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Cave spiders choose optimal environmental factors with respect to the generated entropy when laying their cocoon

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The choice of a suitable area to spiders where to lay eggs is promoted in terms of Darwinian fitness. Despite its importance, the underlying factors behind this key decision are generally poorly understood. Here, we designed a multidisciplinary study based both on *in-field* data and laboratory experiments focusing on the European cave spider *Meta menardi* (Araneae, Tetragnathidae) and aiming at understanding the selective forces driving the female in the choice of the depositional area. Our *in-field* data analysis demonstrated a major role of air velocity and distance from the cave entrance within a particular cave in driving the female choice. This has been interpreted using a model based on the Entropy Generation Minimization - EGM - method, without invoking best fit parameters and thanks to independent lab experiments, thus demonstrating that the female chooses the depositional area according to minimal level of thermo-fluid-dynamic irreversibility. This methodology may pave the way to a novel approach in understanding evolutionary strategies for other living organisms.

The European cave spider *Meta menardi* is preferably found in the twilight zone of most European caves¹. After mating, females produce a drop-shaped egg sac (cocoon) whose silk has been recently studied² underlining its extreme elongation and robustness. The cocoon (2–3 cm in radius) contains an average of 200/300 eggs³ (Figure 1a–d) and is laid in the nearby of the cave entrance at the end of the summer. After hatching, the spiderlings remain in the cocoon until the first molt, feeding on the yolk^{4,5}. They leave the cocoon in spring, move towards the cave entrance^{4,6} and disperse via ballooning outside the cave^{5,6}.

Cocoons avoid the direct exposure of the eggs to the environment, providing protection against predators and parasites, and also from thermal variations^{7,8}. In particular, the insulation function of the spider cocoon is documented in literature, demonstrating its resistance to temperature fluctuations and the consequent achievement of an optimal microclimate for the embryological development^{9–12}.

Although silk properties are extensively studied^{13–17}, to our knowledge, still little is known on thermal insulation properties of arthropod cocoons as only two scientific papers focusing on this matter have been published up to now^{7,18}.

The increase of knowledge on the thermo-mechanical properties of natural materials may potentially reveal new insights about the adaptations of species to the environment from an evolutionary perspective. In particular, the investigation of insulation properties of the spider egg sac may contribute in understanding the driving factors at the base of the female choice on the selection of suitable depositional areas in order to increase the survival of the species.

In order to reach this aim, we provide an innovative approach, based on the Entropy Generation Minimization methods¹⁹ originally developed in the realm of engineering sciences. Such approach analyses thermodynamic imperfection stemming from heat transfer, mass transport and fluid flow irreversibility. Owing to the Gouy-

