Space-use and movement patterns in an arid-zone agamid lizard

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Research

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Abstract

Background

Quantifying the space-use and movement patterns of animals is critical to understanding habitat use and social systems. Little is known of the finer details of lizard movement biology, due to the limitations of observational studies. Advancements in technology has greatly improved our ability to study animal space-use and movement, though new technology has rarely been used to quantify finer-scale lizard movements and space-use. Using Global Positioning Systems (GPS) tags and accelerometers we tracked 36 central bearded dragon (*Pogona vitticeps*) individuals over three seasons, with the aim to describe space-use and movement patterns and to determine how these patterns differ due to individual traits and environmental drivers.

Results

Home ranges were held by 23 out of 36 individuals and wider tailed males were more likely to be floaters (no evidence of a home range). Evidence of floater behaviour was shown by 45% of females and only 20% of males, though both sexes often roamed over distances greater than 1 km. No significant relationships were observed among home range parameters and the individual traits measured. Home range overlap occurred between both neighbouring males and females, and core areas were not exclusive. Air temperatures strongly influenced movement in both sexes. Movement was significantly higher for males than females during late-spring, but not mid-summer, and was inversely related to head sizes and body mass during mid-summer. Interestingly, no correlation was observed between daily movement rates and home range measures. However, the movement rates of home range holders were significantly different from floaters for each season.

Conclusions

These results confirm that wild *P. vitticeps* movement patterns are driven by temperature, though space-use patterns vary from previously studied agamids, with high rates of nomadism, possibly due to drought conditions and high intrasexual home range overlap. Individuals varied widely in their space-use tactics, which seem unrelated to size, a potential proxy for social status or age. Our detailed data highlights the utility of accelerometers and GPS tracking devices in the study of lizard ecology.

Background

Detailed information on the space-use and movement patterns of individual animals within a population is critical to understanding population dynamics, as movement biology controls dispersal, response to environmental change, resource use and the evolution and organisation of social and mating systems [1]. Our ability to study space-use and movement in animals has been greatly improved with innovations in technology [2, 3], however, the use of this new technology is currently lacking in studies of reptiles, particularly lizards [2, 4].

Space-use and social strategies differ amongst lizard species; some species have populations comprising of mainly solitary individuals, and others have complex social communities with both territorial and non-territorial individuals [5–7]. Within populations, individual lizards may show different activity and space-use patterns based on their social rank and/or social system. Visual observations of iguanid and agamid lizards suggest that, in order to defend their territories, dominant territorial individuals are more vigilant and engage in aggressive displays more often than subordinate non-territorial lizards [6, 8]. Differences in activity patterns may underlie an adaptive trade-off between the benefits of defending a territory and the additional energy needed to retain a territory [9]. This may be particularly important where resources are scarce, such as in arid environments where territories may be important for defending limited resources [10]. For example, Australian arid zone mammals have been found to be highly mobile, possibly reflecting an adaptation to the low productivity and variable rainfall of Australian deserts when compared to more mesic environments [11]. Thus, a life history strategy geared towards increased mobility to prioritize locating sufficient resources to survive and reproduce may be a safer evolutionary investment for arid zone animals than establishing permanent home ranges and shelter sites. In the arid zone, quality habitats with abundant resources can be geographically widespread and transient [12], and therefore increased movement strategies would be critical in enabling animals to locate, exploit and defend resources within quality habitats.

Majority of free-range lizard activity studies are based on GPS or VHF radiotracking or visual observations in the field (e.g. [6, 8, 13, 14]). However, the quantification of lizard activity from visual observations in the field can be compromised by the effects of observers on the study individuals [15]. While GPS or VHF based radio tracking methods minimise observer interference, they may miss crucial movements or behaviours that occur between locational fixes [16]. Data loggers, such as accelerometers or pedometers, are able to collect activity information remotely and do not have these limitations. Pedometers have been used successfully to determine spatial and temporal variation in activity among individuals of sleepy lizards (*Tiliqua rugosa*) [17–19]. These studies were the first to use data loggers on lizards and the novel data gained provided new knowledge about how fine scale movement patterns are influenced by ambient temperatures and habitat complexity, and how movement differs between the sexes. Similar research has yet to be attempted for other lizard species, despite the existence of many suitably sized candidate species.

Similar to pedometers, accelerometers provide continuous data on animal movement. Accelerometers are devices that measure the gravitational and inertial acceleration through piezoelectric sensors, usually on three axes [2]. This allows for accurately determining the timing and rate of activity versus rest whilst eliminating the need for direct observations in the field. Whilst accelerometers are currently being used in studies of mammals and birds, resulting in an abundance of novel findings and insights [2, 3], no studies to date have used accelerometers to determine activity rates in free-ranging lizards. Nevertheless, there are many potential applications of accelerometers in lizard ecology studies and they could be used to increase our knowledge of space use, dispersal patterns, foraging behaviours, physiological performance and interactions between conspecifics [3].

