RESEARCH ARTICLE

Home range, sleeping site use, and band fissioning in hamadryas baboons: Improved estimates using GPS collars

Megan C. Henriquez[1,2,3] | Alexis Amann[1,2,3] | Dawn Zimmerman[4] | Carlos Sanchez[5] | Suzan Murray[4] | Colleen McCann[2,6] | Teklu Tesfaye[3] | Larissa Swedell[1,2,3,7,8]

[1]Anthropology Program, The Graduate Center, City University of New York, New York, New York, USA

[2]New York Consortium in Evolutionary Primatology, New York, New York, USA

[3]Filoha Hamadryas Project, Awash National Park, Metahara, Ethiopia

[4]Smithsonian National Zoological Park, Washington, District of Columbia, USA

[5]Oregon Zoo, Portland, Oregon, USA

[6]Wildlife Conservation Society/Bronx Zoo, New York, New York, USA

[7]Department of Archaeology, University of Cape Town, Cape Town, South Africa

[8]Department of Anthropology, Queens College, City University of New York, Flushing, New York, USA

Correspondence
Larissa Swedell, Department of Anthropology, Queens College, City University of New York, 65-30 Kissena Blvd, Flushing, NY 11367, USA.
Email: LSwedell@qc.cuny.edu

Abstract

Variation in spatial and temporal distribution of resources drives animal movement patterns. Links between ecology and behavior are particularly salient for the multilevel society of hamadryas baboons, in which social units cleave and coalesce over time in response to ecological factors. Here, we used data from GPS collars to estimate home range size and assess temporal patterns of sleeping site use in a band of hamadryas baboons in Awash National Park, Ethiopia. We used GPS data derived from 2 to 3 collared baboons over three 8–12-month collaring intervals to estimate annual and monthly home ranges using kernel density estimators (KDEs) and minimum convex polygons (MCPs). The 95% KDE home range was 64.11 km^2 for Collaring Interval I (July 2015–March 2016), 85.52 km^2 for Collaring Interval II (October 2016–October 2017), 76.43 km^2 for Collaring Interval III (July 2018–May 2019), and 75.25 km^2 across all three collaring intervals. MCP home ranges were 103.46 km^2 for Collaring Interval I, 97.90 km^2 for Collaring Interval II, 105.22 km^2 for Collaring Interval III, and 129.33 km^2 overall. Ninety-five percent KDE home range sizes did not differ across months, nor correlate with temperature or precipitation, but monthly MCP home ranges increased with monthly precipitation. Our data also revealed a southward home range shift over time and seven previously unknown sleeping sites, three of which were used more often during the wet season. Band cohesion was highest during dry months and lowest during wet months, with fissioning occurring more frequently at higher temperatures. One pair of collared individuals from Collaring Interval III spent 95% of nights together, suggesting they were members of the same clan. Our results both suggest that previous studies have underestimated the home range size of hamadryas baboons and highlight the benefits of remote data collection.

KEYWORDS
fission fusion, home range size, movement patterns, remote sensing, spatial ecology

1 | INTRODUCTION

The distribution of resources within a given environment is closely linked to animal ranging behavior and movement patterns, and primates adopt a variety of behavioral strategies in response to changes in the spatial and temporal availability of these resources (Altmann, 1974; Milton & May, 1976; Stone, 2007; Terborgh, 1983; Wilson, 1972; Wrangham, 1980). For example, primates may occupy larger home ranges and travel farther each day where food resources are sparse (Barton et al., 1992; Hemingway & Bynum, 2005) or their movement may show temporally predictable patterns reflecting the seasonal availability of preferred resources (van Alberts & Altmann, 2006; Van Schaik et al., 1993).

Nonhuman primate movement patterns reflect not only the need to acquire vital resources, but also predation pressure, mate searching, and human activity (Alberts & Altmann, 1995; Johns & Skorupa, 1987; Sengupta et al., 2015). Predation pressure may cause primates to form large groups temporarily, avoid areas "perceived" as dangerous, or alter the timing of their movement (Coleman & Hill, 2014; Ferrari & Ferrari, 1990; Van Schaik, 1983). Humans may directly threaten or compete with nonhuman primates in addition to modifying the natural distribution of their resources (Chowdhury et al., 2020; Hoffman & O'Riain, 2012). Even the presence of researchers, who often act as passive observers, may influence primate decision making and movement patterns (Nowak et al., 2014). Overall, spatial ecology—the interactions between an organism and its environment with regard to space use, distribution, and movement patterns—provides a useful lens through which to study the way primates adapt to and interact with their environments.

Baboons (Papio sp.) are known for the flexible ways in which they respond to the variable distribution of resources and changing habitats in which they evolved (Alberts & Altmann, 2006; Whiten et al., 1991). These large-bodied terrestrial primates live in large social groups for which home range size and daily path length typically increase with group size (Alberts & Altmann, 2006; Milton & May, 1976), suggesting that within-group feeding competition imposes a cost on all group members that can be mitigated by increasing the amount of time spent foraging by the whole group (Barton & Whiten, 1993; Barton et al., 1992; Koenig, 2002). However, baboons are among the most ecologically and behaviorally flexible primates and there is also substantial variation within species and populations across habitats (Bronikowski & Altmann, 1996; Swedell, 2011). For example, olive baboons (Papio anubis) in eastern Laikipia, Kenya, use different areas of their home range in response to the seasonal availability and location of food items (Musyoki & Strum, 2016). Yellow baboons (Papio cynocephalus) in Amboseli, Kenya, that forage from a garbage dump have more predictable daily activity patterns, shorter travel routes, smaller home ranges, and spend less time resting than unprovisioned baboons from the same population (Altmann & Muruthi, 1988). Similarly, a group of 115 chacma baboons (Papio ursinus) in the Western Cape of South Africa occupies a relatively small annual home range (9.50 km^2) in a resource-rich, human-modified environment in which the baboons

have access to human-derived foods (Hoffman & O'Riain, 2012), while a group of the same size in a less human-occupied area maintains a larger annual home range (16.7 km^2) (Pebsworth et al., 2012). In the same region, a group of less than half that size (49 baboons) maintains an even larger home range (37.65 km^2) in a lower quality habitat with minimal human contact (Hoffman & O'Riain, 2012).

The dietary and behavioral flexibility of baboons in the face of differential human presence and resource availability has undoubtedly played a large role in their success, having allowed them to flourish in a wide variety of ecosystems throughout the African continent (Alberts & Altmann, 2006; Altmann, 1974; Barton et al., 1992). For example, baboons often engage in high-risk behaviors to acquire resources. Crop raiding occurs nearly everywhere baboons come into contact with human agriculture, even though the resultant anthropogenic conflict increases both physiological stress levels and risk of death (Chowdhury et al., 2020; Fehlmann et al., 2017). The diversity of resource acquisition strategies across baboon populations and species may reflect adaptations to variable pressures exerted by changes in resource availability and distribution across environments and over time (Alberts & Altmann, 2006; Hill et al., 2003; Whiten et al., 1991).

