Temperature-related foraging risk in temperate climate ants (Hymenoptera: Formicidae)

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Abstract. Many ant species inhabiting typical desert habitats utilize a risk-prone strategy when foraging for food. They forage near the critical thermal limit because of prey availability or a low competitive status. In a temperate climate, sandy habitats are also inhabited by xerothermic ant species e.g. *Formica cinerea* (Mayr, 1853) or *Manica rubida* (Latreille, 1802). The aim of the experiment was to estimate if these two species increase their thermal-related foraging risk. During a laboratory experiment, workers of both species could freely forage on sandy arenas heated from neutral temperatures up to 50 °C. Generally, the results indicate that workers of both species reduced the foraging time with increasing soil temperature – i.e., utilized a risk-averse strategy – when no food was available. However, when workers of *F. cinerea* had access to the food, they foraged with the same intensity in the range of temperatures from 38 °C up to 47 °C. Temperatures above 45 °C may be considered as stressful; therefore, workers of *F. cinerea* utilized a risk-prone strategy when they had access to the food.

Key words: thermal limits, resistance, ant, *Formica cinerea*, *Manica rubida*.

Introduction

Foraging for food is correlated with various levels of risk and costs, e.g. predation, desiccation or heat stress (Stephens & Krebs 1986, Riechert 1991, Hughes et al. 1994). In case of thermophilic species inhabiting deserts or dunes, the thermal-related stress is a major cost of foraging (Angilletta 2009, Merkt & Taylor 1994). In those environments overheating and water loss are the most important instruments of natural selection leading to shortening of foraging time or taking a risk of heatstroke – if this is profitable (Stephens & Krebs 1986). Studies on many groups of animals lead to formulation of a nutritional-based risk-sensitive theory (Kacelnik & Bateson 1996, Bateson & Kacelnik 1998, Gilby & Wrangham 2007). In the case of ants inhabiting xerothermic habitats, risk can be perceived from the perspective of physiological critical limits; workers may utilize risk-prone strategy (when foraging close to thermal limits) or risk averse strategy (far from critical thermal limits) when foraging for food (Cerda et al. 1998). Many desert ants are scavengers and utilize a typical risk-prone strategy when foraging for invertebrates which died of a thermal stress (Arnan et al. 2012). Subordinate desert species may utilize risk-prone strategy and forage in suboptimum temperatures because of a low competitive status in a hierarchy (Savolainen & Vep-

säläinen 1988). Some desert ant species forage when the surface temperature exceeds 50 °C (*Pogonomyrmex californicus*; Buckley, 1866) and even at extreme level of 60 °C in case of *Cataglyphis* sp. (Förster, 1850) (Bernstein 1974, Bernstein 1979, Wehner et al. 1992). Foraging of thermal specialist is usually supported by morphological, physiological and behavioural adaptations (Cerda & Retana 2000, Cerda 2001, Schultheiss & Nooten 2013). Some species of *Cataglyphis* synthetise and accumulate heat shock proteins in low temperatures (phenomenon called inducible thermotolerance) as preadaptation to foraging in rapidly increasing outdoor temperatures (Gehring & Wehner 1995, Evgen'ev et al. 2007). Other species lower their body temperature by finding thermal refuge like small sticks or stones (Clémencet et al. 2010, Marsh 1985, Christian & Morton 1992, Wehner et al. 1992, Cerdá & Retana 2000).

In temperate climate, xerothermic habitats like dunes or sandy patches are in general very different from typical deserts, but in some periods all sun-exposed sandy habitats are very similar in regard of abiotic conditions. For example, surface temperature in the Sahara desert may rise up to 74 °C, while during my field experiments I recorded 61 °C in central Europe – which is anyhow beyond the thermal optimum of most living organisms (Chen et al. 1991). The main focus of the experi-

ment was to estimate if xerothermic ants from temperate climate may utilize risk-prone strategy when foraging for food like typical desert ants. Species like *F. cinerea* (Mayr, 1853) and *M. rubida* (Latreille, 1802) are dependent on different food sources (comparing to a typical desert species) that may be collected in cooler periods of the day. They do not need to forage in the midday when the surface temperature is the highest, so are they able to take the risk? The main experiment hypothesis assumed that workers increase their temperature-related foraging risk in the presence of food (like typical desert species). To test the hypothesis ant colonies were transported to the laboratory where workers forage on arenas with controlled temperature.

