Applications of thermal infrared imaging for research in aeroecology

Nickolay I. Hristov,[1,*] Margrit Betke[*,†] and Thomas H. Kunz[*]

[*]Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, MA 02215, USA; [†]Department of Computer Science, Boston University, Boston, MA 02215, USA

Synopsis The night sky remains a largely unexplored frontier for biologists studying the behavior and physiology of free-ranging, nocturnal organisms. Conventional imaging tools and techniques such as night-vision scopes, infrared-reflectance cameras, flash cameras, and radar provide insufficient detail for the scale and resolution demanded by field researchers. A new tool is needed that is capable of imaging noninvasively in the dark at high-temporal and spatial resolution. Thermal infrared imaging represents the most promising such technology that is poised to revolutionize our ability to observe and document the behavior of free-ranging organisms in the dark. Herein we present several examples from our research on free-ranging bats that highlight the power and potential of thermal infrared imaging for the study of animal behavior, energetics and censusing of large colonies, among others. Using never-before-seen video footage and data, we have begun to answer questions that have puzzled biologists for decades, as well as to generate new hypotheses and insight. As we begin to appreciate the functional significance of the aerosphere as a dynamic environment that affects organisms at different spatial and temporal scales, thermal infrared imaging can be at the forefront of the effort to explore this next frontier.

Introduction

Novel technologies have always been an indispensable part of the scientific enterprise and a catalyst for new discoveries. Human history is rich with examples of the impact and contribution of such tools as vehicles for the exploration of new frontiers: from the telescope and microscope in astronomy and biology to nuclear magnetic resonance in chemistry, particle accelerators in physics, and computer-aided tomography in medicine. Visual techniques and methods have been especially instrumental for the advancement of biology. The development of electron microscopy in the 1930s, for example, allowed the visualization of structures smaller than the wavelength of visible light and demonstrated in stunning detail, among other things, how form and function are integrated in nature at the microscopic level. More recently high-speed videography has revolutionized our understanding of how organisms move and interact with one another at speeds beyond the temporal acuity of our own eyes. Such tools, however, are predominantly limited to applications in the laboratory and the need remains for similar capabilities in the natural world. Field biologists are especially limited at night when even fewer tools are at their disposal. Originally developed for military use, over the past two decades, thermal infrared imaging has become increasingly available for non-military purposes (Burnay et al. 1988). Nevertheless, despite its growing use in industrial as well as in medical applications, its use in biology and especially field ecology remains limited (McCafferty et al. 1998; Kastberger and Stachl 2003; Simmons 2005; Gauthreaux and Livingston 2006; Betke et al. 2007, 2008; Horn et al. 2008).

In this article, we present examples from our successful applications of thermal infrared imaging in studies of free-ranging bats. Three specific examples were selected to highlight the use of this tool: behavioral observations, thermographic analysis of animal energetics, and censusing large colonies of bats. While these examples represent only a small subsample of possible applications of thermal imaging, they were chosen in an attempt to best illustrate the diversity, power, and potential of this tool for the study of aeroecology. As we begin to appreciate the functional significance of the aerosphere as a dynamic environment that affects organisms at a number of spatial and temporal scales, thermal imaging can be at the forefront of the effort to explore this next frontier. With this review, we hope to promote the advantages of thermal imaging and stimulate its wider adoption in ecological research.

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[1]E-mail: hristov@bu.edu
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How thermal infrared imaging works

Like all imaging approaches, thermal imaging is based on the detection of electromagnetic waves and their conversion to electrical signals for visual display. However, unlike devices that rely on measuring the radiation (visible or infrared) that objects reflect, thermal infrared cameras detect the characteristic infrared (IR) radiation that objects emit. Just like visible light, this radiation can be focused by appropriate optics and detected by specially designed sensors. The higher the temperature of an object of interest, the greater the intensity of emitted radiation and thus the brighter the resulting image (Kastberger and Stachl 2003). All objects above 0 K, emit IR radiation as a result of their molecular motion. The wavelength of this radiation ranges from 0.7 to 1000 μm (DeWitt 1988; Kastberger and Stachl 2003). The range from 0.7 to 14 μm is best suited for thermal-IR imaging and is further subdivided into near-IR (0.7–1 μm), mid-IR (3–5 μm), and far-IR (8–14 μm). Most thermal cameras operate within the mid-IR portion of the spectrum which is most appropriate for imaging in the 90–740 K range.

There are two general designs of thermal-IR cameras: cooled and uncooled, each with distinct advantages and disadvantages. Cooled cameras rely on a sealed cryogenic chamber that lowers the operating temperature of the detector array to a temperature that is much lower than ambient (typically 70–80 K). Since most objects of interest have a higher temperature, such devices have high thermal sensitivity and produce images of high thermal and spatial resolution. At the same time, cooled cameras cost more, are generally bulkier and more fragile, and require a period of time to cool before they are operational.