Unlike most other baboons, hamadryas baboons (Papio hamadryas) have evolved an unusual multilevel social system, possibly in response to their evolutionary history in the semiarid and resource-scarce regions of the Horn of Africa and the Arabian Peninsula (Altmann, 1974; Jolly, 1993; Kummer, 1968; Newman et al., 2004). Consequently, hamadryas are a particularly interesting species in which to study spatial ecology. Their multilevel social system is readily apparent, with bands (the largest consistent grouping), clans (subsets of bands), and one-male units (the smallest groupings, a.k.a. OMUs) existing as nested, spatially distinct social entities (Kummer, 1968; Schreier & Swedell, 2009). Additionally, multiple bands congregate on sleeping cliffs at night to form troops for predator protection (Kummer, 1968). Prior studies have shown that hamadryas employ a fission–fusion strategy to access sparse and widely distributed resources, with bands splitting into clans and OMUs when resource availability is low (Altmann, 1974; Kummer, 1968; Schreier & Swedell, 2012; Stolba, 1979). Here we seek to build on these studies so as to better understand the ecological basis of the relationships that govern fission–fusion dynamics and ranging patterns in this species.

In this study, we used satellite-linked GPS collars to explore spatial ecology in a population of hamadryas baboons at the Filoha site in Awash National Park, Ethiopia. Our first goal was to generate a more accurate estimate of the home range of our study band than had been possible previously with observational data alone. Our second goal was to assess seasonal variation in home range use. Our third goal was to investigate patterns of sleeping cliff use over time. Finally, our fourth goal was to build upon previous studies of seasonality in band separation patterns (Schreier & Swedell, 2012) by assessing where, when, and how often individuals spent nights at different sleeping cliffs. We predicted that home ranges would be

larger than previous estimates using observational data alone and that the baboons would contract their home range during the dry season, centralizing their activity around permanent bodies of water. Correspondingly, we predicted they would travel more, and thus occupy larger home range areas, during the wet season, when standing fresh water was more available throughout the park. We predicted sleeping site use patterns would vary seasonally as well, concordant with seasonal shifts in home range use. Lastly, we predicted that band fissioning would occur primarily during the wet season as suggested by previous studies (Barton et al., 1992; Schreier & Swedell, 2012).

2 | METHODS

This study was approved by the Institutional Animal Care and Use Committee of Queens College (Protocol #93).

2.1 | Study site and subjects

Awash National Park (ANP), located in the central lowlands of Ethiopia on the slopes of the dormant Mt. Fantalle volcano (8.98°N, 39.90°E), is characterized by a semiarid climate (400–700 mm rainfall annually; Zerga, 2015) and a mosaic of *Acacia sp.* scrublands, open grasslands, and palm forests, with outcroppings of volcanic rock (Schreier & Swedell, 2012; Swedell, 2006; Zerga, 2015). The region experiences one major period of seasonal rainfall from late June through September and intermittent short rains during the rest of the year. The Ethiopian National Meteorology Agency collects climatological data (average minimum monthly temperature, average maximum monthly temperature, and total monthly precipitation) for the region from a weather station located in the city of Metahara (8.86°N, 39.92°E) at the southwestern boundary of ANP. According to these data, temperatures in the region ranged from 8°C to 38.6°C (26.5°C average) between 2015 and 2019 and monthly total precipitation ranged from 0 to 228 mm (46.8 mm average).

Band 1 at the Filoha outpost of ANP (9.06°N, 40.0°E) has been studied intermittently since 1996 (Swedell, 2002, 2006) and at the time of this study (2015–2019) consisted of about 230 baboons. Band 1 and other bands in the area use several cliffs in the northern part of the park as sleeping sites (Cliffs A–C; Figure 1a). Most sleeping cliffs are situated within the same semiarid scrubland as the rest of the park, and Cliffs A (Filoha) and C (Ureli) are located within a network of natural hot springs and marshes marked by year-round availability of fresh water and doum palm (*Hyphaene thebaica*) fruit, a dietary staple for this population (Schreier, 2010; Swedell et al., 2008).

2.2 | Data collection

In July 2015, October 2016, and June 2018, respectively, we darted, immobilized, and fitted satellite-linked GPS collars (Africa Wildlife Tracking, Pretoria, South Africa) on nine adult males in Band 1, three during each darting session. To minimize disruption to OMU membership (because leader males can lose their females when immobilized; Swedell, 2006), we preferentially chose males for darting that were fully adult but that did not have any females, while also taking into consideration logistical factors that varied over time such as the availability of personnel and supplies and our ability to dart with minimal disruption to other baboons. The outcome of this strategy, because most fully adult hamadryas males are leaders until they lose their females (Pines et al., 2011, 2015), was that most collared males were previously deposed leaders.

On darting days, we first located the band at their sleeping site at dawn, which in six cases was Cliff D (Dhali Bora) and in three cases was Cliff A (Filoha; Figure 1). After identifying a target male, a certified wildlife veterinarian (authors Carlos Sanchez or Dawn Zimmerman) immobilized the male with a combination of ketamine (3 mg/kg) and medetomidine (0.075 mg/kg) administered intramuscularly via a 1.5 ml (cc) plastic dart (Dan-Inject dart syringe). The dart was fitted with a collared 1.5 × 20 mm needle of the same brand and projected using a Dan-Inject CO_2 pressurized pistol. The pressure used in the pistol (Bar) depended on the distance between the veterinarian and the target animal, the wind factor, and the size of the animal among other considerations. Immediately after darting the target animal, the band left the area; if they did not, designated members of the field team donned apparel resembling the local nomads, to which the baboons are not habituated, and the baboons dispersed in response. Once the target animal was immobilized and the rest of the band was out of view, we collected a set of morphological measurements and other biological data from the immobilized animal and fitted a GPS collar on it. Collars weighed approximately 0.5 kg and included both Iridium satellite and very high frequency (VHF) transmitters. In a few animals, 200–300 ml of subcutaneous fluids were administered to assist with rehydration; these decisions were made by the veterinarian while monitoring the immobilized baboon. When processing was complete and a minimum of 35–40 min had passed since initial injection, we reversed the medetomidine with atipamezole at a dose of 5 mg of atipamezole for 1 mg of medetomidine administered intramuscularly. This time was considered the anesthesia time and, in all cases, never lasted more than 45 min. Before reversing the anesthesia, we assessed whether the terrain was safe for the animal during the initial phases of recovery; if deemed too steep or unsafe due to environmental hazards or local topography, the animal was carried to a safer location for recovery. We then monitored the animal until it was fully recovered.