Combining the use of accelerometers with GPS tags can provide information on how activity relates to animal home range sizes and space-use strategies. As lizards with larger home ranges need to move further distances to traverse their home range [20, 21], does this mean that they spend more time actively

moving? Alternatively, are activity levels similar for lizards with smaller home ranges, who may restrict activities to core areas? Answering these questions can lead to a better understanding of how lizards utilize space within home ranges. Also, the use of both devices allows for the activity and space-use strategies of floaters (non-home-range holding animals) to be understood, as nomadic animals are often removed from observational studies when they leave study areas [6, 8, 22]. The adaptive significance of space-use choices is difficult to determine without information on the full diversity of movement patterns and how these relate to the physical traits, survival and reproductive success of individuals [23].

The central bearded dragon (*Pogona vitticeps*, Ahl 1926) is a large, common, conspicuous agamid found in central Australia [24]. It is a semi-arboreal omnivore that breeds from September to December and ranges in size from 15–25 cm snout-vent length with a body mass of 150–600 g [24]. Despite being often used in laboratory studies (over 120 publications listed in Scopus from 2008–2018), there is almost no published research on the behaviour of *P. vitticeps* in the wild [24, 25]. The overall aim of this study was to use GPS tags and accelerometers to identify patterns of space-use and movement rates of arid-zone *P. vitticeps* and to determine how these patterns are influenced by individual traits and environmental conditions. Specifically, we hypothesised that there would be differences in home range sizes and space use patterns between individuals based on sex and morphological characteristics, and that most *P. vitticeps* would hold home ranges which overlap with neighbouring individuals of both sexes. We expected that a small proportion of the population (younger or smaller individuals) would show evidence of non-territoriality or floater behaviour, based on evidence of multiple social tactics in related species [22, 23]. Additionally, we predicted that the timing of movement patterns of *P. vitticeps* individuals will be dependent on thermal conditions physical traits and home range size. By monitoring animal behaviour during mid-spring, late spring and mid-summer, we aimed to determine lizard movement behavioural responses to changing environmental conditions. Knowledge of the space-use and movement rates of *P. vitticeps* in relation to individual traits and season will provide information on the potential variety of behavioural tactics in this species.

Results

Space-use patterns

A total of 36 *P. vitticeps* were caught and tracked for 3–20 days (Additional file 1.doc: Table S1). The variation in total tracking times was due to staggered tag deployment schedules, tag failure events and the rare occurrence of an individual/tag not being relocated. Twenty-three of these dragons held home ranges.

Tracking resulted in 6849 total successful GPS fixes being taken, an average of 190 (± 135) fixes per dragon (Additional file 1.doc: Table S1). Approximately, 80% of males and 55% of females held home ranges, however logistic regression showed that this difference was not significant ($\chi^2_1 = 2.42$, $P = 0.12$). Male dragons with wider tails were significantly more likely to be a floater, while males with longer tails were more likely to hold a home range, though this trend was non-significant (Table 1).

Table 1
Results of logistic regression between body size measurements and whether a home range was held

Body Measurement	All Periods (n = 29)			
	M (n = 21; 4 floater)		F (n = 11; 5 floater)	
	χ^2	P	χ^2	P
SVL	2.6749	0.101	1.051	0.305
Mass	2.148224	0.143	0.038	0.845
Head Length	2.861263	0.091	1.149	0.284
Head Width	2.257263	0.071	0.790	0.374
Tail Length	6.187265	0.013*	0.123	0.726
Tail Width	7.632024	0.006**	4.279	0.037
Analysis was run for all periods with both sexes, and males and females treated separately. Degrees of freedom are equal to 1 for all analyses. Double asterisk denotes P-values under sequential Bonferroni adjustment [53], single asterisk represents marginally non-significant result (sequential Bonferroni adjustment $\alpha = 0.010$). Analysis was not run for each period separately, as there were not enough dragons in either the home range or floater categories to allow for comparison				

