Higher soil temperatures cause faster running and more efficient homing in the temperate thermophilous ant *Formica cinerea* (Hymenoptera: Formicidae)

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Abstract

Thermophilous ants, which live in many places at very different latitudes, can on occasion face similar thermal conditions. The temperature of the sand in a Euro-Siberian forest clearing can reach 61 °C, a temperature that is above the thermal maximum of most foraging ants. Therefore, we expect that temperature may have a similar effect on the foraging strategy of species living there, for example, *Formica cinerea*, as it has on the foraging strategy of typical thermal specialists. We experimentally tested in the field whether workers with higher mean speed are more efficient than slower individuals by comparing their path shapes as they return to the nest. More specifically, we asked whether workers' time taken to return to the nest and the straightness of their paths from the feeder to the nest are affected by workers' speed and surface temperature. As temperature increases, workers walk faster and take less time to return to the nest. The speed of workers influences the straightness of their path from the feeder to the nest – the workers with the higher mean speed take a less sinuous return path to the nest. We conclude that workers with higher mean speed are more efficient than slower individuals.

Key words: Foraging, risk, speed, thermal stress, straightness.

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Introduction

The principal ecological determinants of the foraging strategy of ants are the distribution of food resources in space, time, quality, and quantity and the combination of competition and predation (Traniello 1989, Dornhaus & Powell 2009). Various foraging strategies exist – from solitary foraging to systems with well-organised communication among foraging workers. Solitary foraging is considered the ancestral state and the simplest foraging strategy possible (Baroni Urbani 1993) and used by the most primitive species, for example, Ponerinae and Myrmeciinae (Traniello 1989). In the systems with well-organised communication among foraging workers, there are very efficient collective behaviours and they occur in many higher organised ant species, for example, Formicinae (Savolainen & Vepsäläinen 1989, Punttila 1996, Johansson & Gibb 2012, Markó & Czechowski 2012, Czechowski & al. 2013). Despite the differences in foraging strategies leading to the most efficient way of finding a food source, the most essential task for all central place foragers after locating the food is returning to the nest (Wehner 2008, Graham 2010, Zeil 2012,

Knaden & Graham 2016, Graham & Philippides 2017, Fleischmann & al. 2018). Quickly returning to the nest with information about food increases the chances that after recruiting nestmates the food will still be available (Elizalde & Farji-Brener 2012).

The speed of information transfer about prey is not only vital for colony fitness. In addition, the time foraging ants spend outside the nest is always correlated with a higher risk of mortality compared with the tasks performed inside the nest (Cerdá & al. 1998, Cerdá & Retana 2000). Therefore, workers carrying food or information about the food source should shorten their exposure time and try to find the most optimal way back to the nest (Harkness 1979b, Schmid-Hempel 1984). There are several factors influencing high mortality risk during foraging, for example, predation and competition, but for ants living in xerothermic habitats, temperature is the most crucial one (Cerdá & al. 1998, Cerdá & Retana 2000). Some thermal specialists can forage even at temperatures exceeding 50 °C, for example, *Pogonomyrmex californicus* (see Bernstein 1974, 1979), and even at the extreme level

of 60 °C, as is the case for *Cataglyphis* spp. (Wehner & al. 1992). Therefore, foraging time is very limited by the inevitable risk of exceeding their critical thermal limits (CT_{max}) (Pfeffer & al. 2019).

In general, ant thermal specialists (with wider thermal breadth ranges) are not present in high latitude areas (Diamond & Chick 2018, Roeder & al. 2021). In the central part of Euro-Siberian forests, there are no typical thermal specialists such as *Cataglyphis* or other desert ants, the most thermophilous species is *Formica cinerea*. Dunes or sun-exposed, sandy patches, which are typical nesting places for this species, are also obviously different from xerothermic habitats of typical desert ants. Nonetheless, under certain circumstances, the conditions in all xeric habitats may temporarily become very similar in terms of extremely high surface temperatures. The temperature of the sand in a Euro-Siberian forest clearing may reach 61 °C (Ślipiński 2017), a temperature that is above the thermal maximum of most foraging ants. Therefore, thermophilous ants living in many different places may temporarily face similar thermal conditions. In their field study, Markó & Czechowski (2004) observed that foragers of *F. cinerea* can be active up to ground temperatures of 48 °C. More recently, in a laboratory experiment, Ślipiński (2017) observed workers of *F. cinerea* foraging at 47 °C and 50 °C in the presence of food. Therefore, despite living at a relatively high latitude, *F. cinerea* behaves similarly to thermal specialists from lower latitudes (desert ants from the Palaearctic arid regions (genus *Cataglyphis*), the south African region (genus *Ocymyrmex*) and Australia (genus *Melophorus*)). Thermal specialists have developed different adaptations to forage in such arid environments (Boulay & al. 2017) – the thermophilia syndrome has evolved independently in ants from arid regions (Wehner & Wehner 2011) and includes the following adaptations: morphological adaptations (e.g., long legs, reflective hairs: Cerdá & Retana 2000, Shi & al. 2015, Willot & al. 2016), behavioural adaptations (high speed, use of thermal refuges: Wehner & al. 1992, Cerdá & Retana 2000, Schultheiss & Nooten 2013), and physiological adaptations (production of heat shock proteins before emerging from the nest: Gehring & Wehner 1995, Willot & al. 2017). However, the thermophilous *F. cinerea* is consistently different from these "true" thermal specialists: It has neither long legs nor reflective hairs; and when Ślipiński & al. (2015) analysed the heat shock protein gene expression, they found no significant effect of temperature between *F. cinerea* workers from the control (23 °C) and workers foraging on the sand surface (47 - 54 °C).

