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Newly discovered populations of the "terrible hairy fly", *Mormotomyia hirsuta* Austen (Diptera: Mormotomyiidae) in Kenya, with further observations on natural history

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ABSTRACT

This paper presents the results of investigations conducted between 2011 and 2013 to discover additional populations of *Mormotomyia hirsuta* Austen. These investigations were conducted primarily in the relatively dry savanna of eastern Kenya, focusing on small hills and rocky outcrops resembling that of Ukasi Hill, the type locality of the "terrible hairy fly". Investigations were conducted at 144 caves and at ground level, directly below 104 above-ground, narrow, horizontally-oriented fissures, often on near-vertical rock faces. Evidence of *Mormotomyia* was not found in any of the caves investigated. During the dry season, however, desiccated corpses of *Mormotomyia* were discovered embedded in a matrix of dried bat guano adhering to the rock face directly below fissures at Ngauluka and Makilu Hills, also located in the Ukasi area. Later, rainy season visits to these two hills revealed populations of living *Mormotomyia* while, contemporaneously, flies were absent from the type locality. Like the type locality, the rock face directly below the fissures on Ngauluka and Makilu was discolored with pink and purple vertical streaking, presumably stained by bat urine and guano. Using the characteristically stained rock face as a search image, expeditions were expanded to include areas further afield and living flies were found at a third site 187 km to the south. Formerly considered "the rarest fly in the world", the conservation status of *Mormotomyia* appears robust. *Mormotomyia* was actively preyed upon in the field by two species of lizards and remains of the fly were found in a jumping-spider nest. During laboratory observations of five live flies, the single male exhibited lengthy periods of female-guarding, with females being enclosed within the span of the much longer and setulose legs of males for more than 10 minutes.

KEY WORDS: Conservation, female-guarding, inselbergs, kopjes, Makilu, Mbuinzau, new populations, Ngauluka, phenology, predators.

INTRODUCTION

Mormotomyia hirsuta, the "terrible hairy fly", was described by E.E. Austen in 1936, based on two male specimens collected in 1933, at Ukasi Hill (as Ukazzi) in the dry eastern Sahelian zone (Coe 1999: 5) of eastern Kenya. The fly is a curious-looking, brachypterous species (Fig. 1), with long, orange-yellow setulae covering the body—a feature particularly well pronounced in males. The non-functional wings are reduced to setulose, strap-like appendages and the halteres are likewise reduced to barely visible nodular processes (Kirk-Spriggs *et al*. 2011). The species was sufficiently distinctive to warrant the erection of the new family Mormotomyiidae to contain it (Austen 1936). *Mormotomyia hirsuta* (confined to Kenya), is currently the sole representative of the family and Mormotomyiidae is the only endemic, monotypic family of flies that occurs in the Afrotropical Region.

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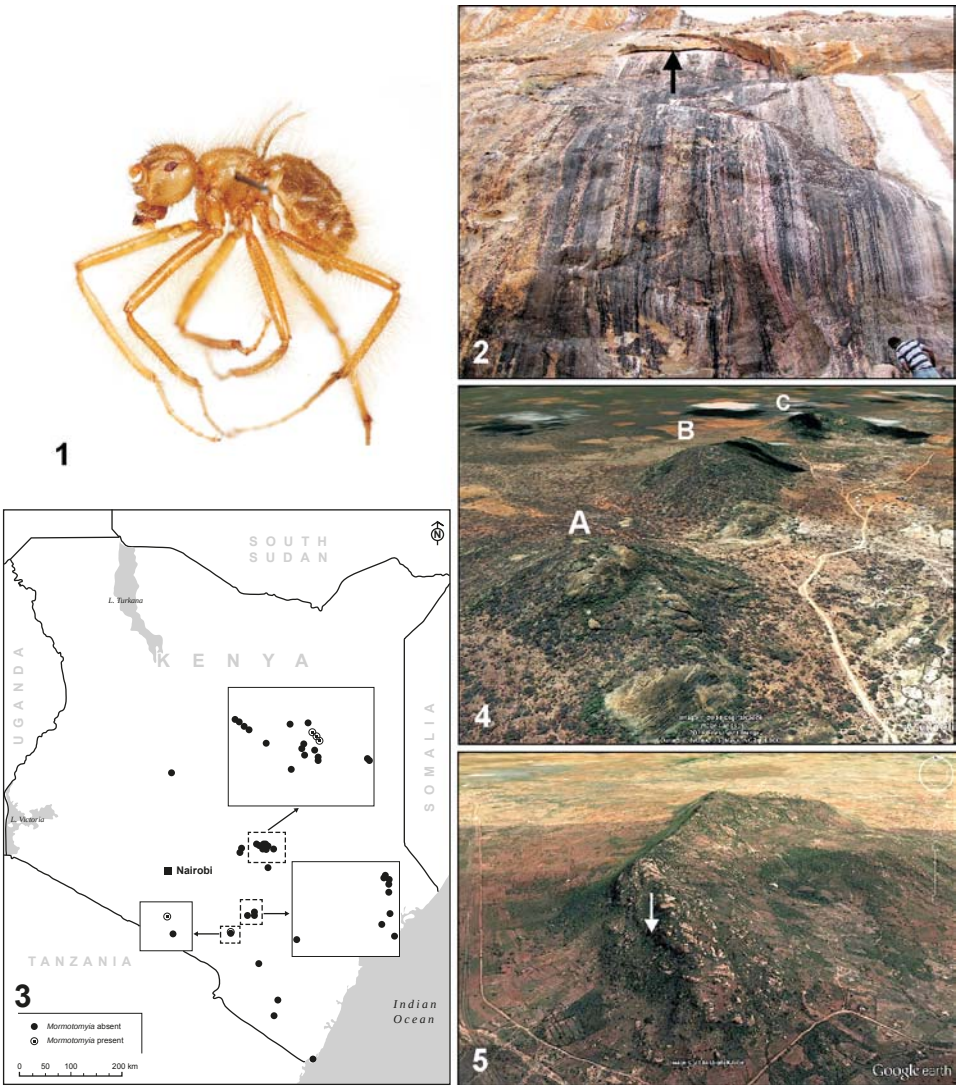

Figs 1–5. (1) Habitus of male *Mormotomyia hirsuta* Austen, lateral view; (2) typical fissure at Makilu Hill, note pink/purple discoloration of rock face immediately below; (3) map of Kenya, indicating distribution of sites with caves and fissures visited during the 2011–2013 survey; (4) aerial view of Ukasi Hill area (type locality) and nearby hills (A – Ukasi Hill; B – Ngauluka Hill; C – Makilu Hill); (5) aerial view of Mbuinzau Hill (arrow denotes location of fissure inhabited by *Mormotomyia*) (Figs 4, 5: Google Earth images, data © Digital Globe 2013).

Mormotomyia was not collected subsequently until 1948, when V.G.L. and G.R.C. van Someren rediscovered the species at the same locality, associated with a vertical fissure in a large rock at the summit of Ukasi Hill (Copeland *et al*. 2011). On this occasion a large number of flies were collected (including the unknown females) and immature stages were sampled in bat guano that had washed out of the rock fissure. These immature stages (egg, larva and puparium) were subsequently described by van

Emden (1950), who further noted that bat guano was the substrate for larval development. Despite sporadic searches, there were no further records of *Mormotomyia* in the wild until 2010, when the species was again discovered at the type locality (Copeland *et al*. 2011; Kirk-Spriggs *et al*. 2011).

Mormotomyia hirsuta has long been of great interest to Diptera systematists and conservation biologists (Courtney *et al*. 2009: 203; Kirk-Spriggs & Stuckenberg 2009: 172; Oldroyd 1964: 184), as a result of its contentious systematic position and rarity. Due to the aberrant form, reduced head and thoracic setation and wing venation, morphological taxonomists have been unable to resolve the phylogenetic relationship of Mormotomyiidae to other families of Diptera. It has variously been placed in the Calyptratae (Pont 1980: 713); or as a possible transitional family between acalyptrate and calyptrate flies, and probably closest to the Scathophagidae (as Cordyluridae) (van Emden 1950); or as related to families of acalyptrate flies, including Sphaeroceridae (as Borboridae) (Austen 1936) and Heleomyzidae (Sphaeroceroidea) (McAlpine 1989: 1484).

Detailed study of the specimens collected in 2010 allowed redescription of the third-instar larva and puparium, using stereoscan microscopy, and description of the female reproductive tract (Kirk-Spriggs *et al*. 2011). This study revealed that the structure of the female reproductive tract suggested that *Mormotomyia* should be ascribed to the acalyptrate superfamily Ephydroidea (Kirk-Spriggs *et al*. 2011) and later McAlpine (2011) noted that the general structure of the antenna of *Mormotomyia* concurred with this view. Recent advances in molecular phylogenetics (e.g. Wiegmann *et al*. 2011) presented an additional technique to help resolve the phylogenetic placement of *Mormotomyia*, and live flies, collected into 96% ethanol, for the first time were used for such an analysis (Copeland *et al*. 2011). Results of this study confirm placement of the Mormotomyiidae in the Ephydroidea, as sister to the remainder of the Ephydroidea, except the Ephydridae (Winkler *et al*., in prep.).

