Microclimate and niche constructionism in tropical bat caves: A case study from Mount Elgon, Kenya

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ABSTRACT

Significant impacts on cave microclimate from large populations of the bat *Rousettus aegyptiacus* have been documented in three simple caves in pyroclastic rock of Mount Elgon National Park, Kenya, one of which, Kitum Cave, with few bats, acts as a control, indicating microclimatic variations in the absence of significant biological activity. Seven days of temperature logger records, and on-site mapping of rock and air temperature, humidity, and air flow provide the basis for modeling of heat, water, and CO$_2$ production and dispersion. Internal temperatures in the presence of bats in Mackingeny Cave and Ngwarisha Cave rise to ~18 °C above ambient (from ~12 °C to ~30 °C), but in the control site by only ~2 °C. Excess bat-generated energy is dissipated by conduction to rock and by ongoing air circulation, the strongest of which accompanies bat entry and exit flights. In Kitum Cave, temperatures that are substantially lower than bat thermo-neutral zone raise concern for Allee effects on long-term colony fitness: Modeling indicates that a population of at least 100,000 bats should promote colony vitality. Metabolic outputs were modeled to yield corrosional potential: At these population densities, were the caves in limestone, rates of surface denudation caused directly by metabolic outputs would be 1 m in ~80,000 yr. These results confirm that tropical bats can be effective niche constructionists, by optimizing microclimatic roost conditions, by longer-term bioerosional optimization of rock surfaces for roosting, and by long-term niche engineering through zoo-speleogenetic enlargement of roost volume.

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INTRODUCTION

Numerous authors have noted that large colonies of cave-roosting bats substantially alter the microclimate of their immediate surroundings, particularly in tropical environments, but these effects have not been well studied due to the limitations of field portable instrumentation and the inaccessibility of the roosts. Here, we report observations on tropical caves of East Africa, where these effects have been studied quantitatively.

Since an original paper in 1969 (Taboada and Pine, 1969), several authors have promoted the idea of “hot caves” as quantitatively distinct habitats in the West Indies (Sampedro et al., 1977; Rodríguez-Durán, 1995), Venezuela (Bonaccorso et al., 1992), and Dominican Republic (Tejedor et al., 2005). Roost-cave temperatures as high as 40 °C have been reported (Rodríguez-Durán, 1995). Unfortunately, some of the reported temperature and humidity values lie outside the range and/or precision of the instruments used, and these studies did not report any of the three-dimensional spatial variation in these parameters, which is known to occur. Marinkelle (1982) reported that temperatures in Mormoopid bat roosts in Colombia may reach 45 °C, but no details were provided; this “observation,” which exceeds the probable maximum thermal tolerance of the animals (cf. Rodríguez-Durán and Soto-Centeno, 2003), is almost certainly spurious. Herreid (1963) made very careful measurements of cave air temperatures around and within tight clusters of large numbers (>1 × 10⁶) of roosting *Tadarida brasiliensis* in Texas caves and reported maximum air temperatures of 28.5 °C immediately above the cluster and 41 °C within the cluster. Rock temperature under the cluster was 31 °C.

The degree to which tropical cave bats can be considered obligate niche constructionists, that is, dependent on substantially modified cave microclimate, is important for conservation planning. Obligate niche constructionists are likely to be more severely impacted by declines in colony size than facultative niche constructionists, a manifestation of the Allee effect (defined as positive effects of increased population size/density on fitness, or, the corollary, decline in fitness at low population size/density, with implications that populations may have critical levels below which they crash; Kramer et al., 2009).

Cave bats may, in some circumstances, reveal themselves as niche constructionists par excellence. Physiological processes in large bat colonies can significantly modify both the microclimate and the morphology of cave roosts, either on a mesoscale (<1 m²), for example, through the development of bell holes (Lundberg and McFarlane, 2009), and/or on a macroscale (10²–10⁶ m²), for example, large-scale passage enlargement (Lundberg and McFarlane, 2012), both of which are examples of allogenic niche engineering sensu Jones et al. (1994). These erosional forms and volumes directly increase colony fitness both by magnifying favorable microclimate effects (e.g., bell holes) and substantially increasing predator-free roosting space (large-scale zoo-speleogenesis), and they are therefore examples of an “extended phenotype,” as defined by Dawkins (1982). As with the case of another much-cited allogenic engineer, the beaver *Castor canadensis*, whose ponds create habitat for a suite of dependent species, allogenic engineering in cavedwelling bats supports entire mesoscale ecosystems of guanophagous invertebrates and their predators. These bats are therefore also keystone species (Krebs, 1985) in these cave ecosystems.

STUDY SITES

The eastern flanks of Mount Elgon, an ~4000 km², 4321-m-high stratovolcano of early Miocene age (25–10 Ma) on the border of Kenya and Uganda (Fig. 1), are penetrated, at altitudes of 2400–2500 m, by several voluminous caves up to ~150 m long, ~60 m wide, and ~10 m high. These caves, developed in pyroclastic agglomerate host rock (which forms the greatest portion of the mountain: Davies, 1952), are most famous for being regularly visited by a variety of animals, including elephants, which “mine” the rock for its sodium-rich salts (e.g., Redmond, 1982, 1992). However, the caves also host significant bat populations, which have received little attention.

Most studies of bat-cave microclimate have focused on temperate zone caves where bats seek out cool, stable conditions appropriate for hibernation (e.g., Kunz, 1982; Ransome, 1990) and where the low metabolism of the torpid bats does not significantly influence the cave climate. In contrast, large-biomass bat roosts in some tropical caves are associated with raised cave temperatures. However, studies such as those of Bonaccorso et al. (1992), which reported a temperature of 36.0 °C in a Venezuelan cave, have not addressed the spatial complexities of in-cave microclimates. The Mount Elgon caves provide a circumstance in which high biomasses of bats, typical of many tropical systems, roost in a cool, high-altitude environment, which accentuates their microclimatic impact.

In this context, we studied three caves—Kitum Cave, Mackingeny Cave, and Ngwarisha Cave—located in Mount Elgon National Park, Kenya, from 28 May to 4 June 2003, and again from 7 to 15 July 2005. Detailed cave maps and locations appear in Lundberg and McFarlane (2006). Although the caves support at least 11 species of bats (Bauer et al., 1981), the largest colonies in these caves by far (10³–10⁶ individuals) are those of the Egyptian fruit bat *Rousettus aegyptiacus*; smaller colonies of the insectivorous bat *Miniopterus schreibersi*, and isolated individual horseshoe bats *Rhinolophus clivosus* are also present. Typical body temperatures are 37.0–41.1 °C (Kulzer, 1963). They forage by night and roost by day, and they inhabit the caves year-round. Further information on their physiology can be found in Kunz (1980, 1982) and Kwiecinski and Griffiths (1999).

The research is based on the following hypotheses: (1) We would expect the greatest impact on microclimate to coincide with the largest bat populations. (2) If bat roost quality is dependent on a significantly modified cave environment, then we would expect there to be some threshold population number and/or density below which colony sustainability may be impacted. (3) If microclimatic modification is substantial, then we would...
expect this to have a significant effect in terms of corrosional potential and enhanced niche construction.

