Satellite tracking Ghost Bats (*Macroderma gigas*) in the Pilbara, Western Australia

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ABSTRACT – Little is known about the extent of the foraging habitat and characteristics of the threatened Ghost Bat (*Macroderma gigas*) in the arid regions of Western Australia. We used GPS satellite tracking technology to accurately measure the Pilbara Ghost Bat's foraging characteristics. We provide detailed foraging and commuting data for ten bats, eight males and two females tracked over multiple nights. From the time and location data collected, results for five foraging characteristics were calculated. These were the minimum time spent outside the diurnal roost, the time spent for short periods in a specific foraging area, the typical area used for during a foraging period, the maximum radial distance flown from the diurnal roost, and the minimum 'cave-to-cave' distance covered. The time spent outside the roost varied widely with bouts lasting from under half the night to the full period of darkness. The average time spent at a particular foraging area was 116 minutes during which the bats used multiple perches for typically 20 minutes each. Little pattern was evident in the areas used for foraging. The bats made use of the majority of an area available once they had begun to forage there. During foraging bouts, the average radial distance from the roost from all available data was 8.5 km and the maximum distances recorded was 17.7 km. The average return flight distance from all data was 19.4 km with a maximum length of 41 km. One bat totaled over 90 km in four nights. A one-way commute of 27.4 km was also recorded. The Pilbara Ghost Bat is confirmed to be foraging across a varied habitat and over distances not previously recognised. Generally, thinly wooded areas of Mulga, other *Acacia* or Eucalypt spp. or linear woodland features are preferred in areas with a moderate percentage of open ground (typically 30–70%) to facilitate the perch and sally 'surface' foraging strategy used for terrestrial prey. No pattern was evident in substrate type.

KEYWORDS: Ghost Bats, foraging, satellite tracking

INTRODUCTION

The Ghost Bat (*Macroderma gigas*) is a large carnivorous bat that is extant across tropical northern Australia in a number of disconnected subpopulations. The population in the Pilbara region of north-western Australia is a remnant of an arid zone dispersal that in historical times has included the western deserts and the central ranges of Western Australia, South Australia and the Northern Territory. Its arid zone range had extended eastwards to the Dulcie, MacDonnell, Musgrave and Mann Ranges of Central Australia in the early twentieth century but is now severely restricted. Fossil evidence shows that it once extended south to the south-west of Western Australia and the Flinders Ranges of South Australia (Richards et al. 2008: Woinarski et al. 2014).

It is the largest zoophagic bat in Australia weighting up to 175 g, larger in the north and east (J. Augusteyn pers comm) and slightly smaller between 125 and 150 g in the Pilbara (Bullen et al. 2016). It is an obligate cave roosting bat that preys upon small mammals, reptiles, frogs, birds, other bats and large insects (Richards et al. 2008; Claramunt et al. 2019: Start et al. 2019). Genetically, regional populations are highly structured (Worthington Wilmer et al. 1994; 1999) and the Pilbara population is geographically isolated and separated by the Great Sandy Desert. The genetic divergence implies virtually no movement between the Pilbara and the Kimberley to the north-east (Worthington Wilmer et al. 1999). Detailed intra-regional genetic analysis is underway in several areas of the Pilbara (e.g. Ottewell et al. 2017; Ottewell et al. 2018; Ottewell et al. 2019; Sun et al. 2021) that show high levels of relatedness over short distances, low levels of relatedness over longer distances up to 300 km and occasional long-distance dispersals (up to 268 km) have been reported (Ottewell et al. 2017).

In the Pilbara the Ghost Bat is widespread (McKenzie and Bullen 2009) however, it is under pressure from loss of roosting habitat, i.e. caves or man-made structures with suitable characteristics and microclimate (TSSC 2016). The Ghost Bat was relisted as vulnerable under federal and state legislation in 2016 (The federal Environment Protection and Biodiversity Conservation Act 1999 and Western Australian Biodiversity Conservation Act 2016). It has been the subject of detailed observations for many years and, more recently, to several mid and long-term monitoring programs at roost caves. These have shown that Ghost Bats are constantly moving between available caves. The evidence from this work shows that the usage of caves falls into four broad categories. Firstly, there are caves and historical underground mines (usually with adits or stopes as entrances but occasionally with broad shafts as entrances) that are used continuously as diurnal roosts by large numbers of Ghost Bats for long periods of time. Secondly there are caves and adits that are used regularly as diurnal roosts by small numbers of Ghost Bats but not continuously. Thirdly there are caves that are used as diurnal roosts only occasionally and as nocturnal roosts more frequently. And finally, survey work in recent years has shown that virtually any deep overhang, shelter or cave is subject to a nocturnal visit and/or an opportunistic roosting visit (Bat Call WA 2021).

