

REFERENCES AND NOTES

- W. N. Meier *et al.*, *Rev. Geophys.* **52**, 185–217 (2014).
- I. Stirling, A. E. Derocher, *Glob. Chang. Biol.* **18**, 2694–2706 (2012).
- S. C. Amstrup, in *Wild Mammals of North America: Biology, Management, and Conservation*, G. A. Feldhamer, B. C. Thompson, J. A. Chapman, Eds. (The Johns Hopkins Univ. Press, Baltimore, ed. 2, 2003), pp. 587–610.
- B. P. Kelly *et al.*, *Polar Biol.* **33**, 1095–1109 (2010).
- J. Whiteman, thesis, University of Wyoming, Laramie, WY (2014).
- S. C. Amstrup, B. G. Marcot, D. C. Douglas, in *Arctic Sea Ice Decline: Observations, Projections, Mechanisms, and Implications*, E. T. Deweaver, C. M. Bitz, L. B. Tremblay, Eds. (Geophysical Monograph 180, American Geophysical Union, Washington, DC, 2008), pp. 213–268.
- L. A. Harwood, T. G. Smith, J. C. Auld, *Arctic* **65**, 35–44 (2012).
- L. A. Harwood, I. Stirling, *Can. J. Zool.* **70**, 891–900 (1992).
- K. D. Rode, C. T. Robbins, L. Nelson, S. C. Amstrup, *Front. Ecol. Environ.* **13**, 138–145 (2015).
- R. A. Nelson *et al.*, *Ursus* **5**, 284–290 (1983).
- M. G. Dyck *et al.*, *Ecol. Complex.* **4**, 73–84 (2007).
- C. T. Robbins, C. Lopez-Alfaro, K. D. Rode, Ø. Tøien, O. L. Nelson, *J. Mammal.* **93**, 1493–1503 (2012).
- A. M. Pagano, G. M. Durner, S. C. Amstrup, K. S. Simac, G. S. York, *Can. J. Zool.* **90**, 663–676 (2012).
- P. F. Scholander, V. Walters, R. Hock, L. Irving, *Biol. Bull.* **99**, 225–236 (1950).
- C. M. Pond, C. A. Mattacks, R. H. Colby, M. A. Ramsay, *Can. J. Zool.* **70**, 326–341 (1992).
- Materials and methods are available as supplementary materials on Science Online.
- B. K. McNab, *The Physiological Ecology of Vertebrates: A View from Energetics* (Cornell Univ. Press, Ithaca, NY, 2002).
- F. Messier, M. K. Taylor, M. A. Ramsay, *J. Zool. (London)* **226**, 219–229 (1992).
- S. Paisley, D. L. Garshelis, *J. Zool. (London)* **268**, 25–34 (2006).
- T. M. Williams *et al.*, *Science* **346**, 81–85 (2014).
- R. J. Galley, B. G. T. Else, S. J. Prinsenberg, D. Babb, D. G. Barber, *Arctic* **66**, 105–116 (2013).
- R. C. Best, *J. Comp. Physiol. B* **146**, 63–73 (1982).
- O. E. Owen, G. A. Reichard Jr., M. S. Patel, G. Boden, *Adv. Exp. Med. Biol.* **111**, 169–188 (1979).
- M. D. McCue, *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **156**, 1–18 (2010).
- E. W. Pfeiffer, L. N. Reinking, J. D. Hamilton, *Comp. Biochem. Physiol. A Physiol.* **63**, 19–22 (1979).
- A. Friebe *et al.*, *PLOS ONE* **9**, e101410 (2014).
- Ø. Tøien *et al.*, *Science* **331**, 906–909 (2011).
- I. L. Boyd, *J. Exp. Biol.* **203**, 1907–1914 (2000).
- Y. Handrich *et al.*, *Nature* **388**, 64–67 (1997).
- G. M. Durner *et al.*, *Polar Biol.* **34**, 975–984 (2011).
- J. F. Bromaghin *et al.*, *Ecol. Appl.* **25**, 634–651 (2015).
- P. K. Molnár, A. E. Derocher, G. W. Thiemann, M. A. Lewis, *Biol. Conserv.* **143**, 1612–1622 (2010).

