



## The secret life of possums: data loggers reveal the movement ecology of an arboreal mammal

BLAKE M. ALLAN,\* DALE G. NIMMO, JOHN P. Y. ARNOULD, JENNIFER K. MARTIN, AND EUAN G. RITCHIE

*School of Life and Environmental Sciences, Centre for Integrative Ecology, Melbourne Burwood Campus, 221 Burwood Highway, Burwood, Victoria 3125, Australia (BMA, JPYA, EGR)*

*Institute for Land, Water and Society, Charles Sturt University, Albury, New South Wales 2640, Australia (DGN)*

*School of Biosciences, University of Melbourne, Melbourne, Victoria 3010, Australia (JKM)*

\* Correspondent: [b.allan@deakin.edu.au](mailto:b.allan@deakin.edu.au)

Understanding animal movement patterns is fundamental to ecology, as it allows inference about species' habitat preferences and their niches. Such knowledge also underpins our ability to predict how animals may respond to environmental change, including habitat loss and modification. Data-logging devices such as GPS trackers and accelerometers are rapidly becoming cheaper and smaller, allowing movement at fine scales to be recorded on a broad range of animal species. We examined movement patterns of an arboreal mammal (bobuck, *Trichosurus cunninghami*) in a highly fragmented forest ecosystem. The GPS data showed males travelled greater distances than females in linear roadside strip habitats, but not in forest fragments. The accelerometer data showed that both sexes exhibited higher activity levels in roadside habitats compared to forest fragments. By coupling GPS and accelerometer data, we uncovered for this species an ecological pattern similar to other mammals: that male bobucks had higher activity levels than females for a given distance travelled. Our findings also suggest that habitat fragmentation changes the amount and type of activity bobucks perform while moving, and that linear forest strips could be considered "energetically challenging" habitats, which informs how we should manage the spatial distribution of key supplementary resources for this species such as nest sites and minimum fragment sizes.

Key words: accelerometer, animal behavior and activity, biodiversity conservation, environmental change, GPS tracking, habitat fragmentation, home range, mammal, niche, *Trichosurus cunninghami*

Anthropogenic landscape modification is the greatest threat to biodiversity globally (Fahrig 2001; Lindenmayer et al. 2008). The modification and loss of habitat affects the spatial configuration and the amount of resources available to species (Fahrig 2001; Rothmel and Semlitsch 2002; Newbold et al. 2015), which in turn impacts their growth, reproduction, and survival. Understanding how biodiversity responds to and in some cases persists in modified landscapes is therefore critical for species conservation (Tschamntke et al. 2005; Cattarino et al. 2015).

Animal movements are a key aspect of responses to habitat variation. Movement of an organism can be defined in two ways: a change in the spatial location of the whole individual in time (Nathan et al. 2008), or changes in behavioral states irrespective of physical location (Nams 2014). These two aspects of animal movement are interwoven, with behavioral states often leading to changes in spatial location, enabling the individual's

overall response to its habitat (Frair et al. 2005; Fahrig 2007; van Moorter et al. 2013). Spatial recording technology such as VHF tracking, and more recently GPS tracking, has been used to provide insights into space use by animals in modified landscapes (Fryxell et al. 2008; Gautestad et al. 2013; Vasudev and Fletcher 2015). However, these technologies measure only one coarse aspect of animal movement: the change in the location of the entire individual over time (Nathan et al. 2008). Some movements pivotal to the fitness of individuals and the growth of populations do not result in spatial displacement: for instance, intense localized foraging or mating (Duckworth 1998; Naito et al. 2010).

The past decade has seen widespread deployment of accelerometer loggers to quantify behavioral states at fine spatial and temporal scales (Shepard et al. 2008; Rothwell et al. 2011; Elliott et al. 2013). Accelerometers are small, reusable,

externally mounted, and relatively inexpensive electronic devices that record movement as a change in acceleration at a very fine scale (0.001 g) and rate (capable of > 100 Hz) across all 3 dimensions of movement. Furthermore, the data recorded can provide finer temporal resolution than many other methods (Halsey and White 2010; Bidder et al. 2012). By examining the fine-scale movement data recorded by accelerometers, researchers can discern movement irrespective of any change in spatial location, and can even infer specific animal behaviors (Naito et al. 2010; Brown et al. 2013). This allows researchers to gather substantial information about animal activity without the need to directly observe the animal, providing unprecedented insight into the “private lives” of wild animals (Naito et al. 2010; Soltis et al. 2012; Wang et al. 2015). Accelerometers have already been used to examine movement and prey capture in cryptic species such as pumas (*Puma concolor*), revealing new information on energy expenditure and individual variations (Williams et al. 2014). However, accelerometers also have shortcomings, namely that they do not provide spatial data. Thus, when combined, GPS loggers and accelerometers have the potential to provide complementary insights into the movement ecology of individuals.

Here, we use GPS and accelerometer data loggers to examine the movement ecology of an arboreal mammal in forest fragments embedded within an agricultural landscape in southeastern Australia. The study species is the bobuck or mountain brushtail possum (*Trichosurus cunninghami*), a medium-sized (2.6–4.2 kg), arboreal, nocturnal, hollow-nesting marsupial (How 1981; Lindenmayer et al. 2002). Habitat availability for the bobuck has decreased since European settlement, primarily by changing the abundance of the two key resources required by this species: large hollow-bearing trees for den sites and the leaves of the silver wattle (*Acacia dealbata*) for food (Lindenmayer et al. 1990; Martin and Martin 2007). Once a continuous forest, the study landscape is now a matrix of agricultural land, and two types of remnant forest: forest fragments and linear roadside strips. Researchers have examined the association between remnant type and bobuck population structure, social systems, and mating systems (Martin and Handasyde 2007; Martin et al. 2007), yet the mechanism for these effects remains unknown.

