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Anna K Kulessa, Paride Balzani, Ismael Soto, Mathieu Toutain, Phillip J Haubrock, et al.. Assessing the potential phytosanitary threat of the house cricket *Acheta domesticus*. *Science of the Total Environment*, 2024, *Science of the Total Environment*, 917, pp.170376. 10.1016/j.scitotenv.2024.170376 . hal-04443348

**HAL Id: hal-04443348**

**<https://hal.science/hal-04443348>**

Submitted on 19 Apr 2024

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## Assessing the potential phytosanitary threat of the house cricket *Acheta domesticus*

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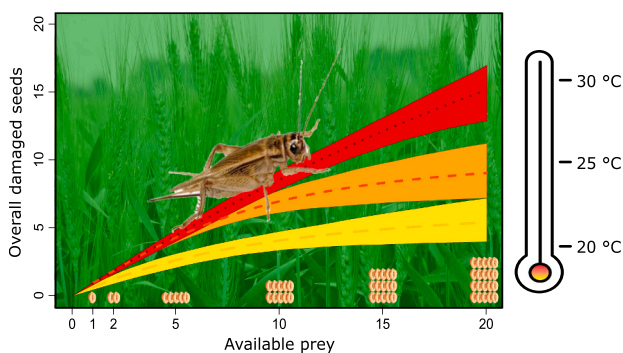
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### HIGHLIGHTS

- Phytosanitary risks intensify globally amid climate change.
- European threat, *Acheta domesticus*, may heighten with climate change.
- Study reveals uniform seed consumption patterns across temperatures.
- Amplified damages, especially to softer seeds, underline threat potential.
- Proactive, science-based strategies urgently needed to counter emerging phytosanitary risks.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

Editor: Rafael Mateo Soria

#### Keywords:

Orthoptera  
Biological invasion  
Pest  
Temperature  
Functional response

### ABSTRACT

Phytosanitary threats can pose substantial risks to global agriculture and ecological systems, affecting biodiversity, human well-being, and food security. Meanwhile, global warming is projected to exacerbate these threats in the future. One in Europe already widely distributed potential phytosanitary threat that may benefit from global warming is the house cricket *Acheta domesticus*. This study explored the potential of *A. domesticus* as a relevant non-native phytosanitary threat under changing climatic conditions by conducting a series of functional response experiments across a temperature gradient (20, 25, and 30 °C). *Acheta domesticus* exhibited comparable patterns of seed consumption and functional responses. Seed type (millet seeds, wheat grains) and temperature increase influenced the damage inflicted on seeds, with softer and smaller seeds being more susceptible to damage, further amplified by warmer temperatures. The study's outcomes underline the phytosanitary threat that *A. domesticus* may pose. Considering the species' established presence and adaptable nature in urban

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<sup>1</sup> Shared senior authorship.

<https://doi.org/10.1016/j.scitotenv.2024.170376>

Received 21 November 2023; Received in revised form 20 January 2024; Accepted 21 January 2024

Available online 27 January 2024

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environments exacerbates the potential for *A. domesticus* to transition to rural and agricultural areas. Its increasing production as a food item, paired with the here-identified potential to damage seeds, emphasizes the need for proactive and science-based strategies to address emerging phytosanitary threats driven by non-native species under changing climatic conditions. As global temperatures continue to rise, the assessment and management of potential pest species like *A. domesticus* will be crucial for safeguarding agriculture productivity and ecological balance.

## 1. Introduction

Phytosanitary threats refer to the risk posed by pests and plant diseases that affect crops, forests, but also the natural environment. These threats can be novel to a specific area where they may affect and encompass a wide range of challenges that pose significant risks to human well-being by impacting agriculture, ecosystem stability, and even global food security (Leal et al., 2010; Lopian, 2018; Papyrakis and Tasciotti, 2019; Kumar et al., 2021). The magnitude of phytosanitary threats is expected to increase due to the effects of global warming and changes in precipitation regimes (Bebber, 2015; Lopian, 2018). These climatic changes may also contribute to the proliferation of pests and diseases, allowing them to spread within the invaded range into previously unaffected regions (Bebber, 2015; Tonnang et al., 2015), thereby weakening plant health and making them more susceptible to secondary infestations (Wawrzynski and Ascerno, 1993).

When species are introduced into new areas, either intentionally or accidentally, where they have no evolutionary history to, they are classified as 'non-native' (Horák et al., 2021; Soto et al., 2024). In the case of successful establishment, non-native populations can grow and spread, thereby being classified as 'invasive' (Traian et al., 2012; Polidori et al., 2018). Meanwhile, depending on e.g. their relative abundance, non-native species can cause a wide range of negative effects (Crowl et al., 2008; Mazza et al., 2014), leading to ecological imbalances in community structures, disrupted biodiversity, and economic consequences (Papyrakis and Tasciotti, 2019; Bella and Aguiar, 2020). Insect species with a high capacity for swift geographical expansions may exert adverse effects on biodiversity, the economy, or human health (Jucker and Lupi, 2011; Hill et al., 2016; Angulo et al., 2022; Fortuna et al., 2022). In agriculture, both non-native and native species can become problematic and pose significant phytosanitary threats, causing extensive damage to crops and incurring massive economic losses (Steedman, 1990; Showler, 2002; Bella and Aguiar, 2020; Wang et al., 2022). One example of such an insect posing a phytosanitary threat is the red imported fire ant *Solenopsis invicta*, which threatens agriculture through its high consumption of agricultural crops and natural environments by feeding on beneficial insects (Menchetti et al., 2023). Another example is the Mediterranean fruit fly *Ceratitis capitata*, which inflicts damage on a wide range of agriculturally relevant fruits (Martinez-Ferrer et al., 2012; Smargiassi et al., 2023). Although not extensively studied, some non-native Orthoptera have recently gained recognition as potential phytosanitary threats, mostly based on their ability to swarm but also their potential to rapidly spread and establish at new localities (Gardiner, 2009; Bella and Aguiar, 2020; Kulessa et al., 2023a, 2023b).