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SUPPLEMENTARY MATERIALS

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THERMAL PHYSIOLOGY

Keeping cool: Enhanced optical reflection and radiative heat dissipation in Saharan silver ants

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Saharan silver ants, *Cataglyphis bombycina*, forage under extreme temperature conditions in the African desert. We show that the ants' conspicuous silvery appearance is created by a dense array of triangular hairs with two thermoregulatory effects. They enhance not only the reflectivity of the ant's body surface in the visible and near-infrared range of the spectrum, where solar radiation culminates, but also the emissivity of the ant in the mid-infrared. The latter effect enables the animals to efficiently dissipate heat back to the surroundings via blackbody radiation under full daylight conditions. This biological solution for a thermoregulatory problem may lead to the development of biomimetic coatings for passive radiative cooling of objects.

The silver ants of the Sahara desert, *Cataglyphis bombycina*, inhabit one of the hottest terrestrial environments on Earth, where they occupy the ecological niche of a “thermophilic scavenger” (1). In wide-ranging foraging journeys, they search for corpses of insects and other arthropods that have succumbed to the thermally harsh desert conditions, which they themselves are able to withstand more successfully. On hot summer days, they may reach maximal foraging activities when temperatures of the desert surface are as high as 60° to 70°C and their body temperatures measured as “operative environmental temperatures” are in the range of 48° to 51°C (2, 3). In order to survive under these conditions, occasionally the ants must unload excess heat by pausing on top of stones or dry vegetation, where, because of the steep temperature gradient above the sand surface, they encounter considerably lower temperatures. Under the midday sun of a summer day, the ants may resort to this thermal respite (cooling off) up to 70% of their entire foraging time (3). In keeping their body temperature below their critical thermal maximum of 53.6°C (4), they need not only to reduce heat absorption from the environment but also to be able to efficiently dissipate excess heat, so that they can minimize the amount of time spent in thermal refuges.

As we showed, through a series of optical and thermodynamic measurements, full-wave simulations, and heat-transfer modeling, a dense array of triangularly shaped hairs, characteristic of *Cataglyphis bombycina*, enables the ants to main-

tain lower body temperatures by (i) reflecting a large portion of the solar radiation in the visible and near-infrared (NIR) range of the spectrum and (ii) radiating heat to the surrounding environment by enhancing the emissivity in the mid-infrared (MIR), where the blackbody radiation spectrum of the ant's body culminates. The thermoregulatory solutions that the silver ants have evolved to cope with thermally stressful conditions show that these animals are able to control electromagnetic waves over an extremely broad range of the electromagnetic spectrum (from the visible to the MIR) and that different physical mechanisms are employed in different spectral ranges to realize an important biological function.

Specimens of *Cataglyphis bombycina* collected in Tunisia (34°10'N, 08°18'E) were used for all of the optical and thermodynamic measurements. In these ants, the dorsal and lateral sides of the body have a silvery glare (Fig. 1A) and are covered by dense and uniform arrays of hairs (Fig. 1B and fig. S4). As scanning electron microscopy (SEM) images show, the hairs, which gradually taper off at the tip, are locally aligned in the same direction (Fig. 1C). Their most remarkable structural feature is the triangular cross-section characterized by two corrugated top facets and a flat bottom facet facing the ant's body (Fig. 1, D and E). Cross-sectional views obtained by focused ion beam (FIB) milling show that the gap between the bottom hair facet and the cuticular surface also varies but is generally larger than a few hundred nanometers.

Optical reflectivity measurements of ant specimens were obtained with two Fourier transform spectrometers, one collecting spectra in the visible and NIR (wavelengths from 0.45 to 1.7 μm) and the other in the MIR (wavelengths from 2.5 to 16 μm). The visible and NIR measurements showed that hemispherical reflection [i.e., the sum of specular and diffuse reflection collected through an integrating sphere (2)] is substantially enhanced

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in regions with intact hair coverage as compared to regions from which the hairs had been removed (Fig. 2A and fig. S1). The hair-covered region reflects 67% of the incoming solar radiation rather than only 41%, as is the case after their removal. This enhancement is due to scattering within the triangular hairs (Mie scattering), where light gets trapped and then reradiates out in all directions (5–7). Individual hairs of given cross-sectional dimensions generate enhanced reflection due to scattering at specific wavelengths where fundamental and higher-order Mie resonance modes are supported (Fig. 2C and fig. S5). Due to the variation in cross-sectional areas, resonance peaks from individual hairs are averaged out, so that the hair cover effectively acts as a coating with enhanced broadband reflection.