Our aim was to use GPS and accelerometer data to examine how habitat modification and fragmentation affect the movement behavior of bobucks in the two types of forest remnants. First, we used GPS data to quantify the nightly distances travelled by bobucks, and accelerometer data to quantify nightly activity and identify key activity states. Next, we examined whether the nightly distance travelled, nightly activity, or the time spent in particular activity states differed between individuals from forest fragments and linear strips and between sexes. We predicted that male bobucks would have higher activity and travel farther than females due to activities such as territory defense (Schmidt et al. 2003; Haan and Halbrook 2015), and bobucks in forest fragments would have higher activity and travel farther than bobucks in linear strip environments as food and nest resources are more widely distributed in forest

fragments (Martin and Handasyde 2007; Martin et al. 2007). Finally, we highlight the complementarity of GPS and accelerometer data for evaluating both aspects of movement behavior.

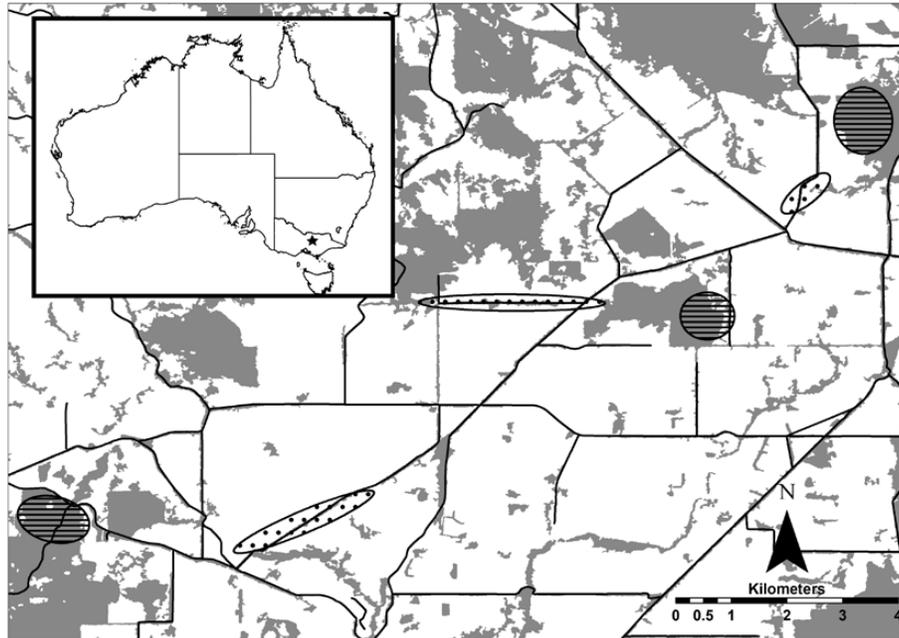
## MATERIALS AND METHODS

*Study area and experimental design.*—Our study area was in the Strathbogie Ranges, northeastern Victoria. The study area ranged from 550 to 750 m above sea level, and has an annual rainfall of ~900 mm. The vegetation consists of open sclerophyll forest dominated by manna gum (*Eucalyptus viminalis*), Victorian blue gum (*Eucalyptus globulus bicostata*), narrow-leaf peppermint (*Eucalyptus radiata*), and broad-leafed peppermint (*Eucalyptus dives*). Key middle and understory species include silver wattle (*A. dealbata*), dogwood (*Cassinia aculeata*), cherry ballart (*Exocarpos cupressiformis*), blackwood (*Acacia melanoxylon*), and austral bracken (*Pteridium esculentum*). Approximately 70% of the native vegetation has been cleared for agriculture and softwood (*Pinus radiata*) plantations (Downes et al. 1997).

We trapped bobucks in three contiguous forest fragments (> 160 ha and an average vegetation width > 750 m, termed “forest fragments” throughout) and three linear roadside strips (> 1 km length and an average vegetation width < 40 m, termed “linear strips” throughout; Fig. 1). Sites (fragments and linear strips) were confined to areas of habitat that consisted primarily of native vegetation and contained trees large enough to provide suitable hollows (diameter at breast height > 50 cm—Smith and Lindenmayer 1988; Pausas et al. 1995). Each site was separated by at least 500 m to reduce the chances of the same individual being caught at two locations, based on home range data from Martin and Handasyde (2007).

We conducted 3 nights of trapping in each of the six study sites. Each site was comprised of two rows of eight large (30 × 30 × 90 cm) wire cage traps, placed on the ground and baited with peanut butter and apple. We transferred trapped individuals from the traps to hessian bags. Traps were approximately 50 m apart. On linear strips, the two rows were placed within the roadside vegetation, and were separated by a minimum of 200 m. In forest fragments, one row was placed along the edge of the fragment, and the other placed within the fragment, starting a minimum of 100 m from the edge, in order to sample both the core and edges of the fragment. We set the traps before dusk and checked them before sunrise. Traps were partially covered with plastic to protect animals from weather.

