attempt to monopolize the resource. Thus, there is no evidence that interference competition has any relation to food. This contrasts to other studies, in which agonistic behaviour between competing species was related to food (Human and Gordon 1996; Lach 2005; Hawes et al. 2013; Damas-Moreira et al. 2020). Harvestmen forage haphazardly in their habitat for widely dispersed food, therefore no resource defense (other than defense of prey under consumption) would be expected.

The present study did not investigate other forms of interaction between *L. gracile* and the two invasive species, that may possibly be implicated in the displacement of native by invasive species (Gao and Reitz 2017). It is worth noting, however, that no cases of predation was observed in the experimental containers, even though the animals were confined in a small space compared to the size (especially leg length) of the animals and their natural activity ranges. This may rule out interspecific predation as a possible factor.

**Conclusion**

The better performance of smaller compared to larger *L. gracile* in conspecific competition even when residual weight change was analyzed, indicates intraspecific competition in *L. gracile*. The strength of the intraspecific competition seems, however, lower than interspecific competition from *O. canestrinii*. This is indicated by the smaller effect size in the conspecific compared with the *L. gracile/O. canestrinii* heterospecific treatment, and by the fact that *O. canestrinii* could increase
considerably in weight in spite of its larger size. The effects of exploitative competition may be
augmented by interference that work in the same direction. It is generally assumed that a weaker
inter- than intraspecific competition may lead to co-existence, whereas stronger inter- than
intraspecific competition may lead to displacement of the weaker species (Petren and Case 1996;
Zaviezo et al. 2018; Damas-Moreira et al. 2020). Our results thus support the hypothesis that the
disappearance of *L. gracile* from urban habitats in Denmark was caused by the overwhelming
invasion success of *O. canestrinii*. As the harvestman populations in forests are presently not in
equilibrium, we hypothesize from these results that *O. canestrinii* may negatively affect *L. gracile*
in the forest habitat in the future, as it has likely done in urban habitats formerly. In contrast, we
regard it unlikely that *D. ramosus* will be a threat to *L. gracile* even if it becomes more abundant
than it presently is.

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Almela VD, South J, Britton JR (2021) Predicting the competitive interactions and trophic niche
https://doi.org/10.1111/1365-2656.13571


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**Author contributions** All authors contributed to the design of the study. KEB, THH and TV performed the experiments. All authors contributed to data analysis. KEB, THH and TV wrote preliminary reports on project parts. ST drafted the combined manuscript and all authors commented and approved the final version of the manuscript.

**Data availability** All data are included in the article and its supplementary information files.

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

**Ethical approval** The study complies with Danish legislation on animal welfare.
Figure legends

Fig. 1 Relationships between initial weight and weight change during four days of competition between conspecific pairs of individuals: L. gracile_{conL} vs L. gracile_{conS} (a), and heterospecific pairs: O. canestrinii vs L. gracile_{can} (b-c), D. ramosus vs L. gracile_{ram} (d-e). Explanation of codes for experimental groups, see Table 1.

Fig. 2 Residual weight change (mean ± SE) of conspecific and heterospecific treatment pairs: (a) conspecific L. gracile/L. gracile pairs, distinguishing large (L) and small (S) members of the pairs; (b) heterospecific O. canestrinii/L. gracile pairs; (c) heterospecific D. ramosus/L. gracile pairs. Closed circles: native species (L. gracile); open circles: invasive species (O. canestrinii, D. ramosus). Letters in top of panels: same letter indicate no significant difference between groups (Student’s t-tests).

Fig. 3 Number of startle events (a) and physical contact time (b) for L. gracile in conspecific (con) and heterospecific (het; with O. canestrinii) treatment pairs (n = 15 for both treatments) counted from video recordings. Box plots show median (horizontal line) and quartiles (boxes), 10/90%iles (whiskers), and outliers (dots).
Table 1. Terminology of treatment groups, sample sizes and body masses (avg. ± SD) of harvestmen in the three treatments.