Because of the ellipsoidal shape of the ant's body, about two-thirds of the dorsolateral surface is obliquely hit by solar radiation (fig. S4). This prompted us to examine the reflectivity as a function of the incidence angle of radiation, which was varied from 0° to 80°, with 0° representing the direction normal to the surface. As the results show, Mie scattering enhances reflectivity over all

angles when regions with intact hair cover are compared to those with hairs removed (Fig. 2B). With increasing angle of incidence, reflectivity enhancement becomes particularly strong at beyond 30°. This is the critical angle at which total internal reflection starts to occur at the bottom facets of the hairs (Fig. 2D, II). At angles approaching 90°, reflectivity drops off when total internal reflection at one of the top facets starts to direct more of the radiation toward the ant's body (Fig. 2D, III).

Next, we performed finite-difference time-domain (FDTD) simulations in order to demonstrate the functional significance of the triangular cross section of the hairs in enhancing reflectivity in the visible and NIR ranges (figs. S5 to S8). These simulations compared the reflective properties of triangular and circular hairs of the same cross sectional area. Even though the enhancement of reflectivity at normal incidence is comparable in both cases, triangular hairs produce an extra enhancement at higher angles of incidence (Fig. 2B). The reason is that although Mie scattering of similar strength occurs in both circular and triangular hairs, in the latter the total

internal reflection at the bottom facets of the hairs enhances reflectivity substantially further. The high reflectivity disappeared when the specimens were wetted by an ethanol-water solution (fig. S3), which removed the refractive index contrast between air and hairs and thus destroyed the conditions required for Mie scattering and total internal reflection.

Reflectivity measurements performed in the MIR range revealed a second important point in the silver ant thermotolerance story. When proceeding from lower to higher wavelengths, at about 8 μm , the enhanced reflectivity of regions with hair cover as compared to those without hairs reverses to reduced reflectivity (Fig. 2E). As Kirchhoff's law of thermal radiation states, reduced reflectivity corresponds to enhanced emissivity (8). At a body temperature of 50°C, which the silver ants may reach when foraging at peak activity times, the blackbody radiation of the ant's surface would lie in the range of 6 to 16 μm (peaked at ~9 μm) and thus allow the silver ants to offload heat more efficiently through radiative heat transfer. The latter decreases the steady-state body temperature and reduces the respite time.

