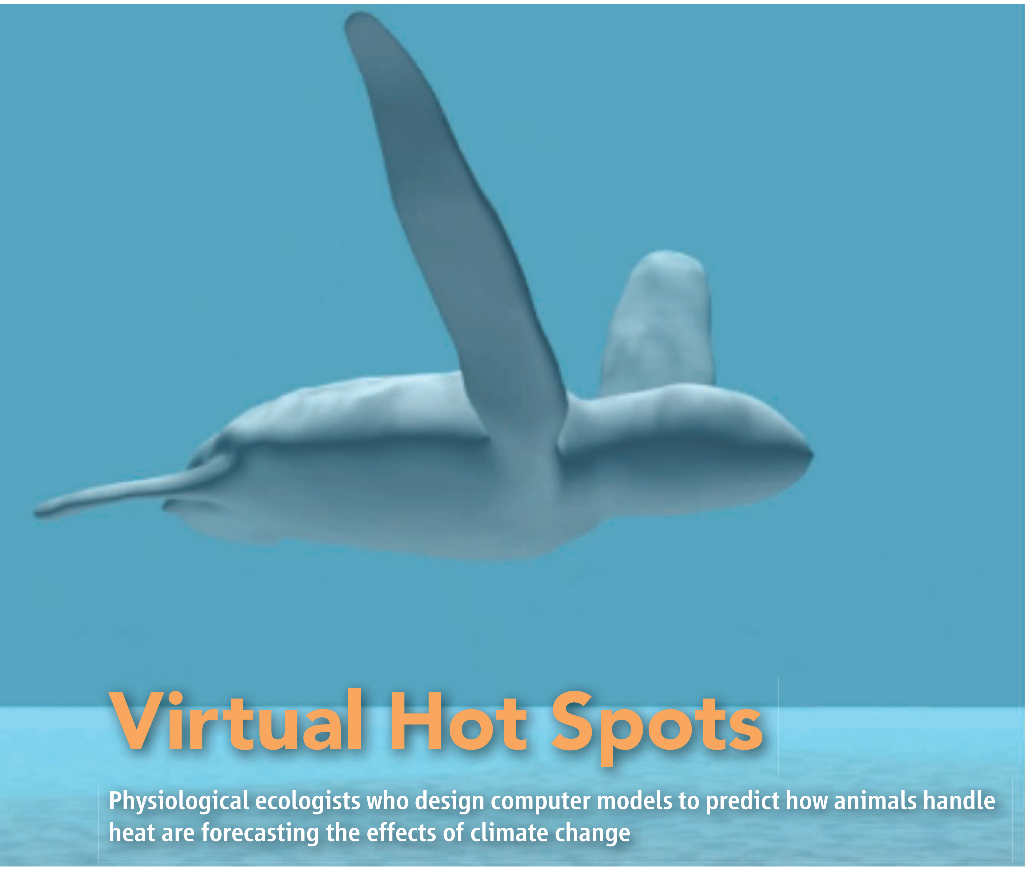

Test case. This virtual sea turtle is helping computer modelers determine where oceans might become too warm for the real leatherbacks.

Virtual Hot Spots

Physiological ecologists who design computer models to predict how animals handle heat are forecasting the effects of climate change

When he was a graduate student in ecology, Warren Porter spent a year in the field watching desert iguanas. Yet a simple question continued to puzzle him: Why did the color of this lizard's skin get lighter during the day? After Porter landed a position in the zoology department of University of Wisconsin, Madison, as an assistant professor, he looked outside his field for answers. He started taking engineering courses to learn about heat transfer and other physical principles that affect animals, and eventually teamed up with two mechanical engineers to build a computer model to test how differently colored lizards would fare as the sun made its way across the sky.

"We found that brightening would extend their activity by 2 to 3 hours a day or more," Porter recalls. The lighter skin absorbed less heat, reducing the likelihood of overheating, and that translated into extra time for foraging. The result sold Porter on the value of computer modeling.

Thirty years later, this biophysical ecologist still sits down at the keyboard to predict how animals make their way through the world. His models are much more sophisticated, but the goal is the same: to understand energy transfer between an animal and its environment and how that affects the organism's behavior, survival, and distribution. Humans can use clothing, heating, and air-conditioning to extend the limits of what they can do at extreme environmental conditions. But other animals are not so lucky. They can seek food and mates only when their bodies fall within a certain temperature range. They may have adaptations, such as changing the color of their skin, that can help, or they can move into the shade or sun depending on the time of day. Yet in the end, temperature still constrains most creatures, whether they are warm- or cold-blooded.

