

Reproductive populations of the Critically Endangered bat *Phyllonycteris aphylla* at two new locations in Jamaica

PHILLIP J. OELBAUM^{*1} , RONALD P. HALL² , DAMION L. WHYTE³ 
RONALD S. STEWART⁴, JAN PAUEL⁴, SILVIA KOUWENBERG⁴ 
ELIZABETH R. DUMONT²  and KENNETH C. WELCH JR.¹ 

Abstract The Jamaican flower bat *Phyllonycteris aphylla* is categorized as Critically Endangered on the IUCN Red List. It is endemic to Jamaica and formerly known only from Stony Hill Cave, where there are an estimated c. 500 individuals. Previously declared extinct twice, its rediscovery in 2010 at Stony Hill Cave marked new hope for the conservation of this important species. Although little is known about its ecology, the species is presumed to be a cave-obligate rooster and to rely exclusively on so-called hot caves, which are defined by high ambient temperatures and low air quality. In March–April 2023, we surveyed bats at seven caves throughout Jamaica. At two of these, Green Grotto Caves, St. Ann, and Rock Spring Caverns, St. Mary, we captured both male and pregnant female *P. aphylla*. At Green Grotto Caves, we captured 24 *P. aphylla*, and 66 at Rock Spring Caverns. We believe Rock Spring Caverns to be one of the largest known roosts of *P. aphylla*. Neither of these sites are hot caves as both are moderated by flowing water, although warmer chambers may be more important to this bat than to other species. Further monitoring of these populations and continued exploration of other potential roosts are vital for the protection of this species.

Keywords Bats, caves, Chiroptera, Critically Endangered, nectarivore, Phyllostomidae, pollinator, roosting ecology

The Jamaican flower bat *Phyllonycteris aphylla* (Chiroptera: Phyllostomidae) is endemic to Jamaica and categorized as Critically Endangered on the IUCN Red List (Koenig & Dávalos, 2015). Kurta & Rodríguez-Durán (2023) estimated there were 500 individuals (up from 250; Koenig & Dávalos, 2015) at Stony Hill Cave, which was purchased by the Natural Resources Conservation Authority in partnership with Bat Conservation International (Donahue, 2019). Despite its significance as a nocturnal pollinator, little is known

about the ecology and natural history of this species, and it has twice been declared extinct. After the species was first described in 1898 (Miller, 1898), only fossilized specimens were collected until the species was rediscovered at St. Clair Cave in 1957 (Goodwin, 1970). Capture records from St. Clair, Riverhead, Mount Plenty, Marta Tick, Wallingford and Oxford Caves all indicated the presence of *P. aphylla* there from the 1960s to the 1980s although they have not been captured at these sites since (Pregill et al., 1991; Genoways et al., 2005). Genoways et al. (2005) found that *P. aphylla* was relatively common in certain localities between 1974 and 1985, but there are no published records of *P. aphylla* after 1985, and the species was believed extinct until its rediscovery at Stony Hill Cave in 2010 (Koenig & Dávalos, 2015).

What is known about the ecology and life history of *P. aphylla* is limited and anecdotal. It appears to form smaller colonies than heterospecifics, as observed by Goodwin (1970) in St. Clair Cave and based on our present knowledge from Stony Hill Cave. The data available suggests this species feeds on fruits, nectar, pollen and insects (Nowak, 1999). It is believed to be a cave-obligate rooster, and based on prevailing descriptions seems to be limited to so-called hot caves (Genoways et al., 2005), which are defined by high bat densities that result in a high temperature and low air quality within particular chambers; often these chambers have small entrances and abundant detritivores consuming guano in passages below the roost, creating additional heat and consuming the limited oxygen (Rodríguez-Durán, 1995; Ladle et al., 2012).

In March–April 2023, we surveyed bats at seven caves throughout Jamaica. During this survey we encountered reproductive male and female *P. aphylla* at two sites where there were no previously documented captures of this species. Here we describe our observations at these two sites, and call for further research on this important species. Over 11 netting nights between 22 March and 2 April 2023, we surveyed caves at Windsor, Green Grotto, St. Clair, Mosley Hall, Riverhead, Mount Plenty and Rock Spring (Fig. 1). All sites except for Rock Spring have been previously surveyed for bats, and there are records of captured *P. aphylla* from Windsor, St. Clair, Riverhead and Mount Plenty (Genoways et al., 2005). At each site, we deployed 1–2 harp traps (Faunatech Austbat, Mount Taylor, Australia)

*Corresponding author, phillip.oelbaum@mail.utoronto.ca

¹University of Toronto Scarborough, Toronto, Ontario, Canada

²University of California, Merced, California, USA

³University of the West Indies, Mona, Kingston, Jamaica

⁴Jamaican Caves Organisation, Ewarton, Jamaica

Received 22 June 2023. Revision requested 28 July 2023.