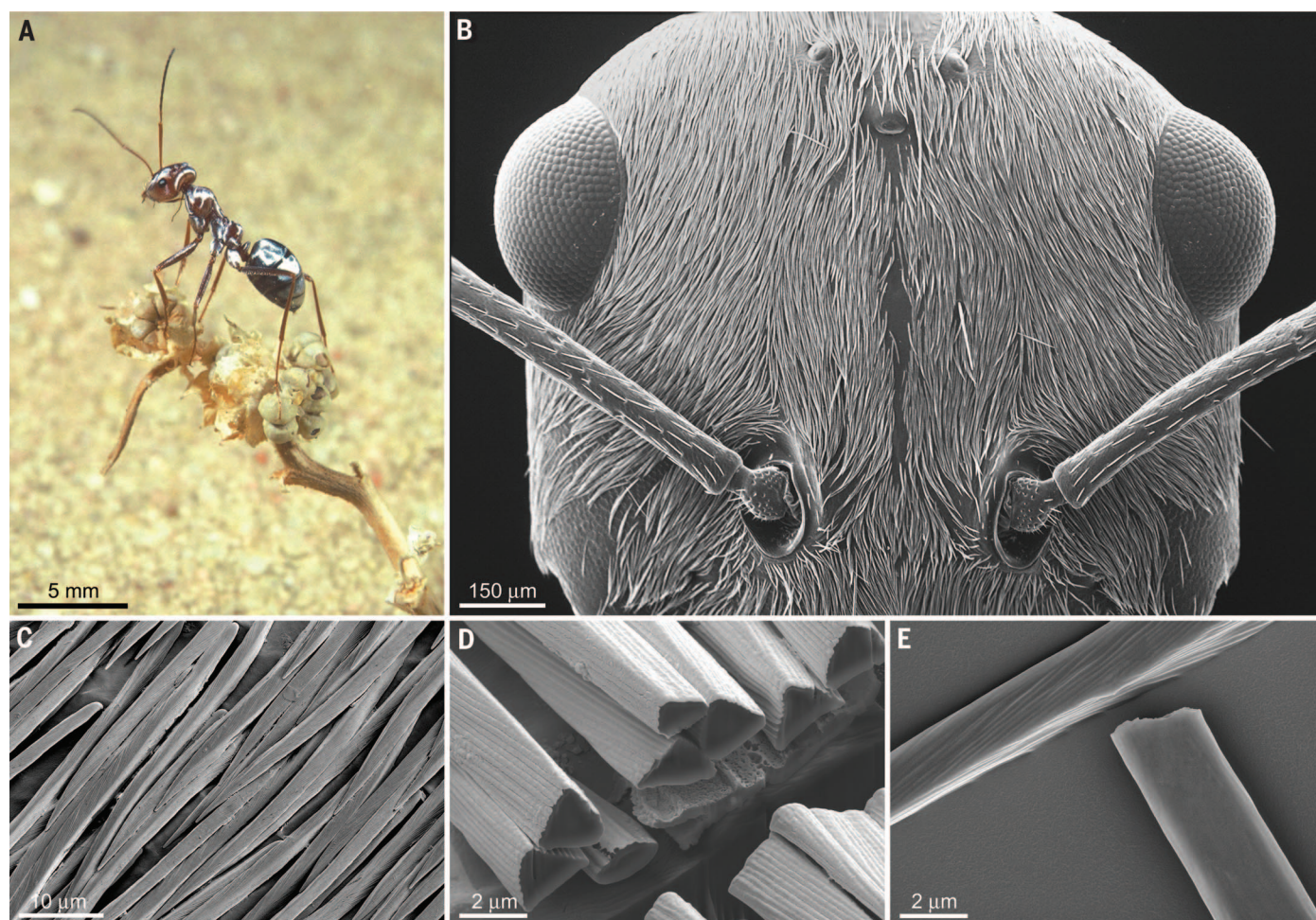
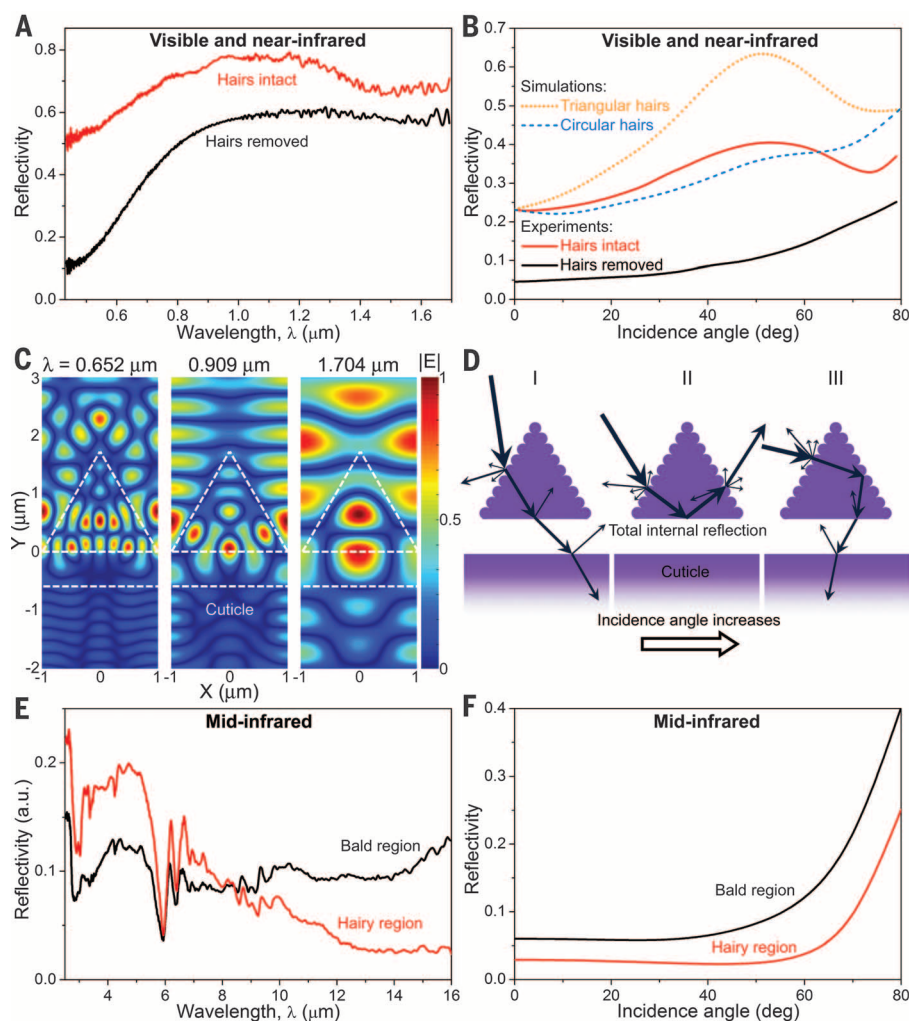


