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To cite this version:

Marion Javal, John S Terblanche, Chantelle Smit, Julien Haran. Comparative assessment of heat tolerance in weevils associated with a fire-prone ecosystem. Ecological Entomology, 2023, 48 (2), pp.240-250. 10.1111/een.13218 . hal-04007187v1

HAL Id: hal-04007187
https://hal.inrae.fr/hal-04007187v1

Submitted on 27 Feb 2023 (v1), last revised 16 Mar 2023 (v2)

Received: 30 July 2022 | Accepted: 22 November 2022
DOI: 10.1111/een.13218

ORIGINAL ARTICLE

Ecological Entomology

Royal Entomological Society

Comparative assessment of heat tolerance in weevils associated with a fire-prone ecosystem

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Associate Editor: Krzysztof Miler

Abstract

1. Fire is an important cause of disturbance which directly shapes many ecosystems worldwide. While the effect of fire on the distribution and regeneration of plant species has been widely documented, little is known on how phytophagous insects are reacting to these disturbances.
2. This study explores the survival strategies of various weevil species, a highly diverse phytophagous beetle group in fire-prone ecosystems of the biodiversity hotspot of the Cape Floristic Region in South Africa. More specifically, we investigated how the lifestyle of species (location of larval development, phenology of adults, and flight ability) correlates with heat tolerance. We hypothesized that wingless species in particular will show better tolerance to heat as they have a limited ability to escape fire rapidly and usually remain hidden in the soil.
3. The thermal tolerance of a set of sixteen species with divergent lifestyles and geographic distribution was measured using a standard heat knockdown protocol at 48°C. Respirometry was then performed on the most resistant species using a ramping protocol in order to determine CT_{max}.
4. Our results show that the species tested exhibit high variation in thermal tolerance across taxonomic groups, clustering into three modalities: weak, intermediate, and high tolerance to heat stress. In addition, life history traits (diurnal vs. nocturnal adult activity and location of juvenile stages in plant tissues) likely better explain thermal tolerance at the species level than flight ability or the fire-proneness of ecosystems. Finally, results revealed that some non-flying weevil species are highly heat tolerant with CT_{max} values reaching up to 50.2 and 51.9°C in species among the Ocladiinae and Brachycerinae subfamilies, respectively.
5. Climate change is leading to an increase in the impact and frequency of fires. In this context, this study highlights the diversity of strategies developed by arthropods to escape extreme heat in fire prone ecosystems. Further work is necessary to examine the generality of these patterns across other fire prone ecosystems to better understand behavioural compensation and evolutionary responses, especially given the forecast increases in fire driven by drying and warming associated with climate change.

KEYWORDS
Bogert effect, fynbos, heat knockdown, thermolimit respirometry, insect, Coleoptera

INTRODUCTION

Fire is an important cause of disturbance which directly shapes many ecosystems worldwide (Bond et al., 2005). Fire regime can be defined by several parameters: the frequency and the intensity of the fire events, but also their seasonality and the size of the surface burnt (Gill & Allan, 2008). Fynbos is a fire-prone ecosystem characteristic of the Cape Floristic Region (CFR, South Africa), in which fire has played a major role in the evolutionary diversification of plants (Keeley et al., 2012). It is associated with sandy and infertile soils and characterised by the prominence of aphyllous graminoids and sclerophyllous shrubs, most of the time including proteoid shrubs (Cowling et al., 1997). The characteristics of this ecosystem such as the vegetation assemblage or the accumulation of dead material make it particularly flammable (Kraaij & van Wilgen, 2014). In the context of climate change, the average temperature as well as the frequency of extreme events such as heat waves or fires are likely to increase on short time scales (Harvey et al., 2022; IPCC, 2022). In the CFR in particular, the total area burnt annually has increased significantly between 1980 and 2010 along with the occurrence of extremely warm and dry weather conducive to fires, which can be directly correlated to climate change (Kraaij et al., 2013). In addition, the increase in the frequency of extreme weather following wildfires, together with the effects of exotic plant species have reduced the regeneration of native plant species, leading to a decrease in botanic biodiversity since 1966 (Slingsby et al., 2017). Understanding the responses of fynbos organisms to these events is, therefore, crucial in estimating how global changes will affect them (Swengel, 2001).

Several strategies to cope with fire have been described in plants and animals (Pausas, 2019). Some species develop traits that allow them to resist fire, by developing a protective structure for vital organs (e.g., thick bark (Pausas, 2015), carapace (Sanz-Aguilar et al., 2011), shell (Kiss & Magnin, 2006)), by resprouting from vegetative buds or by reducing the intensity of fire (the "non-flammable strategy", mainly described in plants (Pausas et al., 2017)). Dormancy is another strategy to survive fire. For example, some species survive in the ground as egg, pupae, or seed whose germination or emergence can be tightly linked to fire (Keeley et al., 2012; Pausas et al., , 2018a, 2018b). Finally, organisms with sufficient dispersal abilities may flee the fire and/or retreat to areas less subject to fire ("refugia", Keeley et al., 2012; Robinson et al., 2013), to recolonise the burnt area exogenously (García et al., 2016). However, fire survival strategies are relatively unstudied in animals compared to plants, probably because of differences in the mobility capacity (Pausas et al., 2018a, 2018b). In insects, in particular, few examples are documented. For these ectothermic organisms, temperature is a key environmental driver of population dynamics since they directly depend on environmental temperature to regulate their physiological functions (Angilletta, 2009). Tolerance to extreme high temperatures associated with fire may involve physiological adaptations (González-Tokman et al., 2020; Ma et al., 2021) that lead to an increase in their maximum temperature for coordinated locomotion, or critical thermal maximum (CT_{max}, Cerdà et al., 1998). Behavioural adaptations are also known. For example, some invertebrate species take refuge in protected parts of plants, where the temperature is buffered (Brennan et al., 2011). Other species survive by burrowing into the soil (Thom et al., 2015), and fire can even be a cue for emergence (Jacobs et al., 2011), as it is for the germination of some plants (Keeley et al., 2012). Finally, exogenous recolonisation, a case in which individuals from unaffected areas relocate in the burnt zone after the fire, is well described, particularly in saproxylic insects (Evans, 2010).