The Ghost Bat has two different foraging strategies. It perches in vegetation or on rock walls to ambush passing prey both on the ground and in the air and it also gleans surfaces including the ground while in flight (Churchill 2008; Richards et al. 2008). This includes foraging on bats exiting caves entrances. It is known to move regularly between suitable points within and between foraging areas (Churchill 2008). Early work by Tidemann et al. (1985) suggested a short-range forager with distances from roosts to preferred foraging areas being limited to under 2 km. More recently, limited work has shown that foraging distances out to 12 km are flown by males (Augusteyn et al. 2017). Given that the species is under pressure from loss of habitat by mining and development in the Pilbara and elsewhere, detailed knowledge of the foraging habitats of the species away from cave entrances is required to be known. Tracking using Very high frequency (VHF) has provided some limited insight to Ghost Bat foraging including data collection over extended periods (Augusteyn et al. 2017; Biologic 2019; Biologic 2020) and confirming longer range flights and larger foraging areas but has limitations in not providing pinpoint foraging site data. Satellite tracking using GPS technology was selected to provide foraging site data at a finer scale to complement the VHF tracking studies underway.

METHODS

GPS TRACKING

During 2020 and 2021, GPS data loggers and radio transmitters were attached to ten Ghost Bats. LOTEK Pinpoint system transducers (tags) (model ARGOS 100 weighing 6.2 g or ARGOS 120 weighing 5.3 g, Lotek, Canada) that collected positional data that was subsequently transmitted via ARGOS system satellites to a ground station (Collecte Localisation Satellites SA, France) for analysis were used. A pattern of fix times was programmed into each tag to ensure the best data collection was achieved during the expected foraging times of the night. This pattern began at 18:00 Australian Western Standard time (UTC+8 hr) and programmed a fix every 25 minutes until 22:00, then two-hour breaks gave fixes at midnight and 02:00 followed by fixes every 25 minutes until 06:00.

The Ghost Bats were netted at widely separated roost entrances spanning the length of the Hamersley Ranges and the Marble Bar area of the eastern Pilbara (Table 1). Murdoch University Animal Ethics approval R3220/20 and the Western Australian Department of Biodiversity Conservation and Attractions Reg. 17 license BA27000278 and Section 40 authorisation TFA 2020-0082 were applicable. At the site of capture, each bat's mass was measured (AVINET spring balance Model S1Kg) and checked for condition and for age by reviewing the state of ossification of the wing bone joints. No heavily pregnant female or adolescent bats were used in the study. The GPS tags were glued to the upper back of eight bats using Ostobond skin bonding latex adhesive (Montreal Ostomy, Canada) and the bats released back into the caves unharmed. The remaining two tags on bats LR-2 and LR-3 were bonded with Torbot latex adhesive (Torbot Group, USA). In all cases the adhesive was applied to the Ghost Bat's back and to the tag underside and sides and allowed to airdry for 4 minutes. After placing the tag in position, the tag was held in place for a further 1.5 minutes by very light finger pressure before the bat's release.

The published accuracy of the fix types for the ARGOS locations are given in Table 2. Prior to field work these were checked in controlled conditions by placing a tag of each type at a control location and allowing it to provide fixes over several days, The achieved accuracies were found to conform to the published data (Table 2).

FORAGING AREA ASSESSMENTS.

All location fixes nominated by ARGOS as OK or OK (corrected) including those with poor accuracy (over 1 km) were recorded with their date and time in a spreadsheet and plotted using Google Earth for subsequent analysis. Locations recorded with high (under 100 m) or acceptable accuracy (under 1 km) were nominated as single point locations when only one record was received. Areas with multiple records at consecutive times within a relatively small perimeter were nominated as foraging areas. The sizes of these foraging areas were assessed by placing a circular polygon over the group of perches that had high accuracy of under 100 m if they were on a plain or hilltop area or by placing a suitable polygon over the area if they were along a linear feature such as a breakaway, drainage or riparian zone. Areas with times intermingled with those of high accuracy but with poor accuracy fixes nearby were assessed as belonging to the foraging area. The time spent in each area was estimated by the elapsed time in minutes between the first and last fixes in that area.

TABLE 1 Details of bats used during the study.

Area	Adit/Cave designations	Latitude	Longitude	Bat	Sex	Mass g	Season	Climate and moon phase during study: Maximum temp. range ^0C	Minimum temp. range ^0C	09:00 relative humidity range %	Moon phase
Eastern Hamersley Range	Cave EastH-A	-23.1	119.3	HD-1	Male	130	Late dry season	30–35	10–15	20–25	First qtr. to full
Middle Robe River Valley	Cave MidR-B	-21.7	116.6	RV-1	Male	130	Late dry season	35	~15	8	Full
Lower Robe River Valley	Cave LwR-A	-21.7	115.9	RV-2	Male	125	Late dry season	30–35	15–20	10–45	Full
Central Hamersley Range	Cave CentH-A	-22.5	117.5	GB-1	Male	130	Wet season	30–40	25–30	20–100	Past full
Central Hamersley Range	Cave CentH-B	-22.3	117.4	GB-2	Male	130	Late wet season	35–40	~25	30–70	Last qtr.
Marble Bar	Adit Comet	-21.234	119.727	COM-1	Female	130	Wet season	35–40	~25	50–70	New
Marble Bar	Adit Lalla Rookh	-21.051	119.278	LR-1	Female	135	Late dry season	40	25	15	First qtr. to full
				LR-2	Male	130					
				LR-3	Male	130					
				LR-4	Male	130					

TABLE 2 Accuracies published and achieved for the ARGOS fix types.