Fig. 1. The bright glare of the silver ant and its structural basis. (A) Silver ant offloading heat on top of dry vegetation (18). (B) SEM frontal view of the head densely covered by hairs. (C) SEM image of the hairs gradually tapering off toward the tip. (D) Cross-sectional view of the hairs milled with FIB. (E) SEM image of two hairs with one flipped upside down to exhibit the flat bottom facet.

Fig. 2. Reflectivity of the silver ant's body surface from the visible to the MIR range of the spectrum. (A) Hemispherical reflectivity measured in the visible and NIR. **(B)** Measurement and simulation results showing visible and NIR reflectivity as a function of incidence angle. **(C)** Cross-sectional view of a two-dimensional distribution of a light field (magnitude of electric field component of light, or $|E|$) around a triangular hair for three exemplary Mie resonances. **(D)** Schematic diagram showing the interaction between visible and NIR light and a hair at small (I), intermediate (II), and large (III) incidence angles. The corrugated upper two facets may enhance diffuse reflection in the ultraviolet and visible ranges. **(E)** Reflectivity measured in the MIR at normal incidence. **(F)** Simulated MIR reflectivity as a function of incidence angle.



How does the hair cover with its enhanced reflectivity in the visible and NIR and its enhanced emissivity in the MIR affect the radiative heat transfer between the ant's body and the environment? To investigate this question, we performed thermodynamic experiments, which mimicked all radiative heat transfer effects in the silver ants' natural foraging environment (fig. S2). To accomplish this task, we used a high-power xenon lamp to simulate the solar spectral distribution at the desert sand surface (9) and a thermoelectrically cooled high-emissivity metal plate to simulate the clear sky with its low level of blackbody radiation (10). The ant specimens were suspended on thin threads to minimize thermal conduction. Thermodynamic experiments were conducted in vacuum to study thermal radiation, as well as in still air to study the interplay of thermal radiation and convection. Under both conditions, the specimens with their natural hair covers were able to maintain significantly lower steady-state body temperatures than the same specimens with the hairs removed (Fig. 3).

The thermodynamic experiments conducted in vacuum comparing specimens before and after hair removal further revealed that the hair

cover decreases the time constants of temperature change (Fig. 3, B and E). The shortened time constants indicate an increased rate of radiative heat transfer and are a direct confirmation of the effect of the hairs in enhancing the MIR emissivity. By using the time constants and the heat transfer model, we computed that the hair cover enhances emissivity by about 15% (table S1). This enhanced emissivity is due to the fact that at large MIR wavelengths (i.e., at wavelengths much larger than the dimensions of the cross sections of the hairs), the hair structure acts as a gradient refractive index layer (fig. S9) (11–13), which provides the surface with broadband, broad-angle antireflective properties in the MIR (Fig. 2, E and F). Because of the influence of convection, the time constants of temperature change decreased by a factor of about 3 when the specimens were brought from vacuum into air (Fig. 3). This indicates that radiative heat dissipation amounted to about one-half of convection and, therefore, still played a significant role in the presence of natural convection.