The average MCP home range area was 2.89 ± 1.82 ha and there was no difference between male and female home range sizes over all seasons (Fig. 2; t-test: $t_7 = 0.429$, $P = 0.682$). There was no significant difference between the size of male and female home ranges within seasons (mid-spring: $t_3 = 1.131$, $P = 0.346$; mid-summer: $t_5 = 0.639$, $P = 0.550$) or for the total average home range size between seasons when both sexes were pooled (ANOVA: $F_{2,20} = 1.40$, $P = 0.270$). Linear regression suggested that the size of MCPs were not influenced by the number of times dragons were recaptured for tag replacement when either all dragons were analysed together or each period was analysed separately (mid-spring: $F_{1,8} = 1.48$, $R^2 = 0.157$, $P = 0.259$; late-spring: $F_{1,4} = 3.34$, $R^2 = 0.455$, $P = 0.142$; mid-summer: $F_{1,7} = 1.83$, $R^2 = 0.207$, $P = 0.218$; all periods: $F_{1,23} = 0.106$, $R^2 = 0.005$, $P = 0.747$). No significant relationships were seen between body measurements and MCP area when all resident individuals were analysed for all tracking periods, or when each sex was analysed separately for each period (based on sequential Bonferroni adjustment, Additional file 1.doc: Table S2).

Across all tracking periods, core area size ranged from 0.029 ha to 1.13 ha and occupied an average of 22.6% ($\pm 2.4\%$) of the size of the 95% KDE. Across all seasons, male core areas were not significantly larger than females (Fig. 2; $t_6 = 0.144$, $P = 0.890$). There were no significant differences between the size of male and female core areas within each season (mid-spring: $t_4 = 0.416$, $P = 0.714$; mid-summer: $t_2 = 0.426$, $P = 0.7057$), nor a difference between core area sizes between seasons when all dragons from each season were pooled ($F_{2,20}=1.41$, $P = 0.267$). The size of *P. vitticeps* core areas were not significantly related to any body measurement, for any tracking period or when sexes were analysed separately or together (Additional file 1.doc: Table S2). No *P. vitticeps* that held a home range used it uniformly, and 19 out of 23 individuals revisited core areas within their home range (Fig. 3a). Three of the four individuals who did not revisit core areas were females. For floater *P. vitticeps*, 6 individuals continuously moved away from the site of capture roughly in the same direction (Fig. 3c), whereas three individuals (two males, one female) roamed in varied directions and returned to previously used areas (Fig. 3d).

Home Range Overlap

In mid-spring, all tracked dragons used in overlap analysis shared areas with at least one other individual for MCP's, 95% KDE's and core areas (Fig. 4a). Overlap between residents occurred only once in late-spring, between male dragons C and P (Fig. 4b; Additional file 1.doc: Table S3). Other resident dragons only had overlap occurring with dragons that did not hold a home range. All floaters crossed through at least one home range (both MCP and 95% KDE) and core areas were also crossed by three floater dragons (Fig. 4b; Additional file 1.doc: Table S3).

Daily Movement Per Individual

The total average daily movement per individual was 162 (± 49) min moving per day. Males had significantly higher daily average movement than females during the late-spring period (Fig. 5a; $t_9 = 1.44$, $P = 0.0403$). No significant difference occurred between male and female movement for mid-summer ($t_9 = 0.48$, $P = 0.322$). There was no significant difference in movement between the seasons when each sex was analysed separately (males: $t_{10} = 1.1311$, $P = 0.142$; females: $t_7 = 1.07$, $P = 0.160$).

Resident dragons, regardless of sex, moved significantly more each day than floaters during late-spring (Fig. 5b; $t_8 = 2.34$, $P = 0.0237$), however, the opposite trend was seen in mid-summer (Fig. 5b; $t_7 = 2.97$, $P = 0.0109$). Linear regression suggested that the size of the MCP home range or core area was not correlated with the daily average movement (MCP: $F_{1,12}=0.103$, $R^2 = 0.009$, $P = 0.753$; core: $F_{1,12}=0.5104$, $R^2 = 0.041$, $P = 0.489$). Daily average movement rates per individual showed significant negative relationships with head length and width, and body mass when data from both sexes from mid-summer were pooled (Table 2). When analysed separately, there was a negative, approaching significant, relationship between movement and tail length in males, and movement and tail width in females (Table 2).

Table 2 Results of linear regression analysis for body measurements versus daily activity rates of *Pogona vitticeps*.

Body Measurement	Late-Spring									Mid-Summer								
	M (df=1,5)			F (df=1,2)			Both (df=1,9)			M (df=1,4)			F (df=1,2)			Both (df=1,9)		
	F	R ²	P	F	R ²	P	F	R ²	P	F	R ²	P	F	R ²	P	F	R ²	P
SVL	0.03	0.01	0.86	0.57	0.22	0.53	1.06	0.11	0.33	0.86	0.18	0.41	1.90	0.39	0.26	2.65		0.29
Mass	0.15	0.03	0.72	4.02	0.67	0.18	0.46	0.05	0.52	1.34	0.25	0.31	13.45	0.82	0.04	10.35		0.53
Head Length	0.20	0.04	0.67	0.27	0.12	0.65	1.12	0.11	0.32	2.28	0.36	0.21	28.26	0.93	0.03	12.55		0.61
Head Width	0.00	0.00	0.97	0.00	0.00	0.98	1.82	0.17	0.21	5.85	0.59	0.07	50.65	0.96	0.02	11.86		0.60
Tail Length	1.59	0.24	0.26	9.13	0.82	0.09	2.24	0.20	0.17	9.55	0.70	0.04	0.61	0.17	0.49	4.96		0.36
Tail Width	1.92	0.28	0.22	6.28	0.76	0.13	0.05	0.01	0.84	0.67	0.14	0.46	31.50	0.94	0.03	8.03		0.50