The caves can be ranked according to estimated bat populations, with Kitum having the smallest population and Ngwarisha having the largest (Reinhardt et al., 2007). The caves are similar in size and geometry. The distance from the entrance to the main bat roost area is ~110 m in Kitum Cave, ~100 m in Mackingeny Cave, and ~90 m in Ngwarisha Cave. The caves (Fig. 2) basically have the same, simple, elongated shape, culminating in a collapse chamber toward the back where bats roost. None has an internal stream, but all have small streams forming narrow waterfalls over one side of the entrance cliff. The simple

Figure 2. (A) Entrance region of Mackingeny Cave, showing the well-ventilated and simple passage form that is typical of these caves (roof height ~12 m). (B) View from the front of the collapse dome of Ngwarisha Cave, looking downslope toward the entrance. Many Rousettus individuals (disturbed from their roost further back in the cave) can be seen on the roof (roof height ~2.5 m).
geometry, development within a single level, absence of multiple entrances, and absence of in-cave stream flow greatly simplify cave climate controls. The potential air-flow routes are generally restricted to vertical circulation cells or horizontal cells. Circulation is not impacted by changes in air pressure between upper and lower entrances (Palmer, 2007; Fairchild and Baker, 2012), or by through-flow between multiple entrances (as in most tropical caves, especially flank-margin caves such as those studied in Tarhule-Lips and Ford, 1998). These caves are thus close to ideal as sites to isolate the impacts of bats on microclimate. In addition, although they house tropical species, the low mean annual temperature at the elevation of the caves magnifies the bat-mediated impacts on microclimate.

External climate is dominated by a bimodal, Intertropical Convergence Zone–driven precipitation pattern, annually delivering over 1270 mm of precipitation on the eastern and northern slopes to just over 2000 mm of precipitation on the southern and western sides of the mountain (Mugagga et al., 2012; Kansiime et al., 2013; Kenya Wildlife Service, 2014). Mean annual temperature for the region is ~16 °C (FAO, 2005; http://www.levoyageur.net/weather-city-MOUNT-ELGON-FORE.html, accessed May 2014). Muggingga et al. (2012) quoted mean minimum and maximum temperatures of 15 °C and 23 °C, respectively, but temperatures vary with altitude. Mean daily temperatures at the elevation of the cave entrances during our study period was 10.8 ± 3.8 °C (July 2005, Ngwarisha site, 2500 m above sea level [masl]) and 13.6 ± 1.1 °C (May–June 2003, Kitum site, 2409 masl). The ~2.8 °C difference is largely explained by the difference in elevation and time of year (average temperatures are ~0.75 °C higher in May–June than in July; http://www.levoyageur.net/weather-city-MOUNT-ELGON-FORE.html, accessed May 2014). Mean annual temperature for 2409 masl elevation is presumed to be 12.6 °C, which is the extremely stable condition recorded at the back of Kitum Cave for both the 2 d of record in 2003 and the 6 d of record in 2005. For Ngwarisha, we can presume that mean annual temperature is ~1 °C lower, i.e., ~11.6 °C.

METHODS

Temperatures, relative humidity (RH), and air flow were documented by a combination of data loggers deployed at key locations in the caves and spot measurements throughout the caves. The air temperature HOBO loggers (Onset Corporation) are accurate to ±0.5 °C, and the EDL loggers (Marathon Products Inc.), calibrated against a National Institutes of Standards precision mercury thermometer, are accurate to ±0.3 °C with a precision of ±0.14 °C at 27–33 °C. Loggers were set to record at 3–30 min resolution. Spot measurements were conducted for air temperature and RH using an Extech Superheat Psychrometer (documented by manufacturer as accurate to ~3% RH at 23 °C, and ±1 °C air temperature; field experience suggests that accuracy for RH is reduced as saturation is approached), for rock temperatures using a Raytek infrared thermometer (Raynger ST™, accurate to ±1 °C), and for air-flow direction and speed using a Testo hot-wire anemometer (±0.025 m/s resolution).

Areas and volumes were estimated from the surveys and cross sections (Lundberg and McFarlane, 2006) using ImageJ software (National Institutes of Health Web site: http://rsb.info.nih.gov/ij/ [accessed 26 June 2012]).

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Average temp. (˚C)</th>
<th>Highest temp. (˚C)</th>
<th>Lowest temp. (˚C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>EDL 6, Ngwarisha, control, outside cave, 2500 masl elevation</td>
<td>2005</td>
<td>10.8</td>
<td>15.2</td>
<td>6.8</td>
</tr>
<tr>
<td>Hobo 1, Kitum, control, entrance cliff, shade, 2409 masl elevation</td>
<td>2003</td>
<td>13.6</td>
<td>14.4</td>
<td>12.1</td>
</tr>
<tr>
<td>H5, Kitum, site 17, back wall</td>
<td>2005</td>
<td>12.9</td>
<td>13.3</td>
<td>12.2</td>
</tr>
<tr>
<td>H2, Kitum, site 15, back wall</td>
<td>2005</td>
<td>12.6</td>
<td>12.9</td>
<td>12.5</td>
</tr>
<tr>
<td>H3, Kitum, site 20, midcave roof</td>
<td>2005</td>
<td>12.8</td>
<td>14.1</td>
<td>11.8</td>
</tr>
<tr>
<td>H6, Kitum, site 20, midcave floor</td>
<td>2005</td>
<td>11.7</td>
<td>13.7</td>
<td>9.4</td>
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<td>Hobo 2a, Kitum, back wall</td>
<td>2003</td>
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<td>12.6</td>
<td>12.6</td>
</tr>
<tr>
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<td>Hobo 2c, Kitum, entrance zone</td>
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<td>14.9</td>
<td>11.8</td>
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<td>EDL 2, Ngwarisha, entrance west of waterfall, roof</td>
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<td>16.4</td>
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<td>EDL 2, Ngwarisha, entrance west of waterfall, floor</td>
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<td>12.7</td>
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<td>EDL 1, Ngwarisha, main bat route, floor</td>
<td>2005</td>
<td>13.7</td>
<td>15.1</td>
<td>12.1</td>
</tr>
</tbody>
</table>

Note: Data loggers EDL 3 (Ngwarisha bat roost 2005), H1 (Kitum bat roost 2005), and H4 (Kitum control 2005, outside entrance) failed. Elevation is included because Ngwarisha Cave is ~100 m higher than Kitum and Mackingeny Caves and can thus be expected to be ~0.64–1.00 °C lower average temp. The data from 2003 are shown in italics; masl—meters above sea level.
RESULTS

In 2003, one logger was set up in the shade outside the entrance of Kitum Cave as a control to record outside ambient temperature at 30 min intervals for 6 d. In 2005, two controls were set up, outside Ngwarisha Cave (EDL6) and Kitum Cave (H4), set at 3 min intervals for 6 d; however, only EDL6 gave data, so this must serve as the 2005 control for all three caves (with the extra ~100 m of elevation, the whole record for Ngwarisha Cave is likely ~0.64–1 °C cooler than for Kitum and Mackingeny). The other loggers were placed inside the caves, some directly in the bat roosts and others in parts of the caves not directly affected by bats. Temperature data are summarized in Tables 1 (loggers, air temperature) and 2 (spot, rock temperatures). Results are presented first as an overview in the context of size of bat population, and then with details for each cave.