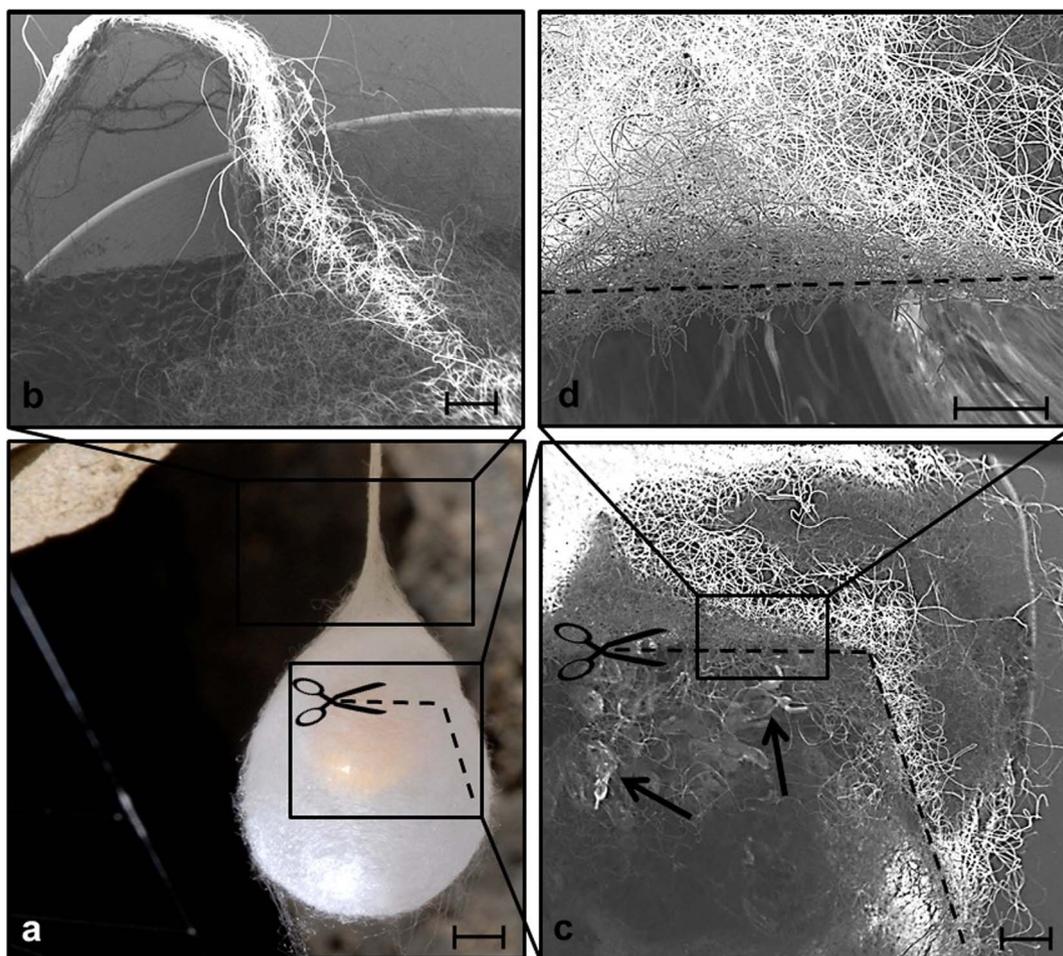


Figure 1 | FESEM characterization of the *Meta menardi* spider cocoon. (a) A cocoon of the European cave spider *Meta menardi*, photo by Francesco Tomasinelli (2009). Scale bar: 5 mm. (b) The upper part and the stalk of the cocoon. Scale bar: 1 mm. (c, d) The walls of the cocoon at different magnifications, scale bars correspond to 1 mm and 500 μm , respectively. The scissors and the black dotted lines indicate cutting of the cocoon wall, which was removed for internal inspection of the cocoon structure and eggs, which are indicated by black arrows.

Stodola theorem, a linear proportionality between the irreversibility level and the more intuitive quantity of useful energy loss (in thermodynamics also known as *exergy* loss) can be proved. As a consequence, design and operation of engineering devices (e.g. heat exchangers, heat pumps) under optimal EGM conditions, imply minimal destruction of useful energy. Ultimately, this leads to a minimal amount of fuel needed for accomplishing a desired task.

The same idea could be referred to a general biological context, in which the fitness of a biological process involving heat transfer, mass transport and fluid flows is maximized when the required energy (i.e. the required amount of food) is minimized. Following similar thermodynamic arguments, Bejan has shown how the optimization of food intake (i.e. useful energy or exergy) can be associated to the optimal size of the organs in animals or to bird flight^{19,20}.

In this study, we first aim at understanding the influence of the environmental factors on the female preference in laying cocoons under natural conditions (Figure 2a). The considered factors included air flow velocity (below also referred to as air speed), light intensity and distance for the cave entrance. As suggested in literature^{4,5,6}, the latter seems to be an important factor conditioning the female, given that the cocoon is laid close to the entrance to facilitate the dispersion of the spiderlings outside the cave. However, apart from caves and artificial cavities such as mines, *M. menardi* is able to colonize the shallow air-filled voids of bare rocky debris²¹ and other hypogean habitats classified as superficial subterranean habitats (SSH, *sensu*^{22,23}). Given the difficulties of

studying the SSH without utilizing subterranean traps, we chose the cave environment for our study as a *proxy* of several other habitats that *M. menardi* can occupy.

Moreover, our purpose was to provide evidence that the preference of the female for specific environmental conditions occurring at the depositional areas are those that minimize the amount of global thermo- and fluid-mechanics irreversibility.

Results

In-field study. According to model selection (Table 1), the most appropriate model (see below the corrected Akaike information criterion - AICc) for the available data set had the following structure: $p \sim d + U_{air} + (1/\text{Site})$, where p = probability of presence/absence of cocoon; d = distance from the cave entrance (fixed factor); U_{air} = mean airflow velocity (fixed factor); Site = collection site (random factor).

In the range of the measured values (Figure 3, Table 2), the probability of presence of the cocoon was found to increase significantly in relation to a corresponding increase in the mean airflow velocity [U_{air} : Beta Estimates: 13.506, Standard Error: 6.624, $p=0.041$ *], reaching 50% around 0.3 m/s and the maximum at 0.6 m/s. Furthermore, the probability of finding a cocoon was also found to increase at minor distances from the cave entrance [d : Beta Estimates: -0.587, Standard Error: 0.324, $p=0.070$ (*)], however with a weaker effect. The maximum probability was reached very close to the cave entrance and decreased to 50% after 8–10 meters.