Weevils (Coleoptera, Curculionoidea) constitute a hyper-diverse lineage of exclusively phytophagous beetles (Oberprieler et al., 2007). This insect group is especially well diversified in the CFR, with entire new clades only described very recently (Meregalli et al., 2021; Haran et al., 2022). More specifically, this region hosts radiating basal weevil lineages adapted to xeric environments (e.g., *Brachycerus* and several tribes among Brachycerini; Oberprieler, 2014) together with more derived clades of various "true" weevil subfamilies among the Curculionidae (Alonso-Zarazaga & Lyal, 1999; Hernández-Vera et al., 2013; Hansen et al. 2021). Due to their high diversity of species, but also of lifestyles or host-plants found in this group, weevils constitute a powerful model to investigate evolutionary dynamics, speciation processes, and adaptation of insects to their environment (Toussaint et al., 2014; Baird et al., 2021; Hévin et al., 2022). A particularly noteworthy feature in the case of xeric and fire-prone ecosystems is the high diversity of terricolous non-flying weevils, where the adults generally live in the leaf litter in the vicinity of their host-plant. This lifestyle is usually associated with larval stages developing in or on the root system or bulbs of the host plant encountered in several subfamilies and tribes of weevils (e.g., Entiminae, Embritini, Oosomini, Tanyrhynchini; Cyclomiinae; Brachycerinae, Brachycerini, Cryptolaryngini; Ocladiinae, Ocladiini; Oberprieler, 1995; Oberprieler, 2014; Haran et al., 2020). The latter contrasts with the expectation that species with good dispersal abilities would better cope with fire-prone ecosystems since they can rapidly escape extreme heat conditions on the soil surface and repeated cycles of fire. This apparent contradiction was noticed during several field observations in the CFR, where species of non-flying genera were observed on resprouting plants in the middle of large, recently burnt areas (*Cryptolarynx pyrophilus* in Montagu, Haran et al., in press; *Tanyrhynchus carinatus* in Du Toitskloof Pass, JH pers. obs.). Though many strategies may be at work in these cases (quick recolonisation, larval stages protected deep in the soil), the assumption that adults of non-flying insects occurring in fire-prone ecosystems exhibit a higher heat tolerance than flying species occurring in neighbouring regions with no fire cycles remains to be explored. This is particularly relevant since other groups of non-flying arthropods such as Collembola were previously found significantly more heat tolerant in the CFR than in other regions (Liu et al., 2020).

In this study, we conducted a first investigation of the relative heat tolerance of adult weevils occurring both in fire-prone and non-burning ecosystems of South Africa. Using both acute constant and dynamic heat exposure protocols, we tested whether non-flying weevil species exhibit a higher tolerance to extreme heat than flying species as an adaptation to survive heat when hidden in the ground. We also produced preliminary data on the potential difference between weevil species occurring in fire-prone ecosystems and in non-fire-prone ecosystems of neighbouring regions in terms of heat tolerance. Patterns of heat tolerance were then contextualised with life history traits of the species tested.

MATERIAL AND METHODS

Species sampling

Weevils are inconspicuous organisms and sampling live specimens of a peculiar species in sufficient amounts can be challenging. In this context, the sampling was conducted opportunistically in 2018 and 2019 during spring, at the vicinity of Stellenbosch in the CFR and further in neighbouring regions. In all, adults of 16 species were obtained, with a number of individuals sampled ranking from 6 to 22 per population (Table 1). Twelve of these species are non-flying, as typical for their subfamilies (Brachycerinae, Cyclomiinae and a part of Entiminae among the Curculionidae (Bouchard et al. 2011; Marvaldi et al., 2014; Oberprieler, 2014; Figure 1)). Due to phylogenetic conservatism in flight abilities, no closely related species to the above groups with flight behaviour occurs in the CFR; therefore, the four flying species included were sampled among the Nanophyinae and Curculioninae subfamilies (Table 1). For two species (*Tanyrhynchus carinatus* and *Cryptolarynx variabilis*), two to three geographically distant populations (1–20 km apart) were obtained and retained for a preliminary assessment of the variability of thermal resistance at population level.

Fourteen of the species were sampled in fire-prone ecosystems of the CFR (Fynbos, and to a lesser extent Renosterveld, Table 1), including ten non-flying. Two species from non-fire-prone ecosystems of neighbouring regions were included: *Ocladius costiger* and *Sciobius pr. brevicollis* (both non-flying) specimen were collected in a desert biome of the Northern Cape province and in coastal tropical forests of KwaZulu-Natal, respectively. These ecosystems show no natural cycles of fires but can exhibit high temperatures, and temperatures in the Northern Cape region in particular are higher than in the CFR (van Wilgen et al., 2016). As these two species share life history traits with non-flying species from the CFR, they are expected to provide insights for a comparative assessment of fire tolerance of weevils in fire versus non-fire prone ecosystems.