**Temperatures and Bat Populations**

From 2003, we have 2 d of record from the highest point in the roof of Kitum Cave, but at the time of sampling, few bats appeared to be using this area (it showed evidence of having formerly been a bat roost). From 2005, we have an excellent record from the roost site of Mackingeny, but unfortunately both loggers placed in the roosts of Kitum and Ngwarisha failed (the solid state sensors are likely very sensitive to condensing conditions). While we did take many spot measurements (in order to map isotherms), bat disturbance by human presence precludes spot measurement of maximum air temperature in bat roosts (and, on the assumption that the loggers would record temperatures, we avoided disturbing the bats as much as possible). The data logger record from the roost in Mackingeny indicates a typical temperature fall of ~0.5 °C some 30 min after bat egress. The maximum spot measurement of rock temperature in the Mackingeny roost roof was 29.9 °C (recorded within a few moments of bat egress), while the air temperature had already dropped to 27.8 °C. The data logger in the roost recorded an average of 29.4 °C and a maximum of 30.4 °C. Hence, we can conclude that spot measurements of rock temperatures (but not so much air temperatures) give a good record of temperatures in the bat roosts when made shortly after bat egress.

Spot measurement of rock temperatures of the roost roof of Ngwarisha, an estimated 60–90 min after bat egress, yielded a maximum of 27.3 °C. Assuming a similar lapse rate as in Mackingeny, this would have been closer to 29 °C before bat egress. The maximum rock temperature for the roost area in Kitum Cave was only 14.1 °C (measured some 30 min after bat egress). Again, if we apply the lapse rate from Mackingeny, this would have been ~14.6 °C while bats were present.

These data indicate that roost temperatures are very significantly raised above ambient in the two caves with substantial bat populations: by at least 16.5 °C in Ngwarisha, and by ~17.6 °C in Mackingeny (assuming, for the lower-altitude caves, an average outside ambient temperature of [10.8 + 1] °C), but by only ~2.3 °C in Kitum, commensurate with its small bat population. Details of the diurnal temperature variations, the spatial temperature variations, and air-flow patterns are given next for each of the caves.

**Kitum Cave**

In this experiment to quantify the impact of bat populations on microclimate (and ultimately on corrosional potential), Kitum Cave (Fig. 3), with the smallest bat population, served as the null hypothesis example: Except for the level of biological activity in the three caves, all other factors are quasi-constant (all caves are about the same size, are in the same region, are in the same geological and hydrological setting, and have almost the same morphology). Therefore, the temperature changes in Kitum can be treated as baseline (i.e., little biogenic impact).

Kitum had the least interesting logger record (Fig. 4) and showed the least variation from the expected: That is, it had greater variation toward the entrance, grading to more constant temperatures inside the cave. Outside ambient air temperature (control) is indicated by EDL6 (red trace in Fig. 4), which was sited just outside Ngwarisha Cave, at ~3 m elevation, shaded from direct sunlight, out of the direct route of bat movement, and away from the cooling effect of the waterfall. The average temperature is consistent with air temperatures at this elevation and season. The diurnal range and simple pattern of change are also as expected, with the highest temperatures around 16:00-18:00 h, and the lowest around 08:00-09:00 h.

In Kitum Cave, temperatures in the floor of the midcave region (logger H6) show diurnal patterns commensurate with the outside air temperature but with lower amplitude; at roof level (H3), it is still more subdued and ~2 °C higher. The two sites at the back of the cave (H2 and H5) have a similar record, so only one is shown in Fig. 4) remained at a very constant 12.6/12.9 °C.
Bat ingress and egress appear to have had no effect on the back wall temperatures (H2). The two days of record from H2b in 2003, sited at the front of the main dome, remained at 14.1 °C regardless of time of day or bat behavior. However, the spot measures of air and rock temperature (Fig. 3) show two warmer regions coincidental with the one small bat-roosting area and the highest part of the central dome. Otherwise, the isotherm map shows one other warm spot, close to the entrance, where the cave wall catches the afternoon sun.

Daytime air-flow records indicated gentle air movement, usually ~20 cm/s, with air flow in the main passage tending toward preferential flow inwards at roof level and outwards at floor level and anticlockwise circulation around the collapse dome. The only site with a significant air flow was the constriction between the southern wall and the waterfall, where air flow exiting the cave at chest height was measured at ~55 cm/s, partly a result of the Bernoulli effect from the waterfall.

Figures

**Ngwarisha Cave**

The Ngwarisha Cave temperature record (Figs. 5–7) shows more complex diurnal patterns than Kitum. Figure 6 depicts a single bat exit-entrance-exit cycle, and Figure 7 shows the complete record. Outside ambient temperature is again shown as the red trace from EDL6. The sites of the data loggers are shown in Figure 5 (note that EDL3, in the bat roost area, failed).

Within the cave, distinctive diurnal patterns are apparent in the temperature data, patterns that are not simply coincidental with the external day-night cycles, and that can be directly related to bat activity:

- Each evening, bats leave the cave en masse around 20:00 h, causing immediate disturbance of air layers (average air flow during bat flight measured in midcave region was 1.2 m/s, with gusts up to ~1.6 m/s, which brings it up to a “light breeze” on the Beaufort scale). A strong outflow of warm air to the western side of the entrance is apparent as a sharp warm spike at EDL2 (floor), sited at floor level to the west of the entrance waterfall. A synchronous influx of cold air at roof level at the eastern side is apparent as a sharp dip at EDL1 (roof), sited in the roof on the main bat exit route, and this can be felt as a strong incoming draft of cold air. Note that the strong air movement engendered by the bat flight is dominant over air density in controlling where the air flows. The emergent mass of bats forces cooler air back into the cave, triggering a counterclockwise air flow that displaces the warm air from the roost area.
- Roof air at EDL1 (roof) then settles over next 2 h and gets warmed from the cave walls. In the absence of bats, this cools gradually over the course of the night. The air at EDL2 (roof and floor), closer to the entrance and on the west side of the waterfall, cools down more rapidly, closely mirroring the outside temperature lapse.
- Returning bats at around 07:00 h trigger another short-lived disturbance, evident mainly in the sharp cold spike at EDL1 (roof) site, accompanied by a sharp warm spike in EDL2 (roof).
- It takes only about 1 h for the settled bats to warm the air at roof level inside the cave (EDL1, roof). Undisturbed roosting keeps air at generally stable high temperatures for 2–4 h. Increasing bat activity (e.g., periodic flying, socializing, grooming; Kwiecinski and Griffiths, 1999) creates more variable and higher roof air temperatures until the 20:00 h emergence time.

The 3 d of record from the floor level at EDL1 are similar to the control record, indicating that the impacts of bat roosting and movement are here most significant at roof level and not so apparent at floor level.