Currently, the order Orthoptera contains 29,500 recognized species (Cigliano et al., 2022), including grasshoppers, crickets, and bush-crickets (Čato and Zagorac, 2021; Essl and Zuna-Kratky, 2021; Kristín et al., 2022). They are characterized by their large hind legs, which are adapted for jumping, and their unique ability to produce chirping sounds through stridulation (Greenfield, 1997; Essl and Zuna-Kratky, 2021; Takahashi and Yoshizawa, 2021). These insects can be found in different types of habitats including chalk downland, tallgrass prairie, savanna, and shrubland steppe, across all continents except Antarctica, showing their high adaptability to different environments and temperature ranges (Smith and Capinera, 2005; Gardiner, 2018). While Orthoptera play a pivotal role in ecosystems, some can become a phytosanitary threat under specific conditions (i.e. a warm and humid

climate) due to their wasteful feeding habits (Gardiner, 2018). Migratory locusts are under normal conditions solitary animals that are quite loyal to their location with low population sizes (Showler, 2002). However, if individuals touch each other's hind legs at an unusual frequency during a certain developmental stage, they release serotonin, triggering a transition to the gregarious (migratory) phase. Larger flights are formed and grasshoppers change their color (Showler, 2002; Hodjat, 2016). In this phase, locusts join together to form swarms with up to 80 million individuals per km<sup>2</sup> and migrate over long distances (Steedman, 1988; Showler, 2002). In this phase, they can consume vast amounts of plant biomass, leading to devastating crop damages, and posing significant agricultural problems in affected regions (Hodjat, 2016; Chunxuan and Enbo, 2003; Zhang et al., 2009; Lourenço et al., 2022). The exact number of locust species that can change to the gregarious phase and form swarms has only been anecdotally described (Hodjat, 2016; Foquet et al., 2021). One such example is the gregarious desert locust *Schistocerca gregaria*, which has been devastating for food security, especially in regions of Africa, the Middle East, and South Asia (Steedman, 1990; Sah et al., 2020; Pandey et al., 2021).

The distribution of Orthoptera species is influenced by various factors, including climatic conditions (Burton, 2003; Čato and Zagorac, 2021; Kaláb et al., 2021; Bauer et al., 2022). Changes in vegetation and habitat induced by climate and naturalization efforts may favor the proliferation of certain orthopterans, leading to the establishment of populations in previously unsuitable areas. Indeed, changes in weather patterns can create more favorable conditions for the survival and reproduction of these insects, thereby contributing to their widening distribution (Showler, 2002; Pandey et al., 2021). The house cricket *Acheta domesticus* belonging to the family Gryllidae is native to arid and semi-arid areas of northern Africa and/or south-western Asia (Ghouri, 1961; Glover, 2003). It is widely distributed globally (Ghouri, 1961; Lu et al., 2023), due to its ability to use various dispersal pathways and vectors, such as the transport of agricultural commodities and ornamental plants as hitchhikers (Bang and Courchamp, 2021; Essl and Zuna-Kratky, 2021). With expanding urbanization and human activities, *A. domesticus* has adapted to human-altered environments and habitats (Weismann and Rentz, 1977; Gardiner, 2009). Its opportunistic and generalist feeding behavior including grains, fruits, and vegetables makes it highly tolerant and capable of surviving and thriving in diverse and changing conditions (Clifford and Woodring, 1990; Wilson et al., 2010), but also a considerable pest for stored crops, threatening agricultural productivity and food security (Ghouri, 1961). Nonetheless, *A. domesticus* has been mostly neglected about its invasiveness, impacts, and potential as a vector for plant pathogens and/or other phytosanitary threats (Kulessa et al., 2023a, 2023b).

Functional response experiments are a crucial tool in ecological and biological research to understand predator-prey interactions (Cuthbert et al., 2019), aiming to investigate the relationship between the density of the prey—which indicates prey availability—and the feeding rate of the predator under controlled conditions (Faria et al., 2023). Functional response experiments can be used to approximate a species' phytosanitary threat, estimating the potential impact of a species on economically relevant prey (e.g., seeds; Pearse, 1980; Tripp, 2001; Zerbe, 2001). Comparing functional responses under different temperatures can indicate a species' response to climatic and environmental changes (Lachenicht et al., 2010; Haubrock et al., 2020). The functional response (i.e. the predator's impact on a presented prey) is expected to vary with

changing temperatures in ectothermic organisms due to accelerated metabolism and faster development and reproduction, leading to a higher demand for resources (González-Tokman et al., 2020). Higher temperatures are also expected to increase the activity level of predators, making them more active and likely to search for and consume more prey (Deutsch et al., 2018).

Here, we used a widely distributed orthopteran, *A. domesticus*, as a model species to conduct functional response experiments, aiming to investigate its impacts on important crops and ultimately to evaluate its potential as a phytosanitary threat. For this, we (i) performed functional response experiments using two different prey (millet and wheat seeds) using male and female individuals of *A. domesticus* and (ii) exposed them to a temperature gradient proxying global warming. We hypothesized that (1) female *A. domesticus* would exhibit higher consumption rates than males due to their reproductive energy demands; (2) the extent of damage depended on the seed type; and (3) increasing temperatures would lead to higher consumption rates due to accelerated metabolism.