While this study focuses on survival of adult weevils, we also recorded the location of larvae in or on the host plant since these stages are the most exposed to hot summers and fires and could unravel insights on survival strategies of the species sampled. All the flying species sampled develop in the aerial part of their host plant and cannot survive fire at larval stages. The adult stage on the other hand, is expected to be able to escape the heat stress by flying. By contrast, the non-flying species sampled develop on or in underground tissues of the host plant and are thus possibly protected by buffering effect of the ground during fire event. Adult stages of these species are generally able to hide in the ground as well and have possibly been selected to resist high heat when staying a few centimetres below the surface of the ground. As a result, the lifestyle of both adults and larvae of non-flying species are relevant in a context of survival to fire events. Adult circadian activity of these weevils is also a relevant feature since they may emerge from the ground only at night and as such escape from extreme heats from solar radiation. Through detailed field observations, lifestyle of larval stages was recorded for all species and host plant taxa was documented for thirteen of them. The sampling further included eight nocturnal species and eight active during daytime at adult stage. The two species from non-fire prone ecosystems were both nocturnal (Table 1).

In order to reduce background thermal history effects (e.g., recent weather fronts; Terblanche & Hoffmann, 2020; Huey & Buckley, 2022), specimens were kept for two to four days after collection (Table 1) at room temperature (about 25°C) with foliage of their host as a food substrate. Species were identified taxonomically based on available literature and using the reference collections housed at Iziko Museum (Cape Town). At least one reference specimen per population was mounted, dried and deposited in the Continental Arthropod Collection at Centre de Biologie pour la Gestion des Populations, Montpellier, France (CBGP; https://doi.org/10.15454/D6XAKL) attached with a specific identification code (see Table 1).

Thermal tolerance assessment

The relative heat resistance of species was first measured using a heat knockdown derived approach to rapidly sort ranking of tolerance (Huey et al., 1992). Specimens were individually set in an Eppendorf tube with ambient air. A thermocouple was used to track the air temperature of the tube, and set in order not to touch the tube walls. Eppendorf tubes were then placed in a water bath at 50°C in order to reach a stable air temperature of 48°C, a lethal temperature for most insects including beetles (Sunday et al., 2011). The duration between the introduction of the tube in the bath and the death of specimens was measured to the nearest second. Weevils exhibited a range of reactions to heat treatment, from rapid escape movement to resistance position without movement. In this last case, we observed that at time of death, weevils could not keep the position of resistance (legs and antennae relaxed) and regurgitate. At time of death, tubes were removed from the bath and left for 45 min at ambient temperature. Specimens that recovered from heat coma were not considered in the analyses. Specimens were dried and weighed individually after experiment microbalance (to 0.1 mg; AB104-S/Fact, Mettler Toledo International, Inc., Columbus, OH, United States).

In a second approach, we selected species that were the least affected by the HKD experiment (which suggests a high thermal tolerance) and could not fly (and, therefore, cannot escape thermal stress