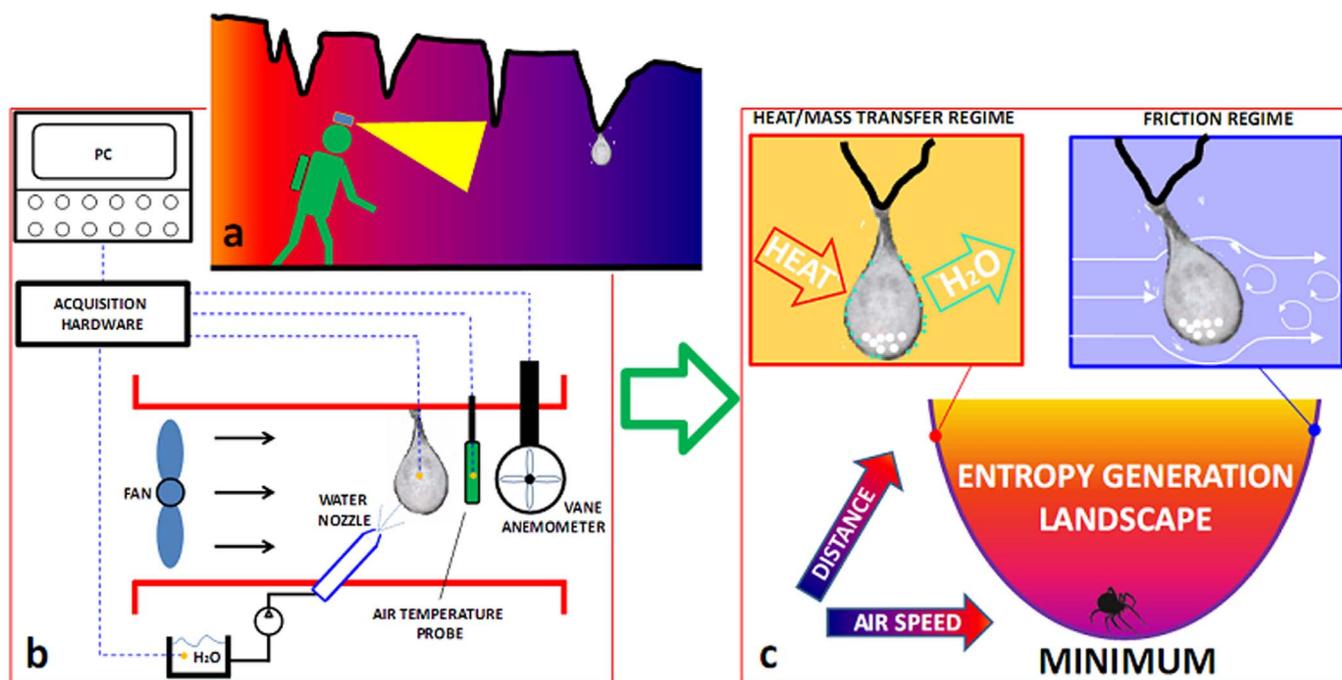


Figure 2 | Summary of the work flow. (a) *in-field* 1-year monitoring and measurements of airflow velocity, distance from cave entrance, presence of the cocoons and final cocoon collecting procedure; (b) laboratory experiments for characterizing the cocoon thermal properties; (c) theoretical modeling based on the EGM method using as input data only the properties measured in phase (b) and direct comparison with observations in phase (a). A relevant agreement is demonstrated without best fit parameters.

Thermal and mass transfer properties of *Meta menardi* cocoon. In a wind channel (sketched in Figure 2b), initial tests were dedicated to the measurements of the thermal transmittance through the cocoon walls as illustrated in detail in the Methods below and the Supplementary Information. The good thermal insulating properties of the cocoon become evident by comparing results referred to as *naked* (i.e. heater not surrounded by a cocoon) with those referred to as *cocoon* (i.e. heater surrounded by a cocoon) in Figure 4a. The latter figure shows that, for vanishing airflow velocities, the transmittance of naked heaters is similar to setups with a cocoon. However, when the airflow velocity increases, the transmittance of the former setup increases as well, attaining (at airflow velocity around 2 m/s) a value three times larger than that observed at zero velocity. On the contrary, the transmittance measured with the cocoon shows a

much more moderate increase with the airflow velocity: at 2 m/s, the transmittance with cocoon is less than 50% larger than the corresponding value at 0 m/s.

As a result, the transmittance of the cocoon wall weakly changes with the airflow velocity proving its insulation capabilities. This is mainly due to its porous structure made of many small interstices (see Figure 1a–d), which induce air stagnation at moderately high airflow velocities, even well above the *in-field* recorded velocity: $0.6 < U_{air} < 2$ [m/s].

Results are shown in Figure 4a in terms of physical quantities (namely transmittance as a function of velocity), or converted in terms of dimensionless quantities (namely the Nusselt number Nu as a function of the Reynolds number Re) in Figure 4b. The latter quantities are often preferred as they allow a more compact form-

Table 1 | Model selection according to corrected Akaike criterion for finite sample size ($AICc^{37}$) ordered from the most to the less appropriate. p = probability of presence/absence of cocoon; U_{air} = mean airflow velocity (fixed factor); d = distance from the cave entrance (fixed factor), L = mean light intensity; Site = collection site (random factor, categorical variable); Df = degrees of freedom; $AICc$ = Corrected Akaike Information Criterion for finite sample size; Wi = Akaike weight

Model structure	Df	$AICc$	$\Delta AICc$	Wi
$Y \sim U_{air} + d + (1 \text{Site})$	4	29.742	0	0.611
$Y \sim U_{air} + d + L + (1 \text{Site})$	5	31.129	1.386	0.305
$Y \sim d + (1 \text{Site})$	3	35.156	5.414	0.041
$Y \sim d + L + (1 \text{Site})$	4	36.653	6.911	0.019
$Y \sim L + d$	3	38.297	8.554	0.008
$Y \sim d$	2	38.864	9.121	0.006
$Y \sim L + U_{air} + d$	4	39.276	9.534	0.005
$Y \sim d + U_{air}$	3	40.144	10.401	0.003
$Y \sim U_{air} + (1 \text{Site})$	3	44.854	15.111	0
$Y \sim U_{air} + L + (1 \text{Site})$	4	47.051	17.309	0
$Y \sim L + (1 \text{Site})$	3	55.692	25.949	0
$Y \sim U_{air}$	2	55.883	26.141	0
$Y \sim L + U_{air}$	3	56.977	27.235	0
$Y \sim L$	2	58.440	28.697	0