While clarification of the phylogenetic placement of Mormotomyiidae represents an important milestone, other issues of biological importance remain unresolved, particularly those related to reproductive and dispersal behaviours and species conservation. Questions that still need to be posed are, for example: what is the biological significance of the pronounced male-biased sexual-size dimorphism observed in the Ukasi population (Copeland *et al*. 2011)?; and was *Mormotomyia* restricted to a single relict population, with the attendant problems of managing the conservation of an endangered species (Courtney *et al*. 2009: 203), or were there other, as yet undiscovered, populations? Analysis of both mitochondrial and nuclear DNA of individuals from the population of flies collected in 2010 presented evidence of outbreeding, suggesting that the Ukasi flies were probably part of a metapopulation of *Mormotomyia* (Copeland *et al*. 2011). If other populations do exist, how does a fly with non-functional wings (Fig. 1) disperse? Examination of the tarsi of *Mormotomyia* (Kirk-Spriggs *et al*. 2011) revealed none of the modifications of the tarsal claws found in other bat-associated fly species known either to be phoretic on Chiroptera, i.e. Mystacinobiidae (Holloway 1976), or ectoparasitic on them, i.e. Streblidae and Nycteribiidae (Oldroyd 1964: 184). To address these questions, further investigations were conducted. In this paper the discovery of three additional populations of *Mormotomyia* in eastern Kenya is reported, together with additional observations on natural history.

MATERIAL AND METHODS

Definitions

For the purposes of this paper a differentiation is made between caves and fissures (rock fissures). The former refer to openings into a rock system, often relatively large, with a floor that is either continuous with ground level, or descends below it. Fissures (Fig. 2) are defined as rock fissures above ground level, usually narrow and horizontally-oriented (i.e. much wider than high), often present on vertical or near-vertical rock faces, making access difficult for mammalian and avian predators. Virtually all fissures located during this study were horizontally-oriented. As is the case with caves, fissures are commonly inhabited by bats.

Expeditions

Between 19 April 2011 and 9 January 2013 expeditions were conducted to sites in Kenya, falling approximately along a northwest-southeast transect, from coordinates 0.4501°N 36.8852°E to 4.6154°S 39.3532°E (Fig. 3). Geological formations similar to those occurring at the type locality of *Mormotomyia* were examined (i.e. small inselbergs/kopjes to medium-sized hills that represent remnants of ancient basement rocks). With the exception of three caves near the Kenyan coast, all were located in dry habitats. The presence of bats was indicated by the occurrence of fresh bat guano within caves or below fissures, and by aural and visual evidence. Evidence of fly presence was sought by searching bat guano on rock faces and on the ground directly below horizontal fissures and by examination of cave floors and walls, using battery operated torches (flashlights). During dry-season expeditions evidence of recent fly occurrence was sought by searching accumulated dry guano deposits for *Mormotomyia* corpses. On six days (2, 3, 5, 7, 8 and 9 December 2012) at Makilu and Ngauluka Hills, lizard predation of *Mormotomyia* was observed through binoculars between 08h30 and 09h00. Lizards were identified using Sprawls *et al*. (2002).

Phenology

During observations of living flies in the field, the relative population size of *Mormotomyia* was monitored below one fissure at the Makilu Hill site over a period of 38 days (29 November 2012 to 7 January 2013). Living flies were counted every second day, between 08h00 and 08h30, both on guano and the rock face, to a height of *c*. 4 m above ground level.

Laboratory observations

When *Mormotomyia* were active, fresh guano was collected from below a fissure on Makilu Hill and placed in two one-litre plastic containers to a depth of *c*. 4 cm. Containers were covered with their original plastic lids, from which a large rectangular section had been cut and replaced with fine-meshed cloth. During transport to the laboratory, cotton material was placed over the containers. Containers were placed in a 60 cm × 45 cm × 45 cm Perspex cage and their covers removed. Emerging adults were provided with cotton wool soaked in sugar water. Containers were left in the cage after the emergence of adults to serve as possible oviposition sites. Twenty adults captured at the Makilu Hill site were placed in a two-litre plastic container containing moistened paper towelling. These were also transported to the laboratory.

TABLE 1
Relationship of caves and fissures to the presence of bats (Chi-square = 20.22; $p < 0.001$).

Presence/absence	Caves	Fissures
Chiroptera present	27	48
Chiroptera absent	117	56

Identification and deposition

Newly-sampled specimens of *Mormotomyia* from Mbuinzau and Makilu Hills were identified by dissection and comparison of the male terminalia with specimens from the original Ukasi Hill population. These were found to be conspecific with *M. hirsuta*. Voucher specimens are deposited in the National Museums of Kenya, Nairobi, the International Centre of Insect Physiology and Ecology, Nairobi and the National Museum, Bloemfontein, South Africa.

RESULTS

Exploration of caves and fissures

A total of 48 sites (Fig. 3) were examined between April 2011 and January 2013. Three of these were subterranean caves; one was a large hole in a Baobab tree, *Adansonia digitata* L. (Malvaceae), that housed numerous fruit bats; and the remainder were rocky hills with caves and fissures. Many of these hills had multiple caves and fissures. A total of 248 caves/fissures were investigated. Some fissures and caves, particularly those in the area of the type locality (Ukasi Hill), were investigated more than once and the total number of visits to caves/fissures was 337. Ukasi is one of a small chain of hills located within 2 km of each other, the others being Ngauluka Hill and Makilu Hill (Fig. 4). These three hills were visited on 31 separate days, comprising a total of 88 investigations of caves and fissures.

Distribution of bats and flies among caves and fissures

Appendix 1 provides a list of the areas and caves/fissures examined that contained resident bat populations, including those that also housed *Mormotomyia*. Caves and fissures that contained neither bats nor flies when visited are listed in Appendix 2. These data were used to test the following two hypotheses: firstly, that the distribution of bats was independent of habitat type (i.e., caves and fissures), and secondly, that the distribution of *Mormotomyia* was also independent of habitat type. During the survey, fissures were significantly more likely than caves to harbour bats. Bats were present in 18.8% ($n = 144$) of unique caves and in 46.2% ($n = 104$) of unique fissures (Table 1). Fissures were also significantly more likely to house *Mormotomyia*. Flies were found in 3.8% of fissures, while they were never observed in caves (Table 2).

Exploration in the area of Ukasi Hill (the type locality)

Twenty-three hills within 20 km of the type locality were investigated (Fig. 3). Although many caves and fissures were found to have resident bat populations (Appendix 1), evidence of *Mormotomyia* was found on only the two hills nearest the type locality, Makilu and Ngauluka Hills (Fig. 4). Living flies were not discovered at the type locality.

TABLE 2
Relationship of caves and fissures to the presence of *Mormotomyia* ($p = 0.03$, Fisher's Exact Test).

Presence/absence	Caves	Fissures
Mormotomyia present	0	4
Mormotomyia absent	144	100

Dry-season expeditions

When visited on 11 August 2012, substantial amounts of dry guano were found below Fissure 3 at Makilu Hill (Fig. 2), much of this adhering to the steep rock face near its base. Close examination revealed what appeared to be the desiccated remains of three dead flies, embedded in a matrix of dried guano. These were highly fragile and were sampled together with the guano and taken to the laboratory for cleaning and microscopical examination, where the insect remains were confirmed as that of *M. hirsuta* (Figs 6, 7). Similarly, during examination of fissures and caves on Ngauluka Hill on 26 September 2012, a single corpse was found, also embedded in dried guano, at the base of the rock beneath Fissure 14. During removal, however, this corpse became detached from the guano and was lost. The rock face below both *Mormotomyia*-positive fissures was stained purple with pinkish streaks (e.g. Fig. 2), as was the rock face below the fissure at the type locality on Ukasi Hill, where *Mormotomyia* was collected in 2010 (Fig. 8). This trend suggested that bat residence in fissures was associated with a characteristic discoloration of the rock face, a feature easily observed at a distance with binoculars. This visual cue was used to focus investigations more finely on fissures with similar characteristics.

Rainy season expeditions

Based on the evidence from dry-season collections of desiccated *Mormotomyia* corpses from Makilu and Naguluka Hills, these and the Ukasi Hill site were closely monitored following the onset of the rains, which began in November 2012. During this time populations of live flies were discovered to be active on fresh guano covering the ground beneath fissures in the rock faces on Makilu and Ngauluka Hills (Appendix 1). Guano had recently been washed out of these fissures by precipitation. *Mormotomyia* were not, however, found on Ukasi Hill. Shortly thereafter, searches in similar habitat, far to the south, revealed a third population on Mbuinzau Hill (Figs 3, 5, 9, 10; Appendix 1), at a distance of 187 km from the type locality. Living flies from below fissures Makilu 3, Ngauluka 16 and Mbuinzau 12 (see Appendix 1) were collected separately into 95% ethanol, providing suitable genetic material for DNA analysis and allowing investigations of whether outbreeding had occurred between the original Ukasi Hill population and the newly discovered ones.

Phenology of Mormotomyia

At the Makilu Hill site, live flies were first observed on 29 November 2012, gradually increasing in number, until peaking abruptly on 9 December 2012 when > 800 individuals were counted (Fig. 12). Live flies were last observed on 3 January 2013.