Uncooled thermal cameras operate at ambient temperature and convert the change in temperature of their detecting array into an electrical signal. Such designs are based on special materials (e.g., vanadium oxide, indium antimonide) that produce electrical potential when heated by the impacting IR radiation. Because uncooled cameras do not require cryogenic cooling, they are cheaper to produce and operate, more compact, and have a faster start up time. At the same time they are less sensitive, have slower thermal response, lower spatial resolution, and generally produce images of lower quality. Regardless of the specific design, most modern thermal-IR cameras are capable of storing the thermal information in digital format at frame rates ranging from 30 to 200 frames per second. Once stored, thermal images can be sampled in a number of ways to reveal the underlying temperature data that produced individual images.

Unlike images from reflectance IR cameras, which are produced by the specific pattern of incident waves reflected by the object of interest, thermal images of objects result in a stereotypical intensity pattern that is generally highest in the center of mass of the body and cooler at the periphery (Fig. 1). This results in a distinct intensity pattern that is ideally suited for analysis by computer vision algorithms, which can detect and interpret the pattern automatically. We have combined thermal imaging with computer vision processing to address the challenges of large colony census as will be discussed below.

Observing animal behavior

Vision is the dominant sensory modality in humans, allowing us to learn more about the surrounding world than we do with any of our other senses. Being able to observe visually where and how organisms behave in their environment is critical for ultimately understanding why they behave as they do and what factors affect given behaviors. While a variety of effective techniques exist for remote and covert observation of diurnal organisms in the field, far fewer options are available to researchers working with nocturnal animals. Traditional devices such as night-vision scopes, IR reflectance cameras (e.g., Sony NightShot), beam-trigger strobes, flash, and radar are restricted in their scale, temporal or spatial resolution, and thus are of limited use to researchers when detailed or prolonged observations are needed. Thermal imaging provides an effective, noninvasive alternative to these traditional methods, with few of their shortcomings.

In our research, thermal-IR imaging has been used successfully to study the behavior of large colonies of

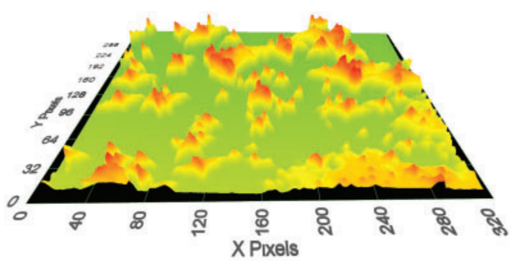

Fig. 1 A 3D representation of the thermal intensities of a thermogram showing a group of Brazilian free-tailed bats (*Tadarida brasiliensis*) in flight, contrasted against the sky. The area closest to the core of the body is warmer than the periphery, thereby producing a characteristic peak in intensity shown here in red.

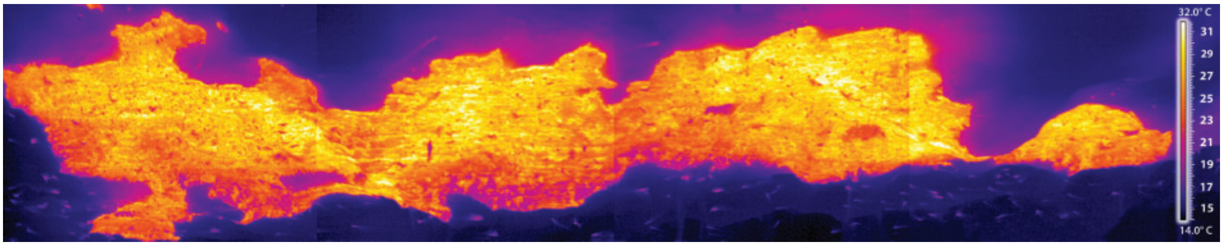

Fig. 2 A composite of four thermal-IR images showing the entire colony of 542,000 Brazilian free-tailed bats roosting in Carlsbad Caverns on September 13, 2007. Changes in the density of the roosting bats results in different surface temperature of the colony. Also visible is a thermal footprint of the recent dimensions of the colony. The physical size of the colony expands and contracts throughout the day as part of the thermoregulatory behavior of the bats. The images were recorded from the interior of the cave with a FLIR S65 camera positioned perpendicular to the roosting bats at an average distance of 28 m. The number of bats was estimated as 542,000 individuals during an evening emergence using our computer vision analysis method (Betke et al. 2007, 2008). The approximate area covered by the colony is 200 m^2.