Material and methods

Study species

F. cinerea is a thermophilic and xerophilic oligotope of dry open habitats. It occurs in sunny, sandy sites, bare or overgrown with sparse herb vegetation. It creates numerous colonies with aggressive individuals. Nests have multiple entrances and are widely spread underground. *M. rubida* is a typical montane species occurring at 500 - 2000 m a. s. l. (usually above 700 - 800 m). *M. rubida* is an oligotope of montane grassy habitats, nests in sunlit open areas overgrown with low xerophilic vegetation. Colonies are usually polygynous with several hundred workers, often forming extensive polycalic systems (Czechowski et al. 2012). In regard of competition hierarchy theory, *F. cinerea* and *M. rubida* are submissive though aggressive species (Savolainen & Vepsäläinen 1988).

Laboratory experiment

For the purpose of laboratory experiment, one colony of *F. cinerea* and *M. rubida* were transported to the laboratory. A colony of *F. cinerea* was collected near the Mazovian Landscape Park near the city of Otwock (central eastern Poland; 50° 1' 34" N, 19° 53' 39" E) and a colony of *M. rubida* was collected in the suburbs of Kraków (south Poland; 50° 10' 26" N). Each colony was kept in large plastic container open at the top with walls coated with paraffin. Initially in each colony there were at least a few hundred workers (and some pupae in case of *M. rubida*), but most probably without a queen. Each container was connected with a short silicone tube to its own feeding arena. Arenas had a layer of sand (collected from the field) spread on the bottom. Ants from each colony could freely leave the nest container and forage on sand arenas. Above the arena there was a terraristic heating lamp (Trixie 76070) warming the sand (100W Trixie neodymium bulb 76008) surface to the required temperature. The temperature was controlled by a digital thermostat (Trixie 76124) that had a probe placed on the arena's sand. Sand temperature was also double checked by infrared thermome-ter (Voltcraft IR 900-30S). When the required sand temperature was achieved, the probe sent a signal to the thermostat, which controlled the heating lamp. Because the lamp did not heat evenly the whole arena and the corners were always a few degrees cooler, the temperature was measured only in the centre of the arena just below the lamp in an area of 70 × 70 mm. In that part of the arena the thermostat probe was placed and also later all the behavioural measurement were made.

After the acclimation period the control phase of experiment was carried out. During control phase the arena was heated from 38 ºC up to 50 ºC in steps of 3 ºC (38 ºC, 41 ºC, 44 ºC, 47 ºC and 50 ºC). When the arena reached the appropriate temperature a camera (Microsoft LifeCam Studio) placed above the arena recorded a video file for one minute (544 × 960 resolution, 30 frames per second) and repeated the recording five more times (six in total) in five minutes intervals for each temperature. A total of 30 records, each 1 minute long, were recorded (five temperature regimes × six recordings). Subsequently, the bait experiment was carried out with the use of exactly the same setup as described above with only modification was the presence of the bait (honey with water) placed in a centre of the frame. The control phase for both species was recorded 15.09.2014-17.09.2014 and the bait phase 16.09.2014-19.09.2014.