Predation on Mormotomyia

During the period that *Mormotomyia* were active on Makilu and Ngauluka Hills, lizards were observed attacking flies. Observations with binoculars revealed that male

Figs 6, 7. (6) Corpse of male *Mormotomyia hirsuta* Austen embedded in dried guano (matrix partially removed; head facing to right, long legs clearly evident); (7) same, detail of head.

and female Red-headed Rock Agamas, *Agama agama* L. (Agamidae), and the Five-lined Skink, *Trachylepis quinquetaeniata* (Lichtenstein) (Scincidae), were actively feeding on *Mormotomyia* at the entrance to Ngauluka fissure 16 and Makilu fissure 3 (Fig. 2). Eight lizards were observed feeding at Makilu Hill on 9 December when *Mormotomyia* numbers were highest. Lizards were not observed to enter the fissure itself.

In addition, the expedition to Ukasi Hill on 18 December 2011 revealed a jumping spider (Araneae: Salticidae) nest *c*. 2 m above the ground, mostly obscured by a tiny

crack in the rock face, below the large fissure that produced *Mormotomyia* in late 2010. The nest was removed and, while one spider escaped capture, the nest and its remaining occupants were placed in a vial containing 95% ethanol. Subsequent examination in the laboratory revealed three nymphal and one adult salticid (probably *Menemerus* sp.; C. Haddad pers. comm. 2014); one mostly intact corpse of *Mormotomyia* embedded in spider silk along with other *Mormotomyia* body parts, including one head and 11 legs; and the head and partial thorax of an acridid (Orthoptera) nymph.

Laboratory observations

Of the 20 adults collected in the field only one female and one male *Mormotomyia* survived the journey to the laboratory. The remainder were either moribund or dead. The female specimen outlived the male specimen and died after 11 days.

Four female and one male *Mormotomyia* emerged in the laboratory from guano collected at the base of Makilu Hill. On two separate days the single male was found to have enclosed a female within the span of his legs (Fig. 11). In neither case was the beginning of the interaction observed and it was not possible to determine whether the same, or a different female, was "guarded". Both "guarding" periods lasted at least 10 minutes. Short video footage was recorded as part of one encounter, and a single, possible attempt at copulation appears in the film between 30 to 32 seconds (pleiocarpa1 2014*a*). Three other short videos of the same male illustrate feeding and grooming behaviour as it sponges sugar water placed on the surface of a rock (pleiocarpa1 2014*b*, *c*, *d*).

DISCUSSION

Exploration

Previous successful and unsuccessful expeditions to the type locality of Ukasi Hill in search of *Mormotomyia* suggested that the appearance of flies was unpredictable, except for an apparent relationship with heavy precipitation events, when moist guano is washed out of fissures, thus providing a suitable medium for larval development (Austen 1936; Copeland *et al*. 2011; Kirk-Spriggs *et al*. 2011; van Emden 1950). Up to now, the dark interior of these fissures has not been examined and it is possible that breeding of *Mormotomyia* continues uninterrupted, even during dry periods, providing bats are in residence.

During recent expeditions, conducted between 2011 and 2013, living flies were not detected at the type locality on Ukasi Hill, where they were encountered in 2010. The absence of living flies at Ukasi Hill, although discovered contemporaneously on two nearby hills, provides further evidence of the ephemeral nature of the presence of living flies. That notwithstanding, when living flies are present at a site they may be active, and readily detected, for a considerable period of time. The presence of *Mormotomyia* at Makilu Hill was documented for a period lasting at least 36 days (29 November 2012 to 3 January 2013), suggesting that properly timed future expeditions would allow more extensive behavioural studies of *Mormotomyia* to be conducted under natural field conditions.

The survey revealed three additional sites with *Mormotomyia* populations, making a total of four sites, one 187 km from the other three. Together, they indicate a much wider geographical distribution than was previously thought. The survey also indicated

Figs 8–11. (8) Sampling of *Mormotomyia hirsuta* adults and larvae below the pink/purple discolored rock face at Ukasi Hill (type locality), in November 2010; (9) Mbuinzau Hill, 187 km south of the type locality (arrow indicates area of collecting site); (10) Mbuinzau Hill, detail (arrow indicates collection site below a fissure in rock face); (11) guarding behaviour of male *Mormotomyia* (above), female (below), enclosed within span of male legs.

that a similar habitat profile (fissures and not caves) was common to all sites at which the fly was found, which should facilitate the location of additional *Mormotomyia* sites.

Fissures were significantly more likely than caves to harbour both flies and bats (Tables 1, 2). Most caves and fissures were visited infrequently, however, and the absence of bats and flies at a site examined on one or a few occasions does not necessarily imply that they are not present at other times. Additionally, access to some recesses of investigated caves was problematic, or impossible, and in general, considerably more challenging than closely examining the well-lit ground and rock faces below fissures. These factors may have affected the detection of bats and *Mormotomyia* in caves and, perhaps, biased the results. Nonetheless, sampling included multiple caves and fissures across an extensive geographical range and these data suggest strongly that fissures provide a preferred habitat for both *Mormotomyia* and the bats on which the flies depend.

Predation on Mormotomyia

Mormotomyia adults are preyed upon opportunistically by lizards and these may play a role in limiting the population size of *Mormotomyia*. It is likely that jumping spiders also prey opportunistically on *Mormotomyia*. Insects associated with the examined salticid nest included a few *Mormotomyia* and a nymphal acridid grasshopper. Although no predation by spiders was observed, the presence of multiple insect bodies suggests that the salticids carry insect prey back to their nest, to consume it within the safety of the crack in the rock face. Similar behaviour has been observed in another salticid species, *Heliophanus termiophagus* Wesołowska & Haddad, that carries its prey into the safety of tunnels within abandoned termitaria prior to consumption (Wesołowska & Haddad 2002).

Lizards were not observed entering fissures, and the association of *Mormotomyia* with narrow fissures on rock faces that are difficult to reach may offer considerable protection for this species, particularly against predation by small mammals. Predation of *Mormotomyia* by small mammals or birds was not observed, nor was there any evidence of predation on immature stages. Vertebrate spoor were not observed on, or near, the moist guano that had accumulated below the fissures.

Female-guarding

Mormotomyia exhibits pronounced male-biased sexual size dimorphism, with seven different body part measurements significantly larger (by 33–61 %) in males than females (Copeland *et al*. 2011). Sexual size differences in insects usually favour females and often correlate with increased fecundity. Nonetheless, there are numerous instances of the reverse being true (Copeland *et al*. 2011, and references therein). Larger size in males may be driven by sexual selection, size being a proxy for male fitness. Larger males may be more likely to win battles for territoriality and access to females. A form of female-guarding behaviour, whereby the male stands above the female, enclosing her within the span of the legs, may also drive increases in male size (Bonduriansky 2006).

Female-guarding behaviour of this type by a *Mormotomyia* male was observed, as reported in some other Diptera families. Adler and Adler (1991), for example, studied three species of Tipulidae, the males of which guard females following copulation, by standing above them, normally maintaining this position until females oviposit, or until dislodged in conflicts with conspecific males. As is the case with *Mormotomyia* (Copeland *et al*. 2011), these tipulid males had longer legs than did the females, significantly so for two of the investigated species. Interestingly, in the tipulid *Limonia simulans* (Walker), sexual dimorphism was also observed in the shape of the last tarsal segments that in males are sinuate on their inner surface, while in females these segments are linear (Adler & Adler 1991). A similar condition occurs in *Mormotomyia*, although in this case the sexual dimorphism is confined to the first tarsal segment of the mid tarsus (Austen 1936; Kirk-Spriggs *et al*. 2011; van Emden 1950). For both species modified tarsal segments may be involved in guarding and also mating behaviour, although direct evidence for this has not been observed. Kirk-Spriggs *et al*. (2011) suggested that the sexually dimorphic tarsal segments of male *Mormotomyia* may serve such a clasping function during copulation. Post-copulatory female-guarding behaviour is also relatively common in flies of the family Neriidae (Bonduriansky 2006; Mangan 1979; Preston-Mafham 2001) and has obvious benefits in circumstances where male competition for

females is high. Even if another male successfully drives off a guarding male before oviposition is completed, engaging the interloper in battle may be enough to allow the now-unprotected female to deposit all, or most of her eggs (Adler & Adler 1991).

In laboratory observations of confined *Mormotomyia*, events prior to the initiation of guarding were not observed. As a result, it is not possible to distinguish between post-copulatory guarding and pre-copulatory persistence of the male, in the face of one, or more, instances of rejection by the guarded female. The duration of female-guarding was considerably longer for *Mormotomyia* (> 10 min, $n = 2$) than that reported for Tipulidae, where post-copulatory guarding episodes that were not interrupted by another male lasted for 2.3 ± 0.78 min ($n = 25$, *Dactylobis montana* (Osten Sacken)) and for 0.9 ± 0.23 min ($n = 44$, *Limonia simulans* (Walker)) (Adler & Adler 1991). *Mormotomyia*'s longer guarding period suggests that pre-copulatory guarding may have been observed. The apparently rejected attempt at mating by the male in the video footage cited above appears to support this interpretation. The recently emerged females may not have been sufficiently sexually mature to mate. Alternatively, it is conceivable that guarding behaviour may be different when other males are present. The observations of female-guarding behaviour by *Mormotomyia* are based on that of a single male that may have behaved differently in the presence of potential challengers. More extensive observations of non-teneral flies in the laboratory and the field are necessary to clarify the type(s) and significance of female-guarding in this species.