Brazilian free-tailed bats (*Tadarida brasiliensis*) in south-central United States where this species aggregates in enormous colonies in caves during the warm months of the year. Human access to the interior of the caves may be difficult, often hazardous, and potentially disturbing to the bats (Kunz 2003). Thus, traditional observational methods are likely to be ineffective and are discouraged. Brazilian free-tailed bats typically roost in extremely dense conditions (Fig. 2) and, to emerge on the surface, individuals must navigate the interior of caves in dense formations with thousands of other individuals near them [Fig. 3; Movie 1 (see Supplementary Material)]. Researchers attempting to study the unique biology of this species face many questions such as: Why do bats aggregate in such numbers? How large are the colonies? Are the bats territorial in their roost? What triggers their nightly emergence? How often do they emerge from and return to the roost each night? Is there an order to how bats emerge from and return to their roosts? How do bats navigate the complex environments of their roosts in the presence of many other individuals? How do individual bats navigate relative to others within an emergence column or during return flights?

While earlier research has provided answers for some of these questions (e.g., mother–pup interaction, McCracken 1984; social communication, Schmidt-French et al. 2006; courtship and mating, Keeley and Keeley 2004), many questions remain unanswered. Using thermal-IR imaging, we have been able to demonstrate that the behavior of bats in the roost is highly dynamic from one night to the next as individuals change the location of the roost within the cave, as well as the shape of the colony and levels of activity throughout the day. In some parts of the roost, bats cluster densely together while in others they are spaced further apart, presumably as part of their thermoregulatory behavior [Figs. 2 and 4; Movie 2 (see Supplementary Material)]. Such arrangements reflect different thermal environments within the roost that bats seem to actively seek and ultimately influence. In addition, our observations indicate that there is no individual-specific order of emergence from the roost. Bats emerging from the dense areas within the roost often drop from the cave ceiling in large clusters [Fig. 5; Movie 3 (see Supplementary Material)]. Bats from the less dense roosting areas emerge individually, apparently by monitoring the density of flying individuals below them and taking to the wing when conditions permit.

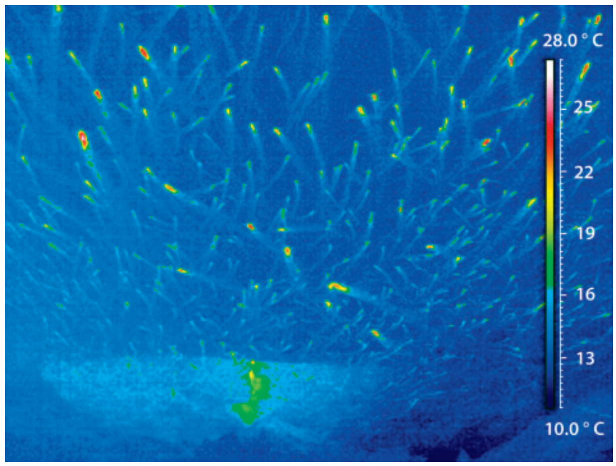

Fig. 3 Thermal-IR image showing a column of Brazilian free-tailed bats flying through the main corridor of Carlsbad Caverns during an evening emergence. The image was taken with a FLIR S65 camera positioned parallel to the direction of flight and below the emerging column. The trails behind the bats are a result of the slower response time of this thermal camera but help visualise the complex flight environment in which these bats fly. The flying bats occupy the entire width of the corridor which at this point of the cave is 27 m.

During pregnancy and lactation, reproductive adult female bats typically emerge before nonreproductive ones. Young bats generally depart later than do adults (J.D. Reichard and T.H. Kunz, unpublished data). These different cohorts, however, do not seem to map to specific locations in the roost. Thus, no spatial organization of emergence from the roost appears to exist, suggesting that the colony is structured by factors other than reproductive status or age. Observations that young bats depart later than do adults may have nothing to do with their position within the roost, but rather reflect differences in energy demands, competency in flight and development of echolocation skills (J.D. Reichard and T.H. Kunz, unpublished data).

Away from their roosts, bats maintain highly organized flight patterns in caves where emerging individuals are restricted to one part of the passage and those returning to the other with little overlap between the two cohorts [Fig. 6; Movie 4 (see Supplementary Material)]. This pattern presumably facilitates the efficient movement of many bats while they fly with reduced sonar performance (Ratcliffe et al. 2004; Gillam et al. 2007).

Thermal-IR imaging also has proven to be a valuable method for investigating the behavior of foraging bats. The aerial interactions between insectivorous bats and their prey, for example, have served as models of predator–prey interactions that have fascinated and puzzled biologists for years.