Recordings were analysed with the use of BehaView software (Boguszewski 2011). In both phases of the experiment the measured variable was the specific time an individual forager spent in 70 × 70 mm part of the arena during one minute of recording time. Each worker entering 70 × 70 mm part of the arena was tracked until leaving it. In the bait phase, the same time variable was used, but only for workers that reached the bait and started feeding. The time each worker spent in a frame was later used as a dependent variable in four (*F. cinerea* control and bait, *M. rubida* control and bait) statistical models (respectively n = 123, n = 193, n = 154, n = 60). For the analysis a generalized linear model (GLM) was prepared with Poisson distribution (Gaussian in case of *F. cinerea* bait). As a main factor, frame temperature was used. Analyses were prepared in the R environment (R Core Team 2013). *Relevel* function was used in order to carry post-hoc sequential comparisons among multiple factor level when performing GLM. Bonferroni-Holm sequential table-wide correction was applied to reveal exact significance levels in these cases.

Results

The workers of *F. cinerea* during the control phase of the experiment generally reduced the foraging time as soil temperature increased (Table 1, Fig. 1). Only at 41ºC there was no significant reduction of foraging time compared to 38 ºC – in all models the reference temperature was set on 38 ºC. In general in all control cases, the median values were very low and similar, indicated that workers

Table 1. Results from GLM models explaining the differences between *F. cinerea* and *M. rubida* workers' foraging time in relation to increasing surface temperature in control and bait (food presence) phases of the laboratory experiment.

Response variable	Predictor	n	z/t	p
F. cinerea - Control	Temp. = 38 °C	14		
	= 41 °C	15	-0.324	0.746
	= 44 °C	30	-3.799	**0.001**
	= 47 °C	25	-2.839	**0.027**
	= 50 °C	12	-4.289	**0.000**
F. cinerea – Bait	Temp. = 38 °C	17		
	= 41 °C	19	-1.480	0.853
	= 44 °C	24	-0.374	1.000
	= 47 °C	21	-1.366	0.875
	= 50 °C	19	-3.071	**0.027**
M. rubida – Control	Temp. = 38 °C	7		
	= 41 °C	69	-3.865	**0.000**
	= 44 °C	35	-4.050	**0.000**
	= 47 °C	32	-4.552	**0.000**
	= 50 °C	11	-4.068	**0.000**
M. rubida – Bait	Temp. = 38 °C	15		
	= 41 °C	18	-4.724	**0.000**
	= 44 °C	7	-9.399	**0.000**
	= 47 °C	8	-8.132	**0.000**
	= 50 °C	11	-13.103	**0.000**

Figure 1. Visualization of *F. cinerea* and *M. rubida* workers' foraging time in regard to different sand temperature in the control and bait phases.

spend only a few seconds on the arena. When workers had access to food the trend was very different. There were no differences in workers' foraging times between control and temperatures up to 47 °C (Table 1, Fig. 1). Only the temperature of 50 °C negatively influenced workers' foraging time.

The relation of foraging time to soil temperature was in case of *M. rubida* workers very different from *F. cinerea*; during the control phase of the experiment workers of *M. rubida* significantly reduced the foraging time along with the increasing soil temperature in all studied cases (Table 1). At 44 - 50 °C, the median foraging time was only about two seconds in all cases (Fig. 1). After supplying food, the situation was exactly the same (Fig. 1). At 50 °C, the median foraging time was close to zero (two seconds).