## 2. Material and methods

### 2.1. Animal stocking and acclimation

Specimens of *A. domesticus* were obtained from a specialized local breeder (Rodinná farma Bušanovice, Czech Republic) and housed in a temperature-controlled laboratory (25 °C) at the Faculty of Fisheries and Protection of Waters in Vodňany, Czech Republic. Directly upon their arrival, all individuals were transferred into large (57,7 × 79 × 44 cm) plastic containers with a portion of their cover replaced by plastic mesh (1 mm) to allow ventilation. To provide shelter to the animals, egg cartons were supplied to the containers. Specimens were fed daily in excess with fish pellets (Tl-2 Tilapia 2.5 mm, Skretting, Norway) and bio-grade apples. The enclosure was cleaned every other day before feeding. To accommodate the nocturnal activity of *A. domesticus*, a controlled day-night light cycle was maintained with daylight between 7 and 10 a.m. and the remainder of the day being in darkness. The acclimation lasted for a week and no elevated mortality of the stock was observed.

Then, a sufficiently numerous subset of animals was moved to three faunaria (EXOTERRA model PT2310, 46 × 30 × 17 cm, HAGEN, Germany) that were each placed into one of three laboratory incubators (Lovibond TC 445 S/445 L, Liebherr, Germany) to acclimate animals to the experimental temperatures of 20, 25 and 30 °C. To gradually reach the final temperatures without stressing the animals, the temperature was changed by 2 °C for two consecutive days in the incubators finally set at 20 and 30 °C. On the third day, the temperature was adjusted by 1 °C only. Similarly to the common stock maintenance, the faunaria were provided with egg cartons and bio-grade apples in excess, and daily cleaned. The same light regime as for the stock was used also in each incubator.

### 2.2. Preliminary trials

To identify suitable prey items (i.e. seed types) for the functional response experiments, a series of preliminary trials with different seed types (oat flakes, wheat bran, wheat grains, and millet seeds) were conducted. For this purpose, a subsample of the *A. domesticus* stock was placed in individual plastic boxes (size: 114 × 114 × 59 mm) with a cap of a 2 ml Eppendorf® tube glued to the center of each box and filled with water and kept at 25 °C under the same light regime. Animals were starved for 24 h, after which the cap was refilled with water and 10 seeds of the respective seed type (10 replicates each) were inserted into the box. In addition, 10 individuals of *A. domesticus* were kept without seeds to monitor the baseline mortality. After another 24 h, individuals were taken out of the box and euthanized by placing them in a fridge (4 °C) to gradually decrease their temperature and were then finally placed in a freezer (−20 °C).

Wheat bran was found unsuitable as seed type for the following experiments. When consumed by *A. domesticus*, the particles broke apart in a way that made it challenging to accurately assess the amount of consumed or bitten food units. On average,  $2.7 \pm 1.25$  (SD) out of 10 oat flakes were eaten completely and additionally,  $4.8 \pm 1.23$  oat flakes were bitten. In general, oat flakes were suitable as a food source, but the uneven size and rough surface hindered precise measurement of consumption. On average, about  $0.2 \pm 0.42$  wheat grains were completely consumed, and approximately  $4.7 \pm 1.8$  grains were bitten additionally. Meanwhile, millet seeds exhibited an average consumption of  $3.6 \pm 1.4$  seeds, and around  $5.5 \pm 1.6$  seeds were partly consumed. The dissimilar sizes of wheat grains and millet seeds resulted in wheat grains being completely eaten less frequently. Both food items appeared suitable for conducting functional response experiments, thus, both were included in the main experiments. No mortality was observed during preliminary trials.

### 2.3. Main experiments

To assess differences in the functional response of male and female *A. domesticus* (hypothesis 1) we conducted 10 replicates (each with one individual of *A. domesticus*) for every seed density of millet seeds (1, 2, 5, 10, 15, and 20) using the same experimental and box set up used for the preliminary trials. To identify possible differences among seed types (hypothesis 2), we also performed 10 replicates using wheat seeds and the same seed densities. For the inference of differences between seed types, only females were used as they constituted the majority of the population, with the number of males not being sufficient for additional experiments without incurring animal reuse (i.e. pseudo-replication). Finally, to consider the potential effects of climate warming on the potential of *A. domesticus* to present a phytosanitary threat (hypothesis 3), each of these trials (for both millet and wheat seeds) was conducted at three temperatures following the acclimatization described above (i.e. 20, 25, and 30 °C).

After each trial, the (i) completely eaten seeds and (ii) partially eaten (i.e. bitten) seeds were counted and the (iii) number of damaged seeds (summing completely and partially eaten seeds) were noted. If individuals had died during the experiment, their death was noted and the trial was repeated. Over a total of 628 trials, only 11 females and 2 males died.

### 2.4. Statistical analyses

#### 2.4.1. Feeding impact across sexes and seed types

To identify (1) differences in the damage (i.e. completely and partially eaten) on millet seeds across the temperature gradient (20, 25, and 30 °C) between male and female individuals and (2) differences by female individuals on millet or wheat seeds, a series of Wilcoxon rank sum tests were performed. For this, the *pairwise.wilcox.test* function of the stats R package (R Core Team, 2021) was used because the pairwise Wilcoxon test is a non-parametric statistical test to compare the medians among groups. The results were adjusted for multiple comparisons using the Holm method (Holm, 1979) because multiple hypotheses are tested, and thus, the likelihood of encountering a Type I error (false positive) increases.