Fix Type	Published estimated positional error	Achieved accuracy at the pre-study control location (m) Ave (Sd; n)	Comments regarding the achieved accuracy	Number of fixes achieved during the study
3D	< 100 m	7.3 (7.55; 98)	Excellent GPS accuracy for defining foraging points	134
2D	< 100 m	17.5 (19.7; 16)	Excellent GPS accuracy for estimating foraging points	23
A3	< 250 m	231.7 (163.4; 33)	Acceptable accuracy for defining foraging areas	15
A2	250–500 m	523.1 (384.0; 11)	Acceptable accuracy for defining foraging areas	14
A1	500–1,500 m	1,479.4 (1,444.2; 6)	Poor accuracy for defining general foraging location only	9
A0	1,500 m	4,647.0 (954.2; 4)	Very poor accuracy. Not used in this study	5
AA	N/A	1,287.6 (2,003. 8; 9)	Poor accuracy for defining general foraging location only	7
AB	N/A	2,980.1 (3,392.7; 20)	Very poor accuracy. Not used in this study	18

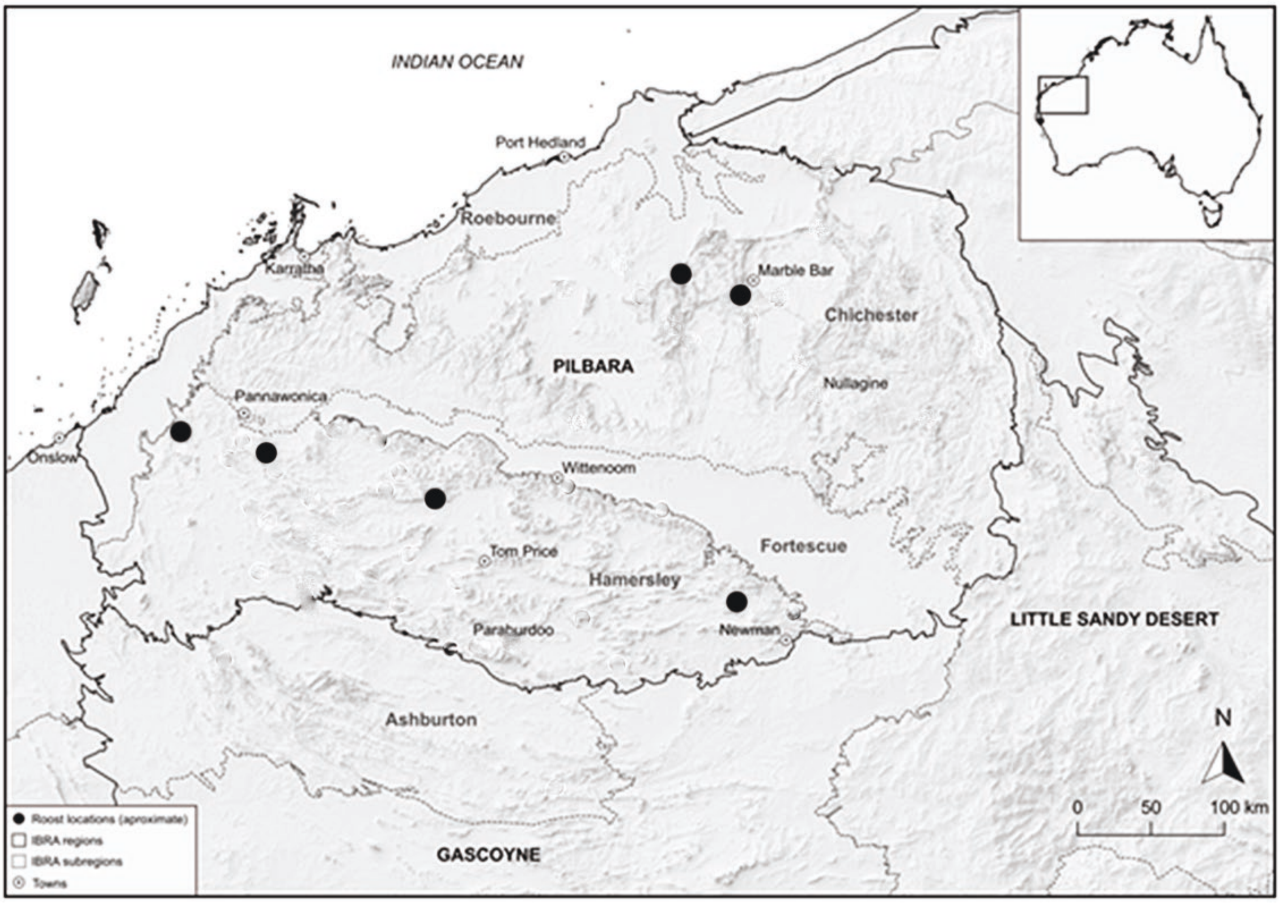

FIGURE 1 General Arrangement showing the locations of tagging sites.