Accepted 2 November 2023. First published online 15 January 2024.

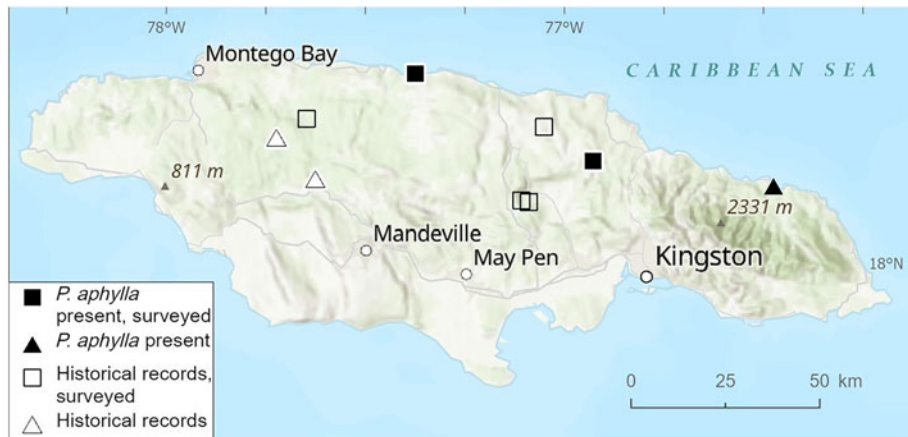


FIG. 1 Caves on Jamaica visited or known to have Jamaican flower bat *Phyllonycteris aphylla* roosts historically and/or currently. Caves surveyed between 22 March and 3 April 2023 are indicated by squares and those not visited as a part of this study are indicated as triangles. One cave surveyed during this study (Mosley Hall) did not have historical records of *P. aphylla* and none were captured there, this has therefore been omitted from this map. There is no confirmed location for Wallingford which has a historical record for the species (Genoways et al., 2005). Because of permit restrictions, we are unable to provide precise locations of caves.

for 2–5 hours. Captured bats were placed in individual cloth bags for subsequent processing and data collection, which involved measuring mass and forearm length, and collecting hair, faeces and wing tissue samples from some individuals. All individuals were released at the point of capture.

On the evenings of 24 March and 2 April 2023, we surveyed Green Grotto Caves, near Discovery Bay, St. Ann

parish. This cave is both a historical site of national importance and a major tourist attraction. Subfossil remains of *P. aphylla* were collected in 1919–1920 from this cave complex (Koopman & Williams, 1951), although there are no published records of *P. aphylla* being captured (Genoways et al., 2005). The principal bat roosting area (known as Bat College) was believed to hold thousands of bats,

TABLE 1 Capture records of 24 *Phyllonycteris aphylla* netted at Lake-Side Bat Exit, Green Grotto Caves, St. Ann, Jamaica. Capture times indicate when bats were extracted from harp traps. The final four bats were released at the trap without processing. All individuals were adults.

ID	Date	Capture time	Sex	Reproductive status	Forearm length (mm)	Mass (g)
JM069	24 Mar. 23	19.00	M	Non-reproductive	46.7	17.43
JM072	24 Mar. 23	19.00	F	Pregnant	46.2	19.90
JM084	24 Mar. 23	21.00	M	Non-reproductive	46.9	19.02
JM085	24 Mar. 23	21.00	M	Non-reproductive	47.6	21.40
JM086	24 Mar. 23	21.00	M	Non-reproductive	48.7	20.79
JM087	24 Mar. 23	21.00	F	Pregnant	47.9	18.14
JM088	24 Mar. 23	21.00	F	Not obviously pregnant	46.8	17.07
JM089	24 Mar. 23	21.00	M	Non-reproductive	45.2	17.04
JM090	24 Mar. 23	21.00	M	Non-reproductive	46.1	20.69
JM091	24 Mar. 23	21.00	M	Non-reproductive	42.4	20.21
JM092	24 Mar. 23	21.00	F	Pregnant	47.5	18.43
JM093	24 Mar. 23	22.00	F	Pregnant	47.7	23.70
JM094	24 Mar. 23	22.00	M	Non-reproductive	46.6	19.54
JM095	24 Mar. 23	22.00	M	Non-reproductive	46.7	17.91
JM325	2 Apr. 23	21.30	F	Not obviously pregnant	46.7	16.23
JM335	2 Apr. 23	21.30	M	Non-reproductive	45.6	18.87
JM336	2 Apr. 23	21.30	M	Non-reproductive	46.4	17.08
JM337	2 Apr. 23	21.30	M	Scrotal	46.9	20.87
JM338	2 Apr. 23	21.30	M	Scrotal	48.1	17.98
JM339	2 Apr. 23	21.30	F	Pregnant	45.3	18.81
	2 Apr. 23	22.30	M	Non-reproductive		
	2 Apr. 23	22.30	M	Non-reproductive		
	2 Apr. 23	22.30	M	Non-reproductive		
	2 Apr. 23	22.30	F	Pregnant		