*Data collection.*—Trapping sessions of 3 nights at each trap site were undertaken over eight consecutive seasons from spring 2011 to winter 2013, inclusive. The methods for capture and handling animals used in this study conformed to the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016) and Animal Ethics Approval from Deakin University (A45-2011). For processing, we anaesthetized individuals with an intramuscular injection of tiletamine/zolazepam (6 mg/kg; Zoletil; Virbac Australia, Peakhurst, New South Wales, Australia) to facilitate handling and minimize distress for the animals. We injected individuals



**Fig. 1.**—Study sites in the Strathbogie Ranges, Victoria, Australia. Gray areas indicate remnant vegetation, striped ovals indicate forest fragments, and spotted ovals indicate linear strips.

with Passive Integrated Transponder (PIT) tags (Trovan, Ltd., Douglas, United Kingdom) for subsequent identification. We then fitted individuals with self-made data-logging collars (80 g, < 3% of individual's body weight) comprised of a VHF transmitter, GPS data logger, and 3-axis accelerometer modified from the design in [Allan et al. \(2013\)](#). We set the collars to start recording data as soon as they were attached to the animal with GPS data set to record at 10-min intervals, and accelerometers at 25 Hz for all three axes. We only used adult individuals for this study (classed as tooth-wear  $\geq 3$ —[Winter 1980](#)). To allow individuals to recover completely from handling and sedation and to avoid releasing bobucks (which are strictly nocturnal) in daylight, we held the animals after processing until dusk on that day. We released the bobucks within 10 m of the site where they were captured. We recaptured all individuals 3–7 days later and removed the data-logging collars.

**Data processing.**—GPS devices determine their position by receiving external data. Factors such as dense canopy cover or an animal's orientation can cause it to take longer to acquire a position fix, increase the error associated with a position fix, or fail to do so ([Williams et al. 2012](#)). As such, although the GPS devices were set to record at 10-min intervals, the interval between fixes was almost never exactly 10 min: some fixes failed to be recorded, and no fixes were recorded while bobucks were denning inside tree hollows. Furthermore, the error of each location fix varies depending on the accuracy with which the location can be triangulated. To standardize the data, we used a continuous-time correlated random walk model to convert the GPS location data into nightly interpolated movement tracks through the environment using the *CRAWL* package in R statistical environment ([Johnson 2012](#)). Correlated movements imply the animal's location at a given time is dependent on all previous locations, not just the last one. The use of

continuous-time formulation allows us to interpolate GPS locations at uniform time intervals based on the nonuniform data recorded ([Johnson et al. 2008](#)).

The total acceleration recorded by the accelerometers is made up of two components: static acceleration and dynamic acceleration ([Shepard et al. 2008](#)). Static acceleration refers to the gravitational field of the earth. An accelerometer not moving is expected to record a cumulative total of 1 g across its three axes due to the gravitational force of the earth. Dynamic acceleration represents the change in velocity as a result of body motion, and has shown great potential as a predictor of energy expenditure ([Wilson et al. 2006](#); [Gleiss et al. 2011](#)). To obtain a measure of dynamic acceleration, we first smoothed each accelerometer channel to derive the static acceleration using a running mean over 3 s, and then subtracted this static acceleration from the raw data, leaving only dynamic acceleration ([Gleiss et al. 2011](#)). The accelerometers we used were capable of measuring  $\pm 8$  g; therefore, any value outside of this range was deemed an outlier and removed (< 0.001% of values). We then converted the values for dynamic acceleration to positive values, and calculated the vector of the dynamic body acceleration to provide a single value for partial vectorial dynamic body acceleration (VeDBA) as per [Qasem et al. \(2012\)](#):

$$\text{VeDBA} = \sqrt{(A_x - S_x)^2 + (A_y - S_y)^2 + (A_z - S_z)^2}$$

$A$  = total acceleration;  $S$  = static acceleration.

These 25 values were then summed in 1-s intervals to create partial VeDBA.

It was not possible to use direct observation for the categorization and validation of behavior as bobucks are nocturnal, spend significant time in very dense vegetation, and their movements are influenced by human presence. Therefore,

we identified behavioral states with the program Ethographer (version 2.02—Sakamoto et al. 2009) in Igor Pro version 6.36 (Wavemetrics, Portland, Oregon). We then categorized the time series accelerometer data into a spectrum via continuous wavelet transformation, then categorized each second of the spectrum into one of 10 specified activity groups by unsupervised cluster analysis, using *k*-means methods. We used 10 activity groups to prevent the lumping of activity; however, due to the possibility for the axes to shift in relation to the orientation of the body, fine-scale behavioral states could not be calculated. Instead the 10 identified groups naturally split into four broad groups, which we termed “activity states,” measured at 1-s intervals, characterized by the periodicities of body acceleration and the time of acceleration:

1. Denning—Measurements taken during the day (mean VeDBA =  $0.028 \pm 0.001$  m/s<sup>2</sup>).
2. Resting at night—Very low VeDBA values, but while the bobucks were out of the den (mean VeDBA =  $0.108 \pm 0.001$  m/s<sup>2</sup>).
3. Moving—Moderate VeDBA values and during the night, including normal foraging behavior (mean VeDBA =  $0.180 \pm 0.001$  m/s<sup>2</sup>).
4. High activity—Activity values much higher than all the others, accounting for behavioral states such as mating, fighting, intense foraging, predator avoidance, etc. (mean VeDBA =  $0.260 \pm 0.002$  m/s<sup>2</sup>).