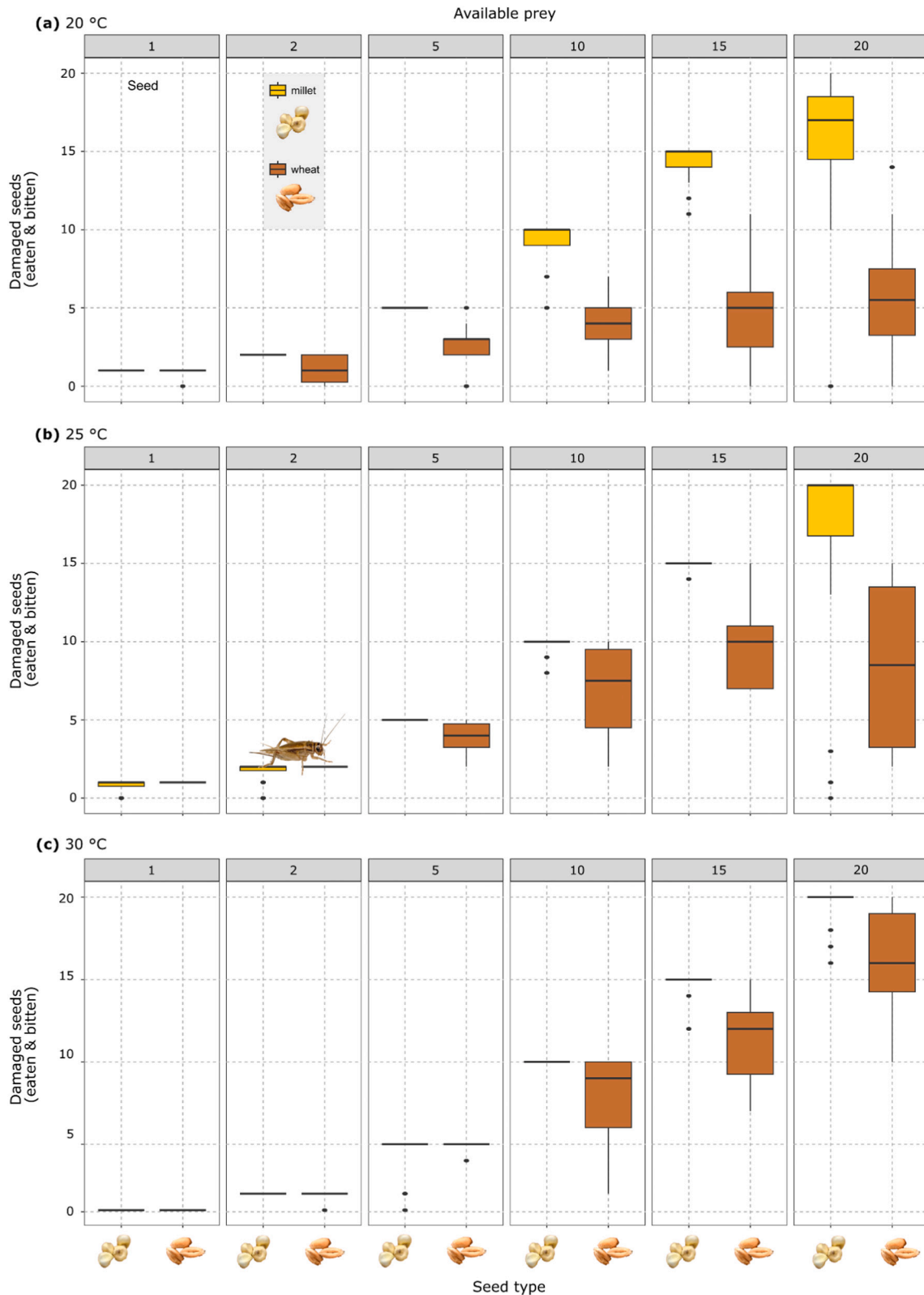
#### 2.4.2. Functional responses

To analyze the functional responses and identify the response type of male and female *A. domesticus* to different seed types and across temperatures, the *fair\_test* function of the *frair* R package (Pritchard et al., 2017) was used. The majority of responses exhibited evidence for Rogers Type II response model (i.e. significant negative first-order term). As we did not replace the consumed seeds, Rogers' random predator equation to each subset was fitted using the *frair\_fit* function of the *frair* R package (Rogers, 1972; Pritchard et al., 2017):

$$N_e = N_0(1 - \exp(-a(N_e h - T))) \tag{1}$$

where  $N_e$  refers to the number of damaged (i.e. completely and partially eaten) seeds,  $N_0$  is the initial seed density,  $a$  is the attack rate (i.e. the rate at which a predator attacks seeds),  $h$  is the handling time (i.e. the

time needed to consume a seed) and  $T$  is the total experimental period (i.e. 24 h). Then, the progression of the functional response curves for the noted subsets was compared using 95 % confidence intervals, calculated using the *frair\_boot* function of the *frair* R package, with 999 non-parametric bootstraps for  $a$  and  $h$  parameters per functional response



**Fig. 1.** Comparison of damages to millet (yellow) and wheat seeds (brown) by *Acheta domestica* females over the temperature gradient (a: 20; b: 25; c: 30 °C) in dependence of their availability (1, 2, 5, 10, 15, 20 seeds).



subset (i.e. sex, seed type, and temperature; Pritchard et al., 2017). Therefore, significant differences among groups were noted when their confidence intervals diverged, or a lack of significance was inferred when the confidence intervals overlapped (Barrios-O'Neill et al., 2015).

Finally, we calculated the functional response ratio (FRR; Cuthbert et al., 2019) to amalgamate information from the attack rate and handling time parameters, by dividing the attack rate ( $a$ ) by the handling time ( $h$ ):

$$FRR = a/h \tag{2}$$

All statistical analyses were conducted in R v. 4.1.3 (R Core Team, 2021).