Discussion

Many typical desert ants utilize a typical risk-prone strategy and forage for food only in the most risky conditions due to a specific dietary requirements. Those desert species are a typical scavengers or opportunistic scavenge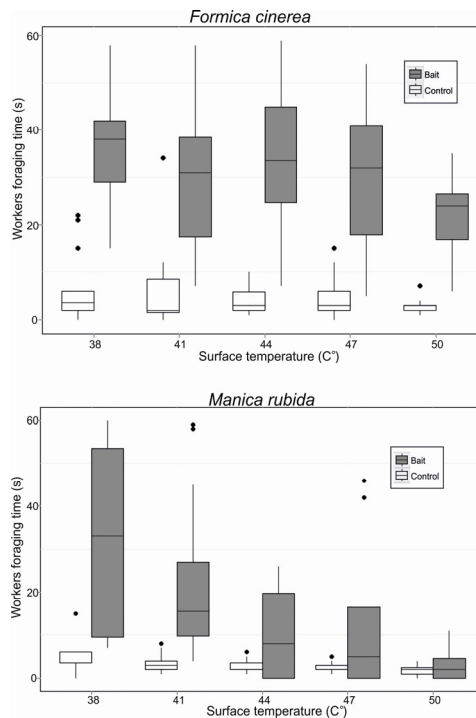rs, collecting other invertebrates that did not survive the thermal stress (Schultheiss & Nooten 2013). This type of foraging involves specific strategy rarely dependent on scent trials and usually requiring solitary foraging. This type of foraging, especially in relatively similar sandy landscapes, requires unusual homing and orientation abilities, discovered for example in *Cataglyphis* sp. (Lenoir et al. 2009). Thermal specialists from deserts are also morphologically, physiologically and behaviourally adapted to harsh habitats (Cerda & Retana 2000, Cerda 2001, Schultheiss & Nooten 2013), whereas many xerothermophilic ant species like *F. cinerea* or *M. rubida* living in temperate climates are dependent on liquid food like honeydew. This type of foraging does not require any special adaptation. Food presence is not dependent on the time of day and not correlated with surface temperature. On the other hand, *F. cinerea* and *M. rubida* are "thermal specialists" in a temperate climate due to their living conditions, and therefore they may be able to increase their foraging risk in the presence of food.

In the case of *M. rubida*, there was no positive effect of the food presence on the risk taken by the

workers. Generally workers avoid patches of hot sand regardless of whether there was food or not. Therefore, *M. rubida* clearly utilizes risk-averse strategy when foraging for food in a suboptimum environment.

Workers of *F. cinerea* also used a risk-averse strategy when there was nothing worth risking for. However, when food was present, the workers' foraging times were similar at temperatures up to 47 °C. Therefore, workers utilized risk-prone strategy. Workers' foraging time was significantly reduced starting at 50 °C. Some literature data indicate that temperatures above 45 °C may be stressful (Cerda et al. 1998, Cerda & Retana 2000, Andrew et al. 2013). Therefore, foraging at temperatures up to 47 °C must be correlated with specified risk for *F. cinerea* workers. Another study that used heat shock proteins emphasised that workers of *F. cinerea* are indeed quite temperature resistant (Ślipiński et al. 2015). The analysis of gene expression surprisingly indicated that there was no significant effect of temperature when comparing workers from the control (23 °C) with workers foraging on the surface of 47-54 °C sand (Ślipiński et al. 2015).

In this experiment, some workers of *F. cinerea* were foraging at 47 °C and 50 °C (Fig. 1). These temperatures are very close to critical thermal limits of even a typical desert ants which anyhow dies at temperatures above 50 °C. The critical thermal maximum (CT_{max}) in ants like e.g. *C. bombycina* (Roger, 1859) is only 53.6 °C during 10 min exposure and for *C. bicolor* (Fabricius, 1793) is 55.1 °C (Gehring & Wehner 1995, Lenoir et al. 2009). Therefore, not many ant species forage above 50 °C; e.g. *Pogonomyrmex californicus* forage in substrate up to 54.4°C, and only *Cataglyphis* sp. forage when the surface temperature exceeds 60 °C and when body temperature exceeds 50 °C (Bernstein 1974, Bernstein 1979, Wehner et al. 1992).

Despite the fact that both species in the experiment are "thermal specialists," they nest in a very different habitats. *F. cinerea* is an oligotope of dry open habitats whereas *M. rubida* is an oligotope of mountain habitats. Both habitats may vary significantly in their abiotic conditions (surface temperature), which may be reflected in species adaptation (Stuble et al. 2013). Analysing the general trend for foraging workers of *F. cinerea* and *M. rubida* we can generally confirm the hypothesis that *F. cinerea* increased their temperature-related foraging risk in the presence of food, whereas *M. rubida* did not. *F. cinerea* seems better adapted to cope with high temperatures compared to *M. rubida*, which avoids any thermal related stress.

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