TABLE 1 Ecology of weevil species used in the study

Species	Family	Subfamily	Noctural/ diurnal	Flight	Host plant	Localisation of larva in plant	Larval stages	Exposure to fire	HKD group (Figure 2)	Geographical coordinates	Localisation	Type of ecosystem	n (HKD)	Date of collection	Date HKD test	Mean weight	Species code
Cryptolarynx variabilis pop. 1	Brachyceridae	Brachycerinae	D	no	Oxalidaceae	Ground	enclosed (bulbs)	yes	C	33°57′01.4″S 18°52′30.6″ E	Stellenbosch Mountain	fynbos	15	29/09/2018	1/10/2018	0.014 g	JHAR01185
Cryptolarynx variabilis pop. 2	Brachyceridae	Brachycerinae	D	no	Oxalidaceae	Ground	enclosed (bulbs)	yes	C	33°55′53.4″S 18°52′29.7″ E	Jean Marais nature reserve	fynbos	22	30/09/2018	2/10/2018	0.017 g	JHAR01497
Cryptolarynx pyrophilus	Brachyceridae	Brachycerinae	D	no	Oxalidaceae	Ground	enclosed (bulbs)	yes	B	33°48′41.4″S 20°08′58.4″ E	Montagu	fynbos	15	24/09/2018	26/09/2018	0.004 g	JHAR01528
Byrsops apicalis	Brachyceridae	Brachycerinae	D	no	unknown	Ground	free	yes	B	33°55′53.4″S 18°52′29.7″ E	Jean Marais nature reserve	fynbos	14	30/09/2018	1/10/2018	0.021 g	JHAR01486
Brachycerus milleporus	Brachyceridae	Brachycerinae	N	no	Liliaceae	Ground	free	yes	A	34°14′28.5″S 18°51′12.8″ E	Kogelbay	fynbos	10	23/09/2019	26/09/2019	0.055 g	JHAR01501
Ocladius costiger	Brachyceridae	Ocladiinae	N	no	Aizodaceae	Ground	enclosed (roots)	no	C	29°41′05.7″S 17°56′36.2″ E	Springbok	other	9	29/09/2019	7/10/2019	0.023 g	JHAR04984
Hexatmetus sp.	Brentidae	Nanophyinae	D	yes	Ericaceae	Aerial	enclosed (fruits	yes	B	33°57′54.1″S 18°52′34.5″ E	Stellenbosch Mountain	fynbos	17	29/09/2018	1/10/2018	0.009 g	JHAR04985
Eremnus setifer	Curculionidae	Entiminae	N	no	Asteracae	Ground	free	yes	B	33°57′01.4″S 18°52′30.6″ E	Stellenbosch Mountain	fynbos	14	29/09/2018	2/10/2018	0.013 g	JHAR00991
Eremnus occatus	Curculionidae	Entiminae	N	no	Asteracae	Ground	free	yes	A	34°03′46.6″S 18°52′25.5″ E	Helderberg	Renosterveld	9	13/10/2018	15/10/2018	0.051 g	JHAR2187
Sciobius pr. brevicollis	Curculionidae	Entiminae	N	no	unknown	Ground	free	no	B	29°42′14.2″S 31°02′40.3″ E	Mount Edgecombe	other	20	09/10/2018	11/10/2018	0.021 g	JHAR04986
Phlyctinus grootbosensis	Curculionidae	Entiminae	N	no	Asteracae	Ground	free	yes	A	34°31′44.9″S 19°29′23.1″ E	Grootbos nature reserve	fynbos	22	13/10/2018	15/10/2018	0.023 g	JHAR01300
Oosomus cf. *varius*	Curculionidae	Entiminae	N	no	Asteracae	Ground	free	yes	A	34°31′44.9″S 19°29′23.1″ E	Grootbos nature reserve	fynbos	19	13/10/2018	15/10/2018	0.003 g	JHAR01301
Tanyrhynchus carinatus pop. 1	Curculionidae	Entiminae	N	no	Poales	Ground	free	yes	A	33°41′52.0″S 19°04′26.3″ E	DuToitskloof pass	fynbos	14	24/09/2018	26/09/2018	0.017 g	JHAR03044
Tanyrhynchus carinatus pop. 2	Curculionidae	Entiminae	N	no	Poales	Ground	free	yes	A	33°57′01.4″S 18°52′30.6″ E	Stellenbosch Mountain	fynbos	22	29/09/2018	2/10/2018	0.015 g	JHAR00806
Tanyrhynchus carinatus pop. 3	Curculionidae	Entiminae	N	no	Poales	Ground	free	yes	A	33°57′54.1″S 18°52′34.5″ E	Stellenbosch Mountain	fynbos	19	4/10/2018	5/10/2018	0.014 g	JHAR01487
Hypocolobus anaglypticus	Curculionidae	Cyclomiinae	D	no	unknown	Ground	free	yes	B	33°48′41.4″S 20°08′58.4″ E	Montagu	fynbos	17	24/09/2018	26/09/2018	0.023 g	JHAR01534
Miarus sp.	Curculionidae	Curculioninae	D	yes	Campanulaceae	Aerial	enclosed (fruits	yes	B	33°57′01.4″S 18°52′30.6″ E	Stellenbosch Mountain	fynbos	7	29/09/2018	4/10/2018	0.011 g	JHAR01646
Tychius placidus	Curculionidae	Curculioninae	D	yes	Fabaceae	Aerial	enclosed (fruits/ stems	yes	C	33°56′30.2″S 18°52′31.0″ E	Stellenbosch Mountain	fynbos	6	29/09/2018	4/10/2018	0.011 g	JHAR01553
Acallopistus guttatus	Curculionidae	Curculioninae	D	yes	Malvaceae	Aerial	enclosed (fruits	yes	C	33°56′30.2″S 18°52′31.0″ E	Stellenbosch Mountain	fynbos	11	29/09/2018	4/10/2018	0.010 g	JHAR01481