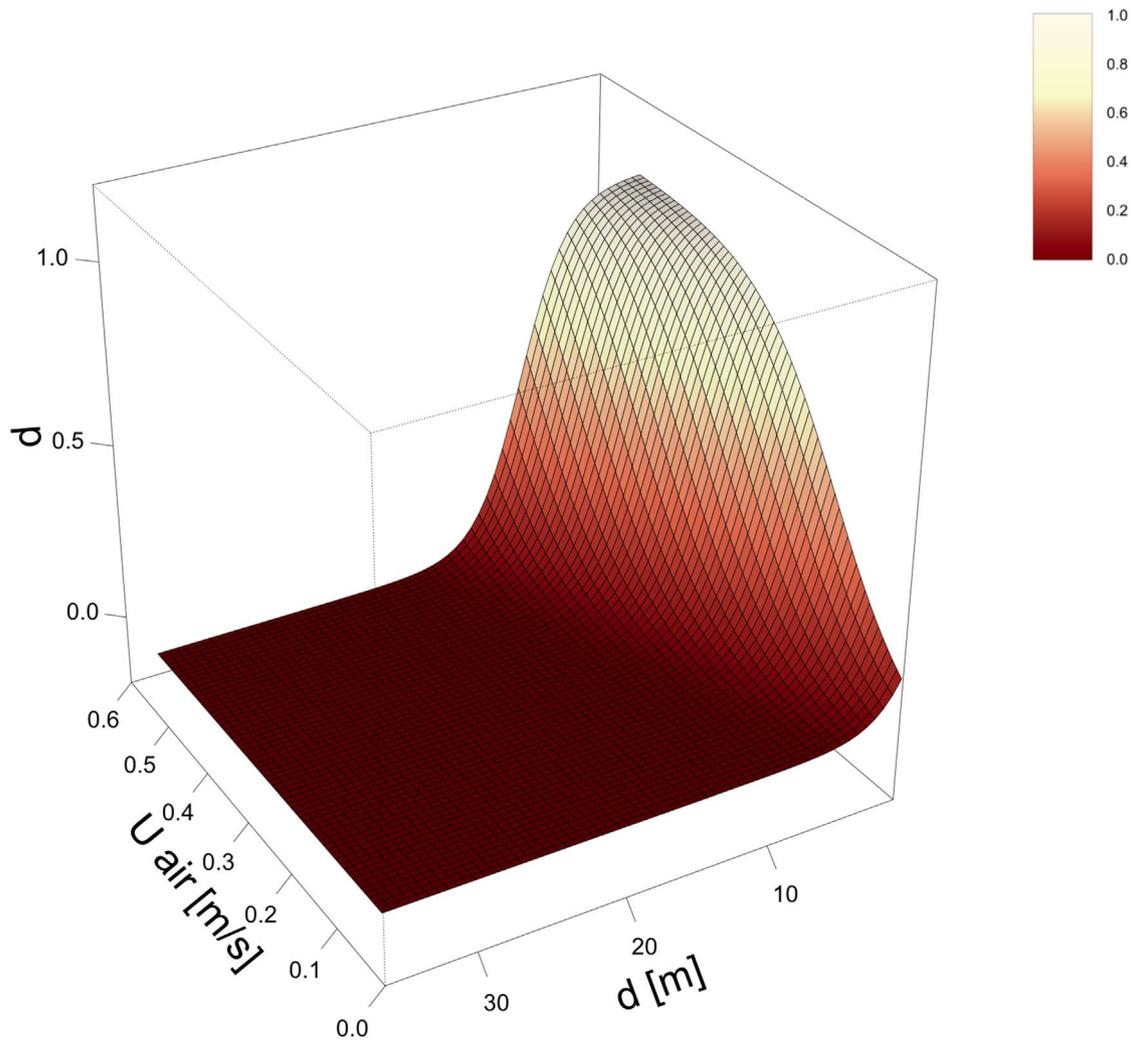


Figure 3 | The binomial Generalized Linear Mixed Model (GLMM). Probability surface shows the relation among mean airflow velocity, distance from the cave entrance and probability of presence of the cocoon of *Meta menardi*, obtained by the binomial GLMM applied to the *in-field* collected data.

alism (e.g. no need to account for the heater size). In the Supplementary Information, we have reported more details on the translation of the physical quantities into the corresponding dimensionless variables. Moreover, relying upon the Chilton-Colburn analogy between heat and mass transfer, we were able to express the analytic dependency of both thermal Tr and mass K transmittances on the velocity value U_{air} (see Supplementary Information). As reported in Figure 4c, those functions were expressed in the following explicit form:

$$Tr = Tr_0 + Tr_1 U_{air}^\alpha; \quad K = K_0 + K_1 U_{air}^\alpha, \quad (1)$$

with Tr_0 , Tr_1 , K_0 , K_1 , and α being appropriately chosen in order to best fit the experimental data. Finally, the characteristic drying time was

also investigated and expressed as a function of the airflow velocity $\tau = \tau(U_{air})$ (see Figure 4d).

The above formulas $Tr(U_{air})$, $K(U_{air})$ and $\tau(U_{air})$ were all utilized to explicitly write the total generated entropy functional S_{tot} and the corresponding probability p of cocoon deposition in terms of the airflow velocity and the distance from the cave entrance as derived in detail in the Methods section below:

$$S_{tot} = S_{tot}(U_{air}, d); \quad p = \exp[-(S_{tot} - S_{tot}^{\min})/S_0]. \quad (2)$$

with S_{tot}^{\min} and S_0 constants. Iso-level curves of both the generated entropy and deposition probability have been shown in Figure 5, where we also reported the results of the 48 *in-field* observations. Cocoon presence probability is in good accordance with the computed function p , thus supporting our preliminary assumption that the preferred environmental factors are those ensuring minimal production of entropy. In particular, the entropic model predicts the highest presence of cocoons at $U_{air} \approx 0.55$ m/s and low values of d .

Discussion

According to the Gouy-Stodola theorem²⁴ a linear proportionality between the irreversibility level and the energy loss can be proved. Ultimately, low irreversibility levels could be related to lower amount of primary energy (i.e. fuel in engineering devices or food in animals) needed for accomplishing a desired task. This same idea has been applied to complex systems such as living organisms^{19,20}.