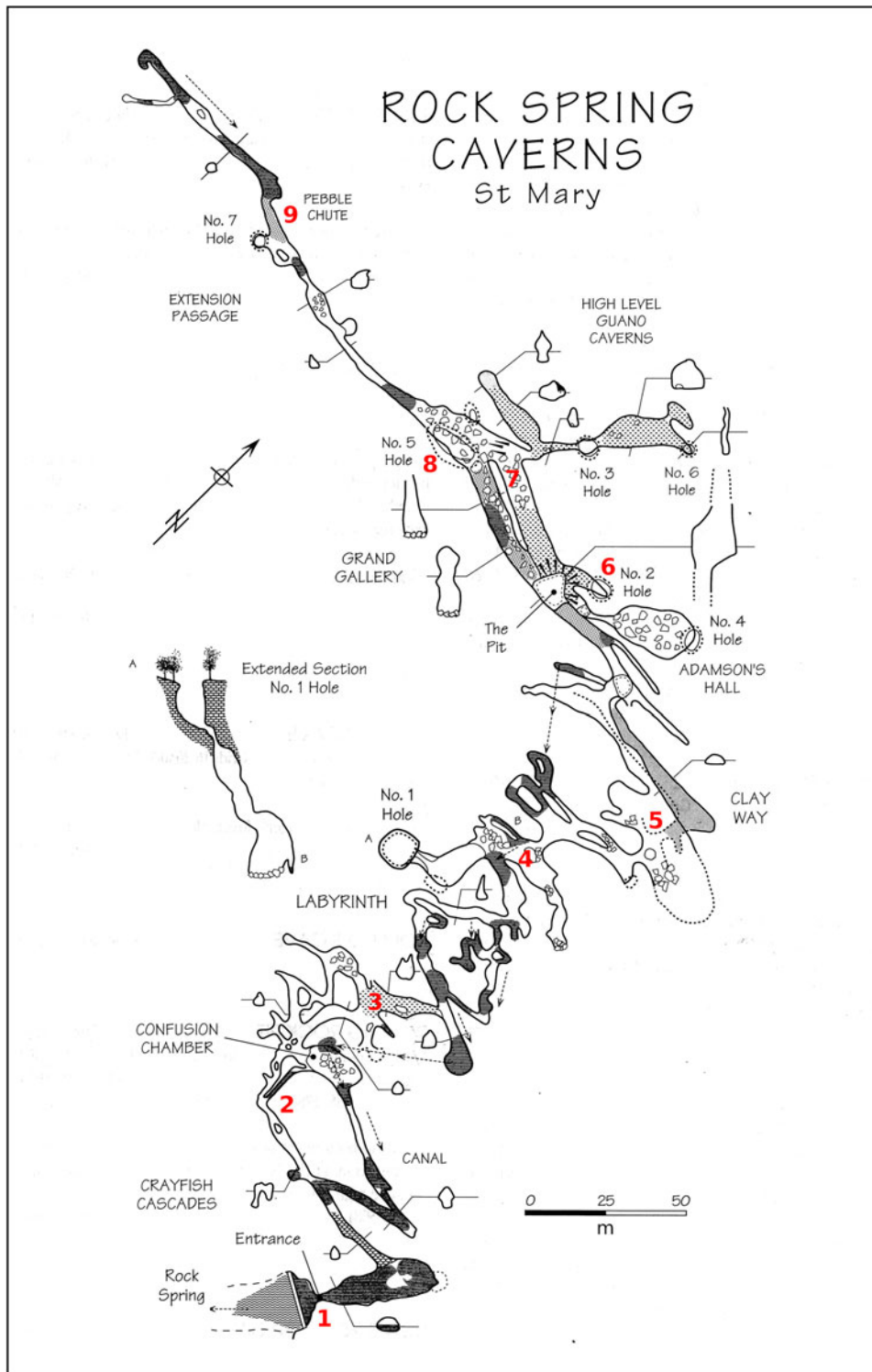


FIG. 2 The internal layout of Rock Spring Caverns, St. Mary Parish, Jamaica (Fig. 1). This map was made as part of a 1963 Leeds University expedition and adapted from Fincham (1997). Temperatures throughout the cave are believed to be stable (23.1–23.6 °C; external ambient 30.0 °C). (1) Constriction < 1 m², periodically submerged; (2) Bat numbers variable, distance below surface c. 30 m; (3) Large roost area, distance below surface c. 35 m; (4) Bats throughout, fewer than location 3, distance below surface c. 40 m; (5) Bats throughout, distance below surface c. 50 m; (6) Big Hole, bats roosting throughout, distance below surface c. 60 m; (7) Deep guano deposits distance below surface c. 30 m; (8) Scary Hole, bats roosting throughout, distance below surface c. 60 m; (9) Constriction c. 1 m² at bottom of Pebble Chute, periodically submerged, distance below surface c. 60 m.

primarily *Erophylla sezekorni*, and potentially *P. aphylla* (D.L. Whyte, pers. comm., 2022). *Phyllonycteris aphylla* were captured there by H. U. Schnitzler sometime between 2000 and 2003, although no specimens were collected and no record was published (Koenig, 2018); acoustic monitoring also supported their likely presence (Koenig, 2018). Fenton et al. (2020) photographically surveyed the

Lake-Side Bat Exit, believed to be connected to Bat College. Among hundreds of bats photographed, they observed four male *P. aphylla* using this exit (Fenton et al., 2020). No female *P. aphylla* were recorded. On both nights of trapping we set a single harp trap perpendicular to the Lake-Side Bat Exit at c. 17.45, and captured bats until 22.30. We captured several hundred bats of seven