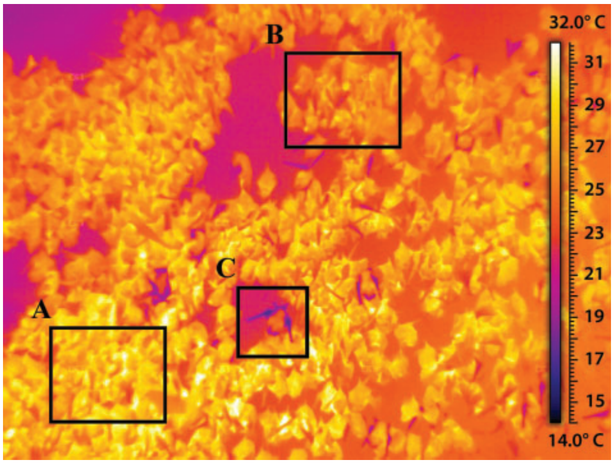

Fig. 4 Close-up thermal IR image of a section of the colony of Brasilian free-tailed bats in Fig. 2. In region (**A**) bats roost closer together and the cluster has a 3°C higher average surface temperature than region (**B**) where fewer bats are roosting. In region (**C**) a bat had just landed. Because of convective cooling during flight, the wings of this bat are 7°C cooler than the body.

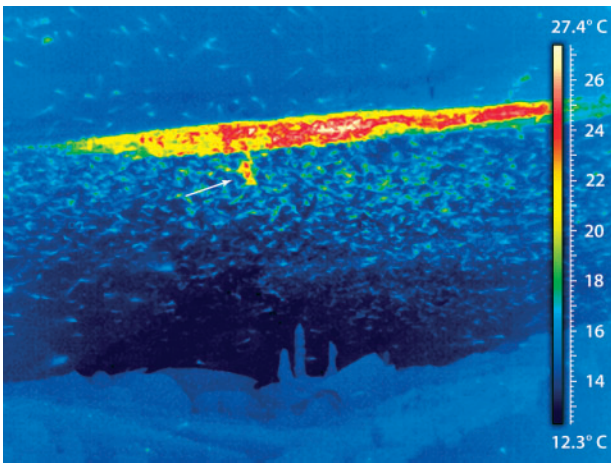

Fig. 5 Thermal-IR image showing a maternity colony of 136,000 Brazilian free-tailed bats in Carlsbad Caverns at the onset of evening emergence on October 15, 2005. The arrow points to a cluster of ~50 bats that simultaneously dropped from the ceiling. The size of the colony was estimated during emergence the previous night using our computer vision method (Betke et al. 2007, 2008).

Fig. 6 Thermal-IR image with superimposed detection and tracking algorithms, showing two-directional pattern of flight of Brazilian free-tailed bats in the interior of Carlsbad Caverns. The camera is pointed perpendicular to the directions of flight trajectories. The entrance of the cave is to the right; the roost is to the left. Emerging bats fly closer to the camera and higher in the cave corridor and field of view. Returning bats fly further away from the camera and lower in the cave corridor and camera field of view. [Movie 4 (see Supplementary Material online)]. The length of the colored trajectories behind bats are 5 frames long.

Decades of experimental work in the laboratory have provided valuable insight into how bats detect, approach, and capture their insect prey (Griffin and Webster 1962; Simmons et al. 1979; Masters 1988; Ghose et al. 2006) and how insects avoid being eaten (Jones and Rydell 2003). Few studies, however, have explored these interactions in the same detail and scope under natural conditions (Kalko 1995; Holderied et al. 2005; Simmons 2005; Holderied and Jones in press). The primary reason for the paucity of such data is the lack of adequate imaging techniques to simultaneously document the movement of free-ranging bats and insects. Using thermal-IR imaging, we have successfully filmed and reconstructed the 3D trajectories of bats in pursuit of moths (Fig. 7). Without the limitations of insufficient lighting or restricted calibrated space, such interactions can be observed in volumes of the aerosphere that extend to thousands of cubic meters versus the typically smaller ones in the laboratory, allowing us to simultaneously follow the interactions of several bats and moths for multiple capture attempts [Movie 5 (see Supplementary Material)]. Such data can be used to answer questions that have puzzled researchers for years and continue to be topics of intensive research: Do bats use a predictive or nonpredictive strategy to intercept prey (Masters, 1988; Ghose et al. 2006)? Do tiger moths (Lepidoptera: Arctiidae) jam, startle, or warn approaching bats (reviewed by Jones and Rydell 2003; Hristov and Conner 2005; Barber and Conner 2007)? Are bats sampling moths of different types in proportion to their availability, or do they select certain types more often than others? The importance of this newly available data, however, is not in single-handedly answering the questions outlined above, but rather in providing the foundation for further experimental work that can ultimately resolve them. Moreover, thermal-IR imaging easily applies to other animal systems [Fig. 8; Movie 6 (see Supplementary Material)] and provides a noninvasive tool for the accurate and unbiased view of natural behavior.