Conservation status of Mormotomyia

Although *Mormotomyia hirsuta* is stenoecious, distributional data presented here indicates that the species is more widespread than previously thought and probably not uncommon in sites resembling those in which it has already been found. Both the macrohabitat (inselbergs) and microhabitat (fissures) in which the species occurs are

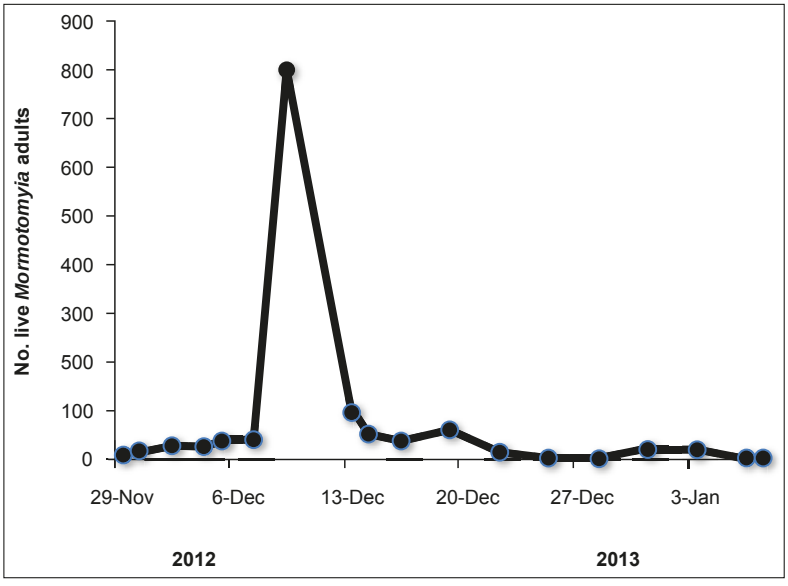

Fig. 12. Phenology of *Mormotomyia* adults at Makilu Hill.

little affected by human activity. Similar rocky outcrops and small hills are widely distributed in the drier areas of Kenya, particularly in the eastern and northern parts of the country. It is likely that the species will also be found to occur in the expanse of Tsavo East and Tsavo West National Parks in Kenya, through to the border with Tanzania and across it into Mkomazi National Park, the southeastern-most extension of the Sahel (Coe 1999: 5). Hitherto, *Mormotomyia* has been considered "the rarest fly in the world" (F.C. Thompson, pers. comm. 2010). The results reported here suggest that the conservation status of *Mormotomyia* is robust and that no special efforts are required to ensure its continuing survival.

Future research

Adult *Mormotomyia* appear to be relatively fragile insects, frequently losing legs in nature and suffering high mortality while being transported from the field to the laboratory (a *c*. four-hour trip over mostly smooth roads). Collection of moist guano at *Mormotomyia* sites is easier, however, and the transport of a reasonably small amount of guano (perhaps 2–3 litres) should produce sufficient adults to study interactions between the sexes in the laboratory, including mating and guarding behaviour. Additionally (as indicated above), at certain times the number of active flies may be substantial and observations made in the field may yield useful information, although activity of adult flies below fissures appears to be limited to individuals that have recently emerged and whose behaviour is limited to ascending the rock face and entering the fissure.

The means by which *Mormotomyia* disperses remain unknown. For practical reasons it was not possible to examine the interior of fissures, or undertake trapping of bats to ascertain whether the flies are phoretic as adults, a possibility that appears unlikely given that *Mormotomyia* lacks the modified tarsal claws apparent in fly families known to be phoretic or ectoparasitic on bats (Kirk-Spriggs *et al*. 2011). Answering this vexing question should be the primary objective of future research.

Finally, the discovery of three additional *Mormotomyia* sites provides the opportunity to compare the genetic makeup of individuals among and within multiple populations of the species. Preliminary results of mitochondrial DNA-barcoding of five individuals each from Makilu, Ukasi, and Mbuinzau Hills yielded two clusters. One cluster included all five Makilu specimens and single specimens from Ukasi and Mbuinzau. The other cluster included the other four Ukasi specimens and the final four specimens from Mbuinzau Hill, nearly 200 km away (R.S.C., unpub. data). These data hint at considerable dispersal of *Mormotomyia* and support earlier suggestions, based on genetic analyses, that the Ukasi population is not a genetically isolated one (Copeland *et al.* 2011). Analysis of nuclear DNA from the three new populations is underway (W. Booth, pers. comm. 2014) and should shed light on the question of dispersal and gene exchange of this interesting fly.

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———2014*c*. *Mormotomyia* feeding and grooming behaviour 2. (https://www.youtube.com/watch?v=YDmVM7tbVmo; accessed 22/04/2014)

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Appendix I.

Presence or absence of *Mormotomyia hirsuta* Austen in bat-inhabited caves and fissures in Kenya.

Prov.	Area	Site name	Cave/fissure name	Cave/ fissure	Date	Coordinates (decimal degrees)	Elev. (m)	Live *Mormotomyia* present?
Coast	Coast	Kisimani cave	Kisimani	cave	26/7/2012	-4.61542 39.35284	20	no
Coast	Coast	Mdenyenye cave	Mdenyenye	cave	26/7/2012	-4.61415 39.35420	20	no
Coast	Coast	Pangani cave	Pangani	cave	26/7/2012	-4.61535 39.35316	20	no
Coast	Kasigau	Kasigau Mountain	Kasigau 2	cave	8/4/2012	-3.84727 38.67464	581	no
Coast	Kasigau	Kasigau Mountain	Kasigau 3	cave	8/4/2012	-3.84713 38.67485	597	no
Coast	Maungu	Marasi Hill	Marasi 1	cave	8/4/2012	-3.57323 38.74625	646	no
Eastern	Kibwesi	Kakindu Hill	Kakindu 12	cave	12/10/2012	-2.08336 38.33989	715	no
Eastern	Kibwesi	Kima Kimwe Hill	Kima Kimwe 3	cave	12/10/2012	-2.06258 38.32144	726	no
Eastern	Kibwesi	Kima Kimwe Hill	Kima Kimwe 3	fissure	21/12/2012	-2.06258 38.32144	726	no
Eastern	Kibwesi	Kima Kimwe Hill	Kima Kimwe 4	fissure	12/10/2012	-2.06229 38.32131	733	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 2	fissure	14/10/2012	-2.02291 38.33135	711	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 2	fissure	20/12/2012	-2.02291 38.33135	711	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 5	cave	14/10/2012	-2.02141 38.33038	676	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 6	fissure	14/10/2012	-2.01911 38.32964	679	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 6	fissure	20/12/2012	-2.01911 38.32964	679	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 7	fissure	14/10/2012	-2.01883 38.32967	681	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 7	fissure	20/12/2012	-2.01883 38.32967	681	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 8	fissure	14/10/2012	-2.01887 38.32968	673	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 8	fissure	20/12/2012	-2.01887 38.32968	673	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 9	fissure	14/10/2012	-2.01864 38.32964	661	no
Eastern	Kibwesi	Kwandula Hill	Kwandula 9	fissure	20/12/2012	-2.01864 38.32964	661	no
Eastern	Kibwesi	Kwayula Hill	Kwayula 1	cave	17/10/2012	-2.00177 38.32431	702	no
Eastern	Kibwesi	Kwayula Hill	Kwayula 2	cave	17/10/2012	-2.00128 38.32418	712	no
Eastern	Kibwesi	Mbale Hill	Mbale 1	cave	16/10/2012	-2.00465 38.33027	672	no
Eastern	Kibwesi	Mbale Hill	Mbale 4	cave	16/10/2012	-2.00367 38.33051	674	no

APPENDIX 1 (*continued*)

Presence or absence of *Mormotomyia hirsuta* Austen in bat-inhabited caves and fissures in Kenya.