TABLE 2 Capture records of 14 *P. aphylla* trapped at Big Hole, Rock Spring Caverns, St. Mary, Jamaica. All bats were captured in two harp traps and were extracted at approximately the same time ± 15 min. These records do not include 52 individual *P. aphylla* captured at 20:30 in the harp traps on the same day; there were 26 males and 26 females (23 pregnant). All individuals were adults.

ID	Date	Capture time	Sex	Reproductive status	Forearm length (mm)	Mass (g)
JM230	1 Apr. 23	19.30	F	Pregnant	48.8	20.69
JM234	1 Apr. 23	19.30	F	Pregnant	47.1	20.32
JM235	1 Apr. 23	19.30	F	Pregnant	47.7	20.69
JM236 ¹	1 Apr. 23	19.30	M	Non-reproductive	45.1	
JM237	1 Apr. 23	19.30	F	Not obviously pregnant	46.1	16.42
JM239	1 Apr. 23	19.30	M	Non-reproductive	47.7	20.78
JM240	1 Apr. 23	19.30	F	Pregnant	44.4	19.87
JM242	1 Apr. 23	19.30	F	Pregnant	46.2	20.09
JM244	1 Apr. 23	19.30	F	Pregnant	45.9	18.42
JM246	1 Apr. 23	19.30	F	Pregnant	47.1	19.20
JM297	1 Apr. 23	19.30	M	Scrotal	48.4	21.52
JM298	1 Apr. 23	19.30	M	Scrotal	47.2	20.69
JM299	1 Apr. 23	19.30	M	Non-reproductive	47.3	21.75
JM301	1 Apr. 23	19.30	F	Not obviously pregnant	47.2	15.99

¹Not weighed.

species, including 20 *P. aphylla* (14 on 24 March 23, 6 on 2 April 23). Among these 20 individuals, we captured five pregnant females and two adult females that were not obviously pregnant at the time of capture. These individuals were processed and an additional four (including another pregnant female) were captured at 22.30 on 2 April (Table 1). These records are the first published captures of *P. aphylla* at Green Grotto Caves, as well as the first confirmation of reproductive females at this site.