Following the initial darting procedure, we regularly observed collared individuals in the field to check for any negative side effects. When possible, we removed or replaced collars on subsequent darting sessions from individuals that had previously been collared. Data collection ceased when the collar's battery failed or the animal was presumed dead, in one case because the collar stopped moving and was then found cut off of the individual, whose remains were never recovered, and in another case because the collar stopped moving and then the battery died before it could be recovered.
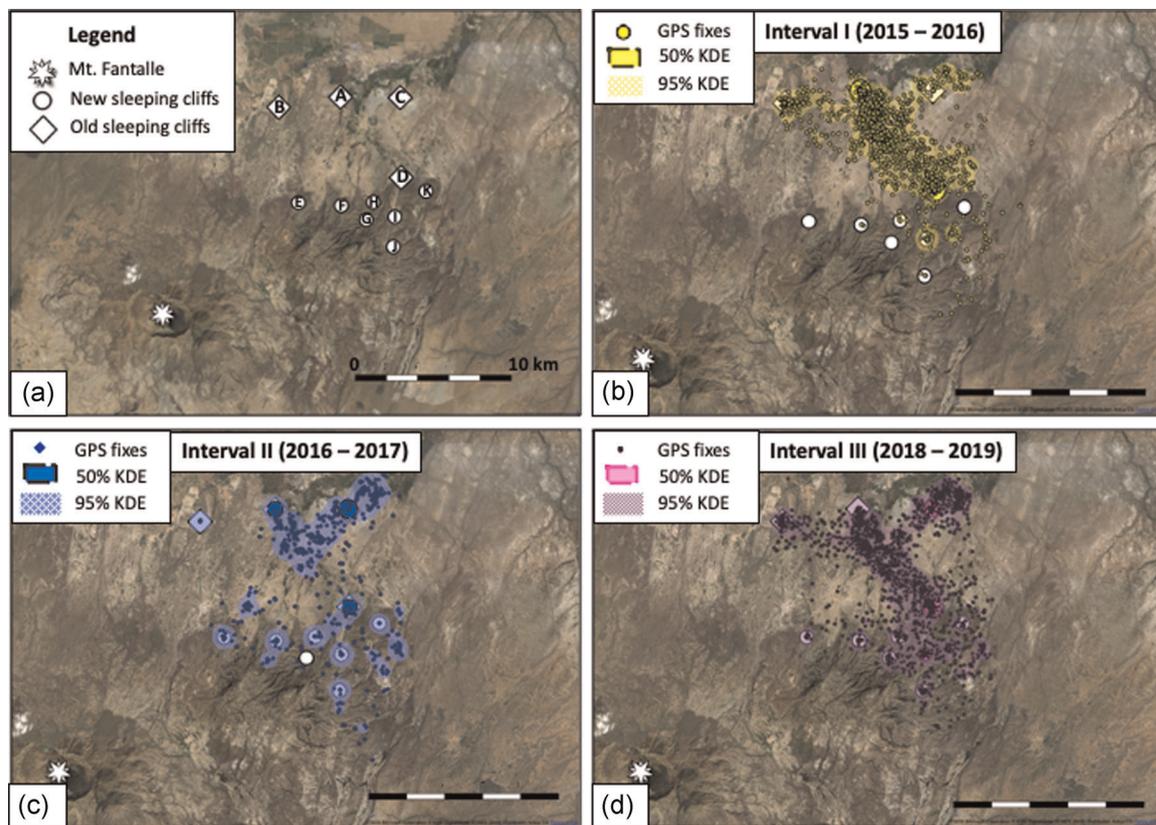
FIGURE 1 (a) Sleeping cliffs used by a band of hamadryas baboons (*Papio hamadryas*) in Awash National Park, Ethiopia, over three collaring intervals from 2015 to 2019. Cliffs A–D (diamonds) had been identified as sleeping sites before this study, while cliffs E–K (circles) were discovered as sleeping sites using data from this study. The scale bar is 10 km in every panel. (b) Annual home range estimate (95% KDE; transparent yellow) and core area estimate (50% KDE; solid yellow with border) for Collaring Interval I (2015–2016). (c) Annual (95% KDE; transparent blue) and core area estimate (50% KDE; solid blue with border) for Collaring Interval II (2016–2017). (d) Annual (95% KDE; transparent purple) and core area estimate (50% KDE; solid pink with border) for Collaring Interval III (2018–2019). KDE, kernel density estimator

For the analyses presented here, we used data collected from seven individuals: two collared in 2015, two collared in 2016, and three collared in 2018 (Table 1).

The collars varied in both their lifespan and their number of daily fixes, ranging from 1 to 12 fixes a day (Table S1). In most cases, collars were set by Africa wildlife tracking (AWT) to a frequency of every 8 h, or three times daily, and in some cases it was possible for AWT to set the collars to attempt to fix locations more frequently (up to every 2 h) but upload less frequently to extend battery life. Additional changes in the rate at which the scheduled fixes were captured, recorded, and stored correctly in the AWT database occurred for reasons such as the collars' inability to connect to satellites due to inclement weather, cloud cover, altitude, and local topography (cf. Hofman et al., 2019). Variation in these individual factors resulted in highly variable data resolution throughout the study. Ultimately, we were able to collect 8 months of data from two individuals in Collaring Interval I (July 2015–March 2016), 12 months of data from two individuals in Collaring Interval II (October 2016–October 2017), and 10 months of data from three individuals in Collaring Interval III (July 2018–May 2019).

We downloaded the recorded data from the AWT database or received it via email from AWT personnel. We then visualized the data in QGIS v 2.18.13 (QGIS Development Team, 2017) and manually removed fixes identified as download errors, duplicates, or outliers (e.g., *xy* coordinates are 0.00, fixes fall over oceans or in other countries).

2.3 | Data analysis

2.3.1 | Home range estimates

We performed all home range analyses in RStudio version 1.2.5001 (RStudio Team, 2019). We estimated annual home range for Band 1 during each collaring interval by combining the GPS fixes collected from all collared individuals during a particular collaring interval (Collaring Interval I, *N* = 2; Collaring Interval II, *N* = 2; Collaring Interval III, *N* = 3). We estimated monthly home ranges for the entire band by dividing the combined data from each collaring interval into calendar months. We also calculated annual and monthly home ranges using only fixes collected during the daytime as a comparison

TABLE 1 Collar ID number, data collection time frame, proportion of nights for which GPS points were collected (19:00–06:00 GMT), and reason for collar data cessation

Collar ID	Data collection time frame	Proportion of night fixes collected	Reason for collar data cessation
Collaring Interval I			
1453	06 July 2015–20 July 2015; 03 Sept 2015–19 Feb 2016	176/183 (96%)	Battery failure
1452[a]	02 July 2015–09 Mar 2016	242/245 (99%)	Battery failure
Collaring Interval II			
254	09 Oct 2016–05 Oct 2017	355/361 (98%)	Presumed dead[b]
253	06 Oct 2016–03 Oct 2017	349/359 (97%)	Battery failure
Collaring Interval III			
2768[a]	03 Jul 2018–03 May 2019	289/304 (95%)	Battery failure
2769	01 Jul 2018–09 May 2019	280/312 (90%)	Presumed dead[c]
2770	01 Jul 2018–08 May 2019	276/311 (89%)	Battery failure

[a]Collars 1452 and 2768 were fitted on the same individual; these two sets of points were treated separately because of their temporal discontinuity.