In any case, despite the seemingly weak thermal adaptation of *F. cinerea*, its workers are active at high temperatures at the similar time of a day as some thermal specialists, so that a strategy similar to that of the "true" thermal specialists is to be expected. Of all the possible thermophilous traits shared by thermal specialist ants, the two that probably most affect their foraging efficiency are worker speed and the trajectory back to the nest. Thermal specialists (1) are very fast, and temperature positively

influences the speed of foragers (Harkness 1979a, Bernard 1984, Marsh 1985, Cerdá & Retana 2000); and 2) follow straight inbound paths (Dietrich & Wehner 2003, Wehner 2008, Schwarz & al. 2017, Buehlmann & al. 2018). Through a field experiment, we will test the hypothesis that speed of *Formica cinerea* foragers and temperature influence the path shape (straightness) of foragers' inbound trajectories. More specifically, we ask whether (1) the time workers take to return to the nest with prey (inbound time) will be negatively affected by workers' speed and surface temperature. The higher the surface temperature and the higher the speed of workers, the shorter the time taken to return to the nest with prey. And we ask whether (2) the factors of workers' speed and surface temperature will influence the straightness of their path from the feeder to the nest. We assume that with increasing surface temperature and speed, ants' paths from the feeder to the nest will be shorter compared with the path of workers foraging at lower temperatures.

Material and methods

Colonies in the experiment

Four colonies of *Formica cinerea* were used during the experiment. The species was identified following Czechowski & al. (2012). Colonies were located in central Poland in two locations near Warsaw: three colonies in Majdan and one colony in Stara Wieś (both localizations were at an elevation of around 90 meters above sea level. Three colonies were inspected three times and one colony twice during summer of 2020 (23 June 2020 - 14 July 2020). During each inspection in the field, between 2 - 5 nest entrances were chosen in each of the studied colonies, with a total 26 independent nest entrances recorded. Recordings were conducted under various thermal conditions, from the beginning of summer period with moderate temperatures to the hottest part of summer, to ensure the largest possible representative group of data (mean sand temperature ± standard deviation of all data: 33.0 ± 8.5 °C; range: 21 °C - 53 °C; median: 30.0 °C; n = 196). Recordings were done between 10 a.m. and 2 p.m. The number of inspected entrances per colony varied because the number of active entrances in each colony also differed due to human / animal activity that often lead to some of them being buried / blocked. Furthermore, abiotic conditions, such as rain, caused some damage to nest entrances that had been still active the day before. For this reason, it was sometimes impossible to determine if a particular nest entrance had been recorded earlier or if it was a completely new one.

Baiting and recording

For the experiment, a fairly short distance between the nest and the bait was established, which enabled the relatively small and fast individuals of *Formica cinerea* to be video recorded.

Bait (20 *Drosophila melanogaster* flies) was placed on a white plastic cap (2 cm in diameter) at a distance of 20 cm