Applying experimentally extracted parameters to the heat transfer model revealed that the enhanced visible and NIR reflectivity and enhanced

MIR emissivity make comparable contributions to reducing the steady-state temperature in the presence of natural convection (figs. S10 and S11). On hot summer days in the Sahara, the foraging activities of silver ants often occur under low wind or even still air conditions, when the ants have to rely on enhanced visible and NIR reflectivity and enhanced MIR emissivity equally heavily to reduce their body temperature during the respite behavior.

It is interesting to note that the hairs cover only the top and the sides of the ant's body, where they are responsible for the effects described above. The absence of hairs on the bottom surface reduces the radiative energy transfer between the hot sand and the cooler ant body, so that the animals can reduce the absorption of blackbody radiation from the desert floor.

In conclusion, Saharan silver ants are covered with a dense array of triangular hairs on the top and sides of their bodies. These silvery hairs protect the ants against getting overheated in at least three ways. First, as a result of Mie scattering and total internal reflection, the hairs enhance reflectivity in the visible and NIR, where solar radiation culminates. Second, in the MIR,

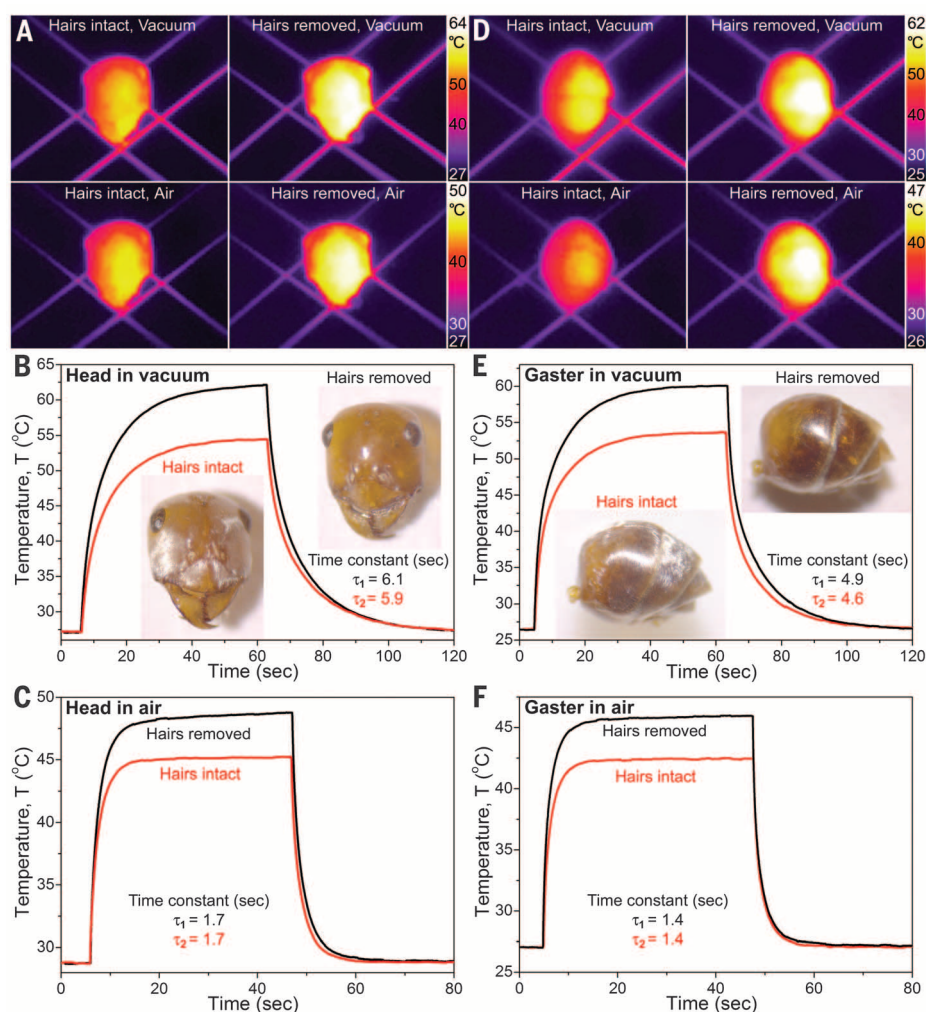


Fig. 3. Results of thermodynamic experiments.