To predict where and when animals will function, "the place to start is temperature," says Raymond Huey, an evolutionary physiologist at the University of Washington, Seattle. It's "better than any other environmental factor." Temperature constraints affect the survival of individual animals, specific populations, and even whole species. "There is a growing awareness of the valuable role that physiological knowledge can play in understanding organism-environment interactions," says Michael Kearney, a physiological ecologist at the University of Melbourne in Australia.

Such knowledge has become increasingly important given the threat of climate change. While some researchers compare historical and current records to assess how warming might affect the range of a species, modelers such as Porter make predictions in silico. "The models allow a direct connection to be made between what we measure about the physiology of an organism and climatic data," Kearney says. "It's an exciting area, and it's a relevant area because of the focus and awareness of environmental change," adds Huey.

For every hour they work at the computer running a model, researchers may spend days in the field taking measurements to validate or refute their virtual animal. Early versions of animal models needed many simplifying assumptions on matters such as the shape of the animal and straightforward scenarios to make them computationally tractable. But researchers can now incorporate many more details, making simulations much more realistic and meaningful, says Michael Sears, an ecologist at Bryn Mawr College in Pennsylvania.

The virtual animals represented by these models still have their skeptics. All models make assumptions, each of which can introduce inaccuracies that some argue add up to be significant. But more decision-makers are making use of them, says Donald DeAngelis, a U.S. Geological Survey ecologist at the University of Miami in Florida. "Models let us put the information that we have together in a rational, orderly way to make predictions about the future," he says. "Without them, all we can do is guess."

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Humble beginnings

When Porter began experimenting with computer models, his goal was simply to predict the body temperature of a lizard of a given size, weight, and color in a particular environment. His first challenge was to convert local temperature, wind speed, and sunlight data into information relevant to the lizard itself—conditions on the ground,

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and even underground. For that, Porter and his colleagues developed a microclimate model and combined its results with lizard physiological and morphological data to predict the animal's temperature under particular conditions.

To see if this crude first model reflected reality, Porter built casts of real lizards using dental wax, plaster of Paris, and aluminum and painted them to reflect sunlight just like the real animals. He placed the casts outdoors with temperature sensors and found that they were within 2°C of what the virtual lizards in his model experienced. "Warren Porter and some of his colleagues were the first people to try to do modeling really looking at the balance of energy in individual organisms," DeAngelis says. "It was a new approach at the time."

Through the years, Porter has refined and adapted his model to different animals and new situations. He gave the virtual lizards the ability to be active when their body temperature allowed it and incorporated food and water requirements to better determine how a lizard would fare under a given condition. To make the model more general, he came up with a version that had a virtual layer of insulation, akin to fur and feathers, thereby letting him study birds and mammals.

At its core, his model incorporates three aspects of energy transfer. Based on the animal's size and color, it calculates the heat loss for a particular microclimate and, consequently, what temperatures the animal experiences. Other researchers have figured out the temperature range at which many species can be active, and the model uses that information to determine how much time an animal might spend eating and drinking. This determines how many calories the virtual animal takes in and burns and the amount of water it consumes and loses, a mix of numbers that adds up to its so-called mass balance. And finally, the model looks at what Porter calls momentum balance, the energy costs of moving.

The models keep getting more sophisticated. In Porter's early work, for example, the bodies of lizards were treated as simple cylinders by the computer programs; now the simulations take into account the real shapes of organisms.

His recent look at leatherback turtles offers further evidence of how far the field has come. As these 2.5-meter-long sea turtles swim, the exertion causes their overall body temperatures to rise, so the animals need to be in water cool enough to keep them from overheating. Porter has begun to determine where in the ocean these lumbering giants are likely to be found. He starts with off-the-shelf 3D modeling and computational fluid dynamics software programs that let him simulate a 3D virtual turtle swimming through water. That simulation enables him and his colleagues to calculate the drag on the animal, which helps them formulate the energy expended by the turtle and the excess heat produced. His model calculates heat loss in different ocean temperatures and from there, the simulation spits out where the seas are cool enough for the leatherbacks.

Porter and his colleagues have applied his computer programs to many species: diving birds, tsetse flies, polar bears, whooping cranes, elk, an extinct Hawaiian honeycreeper, a rare viper in Taiwan, and tuatara, a living fossil reptile found in New Zealand. "We're in the position to design any kind of animal and put it in any place in the world and find out how much food and water it needs," Porter says. The models "are extremely detailed and work remarkably well," Huey notes.