We examined the activity states over 24-h periods (midnight to midnight GMT), including when the bobucks were denning and removed any recordings that did not span the full 24-h time period. Given that animals could potentially display different movement patterns after release, we removed the nights of release and capture from both movement measures.

We created two variables from the GPS data: the total distance travelled in a 24-h period (midnight to midnight GMT), termed “nightly distance travelled” and measured in meters; and distance travelled in 10-min intervals, termed “interval distance travelled,” also measured in meters. Using midnight in GMT meant that the break between one day and the next fell during daylight hours in Australia, which is when the bobucks are denning, meaning no GPS fixes, and a clear break as to when a GPS track finished, and the next began. For nightly

distance travelled, we measured the distance of the interpolated movement tracks for each full night of movement. For interval distance travelled, we determined locations at 10-min intervals along the interpolated movement tracks, and measured the distance between these locations (Table 1).

We created three variables from the accelerometer data: 1) “24-h activity,” which is the sum of the partial VeDBA values over 24 h, commensurate to “nightly distance travelled” and representing the general nightly activity of the animal; 2) “interval activity,” which is the sum of the partial VeDBA values in 10-min intervals, matching “interval distance travelled” from the GPS data, and a representation of activity versus distance travelled; and 3) “activity state,” which is the amount of time animals spent in each of four activity states, measured in 1-s intervals, over 24-h periods (midnight to midnight GMT; Table 1).

To examine the impact of habitat type on bobuck movement, we created a two-level categorical variable indicating the habitat type within which the animal was captured: either forest fragment or linear strip. Second, as the sex of animals can affect movement activity (Beck et al. 2003), a 2nd two-level categorical variable was created indicating the sex (male or female) of the animal. We then concatenated these two predictor variables to create a single, four-level predictor variable that comprised all combinations of habitat type and sex (males in linear strips, males in forest fragments, females in linear strips, and females in forest fragments).

*Statistical analysis.*—We used generalized linear mixed models (GLMMs) to analyze the effects of the predictor variables on measures of animal movement derived from GPS and accelerometer data. Mixed models were required as they can consider both fixed and random effects, the latter of which can account for correlated data (Zuur et al. 2009), including repeated sampling of the same individuals over time (Zuur et al. 2009). Thus, the identity of individual animals was specified as a random effect in all models to account for repeated sampling of individuals over several days. We included the season within which data were collected as an additional random effect to account for season-to-season variance.

We generated GLMMs of the relationship between the movement variables measured over 24 h (nightly distance travelled, nightly activity, and the time spent in each of the four activity states) and the habitat type-sex predictor variable. We ran four

**Table 1.**—Outline of the measures of bobuck (*Trichosurus cunninghami*) movement. VeDBA = vectorial dynamic body acceleration.

Device	Measurement	Unit of measurement	Time frame of measurement	Method of measurement
GPS	Nightly distance travelled	Meters (m)	24 h	Summed distance based on interpolated movement track from GPS points over 24 h
	Interval distance travelled	Meters (m)	10-min intervals	Nightly interpolated movement track broken into 10-min intervals
Accelerometer	24-h activity	Gravitational force (g)	24 h	Summed activity based on accelerometer values measured at 25 Hz over 24 h
	Interval activity	Gravitational force (g)	10-min intervals	Summed VeDBA values, measured at 25 Hz, into 10-min intervals
	Activity state	Categorical	1-s intervals over 24 h	VeDBA values, measured at 25 Hz, used in Ethographer to create four activity states measured in 1-s intervals

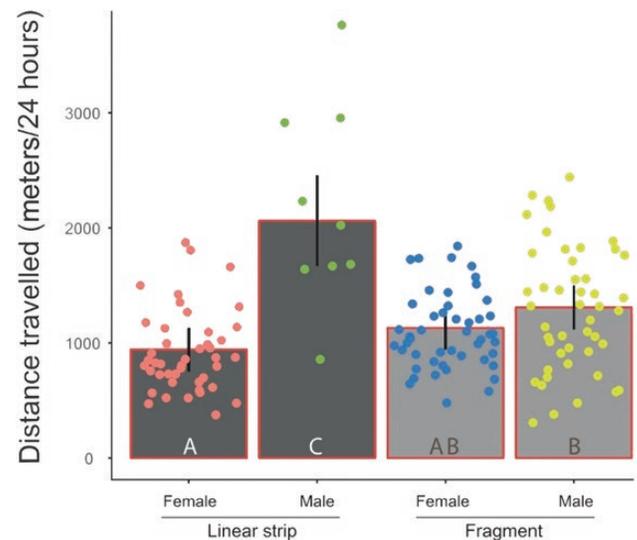
separate models to examine the time bobucks spent in different activity states over a 24-h period, corresponding to each of the four activity states: denning, resting at night, moving, high activity. We ran the models with each group (males in linear strips, males in forest fragments, females in linear strips, and females in forest fragments) as the reference category to determine the differences between all four groups. We applied a Bonferroni correction to the  $P$ -values to infer significant differences between groups after accounting for multiple comparisons. To evaluate the “significance” of differences we observed, we report effect sizes, confidence intervals, and  $P$ -values, with alpha set at  $P < 0.1$ . We chose this value for alpha because we did not have many observations (nights) for some levels of tests, and hence a more conservative  $P$ -value (0.05) might have made it harder to detect “significant differences,” as per results and guidance from Nakagawa and Cuthill (2007) and Jennions and Møller (2003). We assessed model fit using  $r$ -squared calculated using the `r.squaredGLMM` function in the `MuMIn` package.