Prov.	Area	Site name	Cave/fissure name	Cave/ fissure	Date	Coordinates (decimal degrees)	Elev. (m)	Live *Mormotomyia* present?
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 5	fissure	30/10/2012	-2.37266 37.91180	1216	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 5	fissure	19/12/2012	-2.37266 37.91180	1216	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 5	fissure	20/12/2012	-2.37266 37.91180	1216	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 5	fissure	21/12/2012	-2.37266 37.91180	1216	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 5	fissure	22/12/2012	-2.37266 37.91180	1216	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 8	fissure	30/10/2012	-2.36823 37.91150	1227	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 12	fissure	1/11/2012	-2.37011 37.90958	1143	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 12	fissure	19/12/2012	-2.37011 37.90958	1143	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 12	fissure	20/12/2012	-2.37011 37.90958	1143	yes
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 12	fissure	21/12/2012	-2.37011 37.90958	1143	yes
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 12	fissure	22/12/2012	-2.37011 37.90958	1143	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 13	fissure	01/11/2012	-2.36721 37.90947	1207	no
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 24	fissure	20/12/2012	-2.37024 37.90682	1029	no
Eastern	Kibwesi	Vendelani Hill	Vendelani 1	fissure	15/10/2012	-2.01073 38.33111	651	no
Eastern	Kibwesi	Vendelani Hill	Vendelani 5	cave	15/10/2012	-2.00970 38.33023	662	no
Eastern	Kibwesi	Vendelani Hill	Vendelani 6	cave	15/10/2012	-2.00968 38.33059	666	no
Eastern	Kibwesi	Vendelani Hill	Vendelani 6	fissure	19/12/2012	-2.00968 38.33059	666	no
Eastern	Kibwesi	Vendelani Hill	Vendelani 6	fissure	22/12/2012	-2.00968 38.33059	666	no
Eastern	Kibwesi	Vendelani Hill	Vendelani 7	cave	15/10/2012	-2.00975 38.33069	665	no
Eastern	Kibwesi	Vendelani Hill	Vendelani 7	fissure	19/12/2012	-2.00975 38.33069	665	no
Eastern	Kibwesi	Yamalu Hill	Yamalu 2	fissure	13/10/2012	-2.04735 38.33130	912	no
Eastern	Kibwesi	Yamalu Hill	Yamalu 2	fissure	22/12/2012	-2.04735 38.33130	912	no
Eastern	Kibwesi	Yamalu Hill	Yamalu 6	fissure	13/10/2012	-2.04797 38.33171	904	no
Eastern	Kibwesi	Yamalu Hill	Yamalu 6	fissure	22/12/2012	-2.04797 38.33171	904	no
Eastern	Kibwesi	Yamalu Hill	Yamalu 8	cave	13/10/2012	-2.04885 38.33116	837	no

APPENDIX 1 (*continued*)

Presence or absence of *Mormotomyia hirsuta* Austen in bat-inhabited caves and fissures in Kenya.

Prov.	Area	Site name	Cave/fissure name	Cave/ fissure	Date	Coordinates (decimal degrees)	Elev. (m)	Live *Mormotomyia* present?
Eastern	Kyulu	Kyulu Hill	Kyulu 1	cave	9/5/2012	-2.92915 38.40625	593	no
Eastern	Mwingi	Endau Mountain	Sovi 1	cave	19/12/2011	-1.22799 38.56463	650	no
Eastern	Mwingi	Kalanga Hill A	Kalanga A2	fissure	15/8/2012	-0.81018 38.39499	873	no
Eastern	Mwingi	Kangui Hill	Kangui 2	fissure	29/9/2012	-0.79458 38.53382	729	no
Eastern	Mwingi	Kangui Hill	Kangui 3	fissure	29/9/2012	-0.79484 38.53313	737	no
Eastern	Mwingi	Kangui Hill	Kangui 4	cave	29/9/2012	-0.79477 38.53315	735	no
Eastern	Mwingi	Kangui Hill	Kangui 6	fissure	29/9/2012	-0.79445 38.53371	741	no
Eastern	Mwingi	Kavuruti Hill	Kavuruti 3	fissure	13/8/2012	-0.85850 38.51793	622	no
Eastern	Mwingi	Kavuruti Hill	Kavuruti 3	fissure	11/12/2012	-0.85850 38.51793	622	no
Eastern	Mwingi	Kavuruti Hill	Kavuruti 4b	fissure	13/8/2012	-0.85851 38.51819	630	no
Eastern	Mwingi	Kwanduto Hill C	Kwanduto C 5	cave	16/8/2012	-0.79727 38.37453	707	no
Eastern	Mwingi	Makilu Hill	Makilu 2	fissure	11/8/2012	-0.83673 38.55806	677	no
Eastern	Mwingi	Makilu Hill	Makilu 2	fissure	30/11/2012	-0.83673 38.55806	677	yes
Eastern	Mwingi	Makilu Hill	Makilu 2	fissure	2/12/2012	-0.83673 38.55806	677	yes
Eastern	Mwingi	Makilu Hill	Makilu 2	fissure	4/12/2012	-0.83673 38.55806	677	no
Eastern	Mwingi	Makilu Hill	Makilu 2	fissure	9/12/2012	-0.83673 38.55806	677	no
Eastern	Mwingi	Makilu Hill	Makilu 2	fissure	13/12/2012	-0.83673 38.55806	677	no
Eastern	Mwingi	Makilu Hill	Makilu 2	fissure	14/12/2012	-0.83673 38.55806	677	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	11/8/2012	-0.83623 38.55784	686	no[1]
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	29/11/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	30/11/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	2/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	4/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	5/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	7/12/2012	-0.83623 38.55784	686	yes

APPENDIX 1 (*continued*)

Presence or absence of *Mormotomyia hirsuta* Austen in bat-inhabited caves and fissures in Kenya.

Prov.	Area	Site name	Cave/fissure name	Cave/ fissure	Date	Coordinates (decimal degrees)	Elev. (m)	Live *Mormotomyia* present?
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	9/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	13/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	14/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	16/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	19/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	22/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	25/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	28/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	31/12/2012	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	3/1/2013	-0.83623 38.55784	686	yes
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	6/1/2013	-0.83623 38.55784	686	no
Eastern	Mwingi	Makilu Hill	Makilu 3	fissure	9/1/2013	-0.83623 38.55784	686	no
Eastern	Mwingi	Makilu Hill	Makilu 9	cave	8/11/2011	-0.83642 38.55582	999	no
Eastern	Mwingi	Makyui Hill	Makyui B3	fissure	30/9/2012	-0.87016 38.52322	619	no
Eastern	Mwingi	Makyui Hill	Makyui B3	fissure	12/12/2012	-0.87016 38.52322	619	no
Eastern	Mwingi	Makyui Hill	Makyui B5	fissure	30/9/2012	-0.87043 38.52298	639	no
Eastern	Mwingi	Miuni	Miuni baobab	baobab tree hole	12/8/2012	-0.88113 38.55712	564	no
Eastern	Mwingi	Miuni	Miuni baobab	baobab tree hole	6/12/2012	-0.88113 38.55712	564	no
Eastern	Mwingi	Miuni Hill	Miuni 1	fissure	12/8/2012	-0.86047 38.55015	587	no
Eastern	Mwingi	Miuni Hill	Miuni 1	fissure	6/12/2012	-0.86047 38.55015	587	no
Eastern	Mwingi	Miuni Hill	Miuni 6	fissure	12/8/2012	-0.86056 38.54947	577	no
Eastern	Mwingi	Miuni Hill	Miuni 6	fissure	6/12/2012	-0.86056 38.54947	577	no
Eastern	Mwingi	Miuni Hill	Miuni 7	cave	12/8/2012	-0.86031 38.54934	596	no
Eastern	Mwingi	Miuni Hill	Miuni 7	cave	6/12/2012	-0.86031 38.54934	596	no
Eastern	Mwingi	Mulinde Hill	Mulinde 7	fissure	14/8/2012	-0.84208 38.43270	729	no

APPENDIX 1 (*continued*)

Presence or absence of *Mormotomyia hirsuta* Austen in bat-inhabited caves and fissures in Kenya.

Prov.	Area	Site name	Cave/fissure name	Cave/ fissure	Date	Coordinates (decimal degrees)	Elev. (m)	Live *Mormotomyia* present?
Eastern	Mwingi	Ngauluka Hill	Ngauluka 1	fissure	10/8/2012	-0.82251 38.54564	634	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 1	fissure	29/11/2012	-0.82251 38.54564	634	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 2	fissure	10/8/2012	-0.82241 38.54544	619	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 2	fissure	29/11/2012	-0.82241 38.54544	619	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 2	fissure	10/12/2012	-0.82241 38.54544	619	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 13	fissure	26/9/2012	-0.82596 38.55215	749	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 14	fissure	26/9/2012	-0.82576 38.55230	752	no[1]
Eastern	Mwingi	Ngauluka Hill	Ngauluka 14	fissure	1/12/2012	-0.82576 38.55230	752	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 14	fissure	8/12/2012	-0.82576 38.55230	752	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 15	fissure	26/9/2012	-0.82716 38.55269	737	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 15	fissure	1/12/2012	-0.82716 38.55269	737	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 15	fissure	7/12/2012	-0.82716 38.55269	737	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 15	fissure	8/12/2012	-0.82716 38.55269	737	yes
Eastern	Mwingi	Ngauluka Hill	Ngauluka 15	fissure	10/12/2012	-0.82716 38.55269	737	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 15	fissure	13/12/2012	-0.82716 38.55269	737	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 16	fissure	26/9/2012	-0.82702 38.55299	728	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 16	fissure	1/12/2012	-0.82702 38.55299	728	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 16	fissure	7/12/2012	-0.82702 38.55299	728	yes
Eastern	Mwingi	Ngauluka Hill	Ngauluka 16	fissure	8/12/2012	-0.82702 38.55299	728	yes
Eastern	Mwingi	Ngauluka Hill	Ngauluka 16	fissure	10/12/2012	-0.82702 38.55299	728	yes
Eastern	Mwingi	Ngauluka Hill	Ngauluka 16	fissure	13/12/2012	-0.82702 38.55299	728	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 16	fissure	14/12/2012	-0.82702 38.55299	728	yes
Eastern	Mwingi	Ngauluka Hill	Ngauluka 17	fissure	8/12/2012	-0.82681 38.55320	711	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 17	fissure	10/12/2012	-0.82681 38.55320	711	no
Eastern	Mwingi	Ngauluka Hill	Ngauluka 17	fissure	13/12/2012	-0.82681 38.55320	711	no

APPENDIX 1 (*continued*)

Presence or absence of *Mormotomyia hirsuta* Austen in bat-inhabited caves and fissures in Kenya.