[b]Collar 254 stopped moving and was then found cut off the subject, who was presumed to have been killed.

[c]Collar 2769 stopped moving in May 2019, from which we inferred death of the baboon (thereafter the collar's battery failed, and we did not recover it).

to our overall home ranges, which included nocturnal GPS fixes. To do this, we trimmed the data collected in all three collaring intervals to include only points collected between 06:00 and 19:00 East Africa Time, GMT + 3. We then conducted the same analyses in RStudio as we did for the full data set.

The number of days for which GPS fixes were collected in a given month was highly variable (0–31 days; Table S1). To assess whether the number of days recorded per month had any effect on the home range estimate or core area estimate, we created linear models using the "lme4" (Bates et al., 2015) package in R. We set the number of days for which we had data in a given month as the independent variable and the monthly 95% KDE and 50% KDE estimates as the dependent variables.

GPS fixes were downloaded or received as local xy coordinates. Using the R packages "sp" (Pebesma & Bivand, 2005), "raster" (Hijmans and van Etten, 2012), and "rgdal" (Bivand et al., 2016), we transformed the data to WGS 84 before projecting them to UTM37N, the CRS that includes all of Ethiopia. Using the package "adehabitatHR" (Calenge, 2006), we estimated annual and monthly home range size using the fixed kernel density estimation with both a 95% probability distribution and a 50% probability distribution (to estimate the band's "core range") using the h_{ref} algorithm. We also estimated annual home range using the minimum convex polygon (MCP) method in adehabitatHR as a comparison.

2.3.2 | Seasonality

To test for variation in home range size between months, we first pooled all 95% KDE monthly home range estimates over all three collaring intervals. We then performed a Kruskal-Wallis test in RStudio to assess whether there were any significant differences between the means for each month. To test for home range size variation between months within a particular collaring interval, we performed individual Kruskal-Wallis tests for each collaring interval.

Using the data obtained from the Ethiopian Meteorological Agency, we tested whether average monthly maximum temperature (°C), average monthly minimum temperature (°C), and total monthly rainfall (mm) affected monthly home range size by creating multiple linear regression models (lm function in R) in which each of our home range measures (95% KDE, 50% KDE, MCP) were the dependent variables and the climate variables (and interactions between them) were the independent variables.

2.3.3 | Sleeping site use

To detect patterns in sleeping site use, we trimmed the GPS data for all study individuals to include only a single GPS fix collected between 19:00 and 06:00 local time (East Africa Time, GMT + 3) on a given night and excluded nights on which no point was recorded during this timeframe. Based on multiple years of observation, we estimated that the band would typically arrive at the sleeping cliff by 18:00 and depart by 07:00, which would make 19:00–06:00 a conservative estimate of which GPS fixes to use in these sleeping site analyses. However, when multiple fixes were recorded on a particular night, we chose to discard fixes that were recorded closer in time to the ends of this time frame, preferentially selecting points that were recorded in the middle of the night, when individuals would be more likely to be resting and immobile. We uploaded the data for each individual separately to QGIS and overlaid them against a map of Awash National Park using the Bing Maps Openlayer plugin. We identified

sleeping cliff sites by locating clusters of three or more nighttime fixes that aligned with visible cliffs on the map. Although hamadryas occasionally use landscape features other than cliffsides as sleeping sites (Schreier & Swedell, 2008), night points that did not correspond with a cliff on a given night (i.e., outliers) were rare in this data set (<5 fixes per individual per collaring interval), so we limited our sleeping site analyses to cliffs because they were identifiable in the satellite imagery.

2.3.4 | Band cohesion

To estimate how often Band 1 fissioned into subunits that used different sleeping cliffs, we compared sleeping site data among the collared individuals in a particular collaring interval. We first aligned and trimmed the data to include only those nights with GPS fixes for two or more individuals. We then compared the cliffs on which each animal was located for that night. If the cliffs did not match, we measured the straight-line distance between the two cliffs using the "measure line" function in QGIS. We calculated the approximate rate of band cohesion per month by dividing the number of days the two collared individuals slept at the same cliff by the number of days that GPS data were collected in that month.

To determine if there were any correlations between band cohesion and climate, we ran linear models with the rate of group cohesion as the dependent variable and the average monthly minimum temperature, maximum temperature, and total precipitation as the independent variables.

3 | RESULTS

3.1 | Home range estimates

As represented by the collared baboons in our study, Band 1's home range varied from 64.11 to 85.52 km^2 over the three collaring intervals using the 95% KDE method, with the 50% KDE "Core Areas" ranging from 9.21 to 14.47 km^2 (Table 2). Home range estimates using the MCP method were larger in all collaring intervals and ranged from 97.90 to 105.22 km^2. The overall 95% KDE home range estimate using fixes from all three collaring intervals was 75.25 km^2, the overall 50% "core area" was 10.23 km^2, and the overall MCP home range estimate was 129.33 km^2. Similar trends persisted when we considered only diurnal fixes (Table S2 and Figure S1). The overall 95% KDE home range using only GPS fixes recorded during the day from all three collaring intervals was 79.12 km^2, the 50% KDE "Core Area" was 12.48 km^2, and the MCP home range estimate was 123.41 km^2. Ninety-five percent KDE home range estimates ranged from 65.11 to 93.41 km^2, while 50% "Core Areas" ranged from 9.54 to 19.44 km^2. Day-only MCP home range estimates ranged from 91.43 to 103.43 km^2.

TABLE 2 Home range estimates for a band of hamadryas baboons in Awash National Park, Ethiopia calculated using GPS data collected from multiple individuals over three collaring intervals using three different home range area estimation methods

Collaring interval (individuals)	Data collection time frame	Total number of GPS fixes	MCP home range (km^2)	95% KDE home range (km^2)	50% KDE "Core area" (km^2)
Collaring Interval I (N = 2)	02 July 2015–09 Mar 2016	2310	103.46	64.11	9.21
Collaring Interval II (N = 2)	06 Oct 2016–05 Oct 2017	1948	97.90	85.52	14.47
Collaring Interval III (N = 3)	01 Jul 2018–09 May 2019	5268	105.22	76.43	12.12
Overall (N = 7)	02 July 2015–09 May 2019	9526	129.33	75.25	10.23