### 3. Results

#### 3.1. Feeding impact across sexes and seed types

The number of damaged seeds did not differ between male and female individuals (20 °C:  $p = 0.85$ ; 25 °C:  $p = 0.89$ ; 30 °C:  $p = 0.48$ ). Across all three temperatures, the applied Wilcoxon test however identified that the number of eaten millet seeds exceeded the number of consumed wheat seeds (20 °C:  $p < 0.001$ ; 25 °C:  $p < 0.005$ ; 30 °C:  $p < 0.05$ ). This contrast was particularly evident at higher seed densities, regardless of temperature. At lower seed densities (one and two seeds), the extent of damage to seeds was comparable (Fig. 1a-c).

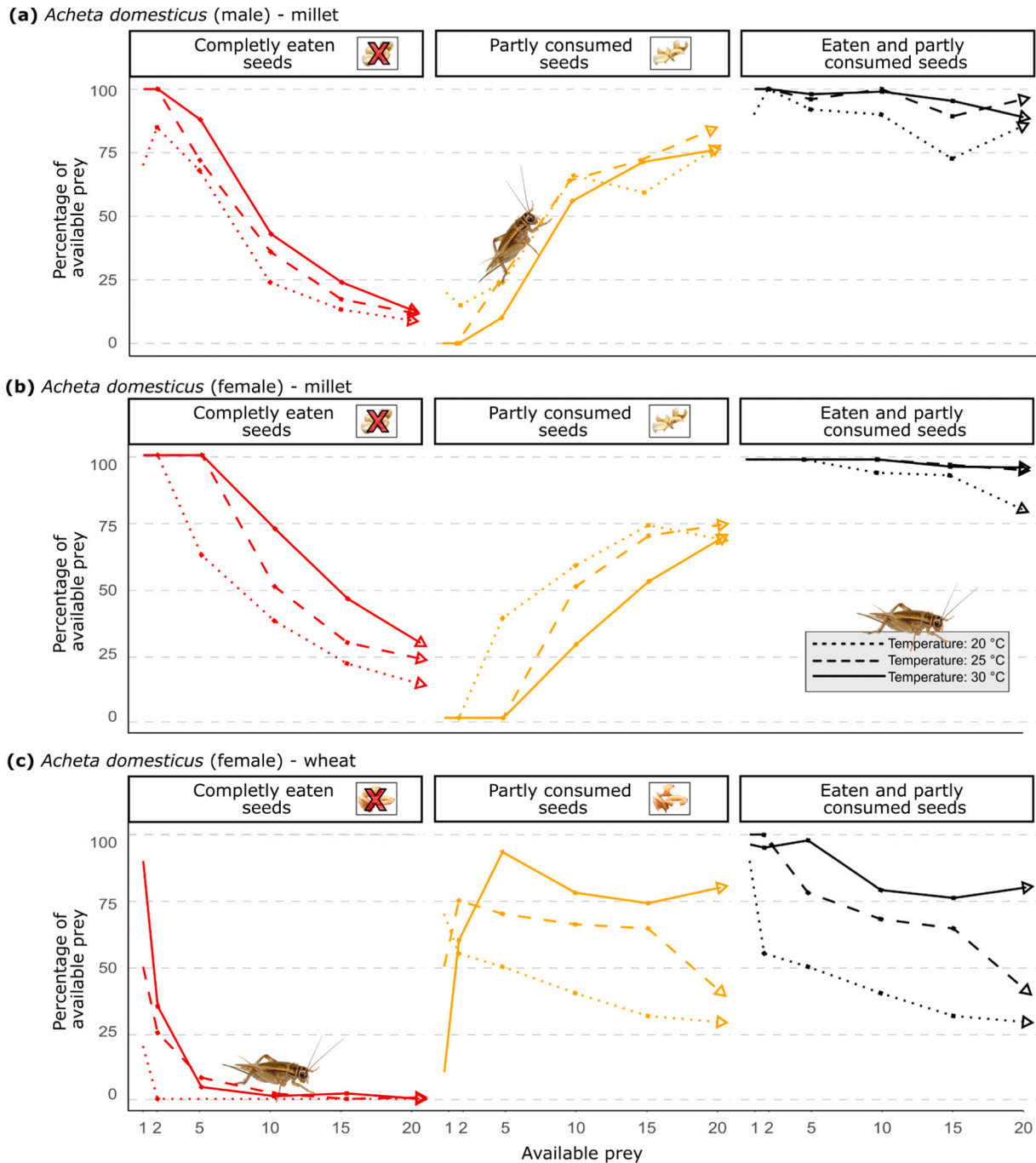


Fig. 2. Comparison of *Acheta domestica*' consumption for male (a) and female (b) individuals consuming millet seeds and respectively female individuals consuming wheat grain (c) over a temperature gradient (20, 25 and 30 °C) with different seed availability. Shown are the completely eaten seeds (red), partly consumed seeds (orange), and the overall damage (black).

As seed density increased, there was a noticeable decrease in the ratio of completely consumed seeds (Fig. 2a-c). Temperature exerted a significant influence, as higher temperatures correlated with increased millet seed consumption when available (Fig. 2a, b). In the case of wheat grains, there was no such trend observed, with the consumption of whole grains remaining constant across all temperatures (Fig. 2c). This temperature effect extended to partially eaten seeds, particularly impacting wheat seeds, and an increase in the temperature led to a higher ratio of partially eaten seeds. While the partially consumed millet seeds remained relatively stable across all temperatures, distinct variations emerged in wheat damage. At 30 °C, more wheat grains were bitten compared to millet seeds at the same temperature (Fig. 2a-c). Millet exhibited consistent overall damage, reflecting its smaller size and softer consistency (Fig. 2a, b). In contrast, the overall wheat damage increased with rising temperatures (Fig. 2c).