The isotherm map (Fig. 5) and maximum-minimum temperatures (Table 2) indicate that the focus of energy concentration
Figure 5. Isotherm map of Ngwarisha Cave. Data logger sites are shown as black squares. Main air movement during bat emergence is shown as heavy dashed arrows.
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coincides with the main bat roost and that within this one small, dry cave, the temperature ranges from under 10 °C to just over 27 °C (i.e., more than double the mean annual temperature, and, as noted already, this range has to be conservative since it was recorded after bat exodus).

Daytime air-flow measurements show a very similar pattern to that in Kitum Cave: The main air flow is in the center of the main passage (~20 cm/s), with little air movement in the low parts of the cave close to the walls, and counterclockwise circulation around the main collapse pile (increasing during bat flight to ~50 cm/s). The waterfall over the entrance did not appear to affect air flow.

Mackingeny Cave

The record from Mackingeny Cave (Figs. 8–9) is the most interesting because it includes data from the bat roost. Temperatures in the roost at roof level (EDL5) averaged 29.4 °C, a remarkable 17.6 °C above outside ambient temperature of 11.8 °C (i.e., EDL6 average plus 1 °C), never falling below 27.9 °C. The periodic relatively small, but sharp, changes in temperature can be directly correlated with bat activity: Each evening, temperatures drop with bat egress (cooler air is forced backward to replace the warm roost air) and then gradually drop further until ~07:00 h, and each morning, after bat entry, they rise. They never drop as far as ambient temperature, nor even as far as any of the other parts of the cave, suggesting that, although considerable mixing takes place, the air is not completely exchanged during bat flight (an observation that is relevant to our modeling experiments; reported later herein).

The sensor EDL4 was placed on the right back wall of Mackingeny Cave in a very similar situation to the placement of H5 in Kitum Cave. Both were in a remote corner, out of the bat roost area, and presumed to be out of the range of influence of bat activity. Both were close to the layer of green clay that was observed to constantly ooz ground water (Lundberg and McFarlane, 2006), and both were expected to show similar records. All the records from the back wall of Kitum (H5, H2 from 2005 and Hobo 2a from 2003) showed the same, almost unvarying trace between 12 °C and 13 °C. The greater range of variation at the Mackingeny back wall (almost three times that of the Kitum back wall) indicates that no part of this cave is immune to the influence of the substantial bat presence.

Mackingeny Cave is narrower than Ngwarisha and Kitum, and the collapse pile is a little more pronounced. The isotherm map (Fig. 8) shows the same simple pattern as in Ngwarisha Cave, with the greatest concentration of energy at the roost site, but here the temperature gradient is steeper. Air tends to circulate...
Mackingeneny Cave plan
Isotherm map and climate sampling sites
Friday, 8th July 2005, morning-midafternoon

**Legend**
- Edge of undercut
- Collapse slabs on floor
- Extended long section
- Standing water
- Wet mud, shallow puddles

**Isotherm classes (°C)**
- 9.0-12.9
- 13.0-16.9
- 17.0-20.9
- 21.0-24.9
- 25.0-28.9

Figure 8. Mackingeneny Cave isotherm map and data logger sites.
by convection along the roof and floor more than by circular flow. Daytime observations showed incoming air at roof level and outgoing air at floor level, with flow rates around 20 cm/s. As in the other caves, the extremities have little to no air flow. Air flow approaching the bat roost area recorded during bat movement was ~35 cm/s incoming at low level and ~25 cm/s outgoing at roof level (but generally very variable). We also observed a counterclockwise component during the bat disturbance caused by our presence. This is likely more pronounced at dusk when the whole roost is mobilized.

MODELING CLIMATIC IMPACT OF BAT PRESENCE

For this part of the research, we wanted to understand the energy changes and microclimatic modification resultant from the large/dense bat populations. We also wanted to understand why Kitum Cave is so much less impacted than the other two caves, and predict whether the Allee effect may be operating here. Third, we wanted to estimate the potential for larger-scale niche modification in terms of geomorphological activity that might be caused by these bats, were the caves in limestone.

Modeling Metabolic Outputs

Reinhardt et al. (2007) published very rough estimates of bat populations for the three caves, but without good aerial survey control. The estimates we present here in Table 2, with good survey control, are more conservative. We based our estimate of the population of bats, as they did, from photographs of the roosts. At maximum density, the bats averaged 82% coverage of the rock face, with a packing density of 400 bats/m² (McFarlane and Lundberg, 2009). This estimate of maximum density is exactly the same as that by Reinhardt et al. (2007). The difference in the population estimates is in the density assumed for the whole roost and the total roost area. We assume that only half of the roost is at maximum density, so we use an average density of 250 bats/m². This yields, for Mackingeny Cave with a roost chamber 113 m² in area, a total population of ~28,250 bats.

For energy output estimates, we used the average of the two basal metabolic rates (BMR) quoted in Kwiecinski and Griffiths (1999): 0.895 cm³ O₂/g bat/h. The energy output for this population of *Rousettus* bats, with an average body mass of 130 g, is 18 J/g bat/h, or 2.34 kJ/bat/h. For the Mackingeny population,
this gives 585 kJ/m²/h, or, from the whole colony for the whole 12 h roosting period, 792,795 kJ/d (Table 3).

CO₂ output (Table 3) is also calculated using the BMR. Each bat produces 2.74 g CO₂ during the 12 h roosting period. At a density of 250 bats/m², the total output per day for the Mackingeny population is 77.5 kg.

In a similar way, water output is estimated (Table 3). Average daily evaporative water loss is quoted in Kwiecinski and Griffiths (1999) at 28% of body mass (which is ~36 g). However, during roosting, this is considerably lower, so it is more appropriate to use the evaporative water loss equation from Studier (1970). Water output during the 12 h roost period is 5.24 g H₂O/bat/d, and the total output for the whole Mackingeny roost is 148 kg H₂O.

Modeling Energy Dispersion

The region of microclimate modification (and therefore niche construction) and dissipation of energy, CO₂, and H₂O is in the immediate vicinity of the roost, and in the surrounding chamber at the back of the cave. Toward the entrance, the outer part of the cave is more open to external air circulation and thus is not directly affected by bat presence. The modeling presented here was initially based on the Mackingeny Cave roost and then applied to the other two caves. Temperature data used in the modeling are shown in Table 4.

What Happens to the Energy?

The energy produced by the bats is dissipated in stages. It warms the air in their immediate vicinity and the rock surface in contact with the roost. The warm front then expands to warm more of the surroundings, in the roost itself and beyond, with the extent of heating indicated by the isotherm maps. On a typical day (e.g., 10 July 2005), the record from EDL5, in the Mackingeny roost (Fig. 9), shows the first stage of rapid temperature rise lasting ~1 h, from 06:38 h (28.8 °C) to 07:26 h (29.9 °C) at a rate of 1.38 °C/h. This stage includes the time required for all the bats to enter and settle down, and the time required to heat the rock surface and the air in the roost. The second stage of slower temperature rise lasts ~6.5 h, until 13:59 h (30.1 °C) at a rate of 0.03 °C/h. During this stage, the loss of heat into the rock has reached equilibrium, and the extra heat disperses out into the surroundings (which for convenience, we call “the bubble of warmth”). The third stage is the stable stage, lasting ~6 h, where temperatures remain relatively constant until the bats leave at ~20:00 h. This is the time when the rate of energy production and dissipation is at equilibrium.