from the inspected nest entrance. Only nest entrances with relatively flat sand surface around the nest were chosen for the recordings. Nest entrances located on uneven surfaces or with obstacles blocking the access to the baits were not taken into consideration. A camera (Sony HDR AS-20, Tokyo, Japan) was placed on a tripod between the bait and the nest entrance. The camera recorded the activity of the ants from the moment the food was placed over a maximum period of 30 minutes in HD resolution (1920 × 1080, 30 frames per second). The procedure was repeated 26 times for 26 independent nest entrances. During each repetition, ants collected the flies from the bait and transported them in different directions; some of them were transported to the inspected entrance. During 26 recordings, a total of 196 flies were transported by ants to an inspected nest entrance. For each individual ant, the surface temperature was measured with an infrared thermometer (Voltcraft IR 900-30S, Hirschau, Germany). A laser dot measured the average temperature of the sand surface along the ants' path from the feeder to the nest entrance. The flies were not replenished in the baits. When the ants had collected all 20 flies from the feeder, the recording was stopped. Usually, ant activity was not high and the ants did not collect all of the flies. The average number of workers that successfully collected flies and returned to the inspected nest entrance was 7.5 (workers per recording). Outward trajectories of ants were not considered because ants were randomly searching for food and very often outside of the video-camera frame. In addition, data about the nest activity were collected. During the first two minutes of each recording, the number of ants going out of the inspected nest entrance was recorded.

Video analysis

From all recorded videos (26) in which multiple ants were foraging, 196 slices / fragments were cut using Bandicut software version 3.6.2.647, one fragment for each of the 196 ants tracked. These shorter videos started at the moment when a tracked ant began leaving the feeder with a fly and ended when it arrived at the nest entrance. Subsequently, the movement of each ant was tracked in Fiji software version 2.6.0 (SCHINDELIN & al. 2012), using the manual tracking option. With the software, the position of the moving ant was manually tracked five times per second. The software calculated the speed at each point of the ants' path based on the travelled distance. This procedure was repeated till the individual reached the nest entrance (Fig. S1 and Tab. S1, as digital supplementary material to this article, at the journal's web pages). Ants were constantly tracked from the moment of collecting the prey until they reached the nest. The total time and path of the ants were included in the speed measurement, including the moments when the ants stopped. Finally, all of the speed measurements were averaged (Tab. S2), and the mean speed of the ants on their way to the nest entrance, their time of return with prey (inbound time), and the distance covered by the ants were calculated.
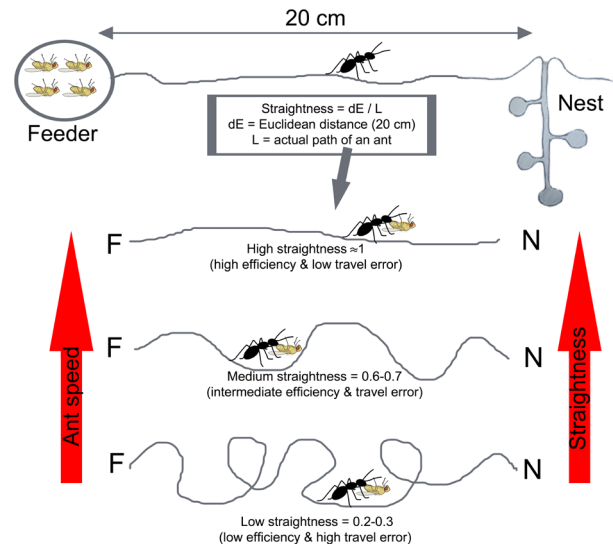

Fig. 1: Schematic drawing of the methodological protocol. Red arrows indicate the influence of ant speed on path straightness.

Variables

For each of the 196 ants, the following variables were collected: mean speed, maximum speed, worker inbound time (time spent from the moment of collecting the prey to arrival at the nest), distance covered by an ant when returning with prey, and sand surface temperature. Furthermore, straightness was calculated based on the distance covered by the ants returning from the feeders to the nest entrance with prey (Fig. 1).

The straightness or linearity index (BATSCHELET 1981) is the net displacement distance (the Euclidean distance between the start and final point) divided by the total length of the movement. The straightness index measures how straight the animal path was relative to the final point; it varies from 0 to 1 and the closer to 1, the straighter and more efficient the foraging path of the ant (ALMEIDA & al. 2010) (Fig. 1). It also quantifies movement efficiency, in our case the movement efficiency of returning to the nest with prey (LEONARD & HERBERS 1986).

Models

To test the influence of sand surface temperature on workers' mean speed, a linear approach (Linear Mixed Model) was used. In the model, the sand temperature was the predictor, whereas workers' mean speed was the dependent variable. The nested random factor was the studied colony ID, the number of recorded videos for a particular nest entrance, and the order of workers which entered a particular nest entrance. The dependent variable was logarithmically transformed.

To test the influence of sand surface temperature and mean speed of workers on their inbound time to the nest and the straightness of their movement, a non-linear approach (Generalized Additive Models) was used. In the models, the mean speed of workers was used and not the maximum speed as both variables were highly correlated and mean speed is a better approximation of workers' behaviour than

Tab. 1: Values of the different parameters calculated from the video recordings of *Formica cinerea* trajectories returning to the nest (n = 196). SD, standard deviation.