We examined activity in relation to distance travelled as a proxy for the energetic cost of spatial movement by bobucks in each of the habitat types and for both sexes. We analyzed these data at a fine scale as variation in activity often occurs over short time periods (Wilson et al. 2006): we used a 10-min time interval in order to match the GPS recording rate. To understand the additional insights from coupling these technologies, we modeled summed partial VeDBA (response variable) as a function of distance travelled. We specified an interaction between these distances travelled and habitat type-sex to allow a separate curve for the relationship between summed partial VeDBA and distance travelled for each habitat type and sex combination. Differences in the slopes of summed partial VeDBA with distance travelled would be indicative of animals investing different amounts of activity per unit of distance travelled, depending on their habitat type and sex. We used the `lsmmeans` function in the `lsmmeans` package (Lenth 2016) to test for differences in the slopes between the habitat type and sex combinations. We again used a Bonferroni correction to account for multiple comparisons, but set alpha to 0.05 given the larger number of samples at the finer temporal resolution. As movements at the scale of 10-min intervals are likely to be temporally autocorrelated, we fit an autoregressive model of order 1 (AR1) to account for residual temporal correlation in the data. The AR1 model residuals at a given time  $t$  as a function of the residuals at previous times  $t - 1$  allowing residuals to be correlated in time, with residuals further away in time less correlated than those closer in time (Zuur et al. 2009). GLMMs were generated using the `nlme` package in the R statistical environment (R Core Development Team 2014).

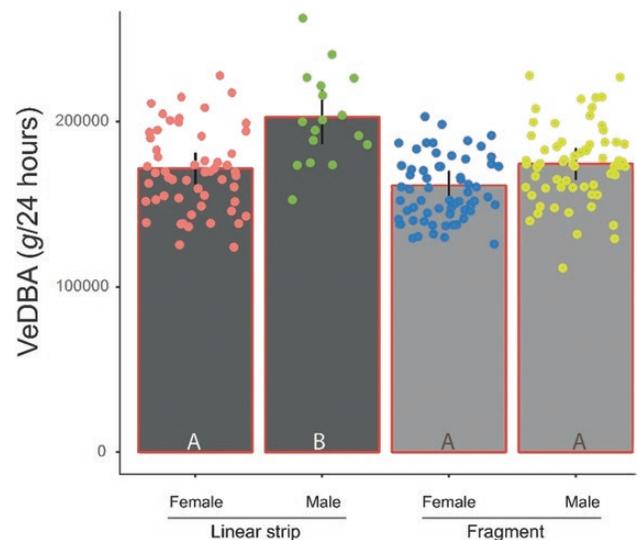
## RESULTS

We tracked 32 individual bobucks for 2–7 nights at a time, totaling 149 nights of data across the eight consecutive seasons (males in forest fragments = 10 individuals and 36

nights; females in forest fragments = 16 individuals and 48 nights; males in linear strips = 6 individuals and 21 nights; and females in linear strips = 12 individuals and 44 nights). Animals classed as inhabiting linear strip environments spent > 80 % of their nightly movement in linear strips, and nine of the individuals strictly inhabited linear strip environments. Animals classed as inhabiting forest fragments ranged more widely, but had > 60 % of GPS points recorded within the



**Fig. 2.**—The average distance travelled (m) over 24 h by bobucks (*Trichosurus cunninghami*) in southeastern Australia, by sex and habitat type. Each point is a 24-h period of movement. The error bars indicate 1 SE. The letters indicate the relationships between the coefficients (see Supplementary Data SD1).



**Fig. 3.**—The average VeDBA (g) measured over 24 h for bobucks (*Trichosurus cunninghami*) in southeastern Australia, by sex and habitat type. Each point is a 24-h period of movement. The error bars indicate 1 SE. The letters indicate the relationships between the coefficients (see Supplementary Data SD2). VeDBA = vectorial dynamic body acceleration.