Initial Stage of Loss of Energy by Conduction through Rock

Energy is conducted through rock over the surface area of the roost, integrated over the time of roosting. The Mackingeny roost record indicates that temperatures rise to 30.1 °C (14:00–20:00 h average) during the 12 h roost period and fall to 28.2 °C (22:00–06:00 h average) in the intervening 12 h foraging period. Using values for thermal conductivity (k) of pyroclastic rock of 1.0204 W/m·°C, density (ρ) of 2099 kg/m³, specific heat (Cp) of 1120 J/kg·K, thermal diffusivity (α) of 4.34 × 10⁻⁷ m²/s (as measured on very similar pyroclastic rocks of India by Krishnaiah et al., 2004), rock surface temperature during roosting of 30.1 °C (Ts), initial rock temperature before bat arrival of 28.2 °C (Ti), and heat flux from bats of 162.4 J/s·m², we can calculate the total integrated heat transferred to the rock over the roost period (Matthew Johnson,

<table>
<thead>
<tr>
<th>Cave</th>
<th>Total (bat/d)</th>
<th>Total (m²/d)</th>
<th>Mackingeny (total roost/d)</th>
<th>Ngwarisha (total roost/d)</th>
<th>Kitum (total roost/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total (kJ)</td>
<td>0.00274</td>
<td>0.00524</td>
<td>792.795</td>
<td>2,806.353</td>
<td>287.651</td>
</tr>
<tr>
<td>CO₂ output (kg)</td>
<td></td>
<td></td>
<td>77.5</td>
<td>274.2</td>
<td>28.1</td>
</tr>
<tr>
<td>Water output (kg)</td>
<td></td>
<td></td>
<td>148</td>
<td>524</td>
<td>54</td>
</tr>
</tbody>
</table>

Notes: Roost temperatures used here are the observed temperatures taken from spot measurements adjusted for lapse rate since bats left (1.0 °C/h, as recorded by data logger in Mackingeny roost): ~30 min for Kitum, ~5 min for Mackingeny, ~60–90 min for Ngwarisha.
2014, personal commun.) as \( k(T - T_0) \sqrt{\text{par}} \) or 726 kJ/m². For Mackingeny, this yields 77,993 kJ of heat transferred to rock and thus 714,802 kJ transferred to the air (Table 5). Assuming the same roost temperatures for Ngwarisha, the respective numbers are 276,081 kJ and 2,530,272 kJ. For Kitum, if we assume a roost temperature of 14.3 °C by day and cooling back down to the average measured by loggers at the back of Kitum Cave (an unvarying 12.6 °C for the 2 d of record in 2003 and the 6 d in 2005), then 25,320 kJ of heat is transferred to rock, and thus 262,331 kJ is transferred to the air.

**Heating the Air in the Roost and Surroundings**

The excess heat not used for conduction to rock goes to raising the roost air temperature and subsequently moves outwards from the confines of the roost to the region of raised temperatures as shown in the isotherm maps. These maps were produced from daytime measurement when the bats were roosting; as discussed already, the temperatures measured in the roosts proper are a little conservative because of bat disturbance, but the non-roost areas are well represented, and they clearly show the extent to which the energy is transmitted to other parts of the caves. The bubble of warmth (delineated by the >13 °C isotherm) occupies ~80% of the volume of Mackingeny and Ngwarisha but is very small in Kitum.

The modeling seeks to explain the pattern of cave temperatures in relation to outside air or mean annual temperatures. We considered three volumes (Table 4):

1. the roost alone;
2. the back half of the cave (plus roost), where we would expect the most impact from energy output (for Mackingeny and Ngwarisha, this is delineated by the edge of the collapse pile and passage constriction; for Kitum, we used the small bubble of warmth, the only area demonstrably affected by bat-generated warmth); and
3. the 80% of the cave volume occupied in Mackingeny and Ngwarisha by the bubble of warmth (but not significantly warmer than mean annual temperature in Kitum).

The temperature rise caused by energy output during each roost period can be estimated, starting with the simple (but unrealistic) case of no air exchange during the 12 h roost period. For calculations of energy required to heat air, we used values for specific heat of air at 30 °C of 1.005 kJ/kg·K and density of 1.1 kg/m³ (http://www.engineeringtoolbox.com/, accessed June 2014). The excess energy was first applied to warming the air in the roost alone. As can be seen from Table 5, these numbers are unreasonable, confirming what we already know—that the energy is not confined to the roost. The fact that the Mackingeny roost temperatures rise only ~2 °C over the roost period indicates that almost all of the energy produced by the bats must be dispersed. Since conduction to rock, radiation to air, and convection alone are local to the roost and minor (radiative heat loss from 113 m² mass of bats at 36 °C to air at 29 °C is only ~0.6 kJ over the whole roost period; it would go up to ~90 kJ if air were at 12 °C, as in Kitum Cave), we conclude that most of the energy dispersion has to be by air exchange.

**Air Exchange Rates**

For the second stage of the modeling, we added air exchange rates. We can calculate the volume of air required to disperse the energy in order to achieve the observed temperatures in the different parts of the caves, and we can change the temperature of the incoming air, for example, to the average outside ambient temperature, or to the average outside temperature during the periods of strongest air flow—the bat flight times. The average outside air temperature at bat exit time (~20:00 h) at the control site was ~11.7 °C (average of temperatures from 19:30–20:30 h, 8–16 July 2005). Since average ambient, mean annual, and average bat exit time temperatures

<table>
<thead>
<tr>
<th>Cave</th>
<th>Area: Roost alone (m²)</th>
<th>Area: Back of cave (m²)</th>
<th>Area: 80% (m³)</th>
<th>Volume: Roost alone (m³)</th>
<th>Volume: Back of cave (m³)</th>
<th>Volume: 80% (m³)</th>
<th>Heat required to raise air temp by 1 °C: Roost alone (kJ)</th>
<th>Heat required to raise air temp by 1 °C: Back of cave (kJ)</th>
<th>Heat required to raise air temp by 1 °C: 80% of cave volume (kJ)</th>
<th>Energy remaining after loss to rock conductance (kJ)</th>
<th>Temp rise if all the energy stays in the roost area (°C)</th>
<th>Temp rise if energy is spread to back of cave (°C)</th>
<th>Temp rise if energy is spread to 80% of cave volume (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mackingeny</td>
<td>113</td>
<td>2140</td>
<td>4600</td>
<td>503</td>
<td>9345</td>
<td>25,904</td>
<td>556</td>
<td>10,331</td>
<td>28,637</td>
<td>792,795</td>
<td>1285</td>
<td>69</td>
<td>25.0</td>
</tr>
<tr>
<td>Ngwarisha</td>
<td>400</td>
<td>4203</td>
<td>6438</td>
<td>3091</td>
<td>14,680</td>
<td>28,756</td>
<td>3417</td>
<td>16,228</td>
<td>31,790</td>
<td>2,806,353</td>
<td>740</td>
<td>156</td>
<td>79.6</td>
</tr>
<tr>
<td>Kitum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8500</td>
<td></td>
<td></td>
<td>63,008</td>
<td>2,530,272</td>
<td>287,651</td>
<td>676</td>
<td>68.0</td>
</tr>
</tbody>
</table>
are all very similar, only the average ambient temperature was used. The average outside air temperature at bat entry time (~07:00 h) was ~8.5 °C, and the average daytime temperature at the control site, from 10:00 h to 18:00 h, was 12.3 °C (for both, 1 °C higher was presumed for Kitum and Mackingeny). The 80% volume represents the minimum volume of heated air observed in Mackingeny and Ngwarisha. Obviously, the larger the volume of air exchanged and the colder the replacement air, the greater is the dissemination of energy: For example, if only the roost volume is exchanged, then many exchanges (of the roost air) are required to reduce the energy level in the roost, whereas if the whole 80% volume is exchanged, only a few exchanges (of the 80% volume) are needed. Table 6 shows the number of exchanges of air that are required to simulate the required temperatures, assuming different starting temperatures for the replacement air (e.g., 4.3 exchanges of 80% volume is required for Mackingeny Cave to keep the average cave temperature 5.8 °C above ambient air temperature).