Table 2 | Results of the Binomial GLMM applied to *in-field* data (Random effect variance: Site = 4 groups, Variance 6.57, Std. dev. 2.563)

Variable	Beta Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.430	2.118	-0.68	0.500
U_{air}	13.506	6.624	2.04	0.041 *
d	-0.587	0.324	-1.81	0.070 (*)

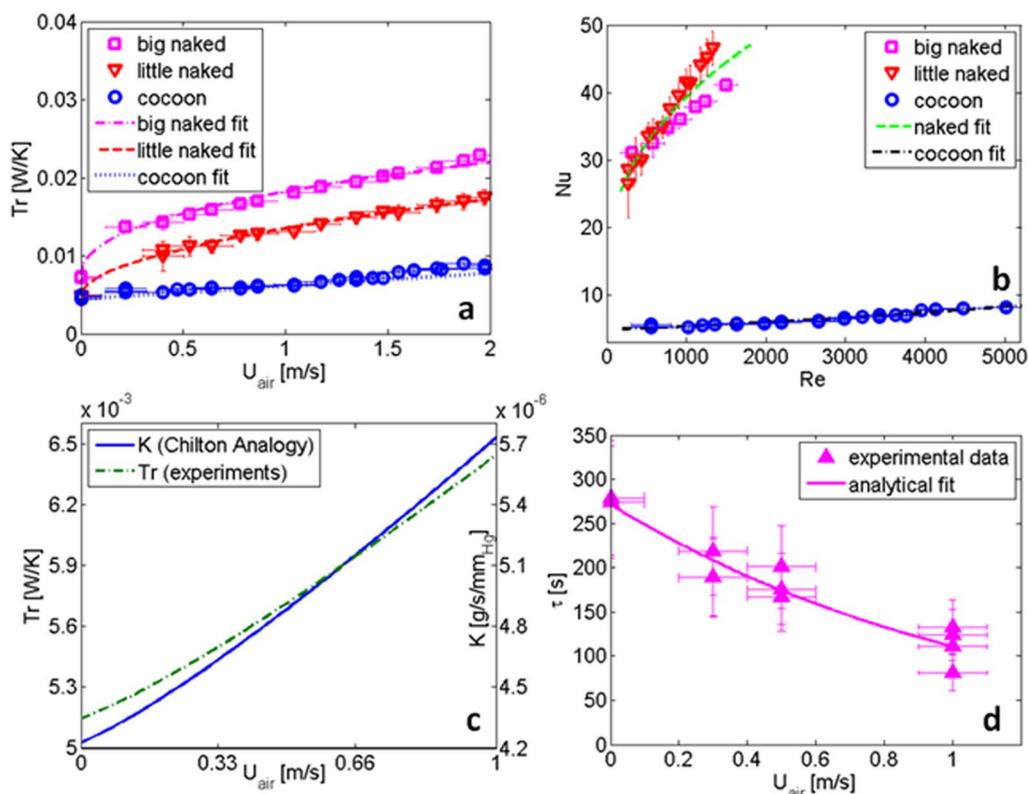


Figure 4 | Experimental results from laboratory tests comparing different setups: naked with BH (big heater), naked with SH (small heater), BH within cocoon, SH within cocoon. (a) Transmittance as a function of the air flow velocity U_{air} . Points refer to experimental data, while lines denote best-fitting curves. (b) Nusselt number as function of Reynolds number. Points refer to experimental data, while continuous lines indicate best fitting curves. (c) Thermal and mass transport transmittances Tr and K as a function of the air flow velocity based on the laboratory experiments. (d) The characteristic drying time τ as function of the air flow velocity U_{air} . Triangles are the experimental points, while continuous line is the corresponding best fitting curve.

In this study, we applied these concepts to study the adaptive significance of the female preference for specific environmental conditions. According to the results of our *in-field* study, the European cave spider *Meta menardi* selects suitable areas for the deposition of the egg sac on the basis of two environmental variables, namely air flow velocity and the distance from the cave entrance within a particular cave. The preferred conditions are found where the air flow velocity ranges between 0.3 and 0.6 m/s within 8–10 meters from the cave entrance. It appears likely that this preference is related to the peculiarity of the life cycle of the spider, in particular to the maintenance of an optimal microclimate for the development of the eggs and to facilitate the migration of spiderlings outside the cave (i.e. dispersion). Moreover, on the basis of a thermodynamic optimization argument, we have observed that such optimal values of those two environmental variables correspond to minimal level of irreversibility. Thermodynamic optimization has been conducted by the EGM method^{19,24,25}, which has the merit of providing a scalar function S_{tot} (see Methods below) to consistently combine in a unique formula several physically non-homogeneous contributions to total irreversibility.

According to the entropic argument, three main irreversibility sources have been considered in our study: i) Fluid dynamics friction (below denoted by S_{drag} and S_{mov}); ii) Mass transport (S_{mass}); iii) Heat transfer (S_{heat}). From the biological standpoint, an increase of fluid dynamic irreversibility plays a twofold undesired role. First, this is responsible for the corresponding increase in the metabolic energy spent by spiderlings while exiting the cave (i.e. the larger the distance d the larger the amount of required energy). It was observed that once the the yolk sac has been consumed, the spiderlings usually do not feed until they disperse outside⁵. Indeed, a large percentage of spiderlings of *M. menardi* emerging from cocoons displays a strong positive