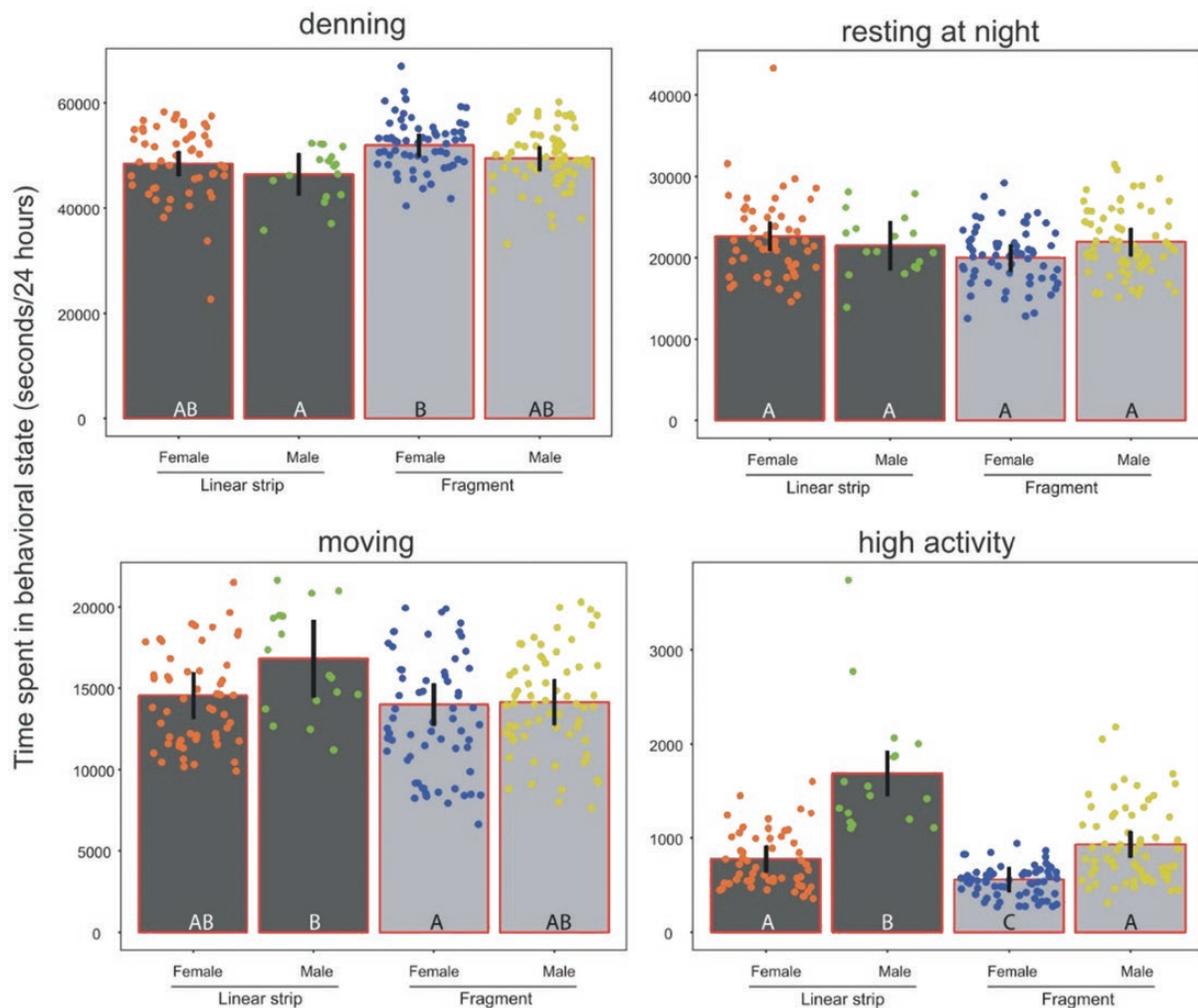
forest fragments, and made use of the forest fragments on a nightly basis. The average time between GPS fixes across the study was 14 min 59 s (range 2 min 04 s to 63 min 29 s). We considered data points with an error > 40 m (6.65% of data) too inaccurate and removed them, resulting in an average estimated horizontal position error (EHPE) of 10 m (range 2.72 to 39.84 m).

The nightly distance travelled by bobucks was significantly higher for males in linear strips than all other groups, and was higher for males in forest fragments than females in linear strips, but there was no significant difference between males and females in forest fragments (Fig. 2; Supplementary Data SD1). The activity of bobucks over 24 h, as measured by VeDBA, was also significantly higher for males in linear strips than all other groups (Fig. 3; Supplementary Data SD2).

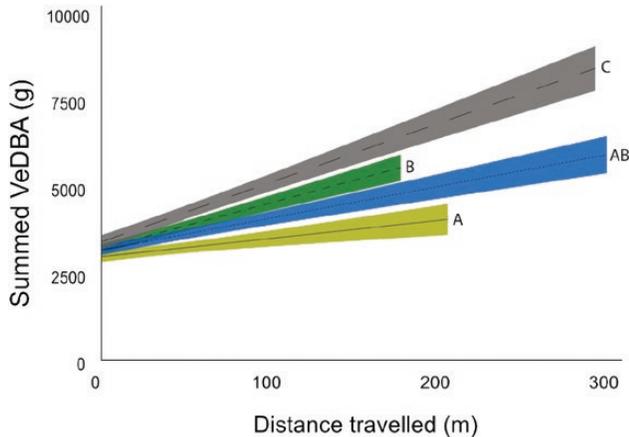
All groups spent a similar amount of time denning, resting at night, and moving (Fig. 4; Supplementary Data SD3). However, differences were observed for time spent in the high activity state. Males in linear strips spent significantly

more time in high activity than all other groups, while males in fragments spent similar time in high activity as the females in linear strips, and significantly more than females in fragments. Females in fragments and females in linear strips spent similar time in high activity (Fig. 4; Supplementary Data SD3).

There was a significant interaction between the “group” an individual belonged to (i.e., male in linear strip, female in linear strip, male in forest fragment, female in forest fragment) and distance moved over 10-min intervals when explaining activity levels. Model predictions showed: 1) that bobucks in linear strips had higher summed VeDBA values when moving the same distance compared to bobucks in forest fragments; 2) that males had higher summed VeDBA values than females for a given distance travelled; and 3) that differences between the four groups (i.e., males in fragments, female in fragments, males in linear strips, females in linear strips) were most apparent when the distance travelled was greater (Fig. 5; Supplementary Data SD4).