<table>
<thead>
<tr>
<th>Treatments – species</th>
<th>$n$</th>
<th>Body mass (mg)</th>
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<tr>
<td><strong>L.gracile/L.gracile conspecific</strong></td>
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<td></td>
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<td>L. gracile_L.con</td>
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<td>-large (L. gracile_L.conL)</td>
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<td>58.5 ± 8.7</td>
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<td>-small (L. gracile_L.conS)</td>
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<td>49.1 ± 10.4</td>
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<td><strong>D.ramosus/L.gracile heterospecific</strong></td>
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Table 2. ANOVA of absolute weight change and residual weight change in the six groups of animals forming the three treatment pairs: homospecific pairs: *L. gracile*<sub>conl</sub> vs *L. gracile*<sub>conS</sub> (abbreviated LgL, LgS); heterospecific pairs: *O. canestrinii* vs *L. gracile*<sub>can</sub> (abbreviated: Oc, Lgc); *D. ramosus* vs *L. gracile*<sub>ram</sub> (abbreviated: Dr, Lgr). Post-hoc comparisons by Student’s *t*-test (superscript lower-case letters); same letter means no significant difference. The factor Week was introduced because data were accumulated over four weeks.

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th><em>F</em></th>
<th><em>p</em></th>
<th>Post-hoc comparisons</th>
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<tr>
<td><strong>Absolute weight change</strong></td>
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<td></td>
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<tr>
<td>Full models</td>
<td>8,97</td>
<td>7.05</td>
<td>&lt;0.0001</td>
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<td>Species</td>
<td>5</td>
<td>8.55</td>
<td>&lt;0.0001</td>
<td>LgL&lt;sup&gt;c&lt;/sup&gt;-LgS&lt;sup&gt;b&lt;/sup&gt;-Oc&lt;sup&gt;a&lt;/sup&gt;-Lgc&lt;sup&gt;b&lt;/sup&gt;-Dr&lt;sup&gt;b&lt;/sup&gt;-Lgr&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>Week</td>
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<td>0.0016</td>
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<td><strong>Residual weight change</strong></td>
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<td></td>
<td></td>
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<tr>
<td>Full models</td>
<td>8,97</td>
<td>8.62</td>
<td>&lt;0.0001</td>
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<tr>
<td>Species</td>
<td>5</td>
<td>11.93</td>
<td>&lt;0.0001</td>
<td>LgL&lt;sup&gt;c&lt;/sup&gt;-LgS&lt;sup&gt;b&lt;/sup&gt;-Oc&lt;sup&gt;a&lt;/sup&gt;-Lgc&lt;sup&gt;b&lt;/sup&gt;-Dr&lt;sup&gt;bc&lt;/sup&gt;-Lgr&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Week</td>
<td>3</td>
<td>4.55</td>
<td>0.0050</td>
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Table 3. Paired t-tests of absolute weight change and residual weight change between members of treatment pairs: homospecific pairs: $L. gracile_{conL}$ vs $L. gracile_{conS}$; heterospecific pairs: $O. canestrinii$ vs $L. gracile_{can}$; $D. ramosus$ vs $L. gracile_{ram}$.

<table>
<thead>
<tr>
<th></th>
<th>Abs. weight change</th>
<th>Resid. weight change</th>
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<tbody>
<tr>
<td></td>
<td>d.f.</td>
<td>t</td>
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<tr>
<td>$L. gracile_{conL}$ vs $L. gracile_{conS}$</td>
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<td>2.28</td>
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<tr>
<td>$O. canestrinii$ vs $L. gracile_{can}$</td>
<td>17</td>
<td>-5.03</td>
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<tr>
<td>$D. ramosus$ vs $L. gracile_{ram}$</td>
<td>21</td>
<td>-1.30</td>
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</table>
Fig. 1. Relationships between initial weight and weight change during four days of competition between conspecific pairs of individuals: L. gracile_{con} vs L. gracile_{con5} (a), and heterospecific pairs: O. canestrinii vs L. gracile_{can} (b-c), D. ramosus vs L. gracile_{ram} (d-e).
Fig. 2. Residual weight change (mean ± SE) of conspecific and heterospecific treatment pairs: (a) conspecific *L. gracile*/*L. gracile* pairs, distinguishing large (L) and small (S) members of the pairs; (b) heterospecific *O. canestrinii*/*L. gracile* pairs; (c) heterospecific *D. ramosus*/*L. gracile* pairs. Closed circles: native species (*L. gracile*); open circles: invasive species (*O. canestrinii*, *D. ramosus*). Letters in top of panels: same letter indicate no significant difference between groups (Student’s *t*-tests).
Fig. 3. Number of startle events (a) and physical contact time (b) for *L. gracile* in conspecific (con) and heterospecific (het; with *O. canestrinii*) treatment pairs (*n* = 15 for both treatments) counted from video recordings. Box plots show median and quartiles (boxes), 10/90%iles (whiskers), and outliers (dots).
Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Harvestmendata.xlsx