Variable	Mean ± SD	Min – Max (Median)
Workers inbound distance	34.1 ± 17.0 cm	20.4 cm - 166.2 cm (28.4 cm)
Workers inbound time	11.1 ± 8.5 s	2 s - 53 s (9 s)
Mean speed	1.25 ± 1.32 cm / s	0.067 - 6.36 cm / s (0.817 cm / s)
Maximum speed	3.27 ± 2.62 cm / s	0.33 - 12.76 cm / s (2.48 cm / s)
Path straightness	0.67 ± 0.20	0.12 - 0.98 (0.70)

Tab. 2: Influence of workers' mean speed and sand temperature on worker inbound time (return time to the nest) and the straightness of their movements. Edf, effective degrees of freedom; Ref.df, reference degrees of freedom.

Dependent variable	Predictor / factor	edf	Ref.df	Chi.sq / F	p
Workers' inbound time	**Sand temperature**	4.537	5.489	8.127	**<0.001**
	Workers order	2.810	18.00	0.282	0.058
	Mean speed	3.161	3.800	216.200	**<0.001**
Straightness	**Sand temperature**	2.379	2.988	1.865	0.136
	Mean speed	4.873	5.756	22.460	**<0.001**
	Colony ID	1.629	3.000	1.545	**0.040**

the temporal (instantaneous) maximum speed (Fig. S2). In the first model (inverse Gaussian distribution), the sand temperature was the predictor, whereas workers' inbound time (return time to the nest) was the dependent variable. In the second model (inverse Gaussian distribution), the mean speed of ants was the predictor, whereas workers' inbound time (return time to the nest) was the dependent variable. In the third and fourth model (Gaussian distribution), also the sand temperature (third model) and mean speed of workers (fourth model) were used as predictors, whereas the straightness was the dependent variable. In all models, the random factors were the studied colony ID, the number of recorded videos for a particular nest entrance and the order of workers which entered a particular nest entrance. To simplify the models, the non-significant random factors were removed before final modelling.

To test the influence of sand surface temperature on the number of workers going out of the nest entrances, a non-linear approach (Generalized Additive Models) was used. In the model (Gaussian distribution), the sand temperature was the predictor, whereas the number of workers going out of the nest entrance was the dependent variable, and the colony ID was a random factor.

The linear model was performed using the lmer function from the lme4 package (BATES & al. 2015). The non-linear models were performed using the mgcv package, REML method (WOOD 2017). All statistical analyses were performed in R (R STUDIO TEAM 2020).

Results

The sand surface temperature positively influenced the mean speed of ants (Fig. 2). The higher the surface tem-perature, the faster the ants moved (degrees of freedom = 58.24, t = 9.19, p < 0.001). Other basic information about speed of ants and their inbound distances are presented in Table 1.

Workers' inbound time is influenced by sand surface temperature and by mean speed of foraging ants (Tab. 2, Fig. 3). Furthermore, in the case of the first model, the order of workers collecting the prey was not significant but close
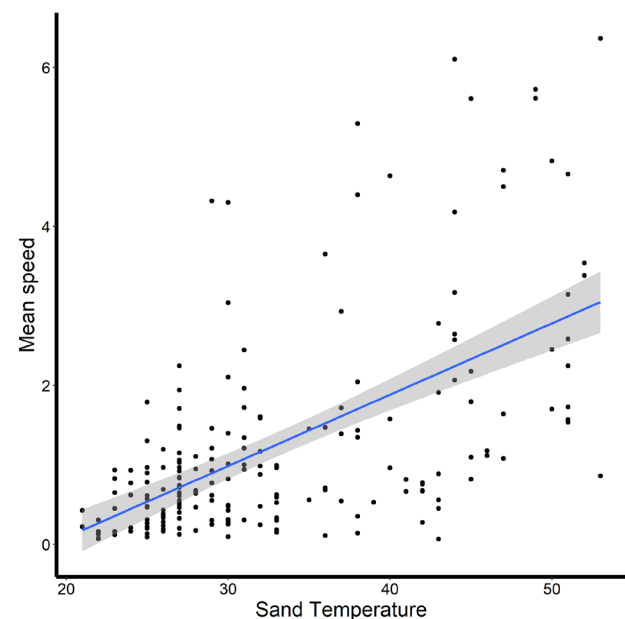