FLIGHT DISTANCE ASSESSMENTS

For each night that fixes were received, a flight path was estimated using satellite imagery by connecting the departure roost with each subsequent fix. The first fixes after departure were often close to the roost. However, being obligate cave roosting bats, no fixes were obtained after the bat had returned to the roost. On nights where the bat exhibited a circular or retraced route, i.e. when the last fix was approaching the originating roost, it was assumed that it returned to that roost. On nights where the bat exhibited a more linear route and showed no evidence of returning to the originating roost, a location with a known cave or known cave forming strata in a rugged area much closer to the final fix than the originating roost was assumed. In all cases, these assumptions were supported by the first fix of the following night being made nearby the assumed location. Flight distances were then calculated by the resulting track.

RESULTS

A total of 170 fixes were recorded of which 151 were of high or acceptable accuracy (Table 2) from ten bats, eight males and two females. High accuracy fixes (i.e. > 20 m) totaled 120 and these were used to characterise the tree perch or the foraging area. The bats generally exhibited similar behaviours however they differed widely in their night-to-night foraging bouts. Often on the first night after tagging the bats stayed relatively close to the roost (average maximum distance was 5.4 km but see RV-1 below for an example of a bat that commuted greater than 10 km on the night it was tagged). On subsequent nights all bats were recorded foraging more widely. During the study, six of ten, departed and returned to the same roost each night. Three bats were recorded using at least two roost caves within 10 km on alternative nights. One bat was detected on a long-range commute to a distant cave at least 27 km from the site of tagging. Vegetation at all foraging areas had similarities with open woodland or drainage line banks having low and scattered Mulga (*Acacia* spp.) or Eucalypt, mostly over shrubs and patchy grasses with typically 30–70% ground cover. The substrate of the foraging areas differed widely though from flat sand and clay plains and ephemeral drainage lines of all sizes to low relief hills of all geologies and the tops of major ridge lines in ironstone and other mafic rocks. The bats did not exhibit a consistent pattern of foraging times with some longer bouts from dusk to dawn (up to ten hours) while other bouts were shorter between dusk and midnight or midnight to dawn (up to six hours).

TRACKED INDIVIDUALS

Bat HD-1

This male was netted at a cave in the eastern Hamersley Ranges during a cool late dry season period. A total of 43 fixes were recorded over seven nights. On each night, this bat foraged within a north-south corridor approximately 15 km long and 5 km wide. He was recorded using seven separate foraging areas (Table 1), two of which he returned to on a subsequent night (HD-1-1 on nights two and four and HD-1-4 on nights three and four). The earliest fixes on all seven nights indicate that he left the roost soon after dusk and the latest recorded fixes indicate that he returned to the roost at various times with the latest being before dawn on nights two and three. Five of the seven foraging areas were in low open Mulga woodland with between 20 and 70% vegetation cover of *Acacia* shrubs and tussock and hummock grasses (Table 2 and 3). The substrates varied between loam, clay and pebbles.

Bat RV-1

This male was netted at a cave (MidR-B) on an unnamed mesa overlooking the Robe River riparian in the Middle Robe Valley during a cool, late dry season period. Only five fixes were recorded before he either scratched the tag off while in the roost or its battery failed prematurely before night three. No fixes were recorded the first night however a single Ghost Bat was detected by an echolocation recorder leaving the cave at 19:12 and was not detected again that night. On the following night, his initial fix was 10 km south-west of the original roost cave (MidR-B). After that he foraged along the Robe River riparian zone nearby the tagging site until 23:00, area RV-1-1, dominated by open *Eucalyptus camaldulensis* woodland over sand and gravel until midnight. No further GPS fixes were recorded; however, a single echolocation call sequence at 03:08 (a diagnostic series of pulses able to be identified by an experienced bat call researcher. See also Hanrahan et al. 2021) inferred that he had returned to cave MidR-B.

Bat RV-2

This male was netted at a cave (LwR-A) in the lower Robe River valley during a warm late dry season period with increased humidity. Eleven fixes, eight accurate, were recorded over three nights. On the first two nights he foraged in two areas to the west and south-west of LwR-A, areas RV-2-1 (both nights) and RV-2-2 on night two. The former was an *Acacia xiphophylla* tall open shrubland over *Triodia epactia* open hummock grassland on loamy plain, over 300 ha, that had adjacent recent clearing disturbance in preparation for development activities. The latter was an undisturbed hilly area approximately 7.5 km south-west with extensive thinly wooded ephemeral drainage lines. On the third night the bat was accurately detected foraging in moderately wooded dry drainage lines (area RV-2-3 of approximately 20 ha) 2.5 km north-east of the cave and on the opposite side of the main Robe River riparian zone.