Prov.	Area	Site name	Cave/fissure name	Cave/ fissure	Date	Coordinates (decimal degrees)	Elev. (m)	Live *Mormotomyia* present?
Eastern	Mwingi	Ngauluka Hill	Ngauluka 19	fissure	10/12/2012	-0.82693 38.55164	713	no
Eastern	Mwingi	Nzewani Hill B	Nzewani B3	fissure	28/9/2012	-0.88033 38.55646	555	no
Eastern	Mwingi	Nzewani Hill B	Nzewani B3	fissure	12/12/2012	-0.88033 38.55646	555	no
Eastern	Mwingi	Sosoma Hill A	Sosoma A1	fissure	27/9/2012	-0.88110 38.67256	503	no
Eastern	Mwingi	Sosoma Hill B	Sosoma B1	fissure	27/9/2012	-0.88130 38.67316	501	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C1	cave	27/9/2012	-0.88357 38.67567	509	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C1	cave	14/12/2012	-0.88357 38.67567	509	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C2	cave	27/9/2012	-0.88342 38.67582	535	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C2	cave	14/12/2012	-0.88342 38.67582	535	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C3	fissure	27/9/2012	-0.88344 38.67584	514	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C3	fissure	14/12/2012	-0.88344 38.67584	514	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C4	fissure	27/9/2012	-0.88325 38.67636	525	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C5	fissure	27/9/2012	-0.88321 38.67635	541	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C5	fissure	14/12/2012	-0.88321 38.67635	541	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C6	fissure	27/9/2012	-0.88309 38.67631	531	no
Eastern	Mwingi	Sosoma Hill C	Sosoma C7	fissure	14/12/2012	-0.88274 38.67634	504	no
Eastern	Mwingi	Tivai Hill	Tivai 4	cave	13/8/2012	-0.84618 38.52211	672	no
Eastern	Mwingi	Tivai Hill	Tivai 4	cave	11/12/2012	-0.84618 38.52211	672	no
Eastern	Mwingi	Ukasi Hill	Ukasi 1	fissure	18/12/2011	-0.81713 38.54225	720	no[2,3]
Eastern	Mwingi	Ukasi Hill	Ukasi 1	fissure	28/11/2012	-0.81713 38.54225	720	no
Eastern	Mwingi	Ukasi Hill	Ukasi 1	fissure	29/11/2012	-0.81713 38.54225	720	no
Eastern	Mwingi	Ukasi Hill	Ukasi 1	fissure	3/12/2012	-0.81713 38.54225	720	no
Eastern	Mwingi	Ukasi Hill	Ukasi 1	fissure	9/12/2012	-0.81713 38.54225	720	no
Eastern	Mwingi	Ukasi Hill	Ukasi 2	cave	18/12/2011	-0.81429 38.54543	667	no
Eastern	Mwingi	Ukasi Hill	Ukasi 2	fissure	1/10/2012	-0.81895 38.54274	664	no

APPENDIX 1 (*continued*)

Presence or absence of *Mormotomyia hirsuta* Austen in bat-inhabited caves and fissures in Kenya.

Prov.	Area	Site name	Cave/fissure name	Cave/ fissure	Date	Coordinates (decimal degrees)	Elev. (m)	Live *Mormotomyia* present?
Eastern	Mwingi	Ukasi Hill	Ukasi 2	fissure	3/12/2012	-0.81895 38.54274	664	no
Eastern	Mwingi	Ukasi Hill	Ukasi 2	fissure	9/12/2012	-0.81895 38.54274	664	no
Eastern	Mwingi	Ukasi Hill	Ukasi 3	cave	18/12/2011	-0.81587 38.54164	670	no
Eastern	Mwingi	Ukasi Hill	Ukasi 3	cave	1/10/2012	-0.81858 38.54328	707	no
Eastern	Mwingi	Ukasi Hill	Ukasi 4	fissure	1/10/2012	-0.81731 38.54401	754	no
Eastern	Mwingi	Ukasi Hill	Ukasi 4	fissure	3/12/2012	-0.81731 38.54401	754	no
Eastern	Mwingi	Ukasi Hill	Ukasi 4	fissure	09/12/2012	-0.81731 38.54401	754	no
Eastern	Mwingi	Ukasi Hill	Ukasi 6	cave	1/10/2012	-0.81692 38.54370	774	no
Rift Valley	Laikipia	Ewaso Nyiro River	Babu's cave	cave	19/4/2011	0.45013 36.88520	1658	no

[1]Dried corpses found, embedded in guano matrix.
[2]*Mormotomyia* was collected below this fissure from November to December 2010.
[3]*Mormotomyia* corpses were found in the nest of a salticid spider, located within a small crack in the rock face below this fissure

APPENDIX 2
Caves and fissures with neither Chiroptera nor *Mormotomyia*.

Prov.	Area	Site name	Cave/ fissure name	Fissure/ cave	Date	Coordinates (decimal degrees)	Elev. (m)
Coast	Kasigau	base of Kasigau Mountain	Kasigau 1	cave	8/4/2012	-3.84724 38.67684	629
Coast	Kasigau	base of Kasigau Mountain	Kasigau 4	cave	8/4/2012	-3.84646 38.68218	653
Coast	Kasigau	base of Kasigau Mountain	Kasigau 5	cave	8/4/2012	-3.84629 38.68196	666
Coast	Kasigau	base of Kasigau Mountain	Kasigau 6	cave	8/4/2012	-3.84621 38.68162	663
Eastern	Kibwesi	Kakindu Hill	Kakindu 1	fissure	11/10/2012	-2.07396 38.33571	796
Eastern	Kibwesi	Kakindu Hill	Kakindu 2	fissure	11/10/2012	-2.07356 38.33587	834
Eastern	Kibwesi	Kakindu Hill	Kakindu 3	cave	11/10/2012	-2.07349 38.33589	833
Eastern	Kibwesi	Kakindu Hill	Kakindu 4	cave	11/10/2012	-2.07335 38.33587	839
Eastern	Kibwesi	Kakindu Hill	Kakindu 5	cave	11/10/2012	-2.07319 38.33575	848
Eastern	Kibwesi	Kakindu Hill	Kakindu 6	cave	11/10/2012	-2.07332 38.33591	866
Eastern	Kibwesi	Kakindu Hill	Kakindu 7	cave	11/10/2012	-2.07333 38.33571	832
Eastern	Kibwesi	Kakindu Hill	Kakindu 8	cave	11/10/2012	-2.07488 38.33629	759
Eastern	Kibwesi	Kakindu Hill	Kakindu 9	cave	11/10/2012	-2.07619 38.33603	715
Eastern	Kibwesi	Kakindu Hill	Kakindu 10	cave	12/10/2012	-2.08290 38.34098	756
Eastern	Kibwesi	Kakindu Hill	Kakindu 11	cave	12/10/2012	-2.08315 38.34038	792
Eastern	Kibwesi	Kanziko Hill	Kanziko 1	cave	17/10/2012	-2.00080 38.32550	713
Eastern	Kibwesi	Kanziko Hill	Kanziko 2	cave	17/10/2012	-1.99869 38.32583	737
Eastern	Kibwesi	Kanziko Hill	Kanziko 3	cave	17/10/2012	-1.99846 38.32587	728
Eastern	Kibwesi	Kanziko Hill	Kanziko 4	cave	17/10/2012	-1.99823 38.32585	725
Eastern	Kibwesi	Kanziko Hill	Kanziko 5	cave	17/10/2012	-1.99802 38.32580	712
Eastern	Kibwesi	Kanziko Hill	Kanziko 6	fissure	17/10/2012	-1.99829 38.32516	680
Eastern	Kibwesi	Kanziko Hill	Kanziko 7	cave	17/10/2012	-1.99851 38.32526	691
Eastern	Kibwesi	Kima Kimwe Hill	Kima Kimwe 1	cave	12/10/2012	-2.06292 38.32174	694
Eastern	Kibwesi	Kima Kimwe Hill	Kima Kimwe 2	fissure	12/10/2012	-2.06263 38.32138	720
Eastern	Kibwesi	Kima Kimwe Hill	Kima Kimwe 5	fissure	12/10/2012	-2.06225 38.32119	744

APPENDIX 2 (*continued*)
Caves and fissures with neither Chiroptera nor *Mormotomyia*.