Abbreviations: GPS, global positioning system; KDE, kernel density estimator; MCP, minimum convex polygon.
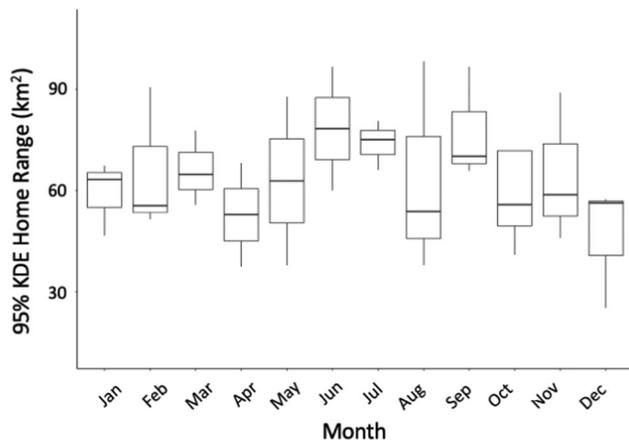
FIGURE 2 Monthly home range estimates (95% KDE, km²) for a band of hamadryas baboons (*Papio hamadryas*) over three collaring intervals from 2015 to 2019. KDE, kernel density estimator

3.2 | Seasonality

Monthly 95% KDE home range estimates varied from 25.27 to 108.98 km², with a mean of 64.72 ± 20.10 km² (Figures 2 and 3). We found no evidence of differences among the monthly 95% KDE home ranges when data from all three collaring intervals were pooled (Kruskal–Wallis $\chi^2 = 7.13$, df = 11, $p = 0.79$). We also found no evidence of differences among months within Collaring Interval I (Kruskal–Wallis $\chi^2 = 8$, df = 8, $p = 0.43$), Collaring Interval II (Kruskal–Wallis $\chi^2 = 11.87$, df = 11, $p = 0.37$) or Collaring Interval III (Kruskal–Wallis $\chi^2 = 11$, df = 11, $p = 0.44$). Additionally, we found no evidence that the number of days for which GPS data were collected in a given month affected the monthly 95% KDE home range estimate

(linear regression: $F = 0.18$, adjusted $R^2 = -0.03$, $\beta = 0.20$, 95% confidence interval [CI]: −0.77 to 1.17, $p = 0.68$) or the 50% KDE "core area" estimate (linear regression: $F = 0.04$, adjusted $R^2 = -0.03$, $\beta = -0.03$, 95% CI: −0.28 to 0.23, $p = 0.84$).

Monthly 95% KDE home range estimates for only diurnal points ranged from 27.65 to 117.10 km², with a mean of 67.00 ± 21.35 km². As was the case with the whole data set, we found no evidence of differences among monthly home ranges when the data from all three collaring intervals were pooled (Kruskal–Wallis $\chi^2 = 6.75$, df = 11, $p = 0.82$), nor did we find evidence of differences among months within any particular collaring interval (Collaring Interval I: Kruskal–Wallis $\chi^2 = 8$, df = 8, $p = 0.43$; Collaring Interval II: Kruskal–Wallis $\chi^2 = 11$, df = 11, $p = 0.37$; Collaring Interval III: Kruskal–Wallis $\chi^2 = 11$, df = 11, $p = 0.44$).

We found no evidence of an effect of maximum monthly temperature on monthly 95% KDE home range (linear regression: $F = 0.47$, adjusted $R^2 = -0.02$, $\beta = 1.34$, 95% CI: −2.68 to 5.33, $p = 0.50$), nor any other home range measurement. Similarly, we found no evidence of an effect of minimum monthly temperature on 95% KDE home range size (linear regression: $F = 3.01$, adjusted $R^2 = -0.06$, $\beta = 1.92$, 95% CI: −0.35 to 4.18, $p = 0.09$), nor any other home range measurement.

While we did not find evidence to suggest that precipitation had an effect on 95% KDE home range size (linear regression: $F = 3.27$, adjusted $R^2 = 0.08$, $\beta = 0.15$, 95% CI: −0.02 to 0.32, $p = 0.08$), we did find a positive effect of precipitation on MCP home range size (linear regression: $F = 6.22$, adjusted $R^2 = 0.16$, $\beta = 0.17$, 95% CI: 0.03–0.31, $p = 0.02$). When we considered only diurnal home range measurements, we found precipitation to be the only climatic variable that predicted ranging patterns, positively affecting both the 95% KDE home range (linear regression: $F = 4.70$, adjusted $R^2 = 0.12$, $\beta = 0.19$,
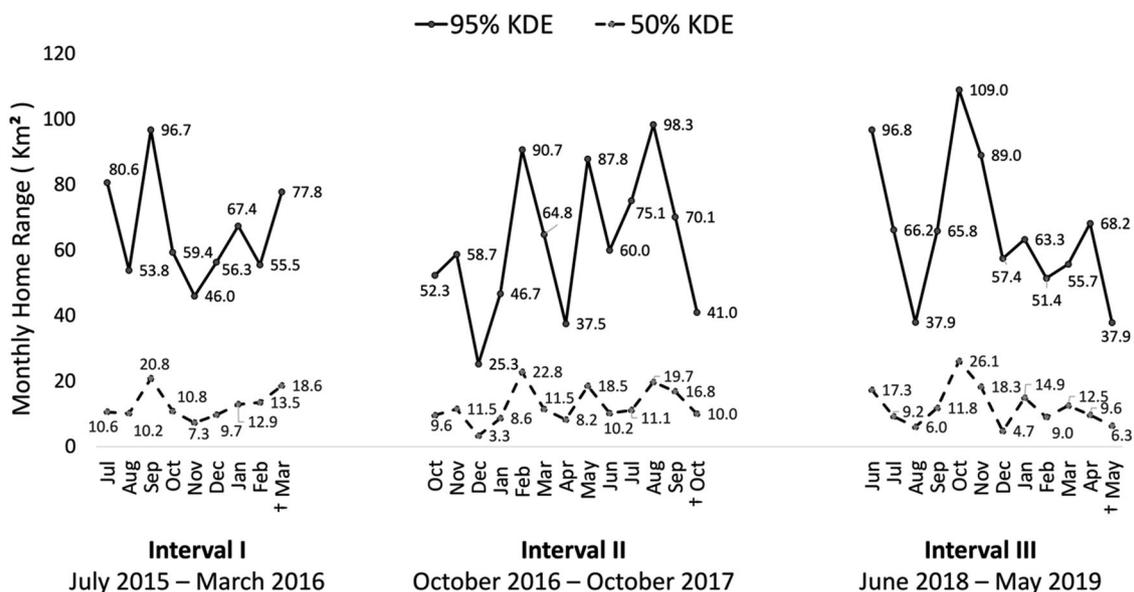
FIGURE 3 Monthly home range estimates (95% KDE, km²; solid line) and "core area" estimates (50% KDE, km²; dashed line) for a band of hamadryas baboons (*Papio hamadryas*) over three collaring intervals from 2015 to 2019. †Months with less than 2 weeks of data. KDE, kernel density estimator

95% CI: 0.01–0.36, $p = 0.04$) and the MCP home range (linear regression: $F = 4.92$, adjusted $R^2 = 0.12$, $\beta = 0.15$, 95% CI: 0.01–0.30, $p = 0.04$).