We now need to see if these rates of exchange would be possible using the observed rates of air flow. Mackingeny Cave has the simplest cross section and an obvious restriction between the main passage and the back of the cave. Passage cross section is ~450 m², of which ~350 m² is used for air flow (the sides having limited circulation). Anemometer readings in the main passage indicated ~20 cm/s incoming air flow at floor level and ~20 cm/s outgoing air flow at roof level, so we modeled flow through half the cross section. Flow rate of incoming/outgoing air is thus ~35 m³/s. At this flow rate, the 80% volume would be flushed in ~12.3 min, allowing ~5 exchanges per hour (which alone would be sufficient to achieve the temperatures observed), or ~58 per roost period. If, instead, we use the average air velocity for the main passage, 13 cm/s, the number of exchanges goes down to 1 per 19 min, 3.2 per hour, or 38 per roost period. Since the greatest rate of exchange is likely during bat flights, we can expect a minimum of two exchanges in addition to those estimated from the average daytime air flow.

### Table 6. Calculation of number of air exchanges (of each appropriate volume) required per roost period to disperse enough metabolic energy to yield the observed temperatures

<table>
<thead>
<tr>
<th>Temp. of incoming air</th>
<th>Mackingeny</th>
<th>Ngwarisha</th>
<th>Kitum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Average ambient</strong></td>
<td>No. exchanges required to keep roost ~18 °C above ambient</td>
<td>No. exchanges required to keep roost ~18 °C above ambient</td>
<td>No. exchanges required to keep roost ~2.5 °C above ambient</td>
</tr>
<tr>
<td>(11.8 °C for K&amp;M, 10.8 °C for N)</td>
<td>71</td>
<td>41</td>
<td>270</td>
</tr>
<tr>
<td>No. exchanges required to keep back of cave ~8.5 °C above ambient</td>
<td>8</td>
<td>16</td>
<td>40</td>
</tr>
<tr>
<td>No. exchanges required to keep 80% of cave ~5.8 °C above ambient</td>
<td>4.3</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td><strong>Average daytime air</strong></td>
<td>No. exchanges required to keep roost ~16.6 °C above daytime</td>
<td>No. exchanges required to keep roost ~16.5 °C above daytime</td>
<td>No. exchanges required to keep roost ~1.0 °C above daytime</td>
</tr>
<tr>
<td>(12.3 °C for N, 13.3 °C for K&amp;M)</td>
<td>77</td>
<td>45</td>
<td>620</td>
</tr>
<tr>
<td>No. exchanges required to keep back of cave ~7.0 °C above daytime</td>
<td>10</td>
<td>19</td>
<td>340</td>
</tr>
<tr>
<td>No. exchanges required to keep 80% of cave ~4.3 °C above ambient</td>
<td>5.8</td>
<td>5</td>
<td>140</td>
</tr>
<tr>
<td><strong>Average dawn air, at bat entry time</strong></td>
<td>No. exchanges required to keep roost ~20.4 °C above dawn air</td>
<td>No. exchanges required to keep roost ~20.3 °C above dawn air</td>
<td>No. exchanges required to keep roost ~4.8 °C above dawn air</td>
</tr>
<tr>
<td>(9.5 °C for K&amp;M, 8.5 °C for N)</td>
<td>63</td>
<td>37</td>
<td>17</td>
</tr>
<tr>
<td>No. exchanges required to keep back of cave ~10.8 °C above dawn air</td>
<td>6.4</td>
<td>13</td>
<td>1.5</td>
</tr>
<tr>
<td>No. exchanges required to keep 80% of cave ~8.1 °C above dawn air</td>
<td>3.1</td>
<td>7.1</td>
<td>8.4</td>
</tr>
</tbody>
</table>

Note: Roost exchange alone is shown in italics because it is not logistically possible. The most likely scenarios, exchange with air at ambient temperature or at daytime temperature, are marked in bold. K&M—Kitum and Mackingeny; N—Ngwarisha.
Kitum has no obvious restriction in the main passage. Cross-sectional area ~40 m in from the cliff line is 246 m² (excluding the dead air at the sides). At average flow rates of 7 cm/s, exchange of 80% volume would take 86 min, i.e., only 8.4 exchanges per roost period. In this cave, the small bat flight would not greatly enhance rates of air exchange.

The question can now be answered of whether the extra bat-produced energy not lost to rock heating can successfully be dispersed by air exchange. The results for roost exchange alone are not useful since such a scenario is not logically possible: If only roost air is exchanged, then it would have to be only with the bubble of warmth, which is not likely to be at ambient temperature unless it had also been exchanged with outside air. Exchange with dawn air is not possible throughout the whole roost period, so it also is not so realistic (but the exercise is valuable because at least one exchange is likely at dawn). Exchange with air at average ambient temperature is more likely, and exchange with daytime air is most likely. Exchanging 80% of cave volume is the only real option, since the bubble of warmth (for Mackingeny and Ngwarisha) shows that at least 80% of the air is warmed. For Kitum Cave, reproducing the observed temperatures is feasible only if exchange is with cold air (i.e., ambient or dawn air, 8 or 1.5 exchanges needed, respectively). For Kitum, it is never possible to dissipate the bat-generated energy by exchange with daytime air alone because the average air temperature in Kitum is ~1 °C lower than the average air temperature.

The fact that the cave temperatures in the main passage of Kitum are below daytime temperatures implies an additional sink for energy. This cave has a large area of standing water/wet mud (420 m²) on the northern side of the main passage that loses energy through evaporation. We used data from 24 measurements at three sites in and beside the mud to calculate evaporative heat loss. Using air flow of 0.030 m/s, water temperature of 11.8 °C, air temperature of 12.0 °C, RH of 82%, and barometric pressure of 70 mbar, evaporative heat loss can be estimated at 24,480 kJ/h (http://www.engineeringtoolbox.com/evaporation-water-surface-d_690.html, accessed June 2014). Since ~250,000 kJ is required to cool the volume of air in the front of the cave by 1 °C, and natural air circulation changes the air ~8 times in 12 h, this rate of evaporative heat loss is about right to keep the main passage 1 °C lower than the incoming daytime air.