Analysis was run for separate periods with both sexes combined for late-spring (n = 11) and mid-summer (n = 11), both sexes separate in late-spring (male n = 7, female = 4), and mid-summer (male n = 6, female n = 4), as well as for males and females separate with all periods combined (male n = 13, female n = 9), and both sexes and all periods combined (n = 21). Asterisk denotes significant P-values under sequential Bonferroni adjustment [53].

Influence of Fine-Scale Weather on Occurrence of Movement

The 10-minute readings of air temperature had a significant parabolic relationship with the proportion of movement of *P. vitticeps* when both seasons were analysed together ($F_{2,30}=78.4$, $R^2 = 0.839$, $P < 0.001$), with the highest proportion of movement occurring at 30 °C (Fig. 6). The occurrence of movement was greatly reduced when air temperatures were below 19 °C and above 37 °C (Fig. 6). Significant parabolic relationships also occurred with air temperature when each season was analysed separately (late-spring: $F_{2,21}=50.2$, $R^2 = 0.827$, $P < 0.001$; mid-summer: $F_{2,26}=60.1$, $R^2 = 0.822$, $P < 0.001$).

Diel Timing of Movement

Total average movement per hour (pooled data) showed that *P. vitticeps* is mainly diurnal, with movements only very rarely being recorded in the late-night hours (22:00–06:00). In late-spring, movement showed a unimodal distribution, with the most movement occurring during the middle of the day (Fig. 7). However, the movement pattern of the mid-summer tracking period had a bimodal distribution, with the highest amounts of movement occurring at 10:00, followed by a large reduction in movement during the middle of the day and then a secondary, smaller peak at 20:00 (Fig. 7), around local sunset at 20:40 AEDT. Hourly temperatures in mid-summer were about 6 °C higher than those in late-spring (Additional file 1.doc: Fig. S1).

Discussion

This study presents the first detailed information on the space-use and movement patterns of the central bearded dragon (*P. vitticeps*) in an arid region, and the first use of an accelerometer in a free-ranging lizard. Two-thirds of individuals held defined home ranges, while the remaining individuals were wide-roaming floaters, often moving distances greater than 1 km. The high proportion of female floaters contrasts with a lower proportion of male floaters and suggests that sexes may have differing space-use tactics. Overall individual movement rates coincided with optimal temperatures as expected [26]. We also found seasonal differences in movement rates; males and residents moved more in late-spring, but floaters moved more mid-summer, possibly indicative of seasonal changes in breeding or territorial behaviours. Findings of the current study corroborate other research which suggests that wild *P. vitticeps* movement patterns may fit well into expected models of ectotherm behaviour associated with optimising movement to preferred temperatures [26, 27], but space-use patterns suggest an unexpected lack of site fidelity and large home-range sizes, particularly for females. These patterns may be driven by variation in resources or social factors.

The large home ranges and high proportion of floaters set *P. vitticeps* apart from other studied Australian agamids. Average home range size (2.9 ha) for *P. vitticeps* were the largest recorded for Australian agamids the next closest being *Chlamydosaurus kingii* (1.9 ha). The proportion of floaters found in this study has not been observed in large agamids previously [6, 28, 29], including the closely related *P. barbata* [30]. While the proportion of territorial males in smaller agamid species ranges widely (< 10% to > 80%), females are commonly sedentary [13, 31–34]. Our results suggesting a large proportion of females do not hold a clear home range is therefore unexpected. The large home ranges and wide-roaming behaviour of both male and female *P. vitticeps* may be driven by environmental factors. This study occurred during a very dry year (2017 annual rainfall was 170 mm below average) and may have driven a switch to wider-ranging behaviours to increase the probability of encountering rare resources in the landscape. Similarly, other species of lizards have been observed to switch space-use tactics towards greater nomadism during drought [5]. Floaters moving more than resident dragons during mid-summer, when resources would be rarer, supports this hypothesis. The trend for females with wider tails to move less, though more likely to have a defined home range, may indicate that animals in better condition (storing more tail fat) are able to range less widely. This is supported by the finding that heavier dragons moved less than lighter dragons after the breeding season. Females with more mass or fat stores would also be more likely to be laying eggs and revisiting a nest site, though we did not see clear evidence of gravid females during our spring monitoring. While less than 45% of *P. vitticeps* females held defined home ranges, 67% of those that did hold a home range revisited core areas. This suggests home range holders revisit a key resource within that range. However, it is also likely that the size and location of home ranges and core areas, as well as movement patterns in *P. vitticeps* depends on the distribution of shelter and perch sites used in social signalling [35, 36], rather than the distribution of food resources. In the future, tracking combined with behavioural observations may be used to determine if shelter or perch sites are revisited or defended by individuals.