On the rocks. Plastic models of mussels provide temperature information important for simulations of how the bivalves fare at a particular site.

CREDIT: BRIAN HELMUTH

Using Porter's research as a starting point, Melbourne's Kearney has recently broadened the scope of such modeling efforts. Working with Brian Helmuth of the University of South Carolina in Columbia, he has linked Porter's model to theories about how animals use energy and food and water for all aspects of their life history, including development, growth, and reproduction. "I can use the integrated models to understand climatic constraints on the entire life cycle and [on] population-level phenomena," Kearney says.

Helmuth studies intertidal organisms, in particular mussels and sea stars, with similar goals. "What we've been doing with terrestrial animals, he's doing with marine animals," Porter says. For Helmuth, a big challenge has been ground-truthing the models. To do that, he's developed "robomussels"—plastic devices shaped and colored like mussels to handle heat the same way—with temperature sensors inside. He's planted them at 40 intertidal zones around the world.

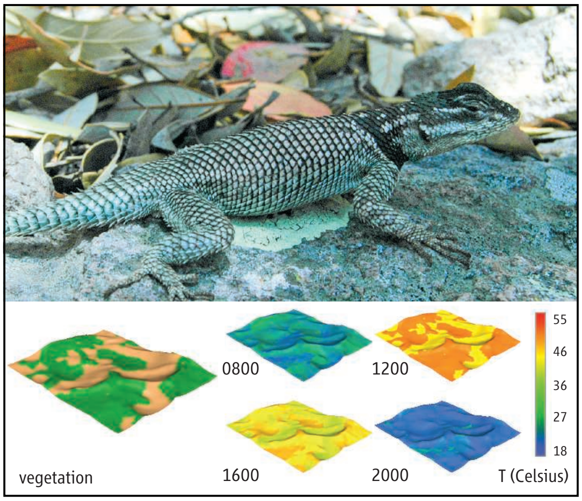
His goal is to find those places where mussels are being, or will be in the near future, pushed to their limits. And although there may not be much that people can do in the short term to stem rising temperatures globally, Helmuth says, "we may be able to ameliorate other stresses," such as pollution or overfishing, that might push mussels at a particular location over the edge. He is now trying to determine just how fine-scale he must model wind speed, cloud cover, and other factors to get the model's predictions to reflect reality. Can remote-sensing data suffice, or are on-site weather stations necessary? "How do you get the local detail that you need without getting so mired in [it] that you don't see the broad pattern," he wonders.

Getting down to spatial details

With his own biophysical models, Bryn Mawr's Sears has found that it's very important to look on the fine scale. Like Porter, he started out as a field biologist with a puzzle: Lizards living at lower elevations were smaller than lizards higher up, even though conventional wisdom held that the cooler climate at high elevations should retard physiological growth. Suspecting that the more desertlike environment lower down constrains the lizards' growth, he and Michael Angilletta Jr., a physiological ecologist at Arizona State University, Tempe, decided to determine how lizards might cope with the heat.

Their simulations and subsequent field studies showed that the hot sun did limit lizard activity, but in a more complex way than researchers had assumed. The limitations imposed by heat depended significantly on the distribution of shade in the particular lizard's environment. "The pattern of [shade] variation has a huge impact on their ability to thermoregulate," Huey says. "They've done a really nice simulation and analysis to show that."

Sears started by creating a realistic simulation of the lizard's desert habitat, which required a visit to sand dunes in central New Mexico to obtain fine-scale temperature measurements. He and his colleagues then wrote a computer program that could specify how hot each 0.5-meter-square spot would be at different times of the day, depending on where the sun was. It's a computationally intense simulation, taking nearly 24 hours to factor in all the shadowing for a 100-square-meter plot with a bumpy, complex landscape—the vegetation coverage incorporated into the model was provided by aerial photos. "They were the first to really factor in spatial [heterogeneity] on a small scale," Huey says.



Daily struggle. The Yarrow spiny lizard (*top*) must move around quite a bit to stay cool, according to simulations of how temperature changes throughout the day in its vegetation-covered landscape (*bottom, left*).