In summary, Mackingeny requires 4.3 and 5.8 exchanges, respectively, for air at mean ambient or daytime temperature and can generate 38–40 exchanges; Ngwarisha requires 9 and 12.5 for the same and can generate 13–14 exchanges; Kitum requires 8 exchanges with air at ambient temperatures or 1.5 with air at dawn temperatures and can generate 8.4 exchanges. So, we can conclude that the bat-produced energy can effectively be dispersed by air exchange. Although relatively crude, this modeling suggests that conduction to rock and air exchange explain most of the energy expenditure and observed temperatures in the caves. Energy is produced in the roost, but dissipated, thereby effecting niche modification throughout the whole of the back of the cave (for Mackingeny and Ngwarisha). The strongest air exchanges are most likely to occur during times of bat entry and exit, with more stable conditions throughout the rest of the day.

Roost Temperatures and a Possible Allee Effect

The observed difference of temperature in the roosts versus the mean annual temperature (only ~2 °C higher for Kitum, but ~17–18 °C higher for the other two caves) indicates the substantial difference in microclimatology among the three caves. The similarity of Mackingeny and Ngwarisha suggests that both have population densities and totals that are sustainable for the bats. The low temperatures in Kitum indicate that the bat population is simply too small to be able to substantially heat a cave of this size (given that air exchange rates are no greater than the other two caves).

Kwecinski and Griffiths (1999) indicated that the thermoneutral zone for *Rousettus aegyptiacus* is 31–36 °C. These bats are adapted to a warm climate and can effectively dissipate heat. However, at temperatures below the thermoneutral zone, oxygen consumption and energy expenditure have to increase, reducing colony fitness. Our field observations in Kitum Cave indicated a lot of old, weathered guano in places where roosting would be expected, suggesting that the bat population may have formerly been higher. Kitum Cave is by far the most heavily visited cave in Mount Elgon National Park, and the accessibility of the roost areas probably encourages regular disturbance. The bat populations in the other two caves appear to be healthy and robust. Therefore, we assume that roost temperatures of ~29 °C are optimal, but we do not know the threshold for long-term population viability. Allee effects (Gregory and Jones, 2011) may be in operation in Kitum Cave, reducing the population’s capacity for recovery. Coupled with the serious human health threats associated with *Rousettus* roosts (e.g., Kalunda et al., 1986; Amman et al., 2012), protecting the further reaches of Kitum cave from visitor disturbance ought to be a cave management priority.

We have used our model to work out the minimum population size required for temperatures to rise in Kitum Cave to similar levels as in Mackingeny and Ngwarisha (i.e., 80% of the cave at least 5 °C above daytime air, or 7 °C above ambient air) and assuming 8 air exchanges per roost period. Assuming a density of bats comparable with the other caves (namely 250 bats/m² on average), a cave the size of Kitum would have to have a roost area of 400–550 m² and a population of at least ~100,000–130,000 bats to have cave temperatures closer to the thermoneutral zone of *Rousettus*. 
MODELING CORROSION POTENTIAL CAUSED BY BAT PRESENCE

The final part of the modeling was to estimate how the microclimatic modifications caused by this level of bat colonization might in turn cause larger-scale niche modification by corrosion of host rock. While corrosional effects directly attributable to bat presence can be seen even in this pyroclastic rock (for example, a tiny roost in Kitum Cave antechamber above a small guano pile shows surface corrosion to a depth of some 10 cm; Fig. 10), it is easier to envisage and model corrosion in limestone. For this part, we calculated rates of erosion that would apply were the rock type limestone, again using Mackingeny as the case example. Knowing the rate of water loss from the bats, and typical rates of air exchange, we can calculate the thickness of water film that can condense on surfaces, and, from this, the rate of potential corrosion.

Table 3 summarizes the metabolic outputs. Chemical weathering of all rocks, but in particular of carbonate rocks, is enhanced in CO₂-acidified water. This is the basis for arguing that the long-term presence of bats will cause geomorphological effects that generally increase niche suitability and size, thereby improving long-term colony fitness. Examples range from the small-scale roughening of the rock surface, creating more footholds and individual protected sites for roosting, to larger-scale chamber enlargement, increasing the total area available for roosting. Corrosional effects in the Mount Elgon caves, although not as dramatic in these pyroclastic rocks as in limestone, were well documented in the study by Lundberg and McFarlane (2006), which showed that most of the rock surfaces in the more humid parts of the caves are corroded or altered to depths of ~10 cm.

Effect of H₂O and CO₂ Production

Geomorphological activity operates only on rock surfaces, and much of it will operate in the immediate vicinity of the site of production of the CO₂ and H₂O vapor, namely, the roost proper. In order to produce a corrosive medium, the CO₂ must dissolve in liquid water. Hence RH must reach 100%, and the water vapor must condense. We know that there is condensing humidity in the roosts when the bats are present (condensation droplets can

Figure 10. (A) Evidence of corrosion, ~10 cm deep, in the roof of Kitum Cave (antechamber), caused by bat presence (here insectivores rather than Rousettus). (B) Evidence of long-term occupation: the guano pile on the floor directly under the center of corrosion. (C) Pristine rock surface, resulting from fracture and collapse of roof block. (D) Detail of corrosional roughening, rendering it more suitable for bat roosting than is the pristine surface.
There is enough bat-water to saturate ~20,000 m³ of cave air; this is 3.7 kg H₂O. From the output of one 12 h roost period (148 kg), 34.7% to reach 100%, which, for the roost volume of air, is 75.3%, so the bat-produced water has to supply only another dense out from the roost air. The average RH for Mackingeny air is 30 g/m³ (engineering toolbox.com) and knowing the output can add air exchanges. With more air to saturate, the volume of condensate goes down; for example, with 6 exchanges, the water film is 0.185 mm thick.

Humidity data were mapped, but values were variable. Nevertheless, simple patterns are apparent, with the highest humidity in the roosts for Mackingeny and Ngwarisha, and at the back of the cave for Kitum.

Knowing that the maximum water content of air at 30 °C is 30 g/m³ (engineering toolbox.com) and knowing the output of water from bats, we can calculate how much water will condense out from the roost air. The average RH for Mackingeny air is 75.3%, so the bat-produced water has to supply only another 34.7% to reach 100%, which, for the roost volume of air, is 3.7 kg H₂O. From the output of one 12 h roost period (148 kg), there is enough bat-water to saturate ~20,000 m³ of cave air; this could saturate the roost air 40 times over. However, not all of this will remain in the roost. Our calculations suggested that 6–10 exchanges of air would effectively maintain observed temperatures, but, in reality, this is likely to be irregular rather than constant over the day, and it is likely to be greater in the more open parts of the cave and less in the more restricted roost area. Air exchange is most effective during bat movement, at bat entry/exit, and during the intermittent episodes of activity during the roost period. The temperature record of the Mackingeny roost shows that, on average, each roost period has ~7 h of stability with very little temperature change. At these times, circulation of the roost air will be limited and RH will be at 100%. Therefore, in order to err on the conservative side, we used 7 h for the rest of the modeling.