Bat GB-1

This male was netted at a cave (CentH-A) in the central Hamersley Ranges during a hot and stormy wet season period. A total of twelve fixes were recorded over four nights with none being recorded on the third due to the passing of a tropical storm that delivered over 200 mm of rainfall. Bats including Ghost Bats are unlikely to leave their roost caves during rain events as the falling rain interferes with their echolocation ability. On the first night the bat stayed within 2.5 km of cave CentH-A however he was recorded at a range of perches with widely varying elevations. After departing from its cave that has an altitude of 650 m ASL, he was detected initially at 1070 m ASL (accurate fix) at a lightly wooded ridge top foraging area (GB-1-1), then at six perches at elevations between 650 and 750 m, all accurate fixes (GB-1-2), comprised of *Corymbia deserticola* scattered low trees over *Acacia* spp. open shrubland over *Triodia wiseana* open hummock grassland onlower slopes of a major ridge line within a 115 ha area. After this he was detected (accurate fix at 02:00) high on the ridgeline nearby GB-1-1, before returning to his diurnal roost cave. Its flight that night covered at least 17 km and twice included climb and descent pairs of over 400 m of elevation. On the second night he was detected 11 km north of CentH-A in thin woodland adjacent to the Nammuldi agricultural pivots (area GB-1-3) on the clay/loam plain before roosting in a different cave in the low relief ironstone hills nearby. On the fourth night, before the tag's battery failed, there were three detections at the ironstone hills approximately 7 km north of the original roost cave and nearby the operating Brockman 2 mine (area GB-1-4). However, only one of these was with acceptable accuracy (A2).

Bat GB-2

This male was netted at a cave (CentH-B) in the central Hamersley Ranges during a hot and humid late wet season period. Over 50 fixes were recorded over four nights. On the first and second nights the bat flew 10 km south where he was recorded foraging close to and within the Nammuldi agricultural pivots (GB-2-1). On the first night he was detected (accurate 3D fixes at 19:39 and 20:05) at two perches 9.15 km apart which corresponds to a flight speed of 22 kph. Later he flew 4 km north where he foraged in a wooded plain (area GB-2-2) before returning to CentH-B to roost. On the second night 14 fixes were recorded between 19:55 and 02:55 on and immediately north of the Nammuldi agricultural pivots as he foraged within an expanded and elongated area GB-2-1, ~3 km long by 500 m across (~450 ha). All but three fixes were accurate locations. Together with the return trip from the roost cave he had flown at least 36 km that night. On nights three and four he flew 5 km north of cave CentH-B to a series of perches between 200 and 300 m higher elevation that the roost. On these nights he was detected foraging at a series of rugged upland perches above the rim of a long cliff line (area GB-2-3). Each of the accurate fixes were on sparsely wooded ground. On the fourth night he returned to the same northern area as the previous night where he foraged in two lightly