**Fig. 4.**—The average time spent by bobucks (*Trichosurus cunninghami*) in each activity state over a 24-h period (midnight to midnight GMT) in southeastern Australia, by sex and habitat type. Each point is the proportion of time (in seconds) spent in an activity state within a 24-h period of movement. The error bars indicate 1 SE. The letters indicate the relationships between the coefficients (see Supplementary Data SD3).



**Fig. 5.**—The relationship between activity and the distance travelled per 10-min interval for bobucks (*Trichosurus cunninghami*) in south-eastern Australia. Lines and shaded area represent the fitted relationship and 95% CIs from generalized linear mixed models, respectively. Solid line = female bobuck in forest fragments; dotted line = male bobucks forest fragments; medium-dashed broken line = female bobucks in linear strip; long-dashed broken line = male bobucks in linear strips. The letters indicate the relationships between the coefficients (see [Supplementary Data SD4](#)). VeDBA = vectorial dynamic body acceleration.

## DISCUSSION

Understanding variation in patterns of animal movement is critical to both theoretical and applied ecology ([Ronc 2007](#)). Despite this, finding techniques that can simply and reliably characterize an individual's movement is challenging. Here, we show the unique insights that can be gained by combining the use of accelerometers and GPS for scansorial and arboreal species. While GPS data showed that male bobucks in linear strips moved farthest compared to other groupings over a 24-h period, accelerometer data showed that these animals also more frequently engaged in bouts of very high activity. These bursts of high activity help explain why male bobucks in linear strips displayed higher levels of activity overall (and probably exerted more energy) per unit of distance travelled.

We found that male bobucks in linear strips travelled significantly farther than all other groups, as we predicted. Males travelling farther than females of the same species is consistent with studies of the movement of a host of mammal species, including rodents ([Maroli et al. 2015](#)), minks (*Neovison vison*—[Haan and Halbrook 2015](#)), wolves (*Canis lupus*—[Jedrzejewski et al. 2001](#)), Iriomote cats (*Prionailurus bengalensis iriomotensis*—[Schmidt et al. 2003](#)), and Arctic foxes (*Alopex lagopus*—[Anthony 1997](#)), as well as lizard and turtle species ([Rose 1981](#); [Thompson et al. 1999](#); [Aresco 2005](#)). In these instances, males travelled greater distances due to larger body sizes and higher energy demands, to maximize home range overlap with females for breeding, and for mate guarding ([Schmidt et al. 2003](#); [Zschille et al. 2012](#); [Haan and Halbrook 2015](#)). On the other hand, the daily movement of females is presumed to be only as far as necessary for efficient foraging ([Dahle and Swenson 2003](#); [Schmidt et al. 2003](#)), and restricted

due to caring for young ([Jedrzejewski et al. 2001](#)). Males in forest fragments did not travel greater distances than females in forest fragments, and females in linear strips travelled the least distance, so we do not believe the increased movement by male bobucks is best explained by foraging requirements as related to food availability. Rather, one possibility, as suggested by [Schmidt et al. \(2003\)](#), is that males in linear strips travel greater distances to guard both mates and territory. [Martin and Martin \(2007\)](#) reported much greater population densities of both male and female bobucks in linear strips than fragments within the Strathbogie Ranges. The higher population density may result in greater vigilance being required to guard mates.

Female bobucks in linear strips travelled distances similar to those travelled by females in forest fragments, and had similar activity patterns over 24 h, yet they had a higher cost of movement per unit distance travelled, contrary to our prediction. This disparity may be due to how arboreal species traverse their environment. An arboreal mammal can move considerable distances climbing up and down trees vertically, without resulting in a change to its two-dimensional position measured by the GPS. Accelerometers are able to capture this three-dimensional activity because they are recording on all three axes of animal movement, providing a much more comprehensive picture of the animal's true movement. [Berry et al. \(2016\)](#) found that disturbed habitats affected both the temporal and spatial movement patterns of bobucks, while accelerometry studies of koalas (*Phascolarctos cinereus*) found that males moved farther and defended territories more, but had the same amount of activity as females ([Ryan et al. 2013](#)). In our case, we propose that females in linear strip environments may undertake more intense foraging, ascending and descending trees, and predator vigilance, all of which can occur within a few meters of horizontal spatial movement, which is within the error of the GPS devices we used.

Male bobucks in linear strips also had the highest activity over 24 h, showing a similar pattern to distance travelled. The analysis of activity states again showed that bobucks in linear strips spent more time in high activity, compared to the activity and distance travelled by the other groups, and this result is likely to be driven by the same factors. Males in fragments also spent more time in the high activity state than females in fragments. This may be due to the additional activities males undertake while moving, such as defending their territories from other males ([Martin et al. 2007](#)). These types of activities are important sources of energy expenditure for a range of species ([Shamoun-Baranes et al. 2012](#); [Christiansen et al. 2013](#)), but are not recorded by GPS technology alone. However, females in linear strips travelled the least distance, so other factors must also be influencing higher activity in linear strips. Female bobucks in fragments were the least active group. We also found no significant difference in any of the activity states between male bobucks in fragments and females in linear strips.