Fig. 2: Relationship between sand temperature (°C) and mean speed (cm / s) of *Formica cinerea* workers in 95% of confidence interval.
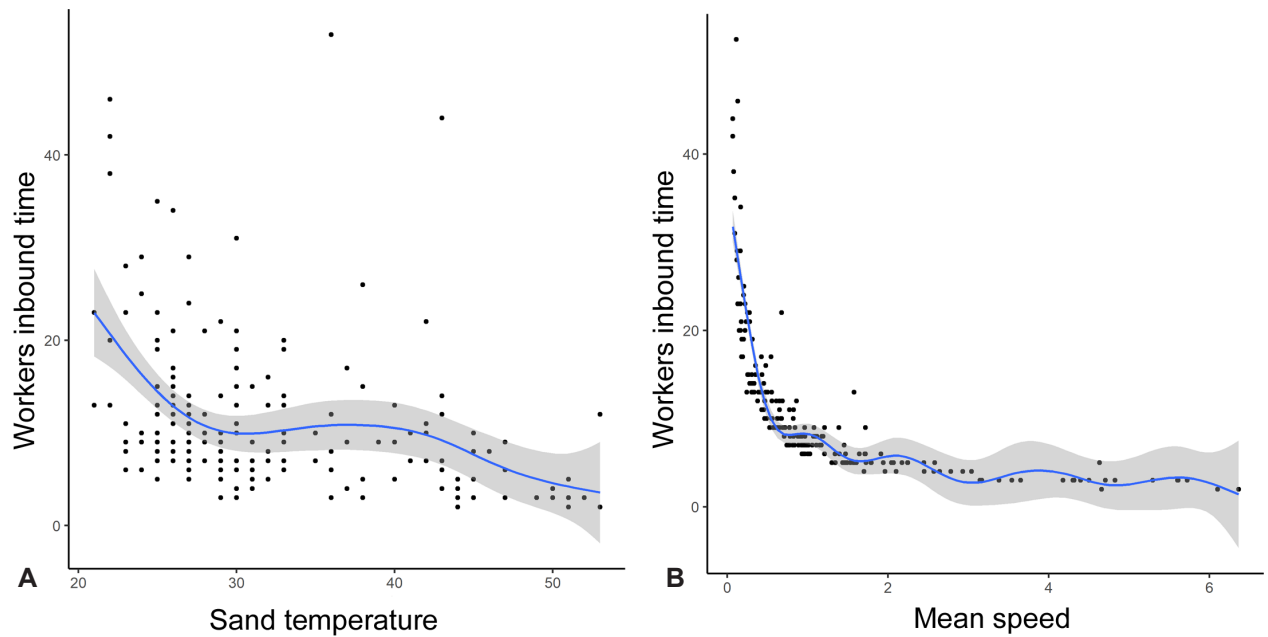
Fig. 3: Relationship between (A) sand temperature (°C) and (B) mean speed (cm / s) of *Formica cinerea* workers with the inbound route time (return) to the nest with prey, fitted with the use of Generalized Additive Models in 95% of confidence interval.
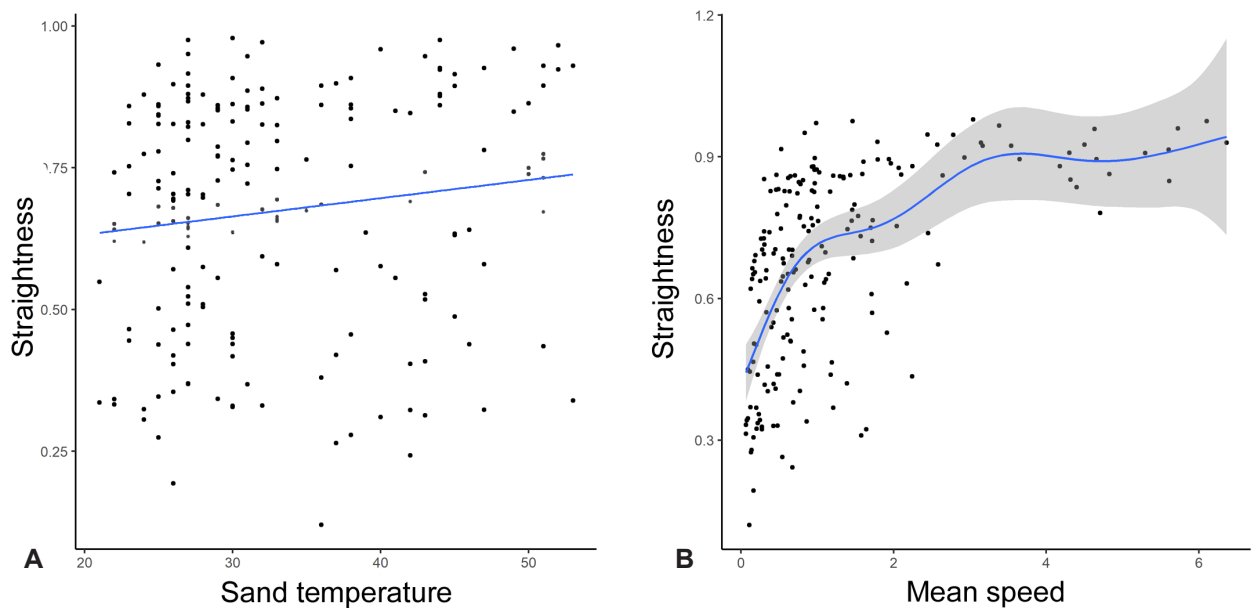