3.3 | Sleeping site use

Table 1 shows the proportion of nights for which we had GPS fixes between the hours of 19:00 and 06:00. Night fix frequency was quite high, ranging from 89% to 99%. In 2015, Band 1 predominantly used Cliffs A (Filoha), B (Wasaro), C (Ureli), and D (Dhali Bora), which had been previously identified as sleeping sites during observational data collection (Schreier, 2010; Swedell, 2002; Swedell, unpublished data). Our GPS data, however, revealed seven additional sleeping sites even farther south of Cliff D, on the ridges leading up to Mt. Fantalle (Cliffs E–K; Figure 1). Use of Cliff A (Filoha) decreased significantly over time (linear regression: $F = 10.32$, adjusted $R^2 = 0.23$, $\beta = -2.00$, 95% CI: −3.27 to −0.73, $p < 0.01$), and visual inspection of the data suggests that use of the more southerly cliffs (E–K) correspondingly increased over time (Figure 4).

We found no evidence of differences among Cliffs A–D in the average number of nights per month they were used. However, visual inspection of the data suggests that the use of Cliff A was greater during months with lower total precipitation (Figure 4). By contrast, Cliff E (Kruskal-Wallis $\chi^2 = 19.82$, df = 11, $p = 0.05$), Cliff F (Kruskal–Wallis $\chi^2 = 20.50$, df = 11, $p = 0.04$), and Cliff H (Kruskal–Wallis $\chi^2 = 21.31$, df = 11, $p = 0.03$) were used significantly more during the wet months of July, August, and September than in any other months of the year (Figure 4b). Monthly use of Cliff E showed no evidence of a relationship with any tested climate variables, but total monthly precipitation was positively associated with monthly use of Cliff F (linear regression: $F = 4.35$, adjusted $R^2 = 0.11$, $\beta = 0.02$, 95% CI: 0.00–0.04, $p = 0.05$) and Cliff H (linear regression: $F = 22.08$, adjusted $R^2 = 0.43$, $\beta = 0.04$, 95% CI: 0.02–0.05, $p < 0.01$). We found no evidence of a significant effect of average minimum and maximum temperatures on monthly cliff use.

Collared individuals typically spent 2–4 consecutive nights at the same cliff before switching sites. Exceptions to this pattern occurred in September 2015 (11 consecutive nights at Cliff H), December 2016 (11 consecutive nights at Cliff C), and February 2019 (11 consecutive nights at Cliff D).

3.4 | Band cohesion

In Collaring Interval I (2015–2016), the two collared individuals spent 124 of 170 recorded nights together (73%) and 46 nights apart (27%). Their average nocturnal distance apart was 14.58 km and they were split the most frequently between Cliffs A and D. They split most often in September (9/28 nights apart; 32%), October (8/28 nights apart; 29%), and November (8/29 nights apart; 28%).

In Collaring Interval II (2016–2017), the two collared individuals spent 269 of 336 recorded nights together (80%) and 67 nights apart (20%). Their average nocturnal distance apart was 4.00 km and they

were split most frequently between Cliffs A and C. They spent most of September 2017 apart (23/27 nights apart; 85%) and spent most of the months between December and May together (7/175 nights apart; 4%).

In Collaring Interval III (2018–2019), the three collared individuals spent 170 of 249 recorded nights together (68%) and 79 nights apart (32%). On 75 of the 79 (95%) nights spent apart, one individual slept on a different cliff than the other two, and on four nights, all three individuals were found on different cliffs (5%). Individuals 2768 and 2770 spent the most nights together (248/261 recorded nights; 95%), while 2769 and 2770 spent the fewest nights together (173/260 recorded nights; 66%).

Generally, band cohesion was lowest (with at least one individual using a different sleeping cliff from the rest) in September (18/21 nights apart; 85%) and October (16/29 nights apart; 55%). By contrast, band cohesion was highest in January (28/31 nights together; 90%) and November (24/28 nights together; 86%). Collared individuals were split most often between Cliffs D and I and Cliffs A and B, and their average distance apart was 6.16 km.

We found no evidence of differences in band cohesion across months (Kruskal–Wallis $\chi^2 = 17.48$, df = 11, $p = 0.09$); however, the data suggest a negative relationship between band cohesion and average minimum monthly temperature (linear regression: $F = 6.40$, adjusted $R^2 = 0.17$, $\beta = -1.29$, 95% CI: −2.34 to −0.24, $p = 0.02$), though there is a considerable amount of variation that is left unexplained, especially at higher temperatures (Figure 5). Neither total monthly precipitation nor average monthly maximum temperature had significant effects on cohesion, although the other recorded climate variables (total monthly precipitation and maximum average monthly temperature) are correlated with the minimum average monthly temperature.

4 | DISCUSSION

This study revealed hamadryas baboon home ranges to be far larger than previously reported for this population and for baboons in general: over 75 km^2 using the KDE method and over 120 km^2 using the MCP method. Previous estimates of home ranges for Band 1 at Filoha were 30 km^2 (Swedell, 2002, 2006) and 38.6 km^2 (Schreier, 2009, 2010), with both authors noting that these values represented an absolute minimum. Those estimates were similar to the home range size of 28 km^2 reported by Sigg and Stolba (1981) for a smaller band at Erer Gota, about 180 km northeast of Filoha. Home ranges as small as 9.3 km^2 have also been reported in Saudi Arabia, albeit in a commensal population (Boug et al., 1994).