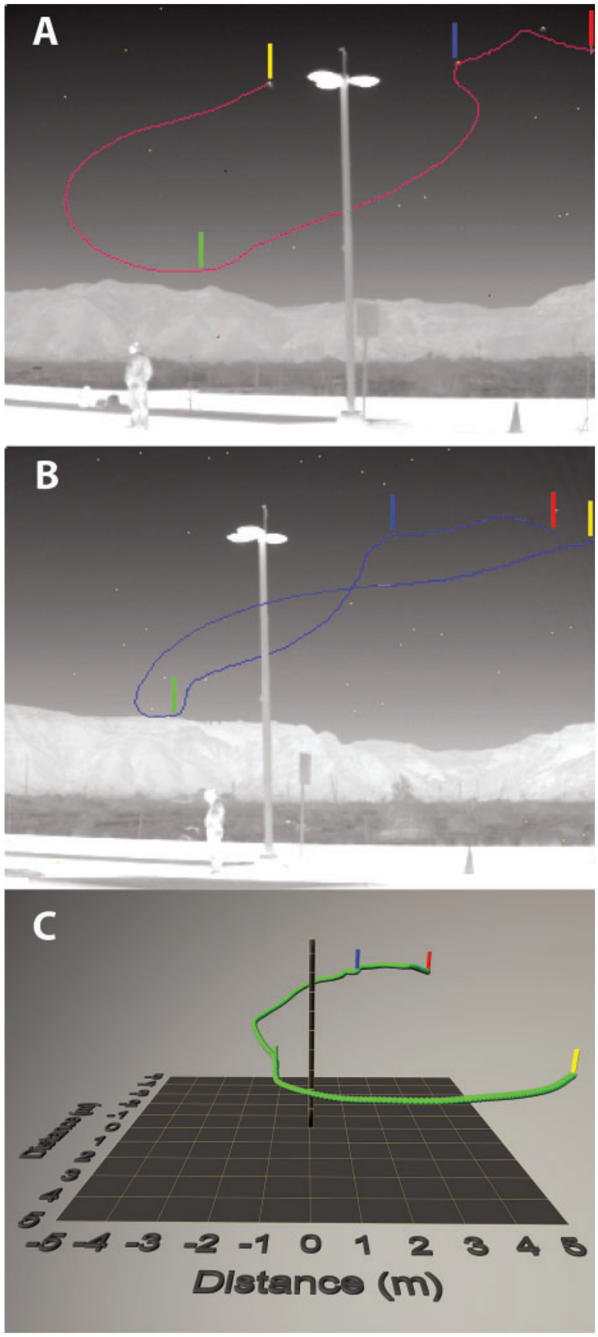

Fig. 7 The 3D reconstruction of the trajectory of a bat attempting to capture a moth near a street light in southeastern New Mexico. The reconstruction is based on images from a pair of Direct Linear Transformation (DLT) calibrated Indigo MERLIN Mid thermal cameras recording at 60 fps and synchronized manually with an external reference point: (**A**) first camera view; (**B**) second camera view; (**C**) resulting 3D reconstruction. The color bars in each image serve as reference points from the beginning of the trajectory (red) to its end (yellow).

Applications in animal energetics

Bioenergetics is another area of biology that faces significant technological challenges when studying physiological processes in free-ranging organisms. Measuring the metabolic cost of flight, in particular, has been of primary interest to biologists because flight is the most demanding form of locomotion, yet it has been adapted to a variety of thermal environments (Schmidt-Nielsen 1972; Speakman and Thomas 2003). It is technically demanding to measure the energetic costs in wild animals. Traditionally this has been achieved through one of three techniques: thermal probe telemetry, doubly labeled water (Speakman 1997), and respirometry (Voigt et al. in press).