While *P. vitticeps* males with wider tails were significantly less likely to hold a home range, there was also a trend towards shorter-tailed males to be floaters. Tail autotomy does not occur in agamids, and many species use their tails to display and communicate to conspecifics, with tail-flicks forming parts of aggressive displays [37]. Thus, territorial owners may use their longer tails to aid in defending their territories either through tail-flicks or as a social status badge. Removal of lizard tails can reduce social status [38] and the two *P. vitticeps* with the largest SVL tracked in late-spring were both missing a large part of their tail (Dragons O and Q, Additional file 1.doc: Table S1), and showed floater behaviour. The wider tails, yet similar movement levels, of floater males may suggest that these dragons expend more energy for foraging than energetically costly mating or territorial behaviours and would allow for floaters to maintain body condition, a scenario which occurs in *C. nubila* [8]. Storage of fat may allow these individuals to roam wider in search of transient resources, which is a tactic used by small mammal species in the arid zone [11], and may result in improved chances of survival during drought. However, more study is needed to fully understand the range of social and spatial strategies of different ranking *P. vitticeps*, and the consequences of those strategies on body condition and survival.

Male *P. vitticeps* moved more than females in late-spring during breeding, perhaps to maximise mating success, as is seen in *T. rugosa* [18] and *Iberolacerta cyreni* [39]. However, enhanced activity rates can impose survival costs and lower daily activity is likely to be selected when not essential [40], resulting in the lower movement seen in female *P. vitticeps* during breeding (late-spring), resident males after breeding (mid-summer), and heavier individuals compared to lighter individuals in mid-summer. Similarly, dominant *C. nubila* males relaxed their territorial behaviour outside of the breeding season, yet little change was seen in subordinate individuals [8]. The increased movement of males in the breeding season and floater behaviour of females may suggest both sexes are maximising mating opportunities and could indicate that *P. vitticeps* has a promiscuous mating system, similar to at least one other agamid (*I. lesueurii*; [41]). Our observed high rates of home range overlap and non-exclusive core areas support this, and may suggest that alternative mating strategies may be occurring [6, 42]. However, while a promiscuous mating system is likely, it cannot be confirmed without genetic parentage studies.

The lack of a relationship between movement and home range measures was not expected, as a larger home range size is often used as an indirect measure of higher activity in lizards [20, 21]. However, this assumption is often based on consecutive radio tracking fixes that measure straight line distances between two points and thus may miss patterns of higher or lower movement between these two points. In this study, movements recorded by the accelerometer were not always from a change in horizontal location, rather they could have been from climbing, feeding, burrowing and displaying to conspecifics. Therefore, individuals that had higher rates of movement in this study may have engaged in these behaviours more often while still occupying home ranges of similar

sizes as individuals that moved less. In addition, a large home range size does not always correlate with dominance, though high activity levels do correlate with dominance in some species [6, 8]. Therefore, the absence of a relationship between home range and core area size with movement levels in *P. vitticeps* is likely due to individuals moving more by feeding, burrowing or social signalling for territorial defence or mating opportunities. If we assume higher activity was used for social signalling, and consider our finding that home range overlap was the norm, this may suggest that *P. vitticeps* has a social system similar based on a dominance hierarchy, in which dominant individuals move more during the breeding season [6, 8]. Nevertheless, how social or resource pressure drive the space-use tactics of *P. vitticeps* is unclear, and greater knowledge of the resource-use and social and breeding systems for this species are needed to make strong conclusions.