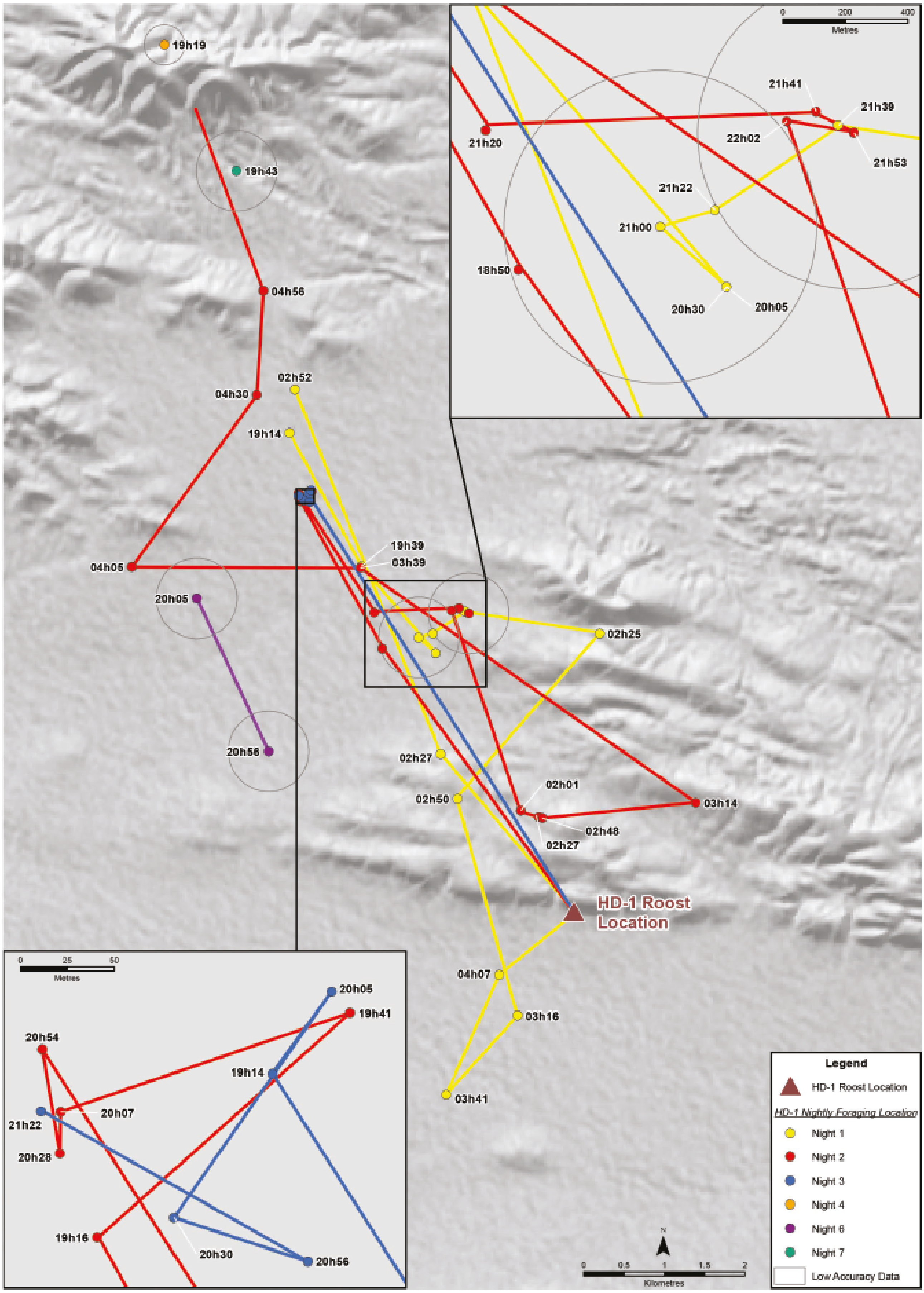

FIGURE 2 Nightly foraging patterns of Ghost bat GB-1. The bat was tagged and roosted on subsequent days at location CentH-A

wooded drainage areas (GB-2-4 and GB-2-5) at 750 m altitude separated by the higher cliff/ridge line at 900 m. Both areas were approximately 125 ha. Over the four nights this bat had flown at least 90 km.

Bat COM-1

This female was netted at the Comet mine near Marble Bar on a hot wet-season night. Only three fixes, all accurate, were recorded over two nights. On the first night, she was recorded in the sparsely wooded low relief hills 2 km west and then on the Coongan River riparian zone, 8.5 km to the south. On the second night her first detection was in the early morning hours 27 km north-east of the roost on an ephemeral tributary of the Talga River in an extensive area of low granite outcrops. Rather than returning to the Comet, she is assumed she either roosted amongst the granite outcrops nearby or more likely, as the granite offers limited roosting opportunities, continued on north or west another 15 km to a range of hills known to have extensive cave forming strata, potentially completing a one-way trip of between 30 and 40 km.

Bat LR-1

This female was netted at the Lalla Rookh adit in the warm to hot, late dry season. A total of 31 fixes (28 accurate) were recorded over five nights. On each night she foraged along the wooded banks of the Shaw River or the adjacent mafic uplands up to 11 km west or south-west of the original roost. The pattern of fixes on nights two to four also indicated that she roosted at an unknown location in the lightly wooded upland before returning to Lalla Rookh after midnight on night four. Her foraging times also varied. On night one she foraged between dusk and dawn, on nights two and four between dusk and midnight and on night three between midnight and dawn.

Bat LR-2

This male was netted at the Lalla Rookh adit in the warm to hot, late dry season and his tag affixed with Torbot adhesive. A total of four accurate fixes were recorded before he scratched the tag off early on night two. On the first night he stayed very close to the roost and returned within approximately one hour. On night two he flew 7.5 km north-west to the woodland along the bank of the Shaw River where a series of identical fixes over subsequent nights indicated that he had removed his tag.

Bat LR-3

This male was netted at the Lalla Rookh adit in the warm to hot, late dry season and his tag was affixed with Torbot adhesive. A total of twelve accurate fixes were recorded before he also scratched his tag off on night three. On night one he stayed close to the roost all night only flying approximately 7 km with a maximum radial distance of 2.8 km. On night two he flew 6 km north-east to the bank of the Shaw River after dusk before returning before dawn. On night three he flew to a similar Shaw River area as the previous night via two upland locations before removing his tag while within the river's riparian zone indicated by a series of identical fixes over many hours.