Prov.	Area	Site name	Cave/ fissure name	Fissure/ cave	Date	Coordinates (decimal degrees)	Elev. (m)
Eastern	Kibwesi	Kwandula Hill	Kwandula 1	fissure	14/10/2012	-2.02398 38.32894	683
Eastern	Kibwesi	Kwandula Hill	Kwandula 3	fissure	14/10/2012	-2.02286 38.33139	721
Eastern	Kibwesi	Kwandula Hill	Kwandula 4	cave	14/10/2012	-2.02272 38.33134	702
Eastern	Kibwesi	Kwandula Hill	Kwandula 10	fissure	14/10/2012	-2.01764 38.32897	643
Eastern	Kibwesi	Kwayula Hill	Kwayula 3	cave	17/10/2012	-2.00106 38.32397	706
Eastern	Kibwesi	Kwayula Hill	Kwayula 4	cave	17/10/2012	-2.00071 38.32389	716
Eastern	Kibwesi	Kwayula Hill	Kwayula 5	fissure	17/10/2012	-2.00025 38.32307	685
Eastern	Kibwesi	Mbale Hill	Mbale 2	cave	16/10/2012	-2.00446 38.33051	664
Eastern	Kibwesi	Mbale Hill	Mbale 3	cave	16/10/2012	-2.00367 38.33088	720
Eastern	Kibwesi	Mbale Hill	Mbale 5	cave	16/10/2012	-2.00368 38.33016	691
Eastern	Kibwesi	Mbale Hill	Mbale 6	cave	16/10/2012	-2.00325 38.32997	714
Eastern	Kibwesi	Mbale Hill	Mbale 7	cave	16/10/2012	-2.00309 38.32973	716
Eastern	Kibwesi	Mbale Hill	Mbale 8	cave	16/10/2012	-2.00326 38.32955	699
Eastern	Kibwesi	Mbale Hill	Mbale 9	fissure	16/10/2012	-2.00207 38.32915	700
Eastern	Kibwesi	Mbale Hill	Mbale 10	fissure	16/10/2012	-2.00260 38.33023	678
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 1	cave	30/10/2012	-2.37274 37.90781	1013
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 2	fissure	30/10/2012	-2.37267 37.90971	1092
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 3	cave	30/10/2012	-2.37361 37.91168	1147
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 4	cave	30/10/2012	-2.37359 37.91176	1162
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 6	cave	30/10/2012	-2.37290 37.91229	1238
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 7	cave	30/10/2012	-2.37079 37.91155	1239
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 9	cave	30/10/2012	-2.36967 37.91082	1238
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 10	cave	30/10/2012	-2.36901 37.91003	1236
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 11	cave	30/10/2012	-2.37248 37.90983	1110
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 14	fissure	1/11/2012	-2.36527 37.91017	1225

APPENDIX 2 (*continued*)
Caves and fissures with neither Chiroptera nor *Mormotomyia*.

Prov.	Area	Site name	Cave/ fissure name	Fissure/ cave	Date	Coordinates (decimal degrees)	Elev. (m)
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 15	fissure	1/11/2012	-2.36369 37.91051	1231
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 16	fissure	1/11/2012	-2.36325 37.91050	1214
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 17	cave	1/11/2012	-2.36221 37.90979	1165
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 18	fissure	3/11/2012	-2.37412 37.91677	1088
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 19	cave	3/11/2012	-2.37417 37.91540	1141
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 20	fissure	3/11/2012	-2.37547 37.91558	1123
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 21	fissure	3/11/2012	-2.37596 37.91427	1146
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 22	cave	3/11/2012	-2.37851 37.91420	1055
Eastern	Kibwesi	Mbuinzau Hill	Mbuinzau 23	fissure	3/11/2012	-2.37942 37.91420	1025
Eastern	Kibwesi	Miusyani Hill	Miusyani 1	fissure	10/10/2012	-2.08115 38.21447	773
Eastern	Kibwesi	Miusyani Hill	Miusyani 2	fissure	10/10/2012	-2.08137 38.21422	799
Eastern	Kibwesi	Miusyani Hill	Miusyani 3	fissure	10/10/2012	-2.08119 38.21420	802
Eastern	Kibwesi	Miusyani Hill	Miusyani 4	cave	10/10/2012	-2.08109 38.21411	794
Eastern	Kibwesi	Miusyani Hill	Miusyani 5	fissure	10/10/2012	-2.08035 38.21337	818
Eastern	Kibwesi	Miusyani Hill	Miusyani 6	fissure	10/10/2012	-2.08006 38.21323	825
Eastern	Kibwesi	Miusyani Hill	Miusyani 7	cave	10/10/2012	-2.07997 38.21319	827
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 1	fissure	2/11/2012	-2.38710 37.91752	1054
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 2	fissure	2/11/2012	-2.38727 37.91777	1059
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 3	fissure	2/11/2012	-2.38760 37.91805	1076
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 4	fissure	2/11/2012	-2.39007 37.91826	1097
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 5	cave	2/11/2012	-2.39031 37.91854	1080
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 6	fissure	2/11/2012	-2.39212 37.91894	1064
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 7	cave	2/11/2012	-2.39243 37.91725	1037
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 8	cave	2/11/2012	-2.39003 37.91654	1056
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 9	fissure	2/11/2012	-2.38770 37.91729	1039

APPENDIX 2 (*continued*)
Caves and fissures with neither Chiroptera nor *Mormotomyia*.

Prov.	Area	Site name	Cave/ fissure name	Fissure/ cave	Date	Coordinates (decimal degrees)	Elev. (m)
Eastern	Kibwesi	Syokivulu Hill	Syokivulu 10	fissure	2/11/2012	-2.38707 37.91659	998
Eastern	Kibwesi	Vendelani Hill	Vendelani 2	cave	15/10/2012	-2.01075 38.33102	652
Eastern	Kibwesi	Vendelani Hill	Vendelani 3	fissure	15/10/2012	-2.01047 38.33075	648
Eastern	Kibwesi	Vendelani Hill	Vendelani 4	cave	15/10/2012	-2.01016 38.33043	659
Eastern	Kibwesi	Vendelani Hill	Vendelani 8	fissure	15/10/2012	-2.00978 38.33082	660
Eastern	Kibwesi	Vendelani Hill	Vendelani 9	fissure	15/10/2012	-2.01034 38.33148	661
Eastern	Kibwesi	Yamalu Hill	Yamalu 1	cave	13/10/2012	-2.04794 38.33131	910
Eastern	Kibwesi	Yamalu Hill	Yamalu 3	cave	13/10/2012	-2.04749 38.33166	923
Eastern	Kibwesi	Yamalu Hill	Yamalu 4	cave	13/10/2012	-2.04779 38.33169	913
Eastern	Kibwesi	Yamalu Hill	Yamalu 5	cave	13/10/2012	-2.04785 38.33169	919
Eastern	Kibwesi	Yamalu Hill	Yamalu 7	cave	13/10/2012	-2.04887 38.33147	883
Eastern	Mwingi	Ethombe Hill	Ethombe Hill 1	cave	20/4/2011	-0.87742 38.09740	1148
Eastern	Mwingi	Ethombe Hill	Ethombe Hill 2	cave	20/4/2011	-0.88003 38.09830	1124
Eastern	Mwingi	Kalanga Hill A	Kalanga A1	fissure	15/8/2012	-0.81272 38.39620	762
Eastern	Mwingi	Kalanga Hill A	Kalanga A3	fissure	15/8/2012	-0.81133 38.39447	793
Eastern	Mwingi	Kalanga Hill A	Kalanga A4	cave	15/8/2012	-0.81169 38.39437	789
Eastern	Mwingi	Kalanga Hill A	Kalanga A5	cave	15/8/2012	-0.81180 38.39421	780
Eastern	Mwingi	Kalanga Hill A	Kalanga A6	cave	15/8/2012	-0.81173 38.39402	770
Eastern	Mwingi	Kalanga Hill A	Kalanga A7	cave	15/8/2012	-0.81207 38.39373	742
Eastern	Mwingi	Kalanga Hill B	Kalanga B1	cave	15/8/2012	-0.80575 38.38523	736
Eastern	Mwingi	Kalanga Hill B	Kalanga B2	cave	15/8/2012	-0.80453 38.38404	748
Eastern	Mwingi	Kangui Hill	Kangui 1	cave	29/9/2012	-0.79422 38.53416	717
Eastern	Mwingi	Kangui Hill	Kangui 5	cave	29/9/2012	-0.79476 38.53317	737
Eastern	Mwingi	Kangui Hill	Kangui 7	fissure	29/9/2012	-0.79392 38.53353	749
Eastern	Mwingi	Kangui Hill	Kangui 8	cave	29/9/2012	-0.79368 38.53318	719

APPENDIX 2 (*continued*)
Caves and fissures with neither Chiroptera nor *Mormotomyia*.