### 3.2. Functional response analyses

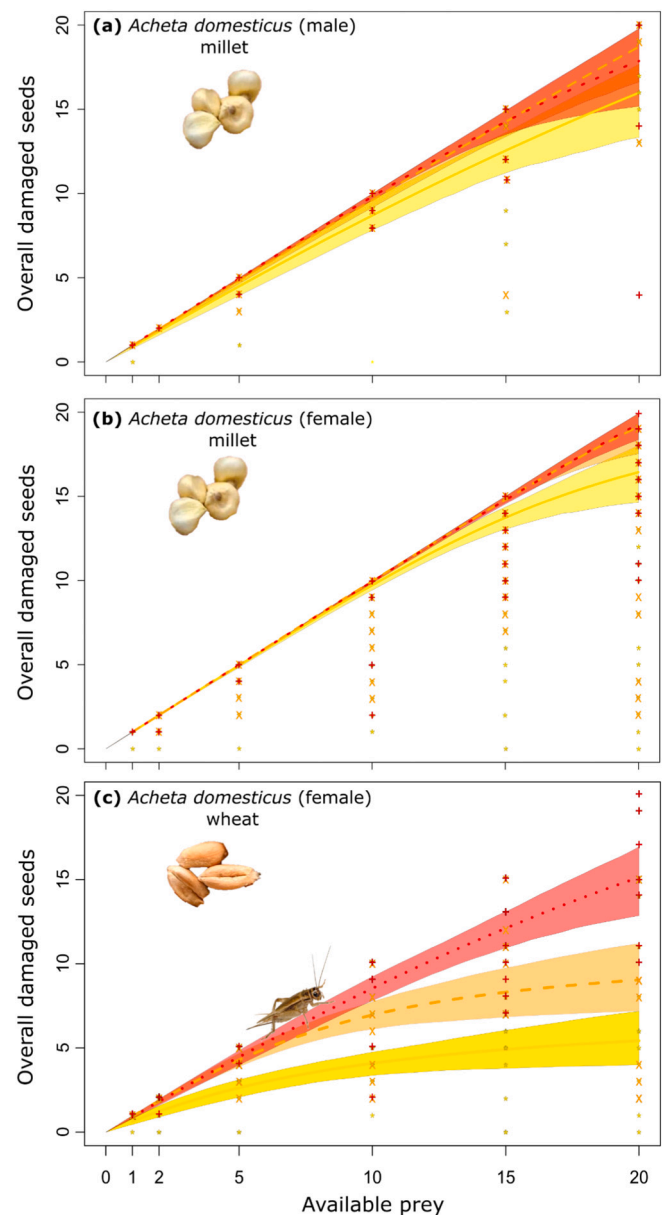
Considering damaged seeds (completely and partially eaten seeds combined), all functional response curves aligned with functional response Type II. The functional response curves for damaged millet seeds revealed minor variation between female and male specimens across the three different temperatures (Fig. 3a, b). For both male and female individuals, the functional response curves at 20 °C remained slightly below those at 25 °C and 30 °C, which overlapped.

At the maximum prey density of 20 seeds, female individuals damaged (i.e. consumed or partially ate) approximately 16 (20 °C) to 19 seeds (25 °C and 30 °C). Male individuals damaged on average 15 seeds at 20 °C, but on average 19 seeds at 25 °C, marginally exceeding the on average 18 damaged seeds at 30 °C. Differences were found between the consumption of millet and wheat (Fig. 3b, c), indicating that higher temperatures correlate with a greater extent of grain damage. At a density of 20 wheat grains and a temperature of 20 °C, an average of five seeds were damaged, while at 30 °C, approximately 15 seeds were damaged on average.

Increasing temperatures affected the attack rates among both sexes (Table 1). Among males, the attack rate increased with rising temperatures (attack rate and handling time for males could not be computed at 25 °C). This trend was also observed for females independent of seed type, but in that case, the attack rate declined beyond 25 °C. Furthermore, when comparing the attack rate between seed types, millet seeds were attacked at higher rates than wheat. Males had a longer handling time as temperature increased, while females displayed a reduction in handling time. Overall, this was reflected in higher functional response ratio (FRR) values in millet seeds compared to wheat, which further increased with a rise in temperature.

## 4. Discussion

Non-native orthoptera such as the house cricket *Acheta domesticus* can be a substantial ecological burden by causing numerous adverse impacts (Ghouri, 1961; Kulessa et al., 2023a, 2023b). However, neither per capita effects nor the functional response of common and widely distributed species like *A. domesticus* have been assessed. With regard to the first hypothesis, we found that, while males and females did not differ significantly in their damage to seeds, seed type and temperature played important roles, thereby confirming our 2nd and 3rd hypotheses that the extent of damage depended on the seed type and that increasing temperatures would lead to higher consumption rates. This was particularly evident at higher temperatures, as the ratio of damaged seeds increased for both food millet seeds and wheat grains. Being the first study to assess the potential impact of Orthoptera species using functional response analysis, the obtained results underline the potential for *A. domesticus* to function as a phytosanitary threat, especially during decades of increasing global temperatures.



**Fig. 3.** Functional response curves for *Acheta domesticus* females exposed to 1, 2, 5, 10, 15, and 20 seeds of wheat (a), millet (b), and male individuals exposed to millet seeds (c) across a temperature gradient from 20 (yellow), 25 (orange), and 30 °C (red). Note that here, the damage to seeds was assessed, i.e. including both completely and partially eaten seeds.