Bat LR-4

This male was netted at the Lalla Rookh adit in the warm to hot, late dry season. A total of ten accurate fixes were recorded over two nights followed by inaccurate fixes on each of the following two nights. On night one he likely returned inside the roost following tagging. On the second night, after dusk he flew north across the sand plain, foraging for 75 minutes along an ephemeral minor drainage line before he moved further north to the wooded banks of the East Strelley River over 18 km north of Lalla Rookh where he is assumed he roosted in a tree. Alternatively, he may have flown 6 km further north and roosted in a station structure. These two alternatives are suggested by an absence of rocky areas with cave forming strata any closer than Lalla Rookh and the timing of the last GPS fixes.

CHARACTERISTIC FORAGING TIMES AND DISTANCES

From the time and location data collected, results showing five particular foraging characteristics were able to be calculated. These were the minimum time spent outside the diurnal roost, the time spent for short periods in a specific foraging area, the typical area used for these foraging periods, the maximum radial distance flown from the diurnal roost, and the minimum 'cave-to-cave' distance covered. Summary data from males, females and all bats combined are presented in Table 3.

The nightly time spent outside the roost varied widely with bouts lasting from under half the night (up to 6 hr), beginning or ending close to midnight, to the full period of darkness (up to 10 hr), beginning in the three hours after dusk and finishing in the three hours before dawn. Overall average time outside the roost was estimated as 348 minutes (Sd 142, n 20). There was no significant difference between the males and females (362 and 311 minutes respectively, $t = 0.17$, $N=20$ $p=0.36$). There was also no apparent difference between the sexes regarding half versus full night foraging bouts (males, 7 half and 10 full: females 2 half and 3 full). The maximum time recorded foraging outside the diurnal roost was over 10 hours for a male and 7 hours for a female.

The time spent in a particular foraging area showed variation overall and no apparent difference between males and females (Table 3). The average time spent at a particular foraging area was 116 minutes during which the bats used multiple perches for between 20 and 30 minutes each. There was insufficient female data to test for significance. Maximum values were 420 and 175 minutes for males and females respectively.

The areas of the sites used for foraging that had multiple fixes varied widely ranging from a minimum of 0.1 ha to a maximum of at least 450 ha at the Nammuldi agricultural pivots (Table 3). Little pattern was evident

TABLE 3 Time and Distance summary statistics.

[1] Unreliable first or last times, or times on nights with single fixes or when the battery failed are excluded.
[2] Sites with single point fixes or sites with times that began or ended between 22:00 and 02:00 were excluded.
[3] First nights, failed battery nights and long distance one-way-commute nights excluded.
[4] First nights and failed battery nights excluded.

Parameter		Average	sd	N	Maximum	Minimum
Minimum nightly time spent outside the roost (minutes)[1]	All data	348	142	20	606	99
	Males	362	159	15	606	99
	Females	311	67	5	427	263
Time spent in a foraging area (minutes)[2]	All data	116	99	22	420	20
	Males	114	101	21	420	20
	Females	175	N/A	1	175	N/A
Size of typical foraging areas (ha)	All data	105	133	19	450	1.0
	Males	121	139	16	450	1.0
	Females	18	28	3	50	1.0
Maximum distance from roost (km)[3]	All data	8.5	3.8	14	17.7	4.5
	Males	8.7	4.1	11	17.7	4.5
	Females	7.9	2.7	3	11.0	6.4
Minimum cave-to-cave distance covered (km)[4]	All data	19.4	9.1	15	41.0	11.6
	Males	18.3	8.0	11	36	11.6
	Females	22.3	12.8	4	41.0	12.2

in the data other than the observation that the bats made use of the majority of an area available by regularly moving between perches once they had begun to forage there. There was no significant difference between the areas that males and females used (t = 0.015 on a two tailed comparison of means, N=19, p=0.31).

The maximum radial distance flown, excluding all first nights, failed battery nights and long-distance one-way commutes of over 25 km, and the minimum cave-to-cave distance covered showed some variation (Table 3). However, neither showed a significant difference between the sexes (max radial distance t = 0.73, N=14, p=0.45; minimum cave to cave distance t = 0.59, N=15, p=0.25). The average radial distance from all available data was over 8 km and the maximum and minimum distances recorded were 17.7 and 4.5 km for males and 11.0 and 6.4 km for females. The return flight distance average from all data was 19.4 km with maximum and minimum lengths of 36 and 11.6 km for males and 41 and 12.2 km for females.