This was the first study to use accelerometers to understand the movement of free-ranging lizards and findings highlight the potential that these devices have in studies of lizard movement and space-use. Although it is not surprising that the highest rates of movement occurred when temperatures were around 30 °C, which is similar to captive *P. vitticeps* [26], the use of accelerometers allowed for this to be simply tested without the impacts of observing individuals. Simple readings of movement rates have also provided insights into other aspects of this species behaviour, such as the potential for multiple social or foraging strategies (see above). In studies of other taxa, accelerometers have been used to determine the timing and duration of specific behaviours [2], though these studies record acceleration data at extremely high resolutions (usually 8–100 Hz, i.e. 8–100 fixes per second; [2, 43]). Currently, the size of accelerometers that lizards can carry cannot store the enormously high volumes of data generated by this sampling frequency. Therefore, we could only focus on determining the daily timing and rate of movement. Future advancement and miniaturization of accelerometer technology may allow for accelerometers to be used in herpetological studies to measure the timing and duration of specific behaviours in the absence of human observation. This would greatly enhance our knowledge of lizard ecology, especially for cryptic species which are difficult to observe.

Conclusions

Through the use of accelerometers and GPS tags, it was found that *P. vitticeps* individuals exhibit a variety of space-use and movement tactics, in which most males occupy home ranges and females less commonly so. Wide-ranging, floater behaviour appeared to be a relatively common tactic and the lack of strong differences between sexes in home range size and overlap suggests that social interactions are more relaxed perhaps particularly during drought periods. Future surveys may determine whether these patterns in space-use and movement are conserved under better climate conditions. This is the first study looking at the space use patterns of this species in the wild, despite *P. vitticeps* being a dominant species in Australia's semi-arid to arid environments, and a commonly used laboratory model. This study shows how *P. vitticeps* utility in scientific research extends with free-ranging individuals and provides baseline information that more complex studies on the space-use tactics, sociality and mating systems of *P. vitticeps* can build upon.

Methods

Study Site

This study took place at Fowler's Gap Arid Zone Research Station (31°20'28.50"S, 141°44'33.18"E), Australia. Fowler's Gap has an arid climate with a mean annual rainfall of 255.3 mm and monthly average maximum temperatures ranging from 17.0 °C to 36.4 °C [44]. The annual rainfall for the year leading up to the study was 84.4 mm, indicating that this study took place during drought [44]. Maute et al. [45] recently identified a diverse reptile assemblage (22 species) at the site in which *P. vitticeps* was widespread. A proportion of animals used in this study were later exposed to locust control pesticide applications in late February 2018 as part of a larger study on the impacts of locust control on non-target species. The data used here is from pre-treatment dates only.

Capture and Tracking of Animals

We tracked bearded dragons over three periods; mid-spring (26 September – 13 October 2017), late-spring (21 November – 9 December, 2017), and mid-summer (19 January – 12 February, 2018). Dragons were hand caught by searching under shrubs or in burrows. Upon capture, we took measurements of snout-vent length (SVL), tail length and width, head length and width, and body mass. Sex was determined by raising the tail to see hemipene eversion. Each dragon was toe-clipped for permanent identification.

We attached Pinpoint Beacon 120 or 240 (Sirtrack Ltd, Havelock North, New Zealand) GPS trackers to the dorsal surface of each dragon's tail (Fig. 1). The GPS tags were set to record latitude, longitude, and Dilution of Precision (DOP; a measure of the precision of a GPS reading) locational data. In mid-spring and late-spring, GPS tags were scheduled to take locational fixes every 40 min from 06:00 or 08:00–21:00. Pilot studies showed that dragons did not move overnight. Tags took fixes all day and all night in mid-summer due to personal observation by the authors that *P. vitticeps* shifts to a semi-nocturnal behaviour in summer, and fix intervals were increased to 2 h to allow for a longer battery life. A VHF beacon enabled relocation of the individual (VHF receiver and antennae; Telonics TR5). We relocated each dragon every 3–11 days to download GPS data and replace tags, with recaptures ranging from 1 to 5 times. Location data with a DOP greater than 5 was excluded from further analysis, as the probability of those fixes being an accurate representation of the dragon's location was low (Recio et al. 2011). At the end of the study, we removed all tags from the animals.

For all dragons tracked in late-spring and mid-summer, as well as three individuals from mid-spring, we attached accelerometers (HOBO Pendant G) underneath the GPS tags (Fig. 1) to measure activity rates. Accelerometers are sensors that measure gravitational and inertial acceleration (g) of three axes (X, Y, and Z) caused by movement (see Brown et al. [2] for a review on their application in studies of the movement of free-ranging animals), thus a change in acceleration indicates a movement performed by the animal. To measure activity, accelerometers were set to record acceleration (from – 3 g to + 3 g) on the X and Y axes (Fig. 1) every 30 seconds.