### 4.1. Males versus females

Sexual dimorphism is common among Orthoptera species, with females generally requiring a higher energy intake due to, but not only, higher investments into reproductive activities (Arrese and Soulaiges, 2010), while also being larger than males (Whitman, 2008). This can be explained in part by the different roles of males and females in reproductive activities, with females generally needing more energy to produce more expensive eggs compared with less energy-intensive spermatozoa (Whitman, 2008; Arrese and Soulaiges, 2010). This sexual dimorphism is also associated with a greater number of pupal stages in females, leading to the earlier emergence of adult males (protandry; Hochkirch and Gröning, 2008), which in turn leads to behavioural or even functional differences. Our results moreover indicated that there were no significant differences in the consumption of millet seed between male and female individuals. Their consumption patterns

**Table 1**

Attack rates and handling time of male and female individuals of *Acheta domesticus* considering damaged seeds (i.e. completely and partially eaten combined) of millet and wheat and temperatures of 20, 25, and 30 °C. See also Supplementary Fig. 1. For the same analysis using only completely eaten seeds, please see Supplementary Table 1.

Temperature	Sex	Seed type	Attack rate [a]	Handling time [h]	Functional response ratio
20 °C	Male	Millet	2.567	0.023	111.623
	Female	Millet	4.081	0.029	140.741
		Wheat	1.166	0.134	8.723
25 °C	Male <sup>a</sup>	Millet	–	–	–
	Female	Millet	7.161	0.028	255.810
		Wheat	3.173	0.090	35.332
30 °C	Male	Millet	6.162	0.036	171.283
	Female	Millet	5.686	0.019	299.334
		Wheat	2.588	0.030	86.361

<sup>a</sup> Not computable due to near maximum feeding activity.

remained remarkably similar, as both sexes inflicted comparable damage to seeds. The functional responses also corresponded to Type II in both sexes, with comparable curvature even with higher temperatures and increased metabolisms, making female individuals an ideal organism and proxy for functional response experiments. The higher reproductive capacity of females also enhances the overall reproductive success of a population, contributing to the species' swift reproduction and extensive distribution, facilitating its ability to spread and thus, its invasiveness (Meade et al., 2017; Soto et al., 2024).

#### 4.2. Different damage between millet and wheat

Many Orthoptera species are known for their opportunistic feeding habitats, consuming a variety of plants, fruits, and also an array of various seed and grain types (Bauer et al., 2022). When orthopterans such as *A. domesticus* reproduce and spread into agricultural areas, they encounter easy access to silos (i.e. harvest supplies) or cultivated fields. The prey (i.e. seeds type) they encounter plays a substantial role in determining the extent of orthopteran infestation. As exemplified in this study, softer and smaller seeds (such as millet) are more prone to be consumed and partially damaged, while larger and harder seeds (such as wheat) are less vulnerable. Meanwhile, using larger and harder wheat grains resulted in more distinct patterns in the functional response under increasing temperatures, while any differentiation observable with millet seeds occurred near the saturation i.e. at the highest offered seed densities. Thus the notable difference in functional responses between seed types confirmed that softer seeds are more strongly impacted, especially considering that the softer millet seeds were damaged, while compared to harder wheat grains, a substantially higher share was entirely consumed. From an ecological perspective, however, it is crucial to acknowledge that there is no distinction between seeds that are entirely consumed and those that suffered damage, as a partially consumed seed is rendered useless (i.e. spoiled). Therefore, we determined that the status as 'damaged' is the decisive factor, given that neither consumed nor damaged seeds are intact and will not be included in the human food chain in food-secure communities or grow into agriculturally viable plants, which will lead to a drop in agricultural yields (Deutsch et al., 2018).

#### 4.3. The effects of global warming

While globally rising temperatures constitute a significant factor influencing the distribution of many non-native species (Kordas et al., 2011), it also affects their metabolism, reproduction, and consumption rates (Rollo and Gunderman, 1984; Willott and Hassall, 1998). Indeed, as increasing temperatures correlate with increased metabolic activities of insects, their activity increases. This leads to higher energy requirements and thus, higher food consumption rates. It is therefore no

surprise that increased temperatures resulted in a higher functional response in both sexes. The attack rate increased from 20 to 25 °C, but decreased towards 30 °C. The handling time also decreased with rising temperatures, reflecting the above mentioned higher metabolic activity. The experiments also demonstrated that the damage to the harder and larger wheat grains also increased with warmer temperatures, thus indicating that higher temperatures will magnify the overall impact *A. domesticus* may have on agriculturally relevant seeds. Comparing our findings for *A. domesticus* to other species like *Melanoplus boulderensis*, *M. sanguinipes*, and *Camnula pellucida*, *A. domesticus* demonstrated comparable enhanced feeding rates at elevated temperatures (Buckley and Nufio, 2014). The observed increased seed damage with rising temperatures was comparable to performance shifts in *M. boulderensis* and *M. sanguinipes* across different elevations, although its responses appeared more consistent across the gradient, unlike the unimodal survival response observed in *C. pellucida* (Laws and Belovsky, 2010). Given its thermal optimum between 26 and 34 °C (Odhiambo et al., 2022), *A. domesticus* could expand its habitat range due to ongoing global warming, especially northwards, posing increased risks to agricultural and ecological systems. These findings, however, underscore the complexity of species-specific adaptations to changing climates, highlighting the necessity to tailor pest management strategies for phytosanitary threats to individual species' ecological dynamics, particularly in the face of global warming, by conducting experimental studies to explore, for example, functional responses.