COMMUTE AND OTHER DATA

On two occasions, bats were assessed as completing long distance (> 15 km) one way foraging or commuting bouts in a basically linear direction without any evidence of a return flight that night. The male LR-1 on his second night flew north-west stopping at a series of points that included area LR-4-1 on a minor ephemeral drainage. His last fix was at midnight on the East Strelley River, 17.7 km north of his departure point. The pattern of fixes on subsequent nights were of insufficient detail to confirm if he had remained in that northerly location or had returned to the original roost. Separately, after foraging to the south on the first night, the female COM-1 departed the Comet mine and was detected at a tributary of the Talga River 27.4 km north-east at 02:30. It is likely that she then continued on to a diurnal roost nearby in the granite outcrops or a further 15 km to the north or west in the uplands of mafic geology. This bat has therefore covered at least 30 and possibly over 40 km in that night. A similar distance of 36 km was flown by the male GB-2. On his second night he departed from and returned to cave CentH-B after foraging at a number of points and areas at and around the Nammuldi agricultural pivots. Four trips of shorter distances under 10 km were also recorded. The male HD-1 moved repeatedly between its original roost and the northern cave for diurnal roosting completing three measured one-way trips. Also, the male GB-1 was interpreted as moving from its original cave to an alternate cave for diurnal roosting approximately 8 km north.

One pair of fixes gave an accurate minimum commuting flight speed estimate. The male GB-2 on his first night was detected at two accurate locations (both type 3D, Table 2) 9.15 km apart, the first at 19:14 and the second 25 minutes later. This corresponds to a flight speed of at least 22.0 kph (6.1 $msec^{-1}$). A similar commute speed was suggested by data from RV-1. He was recorded departing the cave at 19:12 on the first night after tagging. No further GPS or echolocation fixes were detected that night indicating that he commuted away to a second roost cave within the 25-minute fix window The first GPS fix was at 20:15 on night two approximately 10 km to the southwest suggesting that this time was just after he emerged. Taking these data points together indicates that he had flown over 10 km in under 25 minutes on the first night also providing a commuting speed of over 22 kph.

DISCUSSION

The data presented from this study provide an impressive summary of the foraging characteristics of the Ghost Bat away from their diurnal roosts. The existing literature provides some similar details but there are no comparative publications with nightly statistical data for this species. Early data from Queensland that has often been cited suggested that nightly foraging areas were of moderate size averaging 61 ha and were close to the roost, averaging 1.9 km, in Tidemann et al. (1985). Toop (1985) reported winter dispersals of up to 50 km, and possibly as much as 300 km, in central Queensland but no indication of colony mixing at distances over 300 km. He did not address nightly foraging ranges. More recent VHF and GPS data from the Mt. Etna colony in Queensland expanded the foraging range out to a maximum of 11.8 km (Augusteyn et al. 2017) but gave no further detail on areas used for foraging. The averages of our new data are similar to these maxima at 105 ha and over 8 km but then expands the maximum values of both parameters out to 450 ha and nearly 18 km.

Regarding descriptions of foraging areas, our data is similar to and expands upon descriptions from Churchill (2008) and Augusteyn et al. (2017). Churchill summarised habitat as ‘a broad range including arid spinifex hillsides, black soil grasslands, monsoon forest, open savannah woodland, tall open forest, deciduous vine forest and tropical rainforest’. Augusteyn et al. (2017) reported foraging above cleared agricultural land at a few sites on the edges of remaining woodland remnants and others on the edges of ephemeral water courses. That study also reported that bats appeared to transit quite rapidly to the edges of the preferred remnant woodlands without going into that thicker vegetation. Our study confirms both reports while adding detail of the types of foraging areas utilised in the arid areas of the Pilbara region. The overriding pattern of our perches are an upper storey of open woodland to scattered trees over productive shrub and grasslands and all having areas of clear ground (typically 30–70%). This likely allows the perched bat to see and then drop onto its prey as the target moves from covered point to the next covered point. The attraction of the Nammuldi agricultural pivots was apparently associated with the local abundance of mice (*Mus* sp.) which likely coincided with flowering grasses at the pivots. Significantly, none of our bats were detected foraging within deep wood gullies or gorges and the bats apparently preferred to be on or nearby the rims of such deeply incised areas. We note that gorge and/or gully habitats were present in close proximity to the majority of the recorded foraging areas suggesting that these habitats were not preferred rather than the observation being due to lack of opportunity. Again, this is probably associated with the need to see and attack prey without encountering wing membrane damage in heavily cluttered environments. However, it is possible that the tags failed to either receive or transmit in these deeper features.

The limited accurate data we collected on nightly commuting distances and flight speed agrees well with previously published data. Ghost Bats are known (Toop (1985 and other publications) to move long distances seasonally following productive foraging opportunities and to move between cave 6 to 8 km apart and occasionally over 30 km apart (e.g. late dry season movements reported in Sun (2021). One-way commutes and the longest measured nightly round trips of 30–40 km or more from the current study are consistent with the previous data and confirm that long distances are regularly covered by the Ghost Bat and not limited to dry season conditions. Notably the long distance covered by COM-1 was in late wet season and LR-4 in late dry season. Similarly, our single minimum commuting speed data point of at least 22 kph (6.1 $msec^{-1}$) agrees well with the published speed limit of 7.2 $msec^{-1}$ for aerobic flight (Bullen et al. 2016).

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