With no air exchange, the water vapor produced by 7 h of bat roosting would saturate the air in the roost volume and have enough water left to produce a film of condensation on all surfaces (roof, walls, floor) 0.239 mm thick. This is likely the maximum, because air must circulate a little to prevent bat asphyxiation. To account for diffusion and convectional circulation, we can add air exchanges. With more air to saturate, the volume of condensate goes down; for example, with 6 exchanges, the water film is 0.185 mm thick.

CO₂ production is in excess of the amount that can dissolve in this film, so the film always becomes saturated with CO₂. Dissolution is therefore limited by the amount of water condensation. We modeled dissolution using typical values for saturated water of 400 ppm CaCO₃. A water film of 0.239 mm (no air exchange) would result in dissolution of 95 mg CaCO₃/m²/d, which translates to a surface denudation rate of 0.013 mm/yr, or 13 mm/k.y., and the time required for surface denudation of 1 m would be ~76,000 yr. For the water film of 0.185 mm thickness, the rate of surface denudation is 10 mm/k.y., and the time required for 1 m of surface denudation is 98,000 yr (Table 8). This rate is applied to the roost ceiling, walls, and floors, thus enlarging the volume over time and providing more niche space for roosting. Applying this model to Ngwarisha yields times for surface denudation of the same order of magnitude.

### Table 7. Relative Humidity (RH) Data

<table>
<thead>
<tr>
<th>Location</th>
<th>RH average (%)</th>
<th>RH maximum (%)</th>
<th>RH minimum (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kitum 2005 (spot throughout cave)</td>
<td>79.6</td>
<td>92.0</td>
<td>65.4</td>
</tr>
<tr>
<td>Kitum 2003 Hobo logger 2a, back wall</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Kitum 2003 Hobo logger 2b, main chamber roof</td>
<td>93.6</td>
<td>93.8</td>
<td>91.8</td>
</tr>
<tr>
<td>Kitum 2003 Hobo logger 2c, entrance zone</td>
<td>91.9</td>
<td>100</td>
<td>82.7</td>
</tr>
<tr>
<td>Mackingeny 2005 (spot throughout cave)</td>
<td>75.3</td>
<td>99.9</td>
<td>48.7</td>
</tr>
<tr>
<td>Ngwarisha 2005 (spot throughout cave)</td>
<td>74.7</td>
<td>84.5</td>
<td>52.5</td>
</tr>
</tbody>
</table>

### Table 8. Potential Surface Denudation Rates That Would Result from Metabolic Outputs of These Populations of Bats, Applied to Corrosion of Limestone

<table>
<thead>
<tr>
<th>No. of exchanges</th>
<th>Water film thickness (mm)</th>
<th>Mackingeny Wall denudation (mm/k.y.)</th>
<th>Time (yr) for surface retreat of 1 m</th>
<th>Water film thickness (mm)</th>
<th>Ngwarisha Wall denudation (mm/k.y.)</th>
<th>Time (yr) for surface retreat of 1 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.239</td>
<td>13.16</td>
<td>75.991</td>
<td>0.307</td>
<td>16.94</td>
<td>59.042</td>
</tr>
<tr>
<td>2</td>
<td>0.228</td>
<td>12.57</td>
<td>79.579</td>
<td>0.283</td>
<td>15.57</td>
<td>64.244</td>
</tr>
<tr>
<td>3</td>
<td>0.217</td>
<td>11.97</td>
<td>83.523</td>
<td>0.258</td>
<td>14.19</td>
<td>70.452</td>
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<tr>
<td>4</td>
<td>0.207</td>
<td>11.38</td>
<td>87.878</td>
<td>0.233</td>
<td>12.82</td>
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<td>5</td>
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<td>10.79</td>
<td>92.712</td>
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<td>87.330</td>
</tr>
<tr>
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<td>0.185</td>
<td>10.19</td>
<td>98.108</td>
<td>0.183</td>
<td>10.08</td>
<td>99.214</td>
</tr>
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</table>
This modeling indicates that, were these caves in limestone, the times required to produce 1 m of surface retreat in the roost area are in the order of 80,000 yr, a time frame well within the late Quaternary and commensurate with many rates of speleogenesis. Over these time frames, bats can alter their niches in terms of the immediate microclimatic conditions, longer-term modification of surfaces by local corrosional roughening to produce more useful/comfortable roosting sites, and long-term creation of larger roost spaces by surface denudation.

The question of the fate of the CO$_2$- and CaCO$_3$-saturated water applies in all cases of condensation corrosion, where water is not usually observed flowing down the walls. Some of the water simply drips to the floor and percolates to groundwater. Some is evaporated in situ, leaving powdered rock that either falls directly, or is rapidly displaced by bat activity, to the guano-covered cave floor.

CONCLUSIONS

In this report, we have shown that bats in tropical caves of Mount Elgon National Park, Kenya, effectively and significantly modify cave microclimates and are, in turn, very likely to be dependent on the modified conditions for colony fitness. They also effect niche construction by stimulating corrosional roughening and enlargement of their habitat. Simplicity of cave geometry allowed us to isolate impacts of bat metabolic outputs from other potential microclimatic effects. The similarity in size and morphology of the three caves but a distinct difference in the level of bat colonization provided a natural experiment where one cave acted as a low-biological-activity control. Documentation of the cave microclimate, by means of data loggers and spot measurements of air and rock temperatures, RH, and air flow, allowed us to model energy production from the bat populations and dispersion throughout the cave. Our findings are, in summary:

1. Populations of Rousettus aegyptiacus are estimated for Mackingeny Cave at ~28,000, for Ngwarisha Cave at ~100,000, and for Kitum Cave at ~10,000 individuals.
2. Bat exit and entry flights cause significant air flow, and a large-scale counterclockwise circulation cell (as exemplified in Ngwarisha Cave) flushes much of the warm air out from the cave (and, probably, a small percentage of the expired CO$_2$ and H$_2$O vapor).
3. For the caves with large bat populations, roost temperatures reach ~30 °C during the daytime bat roost period and fall to ~28 °C during the nighttime bat-foraging period (i.e., they remain at least 16 °C above ambient), but for the Kitum, with few bats, roost temperatures are raised by only ~2 °C, and temperatures at the back of the cave remain close to mean annual at 12.6 °C.
4. Observed temperatures in the caves can be maintained if energy from bat metabolism (~800,000 kJ for Mackingeny, ~3,000,000 kJ for Ngwarisha) is dispersed by conduction to rock and heating of air with ~6–13 exchanges per day. While the majority of the exchange occurs during bat flight, observed rates of air movement would allow sufficient air exchange to effectively disperse the energy while maintaining the high roost temperatures.
5. Temperatures in Kitum Cave roost, which are substantially below the thermoneutral zone, suggest that the population is too small to maintain conditions optimal for colony fitness, and that Allee effects may be in operation. Modeling suggests that, for its size and rate of air exchange, Kitum Cave would need a bat population of 100,000–130,000 bats to raise roost temperatures into a more equitable range.
6. Corrosional potential from these bat populations, were these caves in limestone, is controlled by the amount of condensed water vapor. Condensation of water vapor, after saturation of the circulating air, would trigger surface denudation rates of ~10 mm/k.y., and the time required for surface retreat of 1 m would be ~80,000 yr.

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