(A) Thermal camera images showing the head of an ant specimen at the thermal steady state under different conditions. Temporal temperature profiles measured for the head before and after hair removal in vacuum (B) and in still air (C) are shown. (D to F) Results obtained for the hind part (gaster) of an ant specimen. Insets in (B) and (E) are photos of specimens before and after hair removal. In the “hairs intact” pictures of head and gaster, because of the limited solid angle of illumination, the silvery glance is not shown all over the body surface portrayed in the figures.

where solar radiation becomes negligible for wavelengths $>2.5 \mu\text{m}$, the hairs acting as an antireflection layer enhance emissivity and thus increase the ants' ability to offload excess heat via blackbody radiation. Third, the ants' bare bottom surface reflects MIR radiation from the hot desert floor more efficiently than if it were covered by hairs. Taken together, these effects result in decreasing the ants' steady-state body temperature and thus enable these thermophilic scavengers to forage at exceedingly high environmental temperatures. Finally, the present interdisciplinary account on the silver ants could have a significant technological impact by inspiring the development of biomimetic coatings for the passive cooling of objects (14–16). A recent article reported the demonstration of a multilayered film that can cool down an object by using essentially the same mechanisms as the silver ants: high reflectivity in the solar spectrum and high emissivity in the MIR (17).

REFERENCES AND NOTES

- R. Wehner, S. Wehner, *Physiol. Entomol.* **36**, 271–281 (2011).
- Materials and methods are available as supplementary materials on Science Online.
- R. Wehner, A. C. Marsh, S. Wehner, *Nature* **357**, 586–587 (1992).
- W. J. Gehring, R. Wehner, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 2994–2998 (1995).
- C. F. Bohren, D. R. Huffman, *Absorption and Scattering of Light by Small Particles* (Wiley, New York, 1998).
- J. Schuller, T. Taubner, M. L. Brongersma, *Nat. Photonics* **3**, 658–661 (2009).
- D. Lin, P. Fan, E. Hasman, M. L. Brongersma, *Science* **345**, 298–302 (2014).
- J. R. Howell, R. Siegel, M. P. Mengüç, *Thermal Radiation Heat Transfer* (CRC Press, Boca Raton, FL, ed. 5, 2010).
- K. L. Coulson, *Solar and Terrestrial Radiation: Methods and Measurements* (Academic Press, New York, 1975).
- J. Monteith, M. Unsworth, *Principles of Environmental Physics* (Academic Press, Oxford, ed. 3, 2007).
- C.-H. Sun, P. Jiang, B. Jiang, *Appl. Phys. Lett.* **92**, 061112 (2008).
- J.-Q. Xi et al., *Nat. Photon.* **1**, 176–179 (2007).
- M. J. Minot, *J. Opt. Soc. Am.* **66**, 515–519 (1976).
- C. G. Granqvist, A. Hjortsberg, *Appl. Phys. Lett.* **36**, 139–141 (1980).
- P. Berdahl, *Appl. Opt.* **23**, 370–372 (1984).
- E. Rephaeli, A. Raman, S. Fan, *Nano Lett.* **13**, 1457–1461 (2013).
- A. P. Raman, M. A. Anoma, L. Zhu, E. Rephaeli, S. Fan, *Nature* **515**, 540–544 (2014).
- R. Wehner, *Jahrb. Akad. Wiss. Lit. Mainz* **89**, 101–112 (1989).

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SUPPLEMENTARY MATERIALS

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Keeping cool

Silver ants inhabit one of the hottest and driest environments on Earth, the Saharan sands, where most insects shrivel and die moments after contact. Shi *et al.* show that the triangular shape of the silver hairs that cover their bodies enables this existence. The hairs both increase the reflection of near-infrared rays and dissipate heat from the ants' bodies, even under full sun conditions. Evolution's simple solution to intense heat management in this species could lead to better designs for passive cooling of human-produced objects.

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