Rock Spring Caverns, St. Mary parish, has not been previously surveyed for bats, although it was geologically surveyed and mapped by a team from Leeds University, UK, in 1963 and is well known to local people and cavers (Fincham, 1997). Exploration by the Jamaican Caves Organisation from 2020 onwards documented 11 holes that appear to give access to the caverns, seven of which were numbered by the original expedition and four subsequently named; e.g. Big Hole and Scary Hole (Fig. 2). Assessments revealed that bats roost throughout most of the cave at varying densities, and based on knowledge of caves throughout the island, it is believed to be one of the largest communities of roosting bats in Jamaica (R.S. Stewart, pers. comm., 2023). On the evening of 1 April 2023, we visited Rock Spring Caverns at Big Hole and set two harp traps at the south-facing edge at c. 18.00. Bats began to emerge at c. 18.20 and through to 20.00 we captured c. 200 individuals of six species; among these were 14 *P. aphylla* (Table 2). By 20.30 the harp traps had captured c. 100 additional bats, the majority being *P. aphylla*. We assessed age-class, sex and reproductive status of each *P. aphylla* before it was released. Among this later group we captured 26 non-reproductive adult males and 23 pregnant females; there were an additional three adult females that were not obviously pregnant. Assuming no individuals

were recaptures (we were unable to mark these bats because of permit restrictions), we captured a total of 66 mature *P. aphylla*. Based on the IUCN Red List assessment, this is likely the largest known population of the species (Koenig & Dávalos, 2015).

The capture records presented here substantially alter what was previously known about this species. Not only do they increase the number of sites and reproductive individuals known, but they also the assumption that *P. aphylla* is only found in hot caves. Although Stony Hill Cave is hot (ambient temperatures of ≤ 38 °C), both Green Grotto and Rock Spring contain flowing or pooled water that moderates temperatures within these caves, and both are described as cool (i.e. below external ambient temperatures) with regard to their overall temperature profile (R.S. Stewart, pers. comm., 2023). At Rock Spring Caverns, although some roosting areas are perceived to be warmer than other areas, no surveyed locations in the cave are hot (23.1–23.6 °C in passages and roost spaces; ambient 30.0 °C). Likewise, at Green Grotto Cave, although some unexplored areas may have temperatures above ambient, the principal bat roosting areas are cooler than external temperatures (27.5–29.2 °C; ambient 35.6 °C; D.L. Whyte, unpubl. data, 2023). McFarlane (1986) suggested that *P. aphylla* may also be restricted to caves associated with abandoned river resurgences, however this is not the case at Stony Hill, Green Grotto or Rock Spring. There are no known uniting geological or other physical features between current and previously known roosts. Thus, we believe there is no known limitation for a cave to host a *P. aphylla* colony and more caves should be surveyed to examine this.

Future work on *P. aphylla* should focus on locating additional roosts and safeguarding the three known populations. The primary threats to this species include

disturbance from guano harvesters and predation by feral cats (J. Flanders, pers. comm., 2023; M.B. Fenton & D.L. Whyte, unpubl. data, 2019). However, it is unclear why we did not record the species at previously known roosts such as St. Clair Cave; we do not know whether this is a result of abiotic factors, such as changes in cave microclimate, or disturbance by people or feral cats. Monitoring of known roosts is required to ensure the survival of this Critically Endangered species, as is improving protection and establishing protected areas around known roosts to reduce disturbance, as Bat Conservation International has done at Stony Hill Cave (Meierhofer et al., 2023). Further surveys of Rock Spring Caverns are required to identify chambers of importance for *P. aphylla*, and deployment of temperature loggers to identify microclimates favourable to roosting within this cave system. We encourage the Urban Development Corporation and National Environment and Planning Agency to create a bat monitoring programme for the Bat College population. Our future work at Rock Spring Cave will focus on monitoring bats at other exits (we only trapped at one of the 11 known entrances) to refine the estimate of population size, and identify areas of ecological importance near the cave to inform management decisions. We feel these new records provide hope for the future of this Critically Endangered endemic species.

Author contributions Study design: PJO, RPH, ERD, KCW; bat fieldwork: PJO, RPH, DLW, RSS; cave fieldwork: RSS, JP, SK; figures: RSS, DLW; writing: all authors.