Space-use patterns

To calculate home range size, we used the minimum convex polygon (MCP) method, using the 100% isopleth. The 95% kernel density estimate (KDE) method was used to determine areas of more intense use (the utilization distribution; Worton 1989). We did not use KDE's as estimates of home range sizes as they have been shown to produce inaccurate estimates in reptiles [46]. Instead, KDE's were used to calculate the core area of usage and to determine if home ranges of dragons overlapped in areas of more concentrated usage. The KDE search radius (sometimes referred to as bandwidth, smoothing parameter, or h) was calculated using the ad hoc method ($h_{ad\ hoc}$) following Kie [47]. To determine core areas of activity, the isopleth of KDE that bounds the core area was calculated following Vander Wal and Rodgers [48]. The AdehabitatHR package [49] was used in R v3.3.1 [50] to calculate MCP's, 95% KDE's and core areas.

To determine the minimum sampling days needed to calculate MCP home ranges we followed the methods outlined by Stone and Baird [21] and Rose [51]. Firstly, nine dragons with MCP measurements that were clear outliers (all were 3 times as large as the average home range size) were considered as not holding home ranges (floaters) and were removed from home range analysis. A plot of the average home range size vs the number of days tracked, from one day to twelve days, was created. To develop an accurate average for each day, individuals that were tracked for less than 12 days were not included. Roughly eight days described 80% of the average MCP and thus was used as the minimum sample size. Four individuals were tracked for less than eight days and were removed from home range analyses.

Home Range Overlap

The distribution of home ranges for individual dragons limited calculations of home ranges to six dragons in mid-spring and five dragons in late-spring. Therefore, due to this small sample size, we were only able to report whether home range overlap occurs in *P. vitticeps*, rather than a statistical analysis of overlap differences between sexes. Neighbouring dragons were considered as overlapping if their MCP, 95% KDE or core area was shared with another tracked dragon. We also determined if the five floaters monitored in late-spring entered resident dragon home ranges by following their trajectory of movement.

Analysis of Movement

A moving individual is represented by large fluctuations in acceleration recorded by that animal's accelerometer [2]. Therefore, we used the variance statistic for the raw acceleration data measured on the X and Y-axis by the accelerometer to define when an animal was moving. As the accelerometers used in this study could only record when an individual is moving and not when it is active (as activity may include basking individuals that do not move for extended periods of times) we refer to measurements taken by the accelerometers as movement rather than activity. To determine what amount of variance constituted movement, a GPS tag was set up on a single individual in spring to take locational fixes every 20 min and the accelerometer was set up as above. Accelerometer data was split into 10 min intervals and was matched with the GPS data to see if movements shown represented an actual change in location. The smallest variance for a 10-minute period where movement occurred was 0.0268 g^2 and the largest variance for a 10 min period without movement was 0.0159 g^2 . Based on this, 0.0199 g^2 was taken as the smallest amount of variance that constituted movement and 10-minute variance subtotals were calculated for each individual using 0.0199 g^2 variance as the movement threshold. Data that were recorded 10 min before recapture, and 20 min after returning the dragon to the point of capture were removed from analysis to reduce the impact of human disturbance on the acceleration readings.

Two types of movement rates were calculated; total average movement per hour (for all dragons pooled) and average daily movement (per individual). Total average movement per hour was calculated by first summing ten-minute moving periods for every hour to determine hourly movements (i.e. 0, 10, 20, 30, 40, 50 or 60 min) for each individual. Next, the average minutes of movement for each hour of the day was calculated by dividing the summed minutes of movement over all days of recording that hour by the number of days that hour was recorded for the focal individual. The total average movement per hour of the day was calculated by averaging data from all individual dragons. These data were used to analyse the patterns in timing of diel movement during the two tracking periods. The total minutes that a dragon moved was divided by the total number of full days that the dragon was tracked to determine the average daily movement rates per individual.

Air Temperature and Movement

Air temperature data was accessed from Fowlers Gap Weather Station [52] ($31^{\circ}4'35.54''\text{S}$, $141^{\circ}44'2.40''\text{E}$) which recorded air temperature ($^{\circ}\text{C}$) every 10 min. To determine how fine-scale air temperature patterns influenced movement, 10-minute temperature data was converted into integer classes, i.e. 30°C represents values from 30.00°C to 30.99°C . The occurrence of movement within each integer class was averaged across all dragons by summing the number of times movement was recorded (with all dragons pooled) within a specific integer class and dividing this sum by the total number of 10-minute intervals when that integer class occurred, resulting in the proportion of movement occurring in each integer class.

Statistical Analysis

For the analysis of space-use patterns we used logistic regressions to see if more individuals from one sex held a home range than the other, and to determine if body measurements were related to the probability of holding a home range. Home range area data were tested with separate t-test's to determine if MCP home range area differed between males and females. An Analysis of Variance (ANOVA) was used to test for differences in MCP area between seasons. We also used a linear regression to see if body measurements characteristics influenced MCP area.