There was a clear significant difference in the movement of bobucks based on sex, such that males had higher activity for a given distance travelled compared to females. We also found that the differences between sexes were amplified in particular

habitats—the difference between males and females was far greater in linear strips than forest fragments, as males in linear strips moved greater distances than females in linear strips. We expected females in linear strips to travel the least distance, as a previous study showed linear strips have greater access to their key food source (silver wattle), and greater access to their key shelter (tree hollows—[Martin and Martin 2007](#)). Movements by males are more influenced by defending their territories, and the greater number of bobucks in linear strips may result in more movement for defense ([Martin et al. 2007](#)).

Bobucks in linear strip environments exhibited different behaviors than those in habitat fragments. Male bobucks in linear strip environments travelled greater distances each night, with many more bursts of high activity, while females maintained similar distances travelled in both habitats; however, their activity levels in doing so increased in linear strips. Linear strip environments often differ greatly in vegetation composition and density when compared to forest fragments, and thus the distribution and availability of resources can vary widely ([Baguette and Van Dyck 2007](#); [Berry et al. 2016](#)). In our study area, linear strip environments have higher abundance of both silver wattle and tree hollows, the key resources for bobucks, than the surrounding remnant vegetation ([Martin and Martin 2007](#)). Based on resource variables alone, bobucks should preferentially select linear strips over other environments to reduce movement ([van der Ree 2002](#); [Pereira and Rodriguez 2010](#)). [Martin et al. \(2007\)](#) hypothesized that males would exert more energy to maintain a home range of equivalent size in the linear strips owing to the much greater distances between the home ranges' extremities. However, the same hypothesis does not explain the activity of females in linear strips, who travelled distances similar to those of females in forest fragments, yet exhibited higher activity. A comparative analysis showed that both males and females in linear strips are investing more energy per meter moved than bobucks in forest fragments. Based on this information, there is an additional cost associated with living in linear strip environments compared with their counterparts in forest fragments that is not identified by distance travelled alone.

Linear strip environments have been shown to affect species by changing movement patterns ([Bonnot et al. 2013](#)), increasing risk of predation ([Estrada et al. 2002](#)) and disease ([Brearley et al. 2013](#)), creating barriers to movement ([Asari et al. 2010](#)), and changing the shape of home ranges ([van der Ree and Bennett 2003](#)). Linear strips also have been shown to increase animal stress levels ([Van Meter et al. 2009](#); [Brearley et al. 2012](#); [Johnstone et al. 2012](#)). We identified detrimental effects such as higher activity states for bobucks in linear strip environments, but the drivers are most likely linked to pressures not able to be examined as part of this study. For instance, predators of bobucks such as powerful owls (*Ninox strenua*) have been found to prey more heavily on the closely related common brushtail possum (*T. vulpecula*) in highly disturbed landscapes ([Cooke et al. 2006](#)), while introduced predators such as foxes (*Vulpes vulpes*) and cats (*Felis catus*) also take advantage of the more-disturbed environments for hunting ([Claridge 1998](#); [Doherty et al. 2015](#)). The added predation pressure is expected

to increase both stress and vigilance for bobucks in linear strip environments. Linear strips also have denser populations of both bobucks ([Martin et al. 2007](#)) and other arboreal species, as they use these corridors to traverse the environment ([Beier and Noss 1998](#)), so encounters resulting in either fighting or fleeing are also expected to be higher, potentially explaining the greater bursts of high activity seen in both males and females in linear strips. The impact of these detrimental effects on growth and survival rates requires further investigation.

We found that GPS data loggers were able to provide broader-scale spatial and temporal information within the environment, while accelerometer data loggers were able to record finer-scale activity and behavioral states. By combining these movement loggers, we were able to build a detailed picture of an individual's spatiotemporal activity budgets as a whole, and specific behavioral states at a very fine scale. Such information could be used in practical conservation applications, such as the design of vegetation corridors or placement of nest boxes relative to food resources within the environment. Individual activity and behavior across different habitat compositions also could be used to predict responses to environmental change (habitat loss and modification). Further research investigating whether greater resource abundance in modified environments also creates higher stress levels would further our understanding of the effects of anthropogenic habitat modification.

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#### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Comparison of the average nightly distance travelled by bobucks (*Trichosurus cunninghami*) in southeastern Australia categorized by sex and habitat type. A positive estimate indicates a relatively higher average distance travelled during the night, while a negative estimate indicates a relatively lower distance travelled. The *P*-values displayed are corrected for multiple comparisons using Bonferroni correction.

**Supplementary Data SD2.**—Comparison of the average vectorial dynamic body acceleration (VeDBA; *g*) measured over 24 h travelled by bobucks (*Trichosurus cunninghami*) in southeastern Australia categorized by sex and habitat type. A positive estimate indicates a relatively higher average distance travelled during the night, while a negative estimate indicates a relatively lower distance travelled. The *P*-values displayed are corrected for multiple comparisons using Bonferroni correction.

**Supplementary Data SD3.**—A comparison of the average time, in seconds, spent in each of the four activity states (denning, resting at night, moving, and high activity) within a 24-h period by bobucks (*Trichosurus cunninghami*) in southeastern Australia categorized by sex and habitat type. Each of the activity states is represented in a separate table.

**Supplementary Data SD4.**—Interval comparison of the average distance travelled (m) versus the average vectorial dynamic body acceleration (VeDBA; *g*), measured in 10-min intervals for bobucks (*Trichosurus cunninghami*) in southeastern Australia categorized by sex and habitat type.

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