Differences among home range estimates derive in part from methodological differences in calculations of home range size. Our annual home range estimates based on the MCP method were larger than our estimates using KDE. It has been suggested that the MCP method may overestimate home range size by including potentially "exploratory points" (Burt, 1943; Grueter et al., 2009; Pebsworth
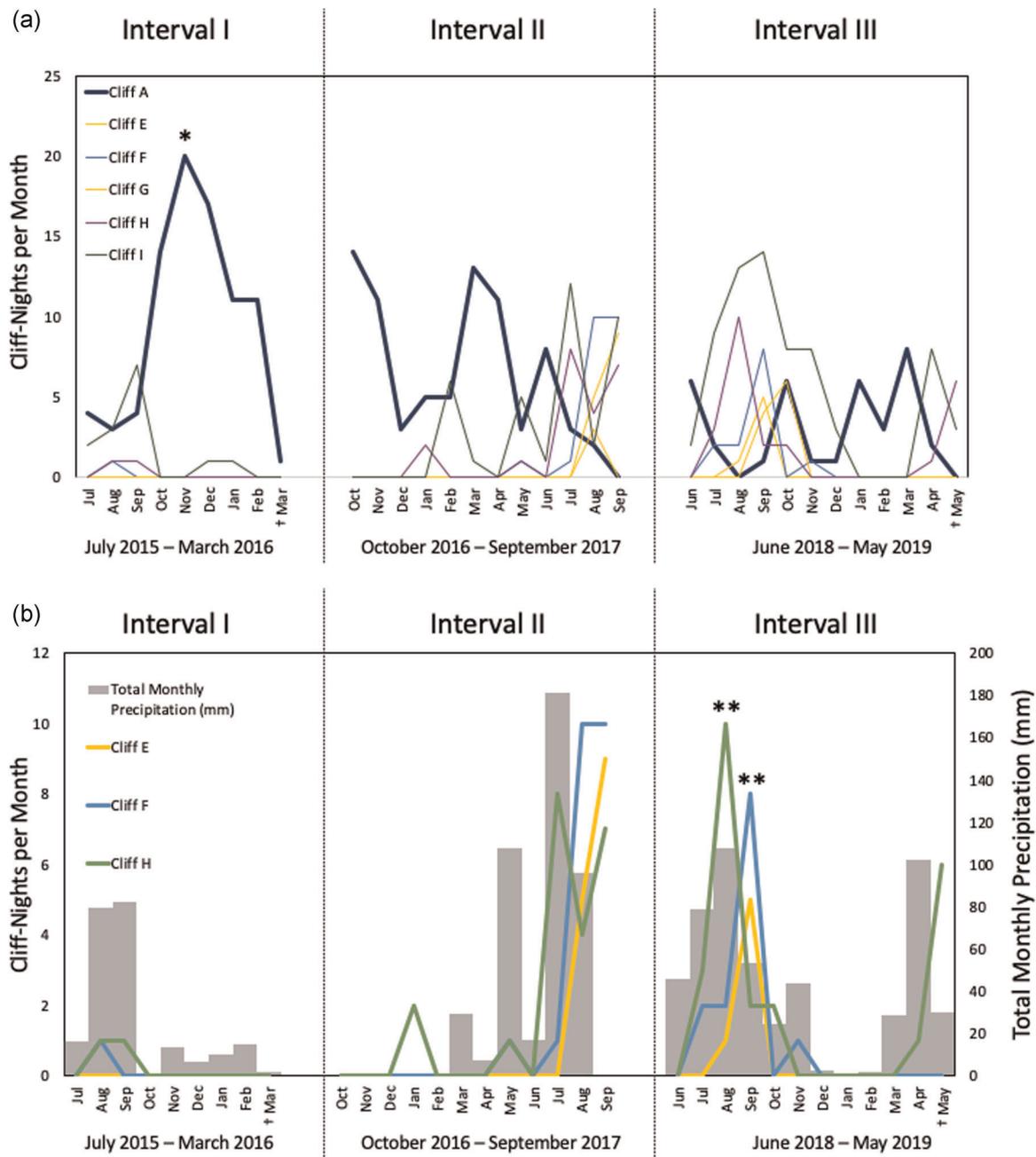
FIGURE 4 Seasonal variation in use of each sleeping cliff by a band of hamadryas baboons. (a) Monthly use of Cliff A (Filoha) over time, compared to Cliffs E–I, showing a greater use of Cliff A during drier months and a decrease in use of Cliff A over time. (b) Monthly use of Cliffs E, F, and H (the southerly cliffs), showing increased use during and following months with higher total monthly precipitation and increased use over time. [†]Months with less than 2 weeks of data

et al., 2012; Powell, 2000), defined by Burt (1943) as "occasional sallies outside the [home range] area." Such exploratory points, however, can provide important information about resource-searching behaviors and future group movement. As landscapes are altered and resource distribution changes, animals must either adjust their behavior or shift their home range to an area with sufficient resources (Powell, 2000). In such circumstances, exploratory points may augment an animal's cognitive map and contain information related to future movement patterns.

More importantly, a key difference between this study and previous work on this species lies in the fact that previous home range estimates were calculated from in-person observations during all day focal follows. Swedell, (2002, 2006), for example, estimated Band 1's home range in 1996–1998 by hand-transcribing daily path lengths onto georeferenced maps of Awash National Park. Similarly, Schreier (2009, 2010) created MCP home range estimates by collecting GPS fixes of the group while conducting full day focal follows in 2005–2006. A drawback of such observational methods is that if
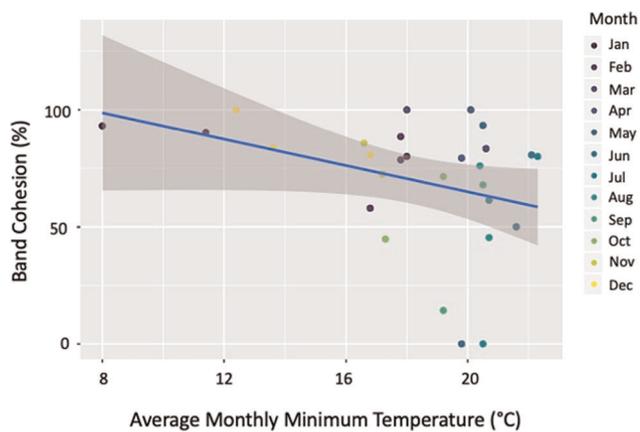
FIGURE 5 Monthly rates of band cohesion in hamadryas baboons as a function of average monthly minimum temperature. Band cohesion decreases significantly, that is, band fissioning into clans increases, as average minimum temperature increases, with warmer months, such as June, July, and August, having the lowest cohesiveness

the group is lost by the research team during the focal follow, or the research team is unable to locate the group on a given day, then the data for that day are incomplete or missing (Kie et al., 2010; Swedell, 2002). Many partial or missed days, in turn, can lead to an underestimate of home range size. Automated data collection methods such as GPS collars allow researchers to collect data remotely, which can result in more robust data sets and better estimates. For the Filoha population, Swedell (2002, 2006) stated explicitly that the home range size for Band 1 was underestimated because of gaps in data collection from incomplete daily focal follows and extended periods when Band 1 could not be found, most notably during the wet season. Both Schreier (personal communication) and Swedell (2002) agree that Band 1 was often lost when the baboons were heading southwest towards Mt. Fantalle, where they suspected Band 1 was located during large portions of the wet season when they could not be found (Swedell, 2002, 2006). Our discovery of seven new sleeping cliffs (E–K) closer to Mt. Fantalle (Figure 1) supports these prior speculations and highlights the benefits of remote monitoring techniques.

Our largest recorded home range estimates are from September 2015 (96.7 km^2), August 2017 (98.3 km^2) and October 2018 (109.0 km^2; Figure 3), which coincide with the wet season and may relate to increased food and water availability during this time. The major period of seasonal rainfall in this region has historically begun in late June or early July and extended into September (Swedell, 2002, 2006), with an abundance of plant and water resources continuing through October. While many primates decrease their home range size in response to higher resource availability (Barton et al., 1992; Milton & May, 1976; Pebsworth et al., 2012; Schreier, 2010), we found the opposite pattern here.

Higher rainfall may be associated with increased home range sizes at Filoha for two reasons. First, the band may be able to move greater distances during the day without sustaining major heat-related stress during periods of increased rainfall (Gordon, 1977).