Acknowledgements We thank the National Environment and Planning Agency, in particular Samantha Grant, Andrea Donaldson and Peter Knight, for granting permission; Brock Fenton, Susan Koenig of Windsor Research Centre, and Jon Flanders of Bat Conservation International for assistance in planning; the Urban Development Corporation and their team, and landowners and communities near Rock Spring Caverns, for access to the caves; and Nancy Simmons, Hugh Broders and Caleb Ryan for the harp traps that made this work possible. Funding was provided by the University of California, Merced (Start-up fund to ERD) and National Science and Engineering Research Council of Canada (NSERC Discovery Grant to KCW).

Conflicts of interest None.

Ethical standards All research was conducted under permits granted by the National Environment and Planning Agency, and work at Green Grotto was conducted under an indemnity agreement granted by the Urban Development Corporation. All capture and handling followed the guidelines of the American Society of Mammalogists (Sikes et al., 2011) and under institutional animal use approval (UTSC AUP #20012113; UC Merced IACUC D16-00791, A4561-1), and this research otherwise abided by the *Oryx* guidelines on ethical standards.

Data availability All capture records published here include pertinent data. As a permit condition, coordinates of our netting sites are not permitted to be published but can be obtained by contacting the authors and/or the Jamaican Caves Organisation. No additional data collected are relevant to this publication.

References

- DONAHUE, M.Z. (2019) Back from the brink: safeguarding the last refuge of the Jamaican flower bat. *Bats*, 14, 14–16.
- FENTON, M.B., FENTON, S.L., KOENIG, S. & WHYTE, D.L. (2020) *Bats Using the Lake-Side Bat Exit, Green Grotto Cave, St. Ann Parish, Jamaica*. Unpublished report. University of Western Ontario, London, Ontario, Canada.
- FINCHAM, A.G. (1997) *Jamaica Underground: The Caves, Sinkholes and Underground Rivers of the Island*. The Press University of the West Indies, Kingston, Jamaica.
- GENOWAYS, H.H., BAKER, R.J., BICKHAM, J.W. & PHILLIPS, C.J. (2005) Bats of Jamaica. *Special Publications of the Museum of Texas Tech University*, 48, 1–155.
- GOODWIN, R.E. (1970) The ecology of Jamaican bats. *Journal of Mammalogy*, 51, 571–579.
- KOENIG, S. (2018) *The Unique Soundscape of Green Grotto: Diversity and Spatial Distributions of Cave- and Forest-Dependent Bats in a Complex Network of Caves (With Additional Notes on Invertebrate Fauna)*. Unpublished report. Windsor Research Centre, Sherwood Content, Jamaica.
- KOENIG, S. & DÁVALOS, L. (2015) *Phyllonycteris aphylla*. In *The IUCN Red List of Threatened Species 2015*. [dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T17173A22133396.en](https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T17173A22133396.en).
- KOOPMAN, K.F. & WILLIAMS, E.E. (1951) Fossil Chiroptera collected by H. E. Anthony in Jamaica, 1919–1920. *American Museum Novitates*, 1519, 1–29.
- KURTA, A. & RODRÍGUEZ-DURÁN, A. (2023) *Bats of the West Indies: A Natural History and Field Guide*. Cornell University Press, Ithaca, USA.
- LADLE, R.J., FIRMINO, J.V.L., MALHADO, A.C.M. & RODRÍGUEZ-DURÁN, A. (2012) Unexplored diversity and conservation potential of Neotropical hot caves. *Conservation Biology*, 26, 978–982.
- McFARLANE, D.A. (1986) Cave bats in Jamaica. *Oryx*, 20, 27–30.
- MEIERHOFER, M.B., JOHNSON, J.S., PEREZ-JIMENEZ, J., ITO, F., WEBELA, P.A., WIANOTORO, S. et al. (2023) Effective conservation of subterranean-roosting bats. *Conservation Biology*, e14157, published online 28 July 2023.
- MILLER, G.S. (1898) Descriptions of Five New Phyllostome Bats. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 50, 334–337.
- NOWAK, R.M. (1999) *Walker's Mammals of the World*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- PREGILL, G.K., CROMBIE, R.I., STEADMAN, D.W., GORDON, L.K., DAVIS, F.W. & HILGARTNER, W.B. (1991) Living and late Holocene fossil vertebrates, and the vegetation of the Cockpit Country, Jamaica. *Atoll Research Bulletin*, 353, 1–19.
- RODRÍGUEZ-DURÁN, A. (1995) Metabolic rates and thermal conductance in four species of neotropical bats roosting in hot caves. *Comparative Biochemistry and Physiology A*, 110, 347–355.
- SIKES, R.S., GANNON, W.L. & THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 92, 235–253.