Fig. 4: Relationship between (A) sand temperature (°C) and (B) mean speed (cm / s) of *Formica cinerea* with the path straightness of the ant trajectories to the nest with prey, fitted with the use of Generalized Additive Models in 95% of confidence interval.

to significance (p = 0.058). The first model explained 29.6% of the deviance, the second 90.0%. Workers foraging at high temperatures (e.g., 50 °C) spend significantly less time on the surface of hot sand compared with workers foraging at low temperatures (20 °C). In addition, relatively fast workers return to the nest before slower individuals.

The straightness of workers' movements – the path they took to the nest – depended on the mean speed of the foraging ants (the model explained 42.1% of the deviance);

there were differences between colonies in this respect (colony ID, Tab. 2), workers with a relatively high mean speed walked straighter paths to the nest. The straightness of workers' movements did not depend on sand temperature (Tab. 2, Fig. 4). The model with sand temperature explained only 3.57% of the deviance.

The sand temperature did not significantly influence the number of the workers leaving the nest entrances (F = 1.72, p = 0.2; Fig. S3). The model explained only 8.19% of the deviance.

153

Discussion

The speed of the workers and the surface temperature influence the time needed to travel from the feeder to the nest entrance. At high temperatures and speed, workers returned to the nest faster than the workers foraging at lower temperatures. Moreover, the speed of workers influences the straightness of their path from the feeder to the nest, and as the speed increases, the straightness of the workers' paths also increases, whereas the variance between the two variables decreases. This indicates that faster workers find their way to the nest in a more precise and direct way.

Thermal stress and the exposure time of workers

Temperature is the most stressful abiotic factor for ants foraging in xeric habitats (Angilletta 2009, Perez & Aron 2020, Yela & al. 2020). Exposure at a high temperature for a prolonged period of time leads to the denaturation of proteins and may cause changes in many cell structures, for example, membrane lipid functions (Quinn 1988, Daniel & al. 2008, Abram & al. 2016, Perez & Aron 2020). Depending on their life strategy, ants may decide to cope with the consequences of thermal stress or stop their activity and wait for cooler periods of the day. Ants utilising a risky strategy and foraging at high surface temperatures are morphologically, physiologically, and behaviourally adapted to minimise the consequences of water loss and overheating. *Formica cinerea* is also physiologically adapted to cope with high surface temperatures (Ślipiński & al. 2015). In laboratory conditions, workers of *F. cinerea* are able to forage at very high surface temperatures of 47 °C and 50 °C (Ślipiński 2017). The results of the current field experiment corroborate the laboratory studies described above. We observed workers of *F. cinerea* foraging at temperatures above 40 °C and even above 50 °C. To our knowledge, this is the first field experiment showing that workers of *F. cinerea* are not only present outside the nest at such temperatures but that they actually successfully forage at these temperatures in field conditions. However, the effect of increasing soil temperature had a very profound effect on workers' inbound time – as the temperature increased, workers carrying prey to the nest returned more quickly (Roeder & al. 2022). The decrease in the inbound time of *F. cinerea* as the temperature increased may be influenced by two factors, the first being the temperature itself. Temperature directly influences the locomotor abilities of ants as increasing temperature affects the metabolic rate and the kinetic properties of muscles (Bennett 1990, Marsh 1990, Rome & Bennett 1990). The increase of running speed with increasing temperatures has been frequently observed in different ants such as *Acromyrmex subterraneus molestans* (see Ramirez-Olier & al. in press), *Pogonomyrmex barbatus* (see Roeder & al. 2022), *Iridomyrmex purpureus* (see Andrew & al. 2013), or *Atta sexdens* (see Angilletta & al. 2008). First Heinrich (1993) and later Hurlbert & al. (2008) concluded in their reviews that individuals of all ant species moved faster at higher temperatures.