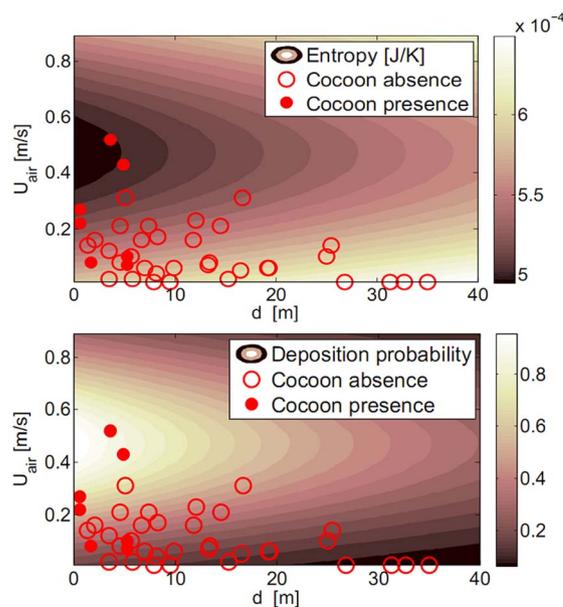


Figure 5 | Entropy isocontours. (a) Isocontours of the total generated entropy according to equation (15) corresponding to: $\phi = 0.65$, $D_c = 1.8$ cm, $T_a = 15^\circ\text{C}$, $D_s = 6$ mm, $U_{spider} = 0.4$ m/s, $N_{spider} = 250$ (see ref. 28). (b) Cocoon deposition probability by equation (16) is reported with a reference entropy of $S_0 = S_{tot}^{min}/8$. *In-field* experimental data are also reported with disks and circles denoting presence and absence of cocoon, respectively.



Table 3 | List of the study sites with the total number of plots considered for the *in-field* study and number of observed cocoons for each cave during the survey, dates of deposition and hatching. The cocoons tested in the laboratory were taken in Grotta del Bandito in October 2013

Cave name	Cadastre number	Type	Municipality	Province	N° of plots	N° of cocoons	Deposition	Hatching
Grotta del Bandito	1002 Pi/CN	Natural cave	Roaschia	CN	16	1	Aug 2012	March 2013
Cave di Marra	Art. Pi/TO	Abandoned mine	Villar Focchiardo	TO	22	11	Aug/Sep 2012	Feb/March 2013
Balma Fumarella	1597 Pi/TO	Natural cave	Gravere	TO	10	2	Aug 2012	Feb/March 2013

phototaxis⁶, moving away from the cocoon towards the light of the cave entrance^{4,5}. In the absence of food intake, it appears likely that the vicinity of the cocoon to the cave entrance minimizes the amount of energy necessary to the spiderlings to accomplish this migration, thus maximizing the reproductive success of the species. On the other hand, the vicinity to the cave entrance may excessively expose the cocoon to a higher predation risk (i.e. by parasitoids coming from the outside, see Ref. 26). In this respect, the external layer of the cocoon has been proved to ensure protection from external attacks^{2,27}. Here it is worth to stress out that the distance from the cave entrance has to be considered with caution. Indeed, the distance from the entrance itself can be regarded as a surrogate of several other environmental and microclimatic conditions, for instance light intensity and air velocity (i.e. microclimatic variability)²⁸. However, our statistical approach deals with this problem via the analysis of collinearity among the covariates and the model selection, aiming to disentangle the effects provided by different covariates on the dependent variable^{29,30}. In particular, light intensity and the distance from entrance were not correlated (given the morphology of the cave, both dark and illuminated plots occurred both near and far from the cave entrance). A similar trend was found for all other combinations of variables. In addition, despite the inclusion in the model of an array of covariates, model selection pointed out a significant effect of the distance from entrance *per se* (Tab. 1), which we interpreted as a factor facilitating the spatial migration of the spiderlings.

A second aspect also included in our thermodynamic model is related to microclimatic conditions at the surface of and within the cocoon. To this respect, fluid dynamic irreversibility (i.e. friction between flowing air and a cocoon) should be minimized as it provides an excess of heat to the cocoon thus altering the internal climatic conditions and possibly the development of the eggs³¹. Heat can be generated by the friction forces between air and the cocoon wall as well as by egg scrubbing.

Similarly, a minimal level of irreversibility generated during water mass and heat transfer is also desirable as this ensures small time-averaged temperature difference and water pressure difference between the cocoon and the environment. Under these conditions (i.e. short temperature and pressure differences regime), the drying process is only experienced for short time thus minimally affecting the microclimatic conditions within the cocoon.

On the contrary, at higher airflow velocity, higher friction generates heat thus altering the optimal conditions within the cocoon. Moreover, if from one side lower air velocity minimizes friction, on the other it may result in lower drying effect thus leading to an excessive wetting of the cocoon. Inside the cave and other hypogean habitats colonized by *M. menardi* (see, e.g., Ref. 21), the relative humidity is very high, usually showing partial or complete saturation^{22,32}. The cocoon can potentially get wet via the running water that often flows over the internal surfaces of subterranean chambers or by the condensation of water droplets over the cocoon external layer when the water content in the cave air is above the saturation. Since the cocoon is suspended from the chamber ceiling by a stalk of silk, it is most often kept away from the running water on the walls⁵. On the other hand, the wetting of the cave surfaces (and thus of the cocoon) through the deposition of water from the atmosphere is by no means an extraordinary event³¹. Under such condition, the

cocoon could grow heavy and collapse as well as become a suitable substrate for fungal attacks⁵. By drying the cocoon, the presence of a flow of air may limit this negative effect connected with the humidity.

In the light of the above considerations, the total irreversibility level S_{tot} can be interpreted as an overall measure of two phenomena: i) the unsuccessful egg development due to unsuitable microclimatic conditions; ii) the unsuccessful migration of the spiderlings toward the entrance due to a large required metabolic energy. In evolutionary terms, the ecological conditions selected by the female in the deposition area ensure a higher reproductive success and thus are promoted in terms of Darwinian fitness.

Moreover, considering the experimental results for the related cocoon thermal properties and the EGM method reported here, the best conditions for the cocoon deposition are found at the same conditions highlighted in the *in-field* study.

The multidisciplinary approach of combining *in-field* ecological study with the thermodynamic arguments, here proposed, may pave the way to a novel understanding of evolutionary strategies for other living organisms.