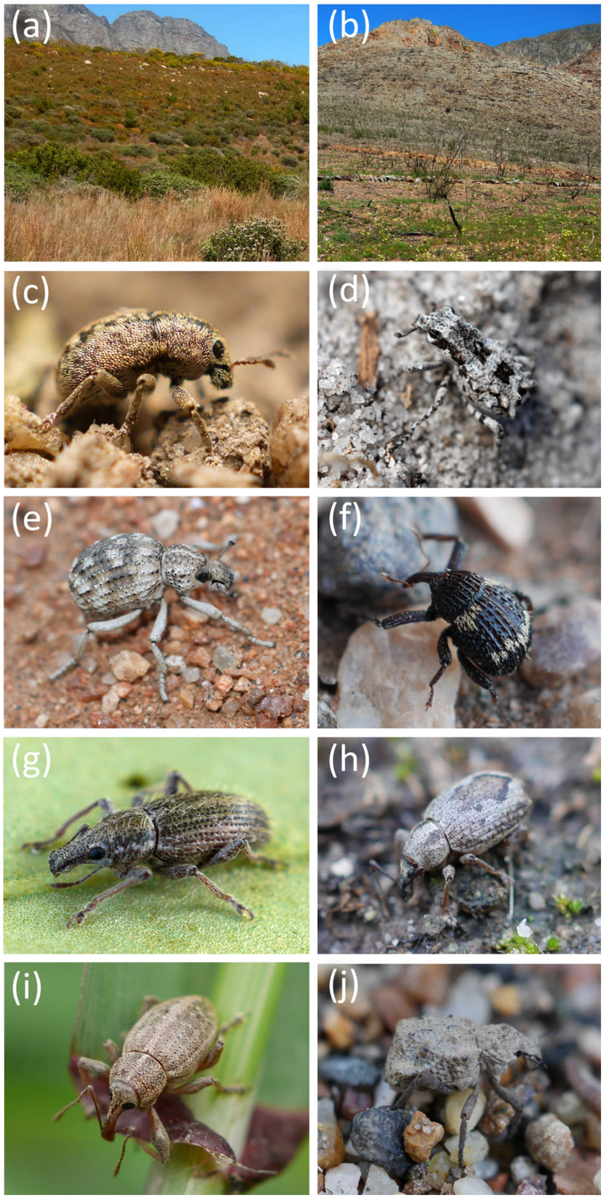

FIGURE 1 Fire-prone vegetation types in the Western cape province of South Africa and habitats of several apterous weevils tested in this study. (a) Fynbos vegetation type in the Theewaterskloof nature reserve. (b) Resprouting vegetation in a burnt area near Montagu where *Cryptolarynx pyrophilus* was collected. (c) *Cryptolarynx variabilis*. (Brachycerinae; Cryptolaryngini). (d) *Byrsops apicalis* (Brachycerinae; Byrsopini). (e) *Brachycerus milleporus* (Brachycerinae; Brachycerini). (f) *Ocladius costiger* (Ocladiinae; Ocladiini). (g) *Eremnus setifer* (Entiminae; Tanyrhynchini). (h) *Oosomus* cf. *varius* (Entiminae; Oosomini). (i) *Tanyrhynchus carinatus* (Entiminae; Tanyrhynchini). (j) *Hypocolobus anaglypticus* (Cyclomiinae; Rhythirrinini).

in their natural environment). The upper thermal limits (CT$_{max}$) of these species were measured using thermolimit respirometry (Lighton & Turner, 2004), following methods adapted from Boardman and Terblanche (2015). All specimens were weighed before and after respirometry on a microbalance. Airflow was regulated at 200 ml min^{-1} (STPD) and controlled by a mass flow control valve (SideTrak, Sierra International, United States) into a Li-7000 infra-red CO2/H_2O analyser fully calibrated for CO_2 at 386 ppm (balanced nitrogen) and water. The CO_2 production was recorded differentially (to ultimately produce an estimate of $\dot{V}CO_2$) in ppm by the standard LiCor software (Li-Cor, Lincoln, NE, United States). Activity was monitored using an infra-red activity detector (AD-2, Stable Systems International, Las Vegas, NV, United States). Animals were given a 10-min equilibration period at 25°C, after which the temperature in the chamber was ramped up at a constant heating rate of 0.25°C min^{-1} to 57°C using a programmable circulating and heating water bath (CC410wl, Huber, Berching, Germany). Baseline recordings were taken before and after each run to correct for potential drift, which was typically negligible. Expedata v. 1.9.10 (Sable Systems International) was used to transform recorded CO_2 values in ppm to VCO_2 in ml CO_2/h, to correct for potential baseline drift for all respirometry files, and to visualise activity data. CT$_{max}$ was defined as the point at which spiracles switched from high to low variability indicating loss of spiracular control (see Javal et al., 2019) and computed according to Boardman and Terblanche (2015).

Statistical analyses

Data were analysed using R 4.0.4 (R Core Team, 2021) with appropriate packages including MuMIn (Barton, 2022) and DoBy (Højsgaard & Halekoh, 2021). For the HKD experiment, data were expressed as proportions of specimens able to survive at 48°C over a period of 45 min. Survival data were modelled by specifying a full factorial generalised linear model (GLM) with logistic link function for binary outcome (i.e., dead/alive). Probability and estimated S.E. for survival were obtained from fitted GLMs and were used to draw survival lines that are presented in figures. Visual inspection of HKD data allowed the graphic categorisation of the species/populations in three groups (Figure 2a–c) according to their reaction pattern. The less heat-tolerant group (group A) was represented by species for which all specimens were dead in less than 500 s, the more heat tolerant group (group C) included species for which survival probability was higher than 60% by the end of the trial, and the intermediate group (group B) included all species in between these two extremes. We ran a one-way ANOVA followed by a Tukey post hoc test to explore every possible pairwise comparison within the three groups. The same combination of tests was used to compare flying species ($n = 4$, Table 1) and non-flying populations ($n = 15$, Table 1), respectively.

RESULTS

Survival probabilities of all species (HKD) followed three main types of responses (weak, intermediate, and high heat tolerance, Figure 2a). The less heat-tolerant group (group A) gathered five flightless, nocturnal species at adult stage, one of which was represented by its three populations (*Tanyrhynchus carinatus*). All these species have one