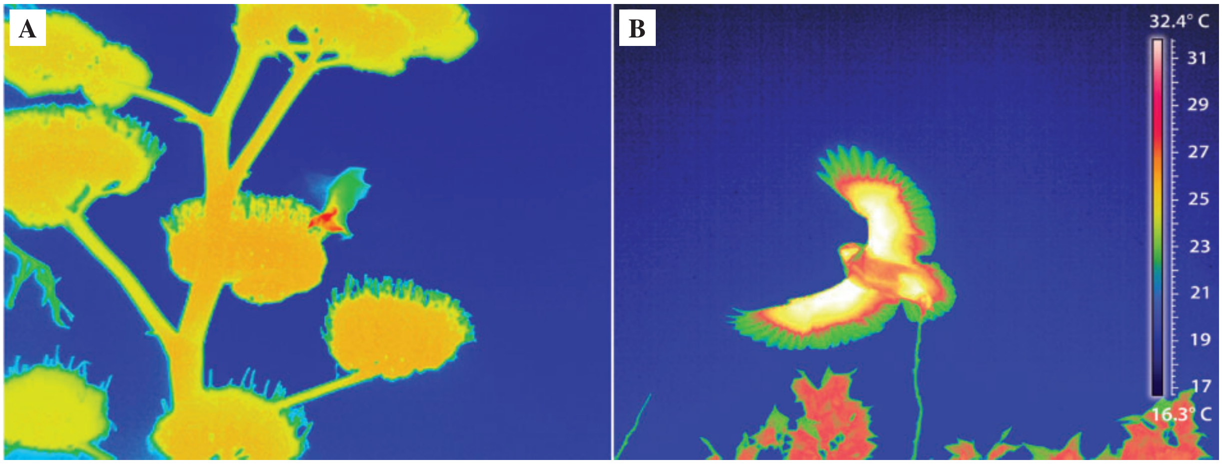

Fig. 8 Thermal IR-images of (**A**) a Mexican long-nosed bat (*Leptonycteris nivalis*) feeding on an *Agave havardiana* plant in Big Bend National Park, Texas and (**B**) a great horned owl (*Bubo virginianus*) departing from the top of a tree. Imagery such as this one makes it possible to study the free-ranging behavior of organisms that have been difficult to observe in the wild.

While these methods have been instrumental in advancing our understanding of how animals manage their energy budgets and how metabolic processes scale to size and across taxa, all three have distinct limitations. Aside from requiring contact with the subject, traditional techniques can involve the attachment of additional hardware to the subject that can affect its performance (e.g., mask respirometry, telemetry probes) or are limited to time-scales outside of the interest of the researcher (e.g., doubly labeled water cannot resolve short-term variation in the cost of free-ranging flight; Wikelski et al. 2003).

The primary advantage of IR thermography as an alternative to conventional techniques is its ability to measure the spatial variation in surface temperature to produce accurate thermal maps of large volumes of 3D space in a way that is not feasible with discrete sensors. In addition, the detection of temperatures by the camera detector is very fast (in the order of nanoseconds), thus allowing for the measurement of rapid thermal events in real time. Moreover, evaluating a thermal scene can be accomplished from a distance of up to hundreds of meters without the need to approach or handle the subject. Unlike thermal imaging used for behavioral observations and population counts, where accurate temperature measurements are not needed, and the camera is used primarily as a detection and imaging device, thermometric applications for the study of thermal physiology and energetics requires the conversion of IR radiation detected by the equipment into accurate temperature readings. The conversion of surface temperature to energy cost is not trivial since the process is affected by several factors such as the emissivity of objects, humidity of the air, distance from the camera, and exposure to solar energy. However, modern hardware and software solutions exist that correct for these variables, with minimal intervention by the user, to produce accurate temperature measurements, making IR thermography a powerful tool for the study of thermal biology in a number of different applications in the field.

In our study of bats, we have relied extensively on thermometric approaches to survey the thermal environment in which bats roost. For example, we were able to interpret our observations of the roosting behavior of Brazilian free-tailed bats in the context of the thermal environment in which they live in order to understand the spatial distribution of individuals in the roost. Thermometric measurements of the roost temperature indicated differences of up to 5°C between areas of densely roosting bats and those with fewer bats. Nevertheless, the combined presence of large numbers of individuals raises the temperature of the cave substrate in the vicinity of the roost by up to 4°C and the air immediately adjacent to bats even higher compared to the rest of the cave away from where the bats are roosting. In addition, we have demonstrated that bats roosting in small groups maintain a lower body temperature during the day than those roosting in large groups. As a consequence, individuals away from the main group are forced to abandon the maintenance of a stable body temperature and spend a significant portion of the day in torpor. Arousal from torpor can be a long and energetically demanding process as we have further shown using time-lapse thermal imaging (Fig. 9). The benefit of shared energetic cost, in combination with the high energetic demand of flight and reproduction in this species, might be one of the explanations for the highly gregarious habits of Brazilian free-tailed bats.

Censusing bats in flight

Insectivorous bats are the dominant predators on insects at night, yet, general lack of knowledge with respect to colony and population size make quantitative estimates of their economic and ecological impact difficult. One of the most prominent examples of the successful integration of thermal-IR imaging and computer-vision processing is the application of this method to the census of large colonies of bats. The aggregations of hundreds of thousands of Brazilian free-tailed bats, for example, present a significant challenge for traditional approaches to censusing. To date, only a handful of studies have attempted to make quantitative