Methods

***In-field* study.** In order to study the influence of specific environmental conditions on the female preference for laying the cocoon, we monitored monthly three natural populations of *Meta menardi* occurring in three subterranean sites in the Western Italian Alps, NW-Italy (Table 3 and the Supplementary Information).

We defined forty-eight plots (squared areas of 1×1 m², Table 3) that were monitored monthly for one year, from April 2012 to March 2013 (12 total surveys). Plots were randomly placed inside the cave within the natural range of occurrence of adult female spiders (1–40 m), derived from previous observations in the sites³³.

The distance from the cave entrance (d) of each plot was measured at the first survey. During each survey, we registered presence/absence of cocoons and measured light intensity (lux) (L) and airflow velocity (m/s) (U_{air}) (median value of four measurements per plot). For light intensity and airflow velocity we used a portable meter (DO 9847 Delta OHM S.r.l.) equipped with a photometric probe (LP 471 Phot) and a hot-wire probe (AP 471 S1).

During the survey, an amount of fourteen cocoons was laid almost simultaneously in the three study sites in August/September 2012 and hatched in February/March 2013 (Table 3). Data of airflow velocity and light intensity gathered between the deposition and the hatching of the eggs (8 surveys) were pooled in one value by calculating the mean of the registered variables (48 total mean observations).

Data exploration was carried out following²⁹. Presence/absence of cocoon was related to the three explanatory variables via a generalized linear mixed model procedure (GLMMs³²) in R environment³⁴. The mixed procedure allowed us to deal with the spatial dependence of the plots, so we included the spatial factor “site” (namely the three subterranean systems in which the plots were located) as a random factor. The Bernoulli distribution was chosen, the response variable containing zeros (absence) and ones (presence). Considering the unbalanced set of zeros and ones in our dataset (14 ones versus 34 zeros), we used the complementary log-log link function (clog-log) as recommended by Ref. 30. The clog-log regression model was fitted via the `glmmAMDB`³⁵ R package (version 0.7.7). The outcome of the models consisted of regression coefficients for the explanatory variables, whose significance was assessed via Wald tests³⁶. We performed model selection by a stepwise selection procedure, according to AICc (corrected Akaike information criterion³⁷) that is appropriate when the number of observations is small³⁸. The AICc values were calculated via the `MuMIn`³⁹ R package (version 1.9.13). The model validation was carried out following³⁰ (See Supplementary Information).

FESEM characterization of the *Meta menardi* spider cocoon. The cocoon walls were cut leaving an opening (see black dotted lines in Figure 1a) in order to scan the wall structure using the Field Emission scanning electron microscope (FESEM, FEI-InspectTM F50, at 1–2 kV) equipped with a field emission tungsten cathode. These have been fixed to aluminium stubs by double-sided adhesive carbon conductive tape (Nisshin EM Co. Ltd.). Samples were used as collected, no fixation processes were made to avoid any alteration of the cocoon structure^{40,41}.



Characterization of thermal and mass transport properties of *Meta menardi* cocoons. For assessing thermal and mass transport performances of *Meta menardi* cocoons, we performed several experimental tests by introducing an electrical heater inside the cocoon along with a thermocouple in contact with the above heater. This enabled us to have an estimate of the temperature T_w inside the egg sac at a given thermal power and external fluid-dynamic conditions.

To ensure a homogeneous temperature distribution, the thermocouple and the heater were wrapped together in an aluminum foil and a good thermal contact was ensured by a thin layer of thermal interface compound (with thermal conductivity larger than 2 W/K/m).

This assembly was introduced inside the cocoon, which was placed on the symmetry axis of the wind channel, whose dimensions are $10 \times 10 \times 40$ cm³ (with a cross section of 10×10 cm²). At the channel inlet, an adjustable velocity fan induced an air stream around the cocoon, thus mimicking the action of wind under natural conditions. An additional thermocouple measured the ambient air temperature T_a in the center of channel middle section.

A hydraulic characterization of the wind channel has been performed before measurements. Namely, using a vane anemometer placed at the center of the wind channel (see also Figure 2b), a characteristic curve has been constructed by recording the electrical power supplied to the fan corresponding to a measured air speed. The latter curve has been used subsequently in the experiments for inferring the air speed value at a given voltage supplied to the fan.

Two different heaters have been utilized in order to investigate possible size effects. The first heater was characterized by a bigger size and smaller electrical resistance (referred to as big heater -BH). The second heater presented a smaller size and a larger electrical resistance (referred to as small heater -SH). The big (small) heater had a cylindrical geometry with height, diameter and resistance of 22.2 mm (10.4 mm), 5.05 mm (4.15 mm) and 22.4 Ohm (98.9 Ohm), respectively.

Evaluation of total irreversibility and cocoon deposition probability. We considered wetting and adiabatic cooling as sufficiently fast processes (compared to the subsequent drying phenomenon), so that starting from t_{start} , the phenomenon of interest was approximated by a sudden cooling with $\Delta T_{max} = T_a - (T_w)_{min} = \Delta T_{max}$ followed by a first-order exponential decay with characteristic time τ . Upon the choice of the relative humidity ϕ and the ambient temperature T_a , ΔT_{max} is dictated by the corresponding wet bulb temperature T_{wb} : $\Delta T_{max} = T_a - T_{wb}$, which was computed by the following empirical correlation⁴²:

$$T_{wb} = (T_a - 273) \left[0.45 + 0.6\phi \left(\frac{p}{1060} \right)^2 \right] + 273, \quad (3)$$

with temperatures expressed in Kelvin, and pressure p in hPa (0.1 kPa).