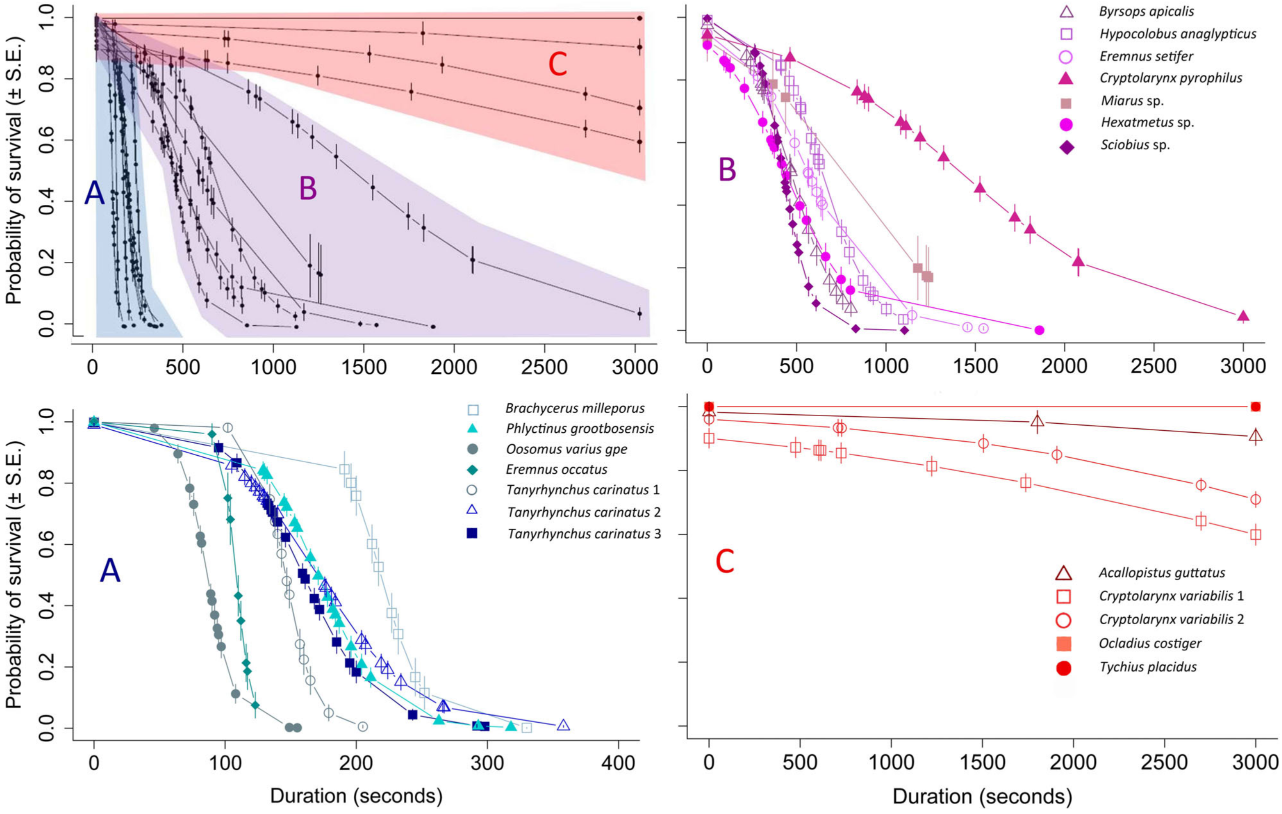

FIGURE 2 Survival probabilities of weevil species during heat knockdown (HKD) experiments at 48°C. top left: Overview of survival probabilities of all species tested clustered in three groups: Weak (a), intermediate (b), and high heat-tolerant (c). Bottom left and right: Details for the species included in the three groups.

thing in common: they all develop in the soil in the larval stage, and feed ectophytically. The remaining flightless species clustered in the intermediate (group B, 5 species) and highly tolerant groups (group C, 2 species). The intermediate group gathered a majority of diurnal species except for *Eremnus setifer* and *Sciobus pr. brevicollis*. Species with flight abilities clustered only in the intermediate and highly tolerant groups (2 species each). Finally, the most heat tolerant species (group C) included mainly diurnal species except for *Ocladius costiger* (Table 1 and Figure 2). The two species from non-fire prone ecosystems fell in the intermediate and high tolerant groups (*Sciobus pr. brevicollis* and *Ocladius costiger* respectively).

Overall, results showed that the three groups we defined were quite homogeneous in terms of survival probabilities: 14 pairwise comparisons out of 21 were non-significant in group A, 15 out of 21 in group B and group C was the only one for which species survival probabilities were all statistically similar (Table S1). In group A, survival probability of *Brachycerus milleporus* was significantly higher than that of *Eremnus occatus* ($p < 0.001$) and *Oosomus* sp. ($p < 0.001$). *Eremnus occatus* survival probability was significantly lower than that of *Phlyctinus grootbosensis* ($p = 0.020$) and *Tanyrhynchus carinatus* pop 2 ($p = 0.023$). Finally, *Oosomus* sp. had a significantly lower survival probability than *Phlyctinus grootbosensis* ($p < 0.001$) and *Tanyrhynchus carinatus* 2 and 3 ($p < 0.001$ and $p < 0.05$, respectively). In group B, *Cryptolarynx pyrophilus* has a significantly higher survival probability than any other species ($p < 0.001$ in all cases but *Miarus* sp. for which $p < 0.05$). The comparison of flying species revealed that only *Tychius placidus* and *Acallopistus guttatus* on the one hand and *Miarus* sp. and *Hexatmetus* sp. on the other hand had a similar resistance to HKD. Among the 15 non-flying species/population, 47 of the 105 pairwise comparisons revealed significant differences ($p < 0.001$; Table S1). Details of the pairwise comparisons are given in Table S1.