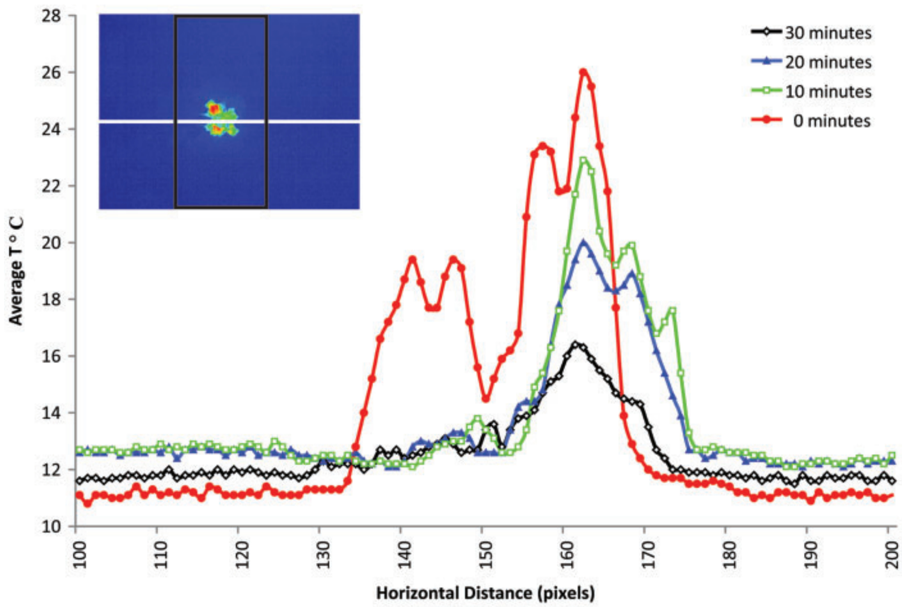

Fig. 9 Variation in mean surface temperature in a group of seven Brazilian free-tailed bats arousing from torpor over a period of 30 min prior to emergence. As the bats slowly arouse, their surface temperature increases 10°C over the 30 min time period. The images were collected using an Indigo Merlin Mid camera recording at 60 fps. The graphs were generated in Rtools v3.5.1, a FLIR analysis software, by sampling the thermal values in the image along the white horizontal line within the highlighted region.

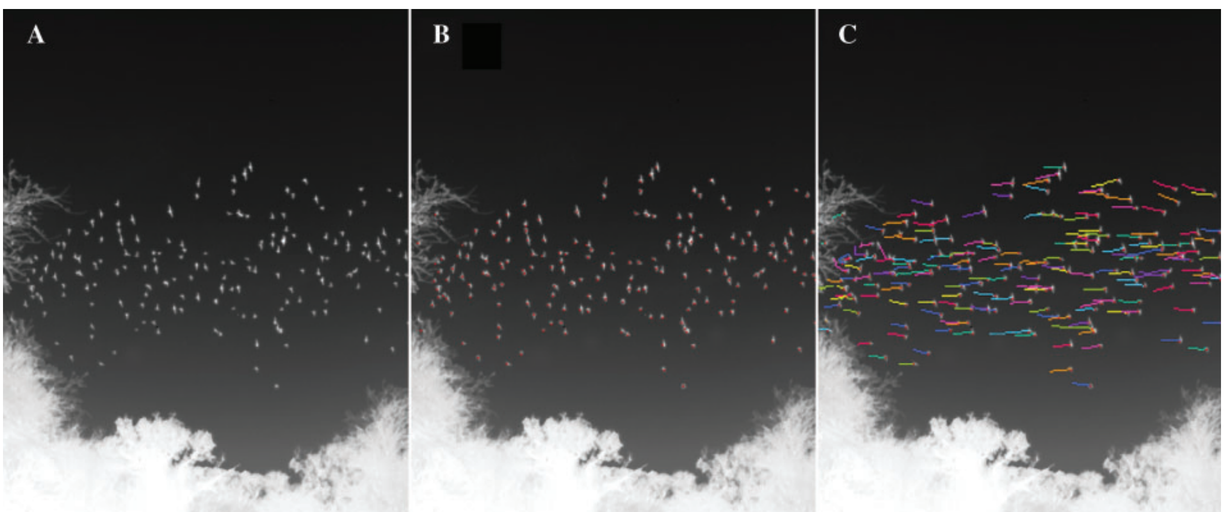

Fig. 10 Thermal IR images of emerging Brazilian free-tailed bats illustrating the application of our computer vision census method (Betke et al. 2007, 2008). (**A**) Raw thermal image of emerging bats. (**B**) Same image of bats with the object detection algorithm applied indicated by a red dot for each successfully detected bat. (**C**) Same image of bats with the automatic tracking algorithm applied showing the trajectory of each bat in the last three frames.

estimates of colony size for this and other species (Sabol and Hudson 1995; Frank et al. 2003; Betke et al. 2007, 2008). Traditional methods for censusing, such as visual counts during emergence, roost-density estimates, and mark-recapture are limited by questionable accuracy, lack of reliability, and the risk of disturbance to the bats (Kunz et al. in press).