During the drying process of a cocoon under forced air convection, mainly three phenomena contribute to the generation of entropy: i) fluid-dynamic drag; ii) heat transfer under finite temperature differences; iii) mass transfer under finite pressure differences. Following a similar argument as in Ref. 24, we can quantify the above three contributions to the entropy production (during the drying process) as follows:

$$\dot{S}_{drag} = \frac{F_D U_{air}}{T_a}, \quad \dot{S}_{heat} = \frac{Tr(T_w - T_a)^2}{T_a T_w}, \quad \dot{S}_{mass} = \frac{K[p_s(T_w) - \phi p_s(T_a)]^2}{\rho_a T_a}, \quad (4)$$

with ρ_a and F_D denoting the air density and the drag force. Under the assumption of spherical cocoon, the latter force can be estimated as:

$$F_D = \frac{C_D \rho_a \pi D_c^2 U_{air}^2}{8}, \quad (5)$$

where D_c is the cocoon diameter and the drag coefficient C_D is computed by means of the well-known correlations⁴³:

$$C_D = \frac{24}{Re} [1 + 0.1315 Re^{0.82 - 0.05w}] \text{ if } Re \leq 20, \quad (6)$$

$$C_D = \frac{24}{Re} [1 + 0.1935 Re^{0.6305}] \text{ if } 20 < Re \leq 260, \quad (7)$$

$$\log_{10} C_D = 1.6435 - 1.1242w + 0.1558w^2 \text{ if } 260 < Re \leq 1.5 \times 10^3, \quad (8)$$

with the Reynolds number $Re = D_c U_{air} \rho_a / \mu$ and $w = \log_{10}(Re)$. The dependence of the saturation pressure on the temperature $p_s(T)$ in equation (4) is accounted by means of a fourth order polynomial as follows:

$$p_s(T) = c_1 T^4 + c_2 T^3 + c_3 T^2 + c_4 T + c_5, \quad (9)$$

where pressure is expressed in Pa, temperatures in Kelvin, $c_1 = 0.000965$, $c_2 = -1.087$, $c_3 = 462.3$, $c_4 = -8.789 \times 10^4$ and $c_5 = 6.297 \times 10^6$.

During the drying process, the above three sources of irreversibility are responsible of a total entropy production which amounts to:

$$S_{drying} = \int_0^{\Delta t} \dot{S}_{drag} dt + \int_0^{\Delta t} \dot{S}_{heat} dt + \int_0^{\Delta t} \dot{S}_{mass} dt, \quad (10)$$

where Δt is a proper multiple of the characteristic time τ (i.e. $\Delta t \approx 3\tau$), after which the

cocoon can be practically considered at thermal equilibrium with the environment. In the following, we focus on a single event during which the cocoon external surface gets fully wet.

The total entropy produced during the drying process can be explicitly expressed as a function of the airflow velocity U_{air} substituting the experimental functions $Tr(U_{air})$, $K(U_{air})$ and $\tau(U_{air})$ plotted in Figure 4c, d in the equations (4):

$$S_{drying} = S_{drying}(U_{air}). \quad (11)$$

Furthermore, the length d is responsible of additional entropy production \dot{S}_{mov} due to the friction generated during the movement of the young spiders while trying to exit the cave. In the following, we report the simplest way of estimating such a contribution:

$$\dot{S}_{mov} = N_{spider} \frac{F_S U_{spider}}{T_a}, \quad (12)$$

where N_{spider} , F_S and U_{spider} are the number of spiders exiting the cocoon, a friction force associated with the spider movement and the traveling speed at which spiders move, respectively.

An estimate of the drag force can be obtained by equation (5): $F_S = F_D$ (upon the choice of a characteristic dimension of the young spiders D_s), while the total amount of entropy generated during the travel from the cocoon to the cave entrance is:

$$S_{mov} = \int_0^{d/U_{spider}} N_{spider} \frac{F_D U_{spider}}{T_a} dt = N_{spider} \frac{F_D d}{T_a}, \quad (13)$$

which, as opposed to equation (11), depends on d : $S_{mov} = S_{mov}(d)$. It is worth noticing that here, for simplicity and without loss of generality, we only consider fluid-dynamic friction and neglect the contribution due for instance to other forms of dissipation, e.g. friction developed while the spider moves upon the cave walls (named F_{SC}). In case of knowledge of F_{SC} , equation (13) can be more accurately expressed as:

$$S_{mov} = N_{spider} (F_D + F_{SC}) d / T_a. \quad (14)$$

According to EGM, optimal deposition conditions are found at the minimum of the following functional:

$$S_{tot} = S_{tot}(U_{air}, d) = S_{drying}(U_{air}) + S_{mov}(d). \quad (15)$$

The above expression is valid under the assumption that the amount of entropy (11) produced during a single complete wetting and subsequent drying process incorporates the entire amount of total irreversibility during the entire life of a single cocoon (see also the Supplementary Information).

Finally, according to classical thermodynamics, we assumed the following exponential relationship between the cocoon deposition probability p and entropy S_{tot} :

$$p = \exp \left[- (S_{tot} - S_{tot}^{min}) / S_0 \right], \quad (16)$$

where S_{tot}^{min} is the absolute minimum value of the functional (15), while $S_0 \propto S_{tot}^{min}$ is a proper reference entropy.

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Author contributions

E.C. and P.A. suggested and developed the E-G-M- approach and designed the experimental laboratory measurements, M.I. and S.M. collected *in-field* data, analysed them with the related statistical models and provided biological arguments, E.L. performed SEM analysis, L.V. conducted laboratory experiments, N.M.P. designed and supervise this research and suggested the type of models. All the authors contributed to the writing of the paper and to the data analysis.

Additional information

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