The results of our current experiment also contribute to and reinforce this interpretation. *Formica cinerea* speed values are far from the record of the Saharan hot-climate specialist *Cataglyphis bombycina* which reaches 85.50 cm / s (Pfeffer & al. 2019), but the maximum speed of *F. cinerea* (12.76 cm / s) is similar to that of the Spanish desert ant *Cataglyphis rosenhaueri* (10.85 cm / s; X. Cerdá, unpubl.). Another factor influencing the inbound time of *F. cinerea* workers as the temperature increased may be high soil temperatures and species' thermal limits. Foraging temperatures of 45 - 50 °C in the case of *F. cinerea* are most probably very close to its critical thermal limit (CT_{max}) because these temperatures are close to CT_{max} of all currently known typical thermal specialists. The critical thermal maximum (CT_{max}) of ants, such as, for example, *C. bombycina* is 53.6 °C during 10 min of exposure and 55.1 °C for *Cataglyphis bicolor* (see Gehring & Wehner 1995, Lenoir & al. 2009). Not many ant species forage above 50 °C; for example, *Pogonomyrmex californicus* forages in a substrate of up to 54.4 °C, and only *Cataglyphis* sp. forage when the surface temperature exceeds 60 °C and when its body temperature exceeds 50 °C (Bernstein 1974, 1979, Wehner & al. 1992). The effect of shortening the time of returning to the nest as the sand temperature increases, as in *F. cinerea*, was also reported for other thermophilic ant species, for example, *C. bicolor* and *Ocymyrmex barbiger* (see Anderson & McShea 2001).

Straightness

The optimization of the path was measured by a straightness index. This index as well as another, for example, the meanderness index, are built on the same principle – to measure how much the moving individual deviates from a straight line as it travels between two points (Fig. 5), which determines the efficiency of its movement (Bernadou & al. 2015, Csata & al. 2017, Vázquez & al. 2020). We expected that with increasing speed, the ants' paths from the feeder to the nest would be shorter than the path of workers foraging at lower temperatures. However, we also considered that, when surface temperatures are very high (e.g., 50 °C), workers with a high body temperature may lose coordination and sense of direction, and therefore their path to the nest may be longer compared with workers foraging at less stressful conditions. The results of our experiment clearly indicate that the fastest workers are actually the ones that find the straightest way to the nest.

There are almost no field studies on the correlation between speed and straightness or other indexes measuring path optimization in ants foraging at high temperatures, which could provide a solid basis for comparing our results (Harkness 1979b, Schmid-Hempel 1984). Leonard & Herbers (1986) failed to find a connection between the speed of *Myrmica punctiventris* and *Aphaenogaster rudis* and its ability to make a straight-line return to the nest, though both species have relatively slow-moving workers. A study on *Cataglyphis fortis,* which utilises path integration combined with visual cues and does not
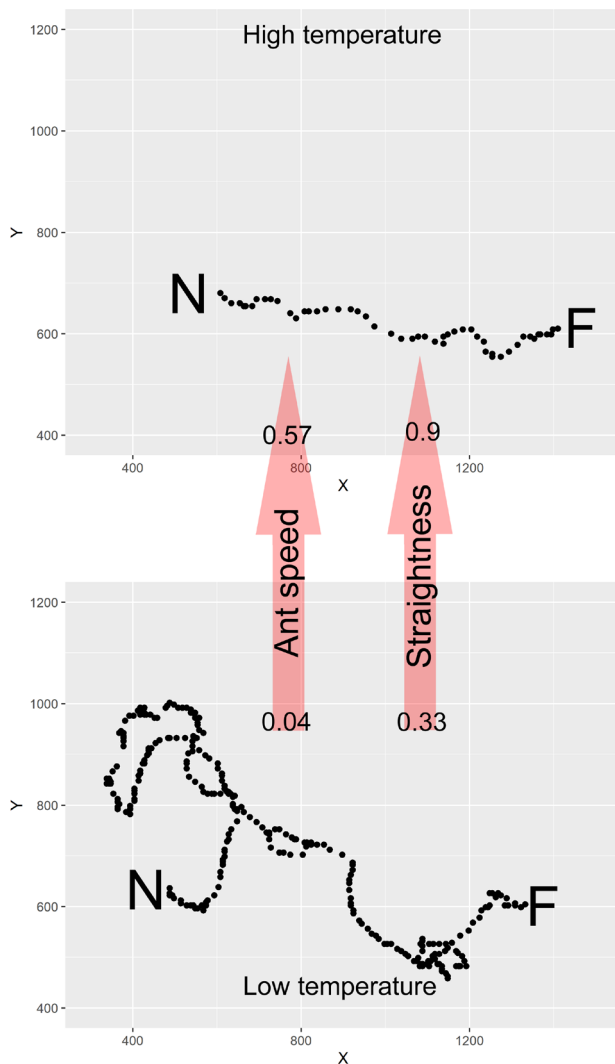
Fig. 5: Example figure showing two workers foraging in opposite extreme thermal conditions, a slow individual (lower panel) and a fast individual (upper panel). Black dots indicate the path of the workers from the feeder to the nest entrance, a short and direct path in the case of the faster individual and a meandering path in the case of the slower worker. Red arrows indicate the direction of speed (cm / s) factor on path straightness. The ant locations are positioned on a X-Y pixel matrix but do not reflect the actual distance in cm.