We analysed core area data similarly to home range data with t-tests being used to determine if core area differed between sexes, and an ANOVA was used to see if core area differed between seasons. Linear regressions were used to see if body measurements influenced core area size.

We used t-tests on individual dragon daily movement data to see if there was difference between sexes, and t-tests to see if there was a difference between the two tracking periods. To see if home range holding dragons moved more or less each day than floaters, a t-test was used with each season treated separately. Also, linear regressions were used to see if body measurements influenced daily movement rates.

To test the relationship between the occurrence of movement and air temperature, polynomial quadratic regressions were used. We used these tests rather than linear regressions as the data showed a clear nonlinear pattern.

All tests on differences between a response variable and sex were run with for each tracking period and all periods combined, all tests between tracking periods and a response variable were run separately for each sex and both sexes. All tests on body measurement variables were run for each tracking period and all tracking periods combined, as well as separate tests for each sex and both sexes. As six body measurement variables were being tested on the same set of home range, core area and movement data, the significance level (α , nominally 0.05) was adjusted following the sequential Bonferroni method [34] for these tests. All data were explored to ensure assumptions of statistical analyses were met by following the protocols in Zuur et al. [35]. Statistical analyses were undertaken using JMP Pro v11.0 [36] and all averages are quoted as mean $\pm$ standard deviations (SD).

Abbreviations

GPS:Global Positioning Systems; GIS:Geographic Information Systems; VHF:Very High Frequency; MCP:Minimum Convex Polygon; KDE:Kernel Density Estimate; SD:Standard Deviation; SE:Standard Error; ANOVA:Analysis of Variance.

Declarations

Ethics approval and consent to participate

All applicable international, national, and institutional guidelines for the care and use of animals were followed. This study was undertaken under the University of Wollongong Animal Ethics Committee authority AE17/19, and the NSW National Parks and Wildlife Service Scientific License (SL100109).

Consent for publication

Not applicable

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

AB, KM and ICC-K collected GPS and movement data. AB analysed the data. All authors made substantial contributions to the conceptualisation and design of the project as well as assistance and guidance on data collection and analysis and the writing of the manuscript. All authors revised and approved the final manuscript.

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Figures

Figure 1

An individual *Pogona vitticeps* tracked in the study. The location and attachment of the GPS and accelerometer tags can be seen, as well as the two axes in which acceleration was measured by the accelerometer

Figure 2

Average ($\pm$ SD) minimum convex polygon (MCP) home range areas and core areas (calculated following Vander Wal and Rodgers [48]) for home range holding (resident) *Pogona vitticeps* tracked at different times in the year. Black bars represent males and white bars represent females. N total = 23, n male mid-spring = 7, n female mid-spring = 3, n male late-spring = 5, n female late-spring = 1, n male mid-summer = 6, n female mid-summer = 3

Figure 3

Locations of *Pogona vitticeps* taken with GPS radio tracking. The locations taken on each day of tracking are represented by different colours. a Shows the home range and core areas of male dragon N, who revisited core areas often. b Home range of female dragon J, who spent time in one core area before moving and staying in another core area. c Shows the trajectory of movement of female dragon S, who moved consistently south from the site of capture over two days. d Trajectory of movement of female dragon T, who roamed widely but returned to previously used areas

Figure 4

Minimum convex polygon (MCP) home ranges, 95% kernel density estimate (95% KDE) utilization distributions, and core areas for: a the 6 dragons tracked at site 1 in mid-spring. Overlapping areas can be seen for neighbouring dragons. Dragons F, G, and J are females, and dragons H, I and K are males. b the 5 home range holding male dragons tracked in late-spring at site 2. Trajectories are shown for dragons that did not hold home ranges, of which dragons O and Q are males, and S, T, and U are females

Figure 5

a The daily average ($\pm$ SD) minutes moved for individual *Pogona vitticeps* tracked at different periods of the year ($n=15$). Black bars represent males and white bars represent females. b The average ($\pm$ SD) daily minutes moved for home range holding (resident) and non-home range holding (floater) *P. vitticeps*

individuals in two different tracking periods (n=22). Black bars represent residents and white bars represent floater dragons. Asterisk denotes significant differences ($P < 0.05$).

Figure 6
The proportion of movement occurring ($\pm$ SE) at specific temperatures for *Pogona vitticeps* tracked in late-spring and mid-summer. $n = 22$, black line represents a quadratic polynomial regression line fitted to the data

Figure 7
The average ($\pm$ SE) minutes moved per hour of the day for *Pogona vitticeps* tracked in late-spring and in mid-summer. Black dots represent the late-spring tracking period ($n = 11$). Hollow dots represent the mid-summer tracking period ($n = 11$)

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