TABLE 2 Summary of data of CT_{max} measurements for *Ocladius costiger* and *Cryptolarynx variabilis*

	Ocladius costiger		*Cryptolarynx variabilis*	
Specimen number	CT_{max} (°C)	Mass (g)	CT_{max} (°C)	Mass (g)
1	47.6	0.0072	53.4	0.0023
2	51.6	0.0088	53.3	0.0105
3	49.8	0.0072	48.9	0.0031
4	49.4	0.0085		
5	52.6	0.0092		
Mean	50.2	0.0082	51.9	0.0053
SEM	1.95	0.0004	2.5	0.0026

CT_{max} was estimated from thermolimit respirometry for *Ocladius costiger* and *Cryptolarynx variabilis* since they were the only species from group C that could not fly and were little or unaffected by the HKD experiment. CT_{max} values ranged from 47.6 to 52.6°C for *Ocladius costiger* ($n = 5$, mean $= 50.2$°C, SEM $= 1.95$) and from 48.9 to 53.4°C for *Cryptolarynx variabilis* ($n = 3$, mean $= 51.9$°C, SEM $= 2.51$), and the mean values were not significantly different between the two species ($p = 0.161$, Table 2). These two species exhibit a small (about 0.015 g for *Cryptolarynx variabilis*) to average (about 0.023 g for *Ocladius costiger*) body weight when compared to all species tested (Table 1).

DISCUSSION

This study provides the first investigation of heat tolerance of multiple species of a phytophagous insect group in fire-prone ecosystems of the CFR. Within the weevil superfamily (Curculionoidea), the species we assessed displayed a remarkable range of reactions to a standardised heat stress at the adult stage. The general trend observed in this study indicates an ability to tolerate heat stress that is mostly species-specific, which is notable for phylogenetically related insects occurring in the same ecosystem. This trend, however, echoes the patterns observed in dung beetles (Scarabaeidae), for example, where substantial variation in heat tolerance exists across species (Gotcha et al., 2021). Within the weevils analysed, some species showed a high sensitivity to the HKD assay while others exhibited a very high heat tolerance, similar to highest records among beetles (i.e., Roberts et al., 1991). It should be noted that these previous records were measured on tenebrionid beetles from the Namib desert with putative morphological adaptations to heat such as long legs, larger size, and thick cuticle (Marden, 1987; Naidu, 2001). Since CT_{max} often correlates positively with body size both within and across species (O'Donnell et al., 2020; Wendt & Verble-Pearson, 2016), high heat resistance of the minute weevils tested here (a few milligrams) is unexpected and calls for further investigations. These results show that in addition to ants and tenebrionid beetles, weevils should be considered among the handful of arthropod lineages whose CT_{max} values exceed 50°C (Bennett et al., 2018). However, a range of intrinsic and extrinsic factors can influence heat tolerance estimates (Mitchell et al. 2017; Clusella-Trullas et al. 2021) and we recommend future investigations to consider larger sample sizes, high resolution microclimatic data, and complementary approaches to refine this finding. We also do not explore thermal acclimation effects and phenotypic plasticity more broadly. In some taxa, high levels of plasticity can be expressed rapidly under specific environmental conditions and may alter conclusions of resistance or heat susceptibility (González-Tokman et al., 2020), especially if fire-prone weevils possess a pronounced ability to mount heat hardening (protective) responses triggered by fire-related cues.

Heat tolerance in flying versus non-flying species

With regard to the first hypothesis we proposed, we found no clear pattern allowing conclusion about a correlation between flight abilities and heat tolerance. Contrary to expectations, all species with flight abilities clustered in the groups of moderate and highly tolerant species. In other words, species with a physical ability to rapidly escape peaks of heat and fire were also the ones showing a strong tolerance to heat stress. A first possible explanation is the positive correlation between flight abilities and heat tolerance due to the heat induced by flight muscles during insects' activity (Stevenson, 1985). A second explanation relates to the specific life-cycle and micro-environment experienced by the immature and adult stages of the flying species tested (*Acallopistus*, *Hexatmetus*, *Miarus* and *Tychius*; all from the CFR). The Bogert effect proposes that the less mobile life stages of ectotherms show greater thermal tolerance than mobile life stages to compensate for their inability to behaviourally escape thermal stress (Marais & Chown, 2008; Mitchell et al., 2013). One could expect thermo-tolerance to decrease with ontogeny and the transition from the larval to the adult stage, since it is associated with the acquisition of an increased mobility and capacity to avoid heat stress (Bowler & Terblanche, 2008). The species studied here follow the phenology of their hosts: they oviposit in tissues of the aerial part of their host plants (seeds or stems) during spring while temperatures are mild, and the development lasts until seed set, during the summer (JH pers. obs.). As such, the last larval instars and the pupae but also teneral adults may experience sustained or extreme heat with little possibility to escape until they emerge as sclerotised, flying adults.

In this context, high heat tolerance might have been selected as it is a requirement for the colonisation and survival of all stages on aerial plant tissues exposed to summer heat typical of the region. Interestingly, the non-flying species showing the highest heat tolerance are also the ones for which immature stages cannot readily escape the plant structures used for development. In the two species of *Cryptolarynx*, larval development takes place enclosed in the bulbs of *Oxalis* species (Oxalidaceae) and teneral adults may stay in this structure for weeks (Haran et al., in press). As bulbs of *Oxalis* are not always standing deep in the ground, the immature may experience extreme heat (due to fire or not) without the possibility to escape. Similarly, the larvae of *Ocladius costiger* occupy the base of the woody root system of its host and remain enclosed in it near to the surface of the ground. Such physical constraints have probably selected resistance to heat stress and the high tolerance observed in these species. Inversely, a common denominator for the least tolerant species (group A) is that the larval stage develops in the soil, but not in a particular plant structure. Consequently, these individuals are potentially able to burrow deeper into the soil in case of severe heat stress, which could be considered as a case of behavioural thermoregulation (Marvaldi et al., 2014; Oberprieler, 2014; Pringle et al., 2015). Thus, these species are not confronted with high thermal stresses and their tolerance is, therefore, low, which highlight the importance of microenvironment in stress resistance.