lay a pheromone trail, revealed that the speed of workers in their inbound path decreases in the final segment, just before reaching the nest (Buehlmann & al. 2018). It would be interesting to compare this finding with species laying a pheromone trail and compare the efficiency of both strategies. There could also be a variance in the interpretation of the straightness depending on the length of the path used for estimating this variable. In the case of our experiment, we can draw conclusions about the final path of ants returning with prey to the nest. The whole foraging range of the *Formica cinerea* colony and its workers can be estimated in several metres, for example, workers of *F. cinerea* colonies located in the dune region of

Hanko Peninsula (Finland) forage to pine trees located at a distance of approximately 10 m (Czechowski & Markó 2005). More studies on thermophilic species are needed to verify the proposed hypothesis about the speed and efficiency of path choice.

Individual foraging or team work

Workers of desert ants form individual routes from a feeding site to the nest and all the way back (Wehner & al. 1996, Cheng & al. 2009, Wystrach & al. 2011, Mangan & Webb 2012). These paths in the case of *Cataglyphis velox*, for example, may be unique to individuals and maintained over time (Mangan & Webb 2012). The main difference between the foraging strategy of a *Formica cinerea* worker and a typical thermal specialist worker, for example, *C. velox*, is that *Formica* generally lays a pheromone trail to the food sources. If workers move along an established route, then in theory the next foraging worker may use it (Ruano & al. 2000), and this could add a repeatability that could be controlled in an experiment. In the case of a field experiment, this is a difficult task. In our experiment, we controlled the order of the workers collecting the prey and getting back to the nest. Generally, there was no effect of the order of workers, however, in the case of measuring the influence of sand temperature on the inbound path of the workers, the effect was close to significance. In our experiment, we additionally tried to control the effect of the order of the workers by limiting the number of prey items during one recording (only 20).

The advantage of a thermal specialist

In general, we can see the similarities among the adaptations of *Formica cinerea* and other thermal specialists. What is unclear, however, is how the foraging of the workers at temperatures above 50 °C affects the colony fitness. There is no data about the importance of such a behaviour in *F. cinerea*. What is the relative number of ants foraging at temperatures above 45 - 50 °C compared with the overall colony size? From the current experiment, it is hard to draw a final conclusion about the effect of temperature on the *F. cinerea* nest activity. There is a significant variance, there are nest entrances where the activity of ants increases with the increasing temperature, but there are also the opposite cases. The differences may be driven by local ecological factors and may vary between colonies. It seems that a larger data set, more focused on this aspect, is needed.

However, we know that the external temperature, as one of the most important ecological factors, may influence the thermal tolerance of workers between different colonies, which could explain the differences between colonies in temperature related activity. One of the potential factors influencing the division of labour and risk strategies of *Formica cinerea* workers is the development temperature of pupae (Ślipiński & al. 2021). The pupal development temperature has been shown to influence thermal tolerance in *F. cinerea* (see Ślipiński & al. 2021) but also in other ant species and other insects, for example,

honeybees or *Drosophila melanogaster* (see CRILL & al. 1996, TAUTZ & al. 2003, JONES & al. 2005, WEIDENMÜLLER & al. 2009, FALIBENE & al. 2016, OMS & al. 2017).

The ecological advantage of most hot-climate specialist ants is that, since they are scavengers, thermophily provides them an evident advantage in collecting dead insects without the presence of other competitors (BOULAY & al. 2017). However, according to ŚLIPIŃSKI (2017), *Formica cinerea* is mainly dependent on liquid food (honeydew), but if it forages at high temperatures, it could also have access to aphids (and also insect corpses) without other interspecific competitors. In the future, it would be interesting to analyse the exploitation of liquid food by *F. cinerea* in different thermal and competitive scenarios.

Acknowledgements

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