Prov.	Area	Site name	Cave/ fissure name	Fissure/ cave	Date	Coordinates (decimal degrees)	Elev. (m)
Eastern	Mwingi	Kangui Hill	Kangui 9	cave	29/9/2012	-0.79331 38.53275	680
Eastern	Mwingi	Kavuruti Hill	Kavuruti 1	fissure	13/8/2012	-0.85716 38.52114	662
Eastern	Mwingi	Kavuruti Hill	Kavuruti 2	cave	13/8/2012	-0.85959 38.52099	643
Eastern	Mwingi	Kavuruti Hill	Kavuruti 4A	cave	13/8/2012	-0.85851 38.51819	630
Eastern	Mwingi	Kwanduto Hill A	Kwanduto A1	fissure	16/8/2012	-0.78889 38.36361	663
Eastern	Mwingi	Kwanduto Hill A	Kwanduto A2	cave	16/8/2012	-0.78884 38.36356	661
Eastern	Mwingi	Kwanduto Hill B	Kwanduto B1	cave	16/8/2012	-0.79583 38.37329	691
Eastern	Mwingi	Kwanduto Hill C	Kwanduto C1	cave	16/8/2012	-0.79711 38.37458	695
Eastern	Mwingi	Kwanduto Hill C	Kwanduto C2	cave	16/8/2012	-0.79722 38.37455	702
Eastern	Mwingi	Kwanduto Hill C	Kwanduto C3	cave	16/8/2012	-0.79724 38.37461	705
Eastern	Mwingi	Kwanduto Hill C	Kwanduto C4	cave	16/8/2012	-0.79725 38.37445	713
Eastern	Mwingi	Kwanduto Hill D	Kwanduto D1	cave	16/8/2012	-0.79607 38.37098	691
Eastern	Mwingi	Kwanduto Hill D	Kwanduto D2	cave	16/8/2012	-0.79606 38.37092	688
Eastern	Mwingi	Kwanduto Hill D	Kwanduto D3	cave	16/8/2012	-0.79617 38.37092	679
Eastern	Mwingi	Makilu Hill	Makilu 1	fissure	11/8/2012	-0.83690 38.55811	680
Eastern	Mwingi	Makilu Hill	Makilu 4	cave	11/8/2012	-0.83535 38.58826	651
Eastern	Mwingi	Makilu Hill	Makilu 5	cave	11/8/2012	-0.83324 38.55795	649
Eastern	Mwingi	Makilu Hill	Makilu 6	cave	11/8/2012	-0.83473 38.55265	609
Eastern	Mwingi	Makilu Hill	Makilu 7	cave	12/8/2012	-0.83894 38.55846	670
Eastern	Mwingi	Makilu Hill	Makilu 8	cave	12/8/2012	-0.83855 38.55812	698
Eastern	Mwingi	Makyui Hill A	Makyui A1	cave	30/9/2012	-0.87019 38.52430	607
Eastern	Mwingi	Makyui Hill A	Makyui A2	cave	30/9/2012	-0.87027 38.52449	611
Eastern	Mwingi	Makyui Hill A	Makyui A3	cave	30/9/2012	-0.86962 38.52448	611
Eastern	Mwingi	Makyui Hill B	Makyui B1	cave	30/9/2012	-0.86978 38.52344	618
Eastern	Mwingi	Makyui Hill B	Makyui B2	cave	30/9/2012	-0.86999 38.52328	628

APPENDIX 2 (*continued*)
Caves and fissures with neither Chiroptera nor *Mormotomyia*.

Prov.	Area	Site name	Cave/ fissure name	Fissure/ cave	Date	Coordinates (decimal degrees)	Elev. (m)
Eastern	Mwingi	Makyui Hill B	Makyui B4	cave	30/9/2012	-0.87057 38.52283	630
Eastern	Mwingi	Mathini Hill	Mathini 1	cave	30/9/2012	-0.90326 38.49417	576
Eastern	Mwingi	Mathini Hill	Mathini 2	fissure	30/9/2012	-0.90361 38.49396	579
Eastern	Mwingi	Miuni Hill	Miuni 2	cave	12/8/2012	-0.86020 38.55010	582
Eastern	Mwingi	Miuni Hill	Miuni 3	fissure	12/8/2012	-0.85887 38.54932	591
Eastern	Mwingi	Miuni Hill	Miuni 4	cave	12/8/2012	-0.86062 38.54931	582
Eastern	Mwingi	Miuni Hill	Miuni 5	fissure	12/8/2012	-0.86052 38.54952	581
Eastern	Mwingi	Mulinde Hill	Mulinde 1	cave	14/8/2012	-0.84257 38.43364	665
Eastern	Mwingi	Mulinde Hill	Mulinde 2	cave	14/8/2012	-0.84242 38.43357	691
Eastern	Mwingi	Mulinde Hill	Mulinde 3	fissure	14/8/2012	-0.84264 38.43279	700
Eastern	Mwingi	Mulinde Hill	Mulinde 4	cave	14/8/2012	-0.84232 38.43269	705
Eastern	Mwingi	Mulinde Hill	Mulinde 5	cave	14/8/2012	-0.84201 38.43250	708
Eastern	Mwingi	Mulinde Hill	Mulinde 6	fissure	14/8/2012	-0.84201 38.43275	732
Eastern	Mwingi	Mulinde Hill	Mulinde 8	cave	14/8/2012	-0.84193 38.43505	689
Eastern	Mwingi	Ngauluka Hill	Ngauluka 3	fissure	10/8/2012	-0.82223 38.54538	628
Eastern	Mwingi	Ngauluka Hill	Ngauluka 4	fissure	10/8/2012	-0.82196 38.54612	675
Eastern	Mwingi	Ngauluka Hill	Ngauluka 5	cave	10/8/2012	-0.82291 38.54604	636
Eastern	Mwingi	Ngauluka Hill	Ngauluka 6	cave	10/8/2012	-0.82112 38.55160	649
Eastern	Mwingi	Ngauluka Hill	Ngauluka 7	fissure	10/8/2012	-0.82122 38.55200	646
Eastern	Mwingi	Ngauluka Hill	Ngauluka 8	fissure	10/8/2012	-0.82481 38.55333	646
Eastern	Mwingi	Ngauluka Hill	Ngauluka 9	fissure	26/9/2012	-0.82312 38.54681	644
Eastern	Mwingi	Ngauluka Hill	Ngauluka 10	cave	26/9/2012	-0.82425 38.55124	754
Eastern	Mwingi	Ngauluka Hill	Ngauluka 11	cave	26/9/2012	-0.82485 38.55102	768
Eastern	Mwingi	Ngauluka Hill	Ngauluka 12	cave	26/9/2012	-0.82543 38.55152	749

APPENDIX 2 (*continued*)
Caves and fissures with neither Chiroptera nor *Mormotomyia*.

Prov.	Area	Site name	Cave/ fissure name	Fissure/ cave	Date	Coordinates (decimal degrees)	Elev. (m)
Eastern	Mwingi	Ngauluka Hill	Ngauluka 18	cave	10/12/2012	-0.82688 38.55154	701
Eastern	Mwingi	Nzewani Hill B	Nzewani B1	cave	28/9/2012	-0.88006 38.55631	552
Eastern	Mwingi	Nzewani Hill B	Nzewani B2	fissure	28/9/2012	-0.88022 38.55677	553
Eastern	Mwingi	Nzewani Hill C	Nzewani C1	fissure	28/9/2012	-0.88067 38.55747	550
Eastern	Mwingi	Nzewani Hill D	Nzewani D1	fissure	28/9/2012	-0.88202 38.55713	559
Eastern	Mwingi	Nzewani Hill E	Nzewani E1	cave	28/9/2012	-0.87752 38.55538	551
Eastern	Mwingi	Nzewani Hill E	Nzewani E2	cave	28/9/2012	-0.87747 38.55520	552
Eastern	Mwingi	Sosoma Hill A	Sosoma A2	cave	27/9/2012	-0.88098 38.67161	502
Eastern	Mwingi	Tiumboni Hill	Tiumboni 1	cave	14/8/2012	-0.79809 38.49091	646
Eastern	Mwingi	Tiumboni Hill	Tiumboni 2	fissure	14/8/2012	-0.79816 38.49090	648
Eastern	Mwingi	Tivai Hill	Tivai 1	fissure	13/8/2012	-0.84853 38.52280	674
Eastern	Mwingi	Tivai Hill	Tivai 2	cave	13/8/2012	-0.84828 38.52303	707
Eastern	Mwingi	Tivai Hill	Tivai 3	cave	13/8/2012	-0.84625 38.52219	672
Eastern	Mwingi	Tivai Hill	Tivai 5	cave	13/8/2012	-0.84584 38.52203	662
Eastern	Mwingi	Tivai Hill	Tivai 6	cave	13/8/2012	-0.84318 38.52161	649
Eastern	Mwingi	Tivai Hill	Tivai 7	cave	13/8/2012	-0.84118 38.52415	676
Eastern	Mwingi	Tivai Hill	Tivai 8	cave	13/8/2012	-0.84126 38.52449	692
Eastern	Mwingi	Tivai Hill	Tivai 9	cave	13/8/2012	-0.84131 38.52458	705
Eastern	Mwingi	Tivai Hill	Tivai 10	fissure	13/8/2012	-0.84115 38.52470	707
Eastern	Mwingi	Ukasi Hill	Ukasi 1	cave	1/10/2012	-0.81947 38.54282	625
Eastern	Mwingi	Ukasi Hill	Ukasi 5	cave	1/10/2012	-0.81717 38.54421	776
Eastern	Mwingi	Ukasi Hill	Ukasi 7	cave	1/10/2012	-0.81680 38.54399	767
Eastern	Mwingi	unnamed Hill		cave	21/4/2011	-0.94212 38.08205	996
Eastern	Mwingi	unnamed Kopje west of Ukasi		cave	18/12/2011	-0.79808 38.49096	660