Non-flying lifestyle comes with a range of strategies to escape or cope with heat

The ten non-flying species of weevil from the CFR exhibited a wide range of reactions to heat stress. Noticeably, several congeneric species clustered in distinct groups based on heat resistance (*Eremnus* spp. in groups A and B and *Cryptolarynx* spp. in groups B and C) and representatives of a single subfamily were found in all three groups (*Brachycerus*, *Byrsops*, and *Cryptolarynx* among the Brachycerinae). A prominent parameter associated with heat tolerance in these non-flying species is the phenology of adult activity, corresponding to active movement for feeding and moving to search for a partner or for an oviposition site. All the less tolerant species (group A) are active at night whereas all species clustering in group B and C (except *E. setifer*) are diurnal. This was also observed in other insects groups such as ants (Garcia-Robledo et al., 2018). It corroborates the thermal adaptation hypothesis, which not only states that more thermally variable environments host eurytherm organisms (Janzen, 1967) but also that ectotherms' thermal limits positively correlate with the temperature extremes of their environment (Addo-Bediako et al., 2000, even though some exceptions are known, especially for high temperatures: Bujan et al., 2020). Diurnal weevil species are exposed to the high summer temperature experienced in the CFR (Altwegg et al., 2014; van Wilgen et al., 2016), which may explain why they evolved high heat resistance. Conversely, the non-flying species active during the night generally hide in the leaf litter at the base of their plant during the day. As they have apparently not developed a physiological adaptation to heat stress, they seem to survive this constraint by escaping it physically burrowed underground and thus protected to some extent from heat extremes.

Burning versus non-burning ecosystems

This study included only a few weevils from neighbouring non-burning ecosystems to the CFR (*Sciobius pr. brevicollis* and *Ocladius costiger*). These two species are non-flying and are active at night, but showed a moderate and high tolerance to HKD, respectively. *Ocladius* exhibited CT_{max} values as high as those observed in the highly heat tolerant *Cryptolarynx variabilis*. This species is occurring in the western part of the Northern Cape region, where temperatures are higher than in the CFR but shows no natural cycles of fires (van Wilgen et al., 2016). As previously reported, the larval stages of this species dig galleries in the woody root system of the host plant, with limited possibility to move deeper to escape heat at the surface of the ground. These first insights suggest that heat tolerances of non-flying weevil species are associated with general climate conditions experienced in an ecosystem rather than by the fire regime itself.

CONCLUSION

This study provides preliminary trends on the tolerance to heat of several species of weevils associated with a fire-prone ecosystem. We show that there is no general phylogenetic conservatism for heat tolerance of adults, but rather that lifestyle plays a major role in physiological adaptation to heat stress. Day versus night activity of adults and enclosed versus free lifestyle of larvae were associated with a higher tolerance to heat stress in adults. As fire generally occurs during summer months and mostly affects immature stages, the higher tolerance of species developing as endophagous in the ground with no possibility to escape may represent an adaptation to this disturbance. That said, species with similar lifestyles from neighbouring non-burning regions showed similar heat tolerance. These observations suggest that there is a general adaptation to heat stress due to lifestyle constraints. However, whether the heat is caused by solar radiation or fire does not seem to be a prominent parameter. Among the species tested, *Cryptolarynx* species are probably the best candidates to conduct further investigations on resistance to extreme heat of arthropods. These very small and slow-moving species showed a remarkable tolerance to heat stress in the adult stage while immature stages spend the hottest months enclosed in the sealed bulb of their host plants only a few centimetres below the surface. The physiological adaptations of these species may provide relevant insights on how phytophagous insects cope with extreme temperature conditions and how they will react to a warming climate.

AUTHOR CONTRIBUTIONS

Marion Javal and Julien Haran designed the research; John S. Terblanche provided the equipment; Julien Haran conducted the insect sampling and collected insect data; Julien Haran, Marion Javal, and Chantelle Smit produced the experimental work; Marion Javal analysed the data; Marion Javal and Julien Haran drafted the manuscript. All authors read and approved the final version.

ACKNOWLEDGEMENTS

The authors thank the Western Cape Nature Conservation Board (Permit No. CN44-30-4229) and the Cape Research Centre, South African National Parks (Permit No. CRC/2019-2020/012-2012/V1) for permission to collect specimens in areas under their control. The authors acknowledge Paula Strauss, Gary Beukman, and Michael Lutzeyer for access to the Grootbos Private Nature Reserve and their friendly assistance during sampling. The authors thank Laurène Dubreuil for introducing Julien Haran and Marion Javal to the Montagu region. Henrika Bosua (Stellenbosch University) is warmly thanked for her help with the respirometry measurements. This study was supported by recurring funding from Montpellier University (Marion Javal) and Cirad (Julien Haran).

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

Data for the HKD experiment is available here: https://doi.org/10.6084/m9.figshare.21647015

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1.

How to cite this article: Javal, M., Terblanche, J.S., Smit, C. & Haran, J. (2022) Comparative assessment of heat tolerance in weevils associated with a fire-prone ecosystem. *Ecological Entomology*, 1–11. Available from: https://doi.org/10.1111/een.13218