Next, Sears plops a virtual lizard of a particular size into various versions of his landscape model. In some, there are big patches of shade, as if there are few big trees; in others there are many small patches, the equivalent of small bushes. He gives the virtual animal the goal of maintaining an optimum temperature for finding food. The lizard initially finds shade, but eventually has to move on to another location because of the shifting sunlight, for example. "What our models have done is focus on where those temperatures are available in space and whether animals can actually use them," Angilletta explains.

To see if their models were valid, Angilletta and Sears spent almost 2 summers in the Chihuahuan desert in New Mexico building fenced-in 400-square-meter plots, arrayed with different configurations of shade cloth. They then released about 80 lizards into these plots and carefully monitored the lizards' movements. Their data from these plots support what the models are predicting: Lots of small patches of shade and sun are better for the animals than a few big patches.

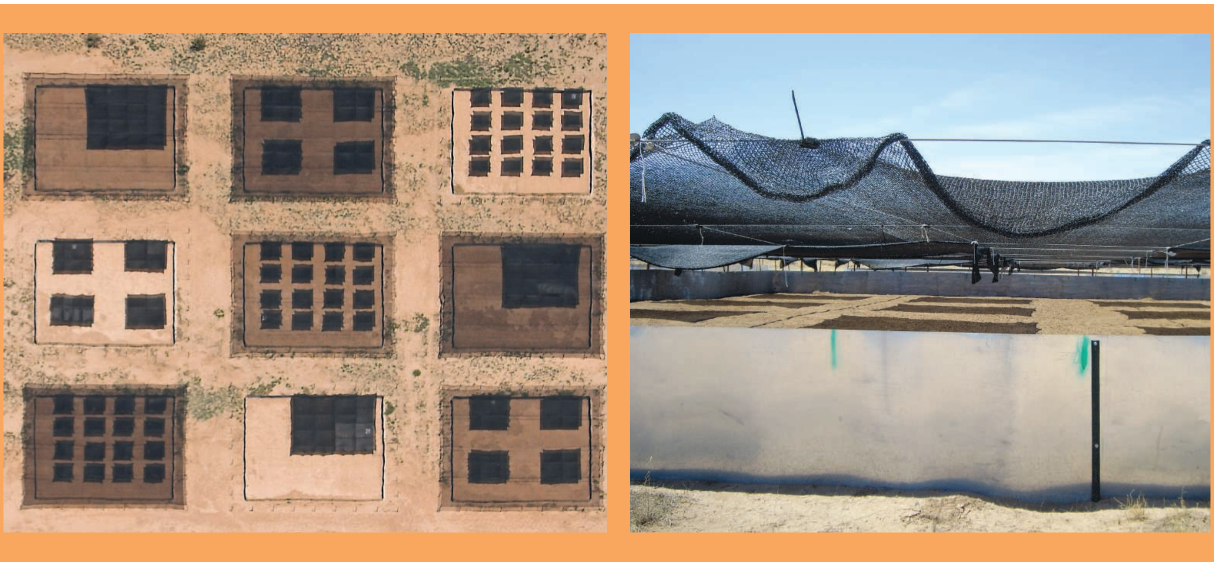
Knowing that heterogeneity of a habitat makes a difference can matter. Conservationists working to protect the dune sagebrush lizard are trying to decide where to set aside land and how to manage these conservation areas. Sears's modeling work shows that the threatened species should be able to be active 20% to 50% longer in complex habitats. "The more complex habitats are probably the ones you should focus on preserving," he says.

While Sears and other animal modelers are typically trying to simulate the current reality, when they tweak their computer programs to plug in temperature changes due to global warming, the situation can become dire for some species. "You're going to have a change in the number of places an animal can find its preferred temperature, but you are also going to have a change in where those are in space and how connected they are," Angilletta explains. For example, lizards may not be as able to reach a preferred place because they would heat up too much as they travel from one to another.

Angilletta and Sears next plan to add other aspects of lizard ecology—such as predators or rivals—to their models to see how that affects the animal's ability to keep its temperature right. And Angilletta is working on other modeling projects to come up with predictions for how an entire species can be affected by climate change. Through such modeling, "the biological consequences of environmental change are addressable, probably for the first time," Huey says.

That's a long way from simply explaining why a desert iguana changes color, but Porter says the underlying principles of the research are the same. "The computational biology is just a tool to understand what it is that makes animals work," he concludes.

–ELIZABETH PENNISI



Shade arrays. Large areas covered with different patterns of shade cloth, as seen in the aerial photo (*left*), helped researchers evaluate simulations showing the importance of diverse shading in hot environments.

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