#### 4.4. Phytosanitary threat

Mass-producing non-native *Acheta domesticus* in Europe for food raises concerns about accidental escapes that lead to high propagule pressure and potentially higher phytosanitary damages to native ecosystems. Especially the combination of a fast reproduction, coupled with high resilience and opportunistic feeding behavior, results in the potential of *A. domesticus* to inflict severe damage to crops and stored grain. Considering that *A. domesticus* is already established in vast parts of Europe (Kulesa et al., 2023a, 2023b), it is unlikely that its presence has no ecologically or economically relevant effects. Especially outside of urban areas, *A. domesticus* may compete with native species and, although no available information was found, possibly damage crops and stored seeds. As prey availability increased, the ratio of completely consumed seeds decreased. This indicated a responsive shift in predator feeding habits, which will magnify the potential impact. This is, because when presented with an overabundance of prey (i.e. in silos), the damage will not be confined to a few seeds entirely consumed, but likely rather result in the partial consumption of multitudes (Gardiner, 2018). This possibility is aggravated considering that both sexes of *A. domesticus* expressed comparable functional responses and exerted similar levels of damage to seeds and that *A. domesticus* is not selective in its food choice (Bauer et al., 2022). The interaction with density dependent factors, as for instance observed in *C. pellicula* (Buckley and Nufio, 2014), suggests that *A. domesticus*'s potential as a phytosanitary threat may be further nuanced, as intraspecific competition intensity could vary with temperature. It should, however, be highlighted that the ecology of non-native species is often detached from the same species' ecology in its native range, and may accordingly not be comparable to other species in their native range.

Climate change positively correlates with numerous factors that can affect the per capita impact of insect pests, thus making it possible that higher temperatures will amplify the phytosanitary threat presented by *A. domesticus*. Considering its high tolerance to temperature changes and ability to adapt to new environments, this may be especially the case of *A. domesticus*, which is native to the climate of arid and semi-arid areas of northern Africa or south-western Asia (Ghourri, 1961; Glover, 2003). The impacts of climate change, characterized by elevated temperatures and changed precipitation regimes could alter crop yields and types in Europe, potentially affecting the availability and diversity of prey for



invasive *A. domesticus*. In a scenario where climate change makes crops more difficult to grow, invasive populations could exacerbate the challenge by directly feeding on limited vegetation and competing with native species, further stressing the already strained agricultural systems. It should, however, be considered that *A. domesticus* is a rather small Orthoptera species (Gray, 1997; Bascuñán-García et al., 2010), insinuating that larger species might be capable of consuming larger and harder seeds. Considering the degree of habitat alteration, as well as the effects increasing temperatures can have on non-native species (Showler, 2002; Pandey et al., 2021), more locally established non-native orthopterans may be enabled to spread. This also included species like *A. domesticus* which is mostly found in cities but might lead to dispersal into more rural or agricultural areas, thereby increasing its potential impact.

#### 4.5. Management biosecurity implication section

Currently, information on the impact of *A. domesticus* is scarce and anecdotal at best, with no information on its impact on native ecosystems or agriculture (Kulesa et al., 2023a, 2023b). In indoor environments, it is however regarded as a nuisance (Busvine and Busvine, 1980). Nevertheless, *A. domesticus* is an established non-native species to continental Europe that is widely distributed in urban areas. As such, it could be considered invasive in Europe due to its past and potentially ongoing spread. With steadily rising temperatures, there is a possibility for its rapid population growth and a stronger impact through higher consumption rates. A study in a 'natural' environment on current European crops (maize, wheat, barley, corn) to assess the impact of *A. domesticus* on seeds, seedlings, and young plants would be the next step. This would lead to the development of localized control strategies, including traps, insecticides, or other known methods commonly used for indoor pests, followed by management strategies, including early detection and research into resilient and resistant plant varieties. Effective management of *A. domesticus* in Europe could involve stringent containment protocols in production facilities, complemented by pre-screening to identify and monitor areas at risk of invasion, thereby preventing or mitigating potential ecological impacts.

#### 4.6. Future perspectives

While the observed functional responses (i.e. the impact) of *A. domesticus* under current climate change scenarios (Scherrer et al., 2005; IPCC, 2022) highlight the need for comprehensive strategies to mitigate its potential as a phytosanitary threat, future studies are imperative to deepen our understanding of this issue. Conducting comparative analyses of the functional responses of *A. domesticus* to seedlings of various agricultural crops, but also other parts of the growing plant that can be affected (e.g. leaves), would be an important avenue for future research. Moreover, exploring this species' temperature limitations, would provide valuable insights into its feeding preferences and potential damage patterns across different crop types. Comparing the behavior and impact of *A. domesticus* with those of native or other non-native species could shed light on the potential interspecific competition with co-occurring native species. Similarly, this could allow us to assess additive, synergistic, or even antagonistic effects of multiple co-occurring non-native orthopteran species on crops. These results could therefore inform targeted management strategies and could be crucial in developing effective, science-based approaches to safeguard agriculture productivity and maintain ecological balance in the face of changing climatic conditions and the spread of non-native species like *A. domesticus*.

#### Funding

This study was supported by The Ministry of Education, Youth and Sports of the Czech Republic, project CENAKVA No. LM2023038. AKK acknowledges the support from ERASMUS+ that enabled her to

participate in this research.

#### Ethics approval

Following ethical guidelines governing research involving animal subjects, this study, which utilized house crickets (*Acheta domesticus*) as experimental organisms, adheres to all applicable legal and ethical standards. The research involving animals was conducted in compliance with the principles outlined by the appropriate institutional and/or national research ethics committee. Furthermore, it is important to note that house crickets are not subject to any legal restrictions or regulations in the context of this research, and their use was characterized by the utmost ethical treatment. Detailed information on the ethical treatment of the animals, including housing conditions, handling procedures, and any measures taken to minimise discomfort or distress, is provided in this manuscript to ensure transparency and adherence to ethical standards in animal research.

#### Consent to participate

Informed consent was obtained from all individual participants included in the study.

#### Consent to publish

Not applicable.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author or can be downloaded from <https://github.com/lsmaSA/Functional-Response-Anna>.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.170376>.

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