Second, increased rainfall may release the baboons from constraints related to having to search for water (Altmann, 1974). Kummer (1968) noted that, at Erer Gota, hamadryas often stop at a watering hole around midday to drink. Whereas the swamps and streams near Cliffs A and C at Filoha provide a year-round supply of fresh water, there is, to our knowledge, no year-round water source near most of the other cliffs. The start of the wet season brings standing pools of water throughout the park, many of which are large enough to sustain the entire band (Swedell, 2002; Swedell et al., 2008). Not being constrained by having to remain near a known water source during this time, the band is likely better able to move in response to other variables, such as preferred food resources, predation pressure, or human activity (Altmann, 1974; Schreier & Swedell, 2012; Swedell, 2002). The exploratory points included in our MCP area estimates may represent forays to potential new sleeping sites or hold some otherwise undiscovered biological value, which may be elucidated by future studies.

The start of the wet season also signals a change in food availability as *Acacia senegal* young leaves and flowers begin to bloom and doum palm fruit availability declines. Schreier (2010) suggested that shifts in home range may reflect ripe doum palm availability throughout the park, with Band 1 shifting their range south to be able to better exploit the southeastern palm forests after depleting all available ripe fruit around the Filoha cliff. Whatever the proximate reasons, the outcome of seasonally increased water availability is a decrease in the use of the Filoha cliff (Cliff A), where there is permanent water from the hot springs; an increase in use of the southerly cliffs, where there is little to no perennial water; and an increase in home range size overall.

In addition to seasonal differences, our data also tentatively support our personal observations of a general southward-bound directional trend in home range and sleeping cliff use over time. While water availability may be a limiting factor for this population, annual patterns of precipitation remained similar throughout the study period, suggesting that the increased southern cliff use over time is driven by factors other than water availability and may represent a home range shift. One such factor may be anthropogenic disturbance: Belay et al. (2014) documented substantial habitat change throughout Awash National Park over three decades due to increased pressure from local communities in the form of grazing livestock and extracting resources. The expansion of farmland and grassland within the park is thus likely one of the main drivers of the band's home range shift.

In parallel with the increased use of the southern cliffs, the use of Cliff A in particular has decreased over time. Cliff A, at the Filoha outpost, is a popular destination for both wildlife and people due to its year-round abundance of fresh water, locally thought to be medicinal, from the hot springs at the base of the cliff. Many local nomadic people come to Filoha to feed and water their herds of camels, goats, and cattle. By increasing their use of the southern cliffs, which are more remote and harder for humans to access, the baboons may be trying to minimize contact with humans or reduce competition with other animals, whether wild or domestic.

The ranging patterns of the baboons in this study may also be influenced by avoidance of local predators, such as lions, leopards and hyenas. Hamadryas baboons adopt defensive strategies, such as remaining in large troops for longer periods, in response to the presence of predators around their sleeping cliffs (Schreier & Swedell, 2012). Similar defensive strategies are seen in other primates, which appear to select habitats that minimize predation risk, regardless of resource availability (Coleman & Hill, 2014). Predator densities and ranging patterns have yet to be studied extensively within Awash National Park, but preliminary data from 2014 suggest that lions and leopards are found centrally within the park, mostly in the mountainous areas where the new sleeping cliffs (E–K) are located (Chernet, 2015). Further studies on the distribution and ranging patterns of hamadryas baboons and their known predators may shed light on the relationship between predation risk and patterns of cliff use observed in this study.

Consistent with the findings of Schreier and Swedell (2012), the fissioning of Band 1 into subunits at sleeping sites was highest during the month of September in all three collaring intervals (9/28 nights apart in 2015, 23/27 nights in 2017, 19/23 nights in 2018), and lowest from November to May. The months of July, August, and September are typically the wettest months at Filoha, when the baboons are not limited by water (Swedell, 2002) but when a number of preferred food items, such as doum palm fruit, decrease in abundance throughout the park (Schreier, 2010). Interestingly, monthly rates of band cohesion were not directly associated with total monthly precipitation. Band cohesion was, however, negatively correlated with average monthly minimum temperature, with individuals sleeping at the same cliff more often during cold months and sleeping at different cliffs more often during warm months, which overlap with the wet season. Whether this pattern represents a thermoregulatory strategy or is an artifact of some other ecological relationship is still unknown. Either way, the change in diet, southwardly shift in home range, increase in home range size, and more frequent subgrouping during these months may all be ways for members of the same band to reduce feeding competition.

This study also revealed differences in sleeping site use by collared males that likely reflect membership in these subgroups, or clans. Clans are sets of one-male units and solitary males that are linked by male kinship and associate more frequently than they do with other members of the band (Abegglen, 1984; Schreier & Swedell, 2009; Staedele et al., 2015). Prior work at Filoha suggests that bands subdivide into clans at least partly in response to periods of food scarcity (Schreier & Swedell, 2009, 2012), as a means to mitigate food competition. Compared to the other pairs of collared baboons, individuals 2768 and 2770 from Collaring Interval III (2018–2019) spent the most nights at the same sleeping cliff (200/209, or 95.0%, of nights), higher than any other two collared males over the duration of the study (66.5%–80.0%), suggesting that these two individuals are members of the same clan (Abegglen, 1984; Schreier & Swedell, 2009). The difference in cohesion between this pair of males and all others suggests that the other pairs of collared males may not have shared clan membership.

Studies of movement patterns and home range use provide researchers with important information linking an animal's behavior to its environment. Future studies at Filoha have the potential to relate GPS data to resource availability, nutritional strategies, and pathogen and predator avoidance strategies to more fully elucidate the ecological factors that drive movement patterns in this population. Technological advances in the field of spatial ecology, such as the use of satellite GPS collars, allow researchers to study movement patterns in greater detail and at larger scales (Hofman et al., 2019; Kays et al., 2015). Although variable data resolution was one of the largest issues in this study, the variation in the quantity and quality of data collected for each individual improved throughout the study, potentially improving the accuracy of our estimates over time. This study highlights the utility of using automated data collection methods to complement in-person observation. The sheer volume of data that can be collected from automated devices such as GPS collars can increase the accuracy of a wide range of measurements in ecological research.

AUTHOR CONTRIBUTIONS

Megan Henriquez: conceptualization (equal); formal analysis (lead); investigation (supporting); visualization (lead); writing original draft (lead); writing review and editing (equal). **Alexis Amann**: investigation (supporting). **Dawn Zimmerman:** investigation (supporting); writing review and editing (supporting). **Carlos Sanchez**: investigation (supporting); writing review and editing (supporting). **Suzan Murray**: funding acquisition (supporting); resources (supporting). **Colleen McCann**: funding acquisition (supporting); writing review and editing (supporting). **Teklu Tesfaye**: investigation (supporting). **Larissa Swedell**: conceptualization (equal); funding acquisition (lead); investigation (lead); project administration (lead); supervision (lead); writing review and editing (equal).

ORCID

Dawn Zimmerman 🔟 http://orcid.org/0000-0001-7003-5258

Larissa Swedell 🔟 http://orcid.org/0000-0001-6909-2669

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