Using advanced thermal-IR imaging and computer-vision processing, we have developed and successfully applied a new method for censusing large colonies of bats (Betke et al. 2007, 2008). In thermal IR video, emerging bats appear as bright, relatively warm objects, silhouetted against the dark, relatively cooler sky. Computer-vision algorithms use the thermal signature of bats to automatically recognize and track each individual in flight, ultimately producing a complete census of the emerging colony (Betke et al. 2007, 2008). The process is completed in two main steps. First, the algorithm detects each bat by recognizing warm regions in the field of view (typically the body) from vegetation, clouds, and other potentially warm objects in the background (Fig. 10A and B). Second, each bat is tracked by predicting its position in the current frame from the positions and velocity in previous frames (Fig. 10C). Bats successfully detected and tracked for a number of frames are then counted to estimate the total number of bats present in the colony.

Thermal imaging and computer-vision processing solve two of the greatest challenges of traditional methods for censusing bats: the dependency on ambient or introduced light, and the requirement for long and tedious analysis. For the past several years, we have embarked on a major effort to estimate the colony sizes of six of the largest and most prominent natural colonies of Brazilian free-tailed bats in south-central United States. Results from this work show that there is large variation in the size of these colonies, on a daily, seasonal, and inter-year basis, indicating that the behavior of bats is more complex and dynamic than previously thought (Fig. 11). While the nature of daily changes in the size of these colonies is not entirely clear, seasonal and inter-year fluctuations appear to be in response to local and large-scale weather patterns and their effect on insect availability. In addition, our ability to quantitatively assess the nightly emergence flights of bats has allowed us to test the validity of historic estimates for the size of Brazilian free-tailed bat colonies, and from these evaluations we have determined that previous ones were inaccurate (Betke et al. 2008; N.I. Hristov and T.H. Kunz, unpublished data).

Conclusions and future directions

Until recently, research on the behavior and ecology of free-ranging nocturnal organisms has been limited by significant technical challenges. New advances in

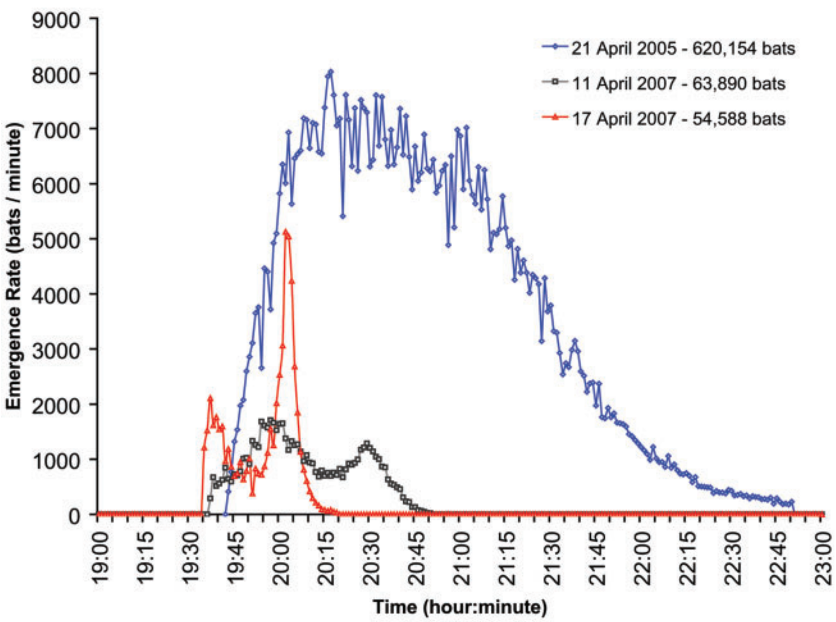

Fig. 11 Emergence profiles and estimates of colony size of Brazilian free-tailed bats at Carlsbad Caverns on three different nights April 21, 2005 and April 11 and 17, 2007, showing variation in size of colony and in emergence behavior. The total number of bats and emergence profiles were estimated during evening emergences of the bats using our computer vision analysis method (Betke et al. 2007, 2008).

affordable thermal-imaging cameras have given researchers of aeroecology one of their most powerful tools yet. The noninvasive nature of this technology is expected to stimulate application in other areas of field ecology. To realize the full potential of this tool, however, will require multidisciplinary collaboration among biologists, computer scientists, and engineers from diverse areas of expertise. For example, estimates of colony size of Brazilian free-tailed bats can be used as ground validation for NEXRAD, tracking, and vertical profiler radar to allow the successful scaling from one level to the next. Similarly, this approach can be applied to the study of large-scale bird and bat migration (Kunz et al. 2007), or to nightly or daily dispersal and foraging behavior (Horn et al. this symposium). Likewise, 3D acoustic tracking of echolocating bats can be augmented by thermal-IR imaging as a modified variation of a "visual" tracking system to permit the complete resolution of positional and acoustic data (Holderied et al. 2008). The successful integration of such diverse approaches ultimately will not only lead to refining of established ideas but also to new directions of research into the biology of birds, bats, and arthropods in the aerosphere.

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Supplementary data

Supplementary data are available at ICB online.

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