

Estimating encounter location distributions from animal tracking data

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Abstract

1. Ecologists have long been interested in linking individual behaviour with higher level processes. For motile species, this 'upscaling' is governed by how well any given movement strategy maximizes encounters with positive factors and minimizes encounters with negative factors. Despite the importance of encounter events for a broad range of ecological processes, encounter theory has not kept pace with developments in animal tracking or movement modelling. Furthermore, existing work has focused primarily on the relationship between animal movement and encounter *rates* while the relationship between individual movement and the spatial *locations* of encounter events in the environment has remained conspicuously understudied.
2. Here, we bridge this gap by introducing a method for describing the long-term encounter location probabilities for movement within home ranges, termed the conditional distribution of encounters (CDE). We then derive this distribution, as well as confidence intervals, implement its statistical estimator into open-source software and demonstrate the broad ecological relevance of this distribution.
3. We first use simulated data to show how our estimator provides asymptotically consistent estimates. We then demonstrate the general utility of this method for three simulation-based scenarios that occur routinely in biological systems: (a) a population of individuals with home ranges that overlap with neighbours; (b) a

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pair of individuals with a hard territorial border between their home ranges; and (c) a predator with a large home range that encompassed the home ranges of multiple prey individuals. Using GPS data from white-faced capuchins *Cebus capucinus*, tracked on Barro Colorado Island, Panama, and sleepy lizards *Tiliqua rugosa*, tracked in Bunday, South Australia, we then show how the CDE can be used to estimate the locations of territorial borders, identify key resources, quantify the potential for competitive or predatory interactions and/or identify any changes in behaviour that directly result from location-specific encounter probability.

4. The CDE enables researchers to better understand the dynamics of populations of interacting individuals. Notably, the general estimation framework developed in this work builds straightforwardly off of home range estimation and requires no specialized data collection protocols. This method is now openly available via the `ctmm` R package.

KEYWORDS

animal movement, *Cebus capucinus*, contact, home range, interactions, *Tiliqua rugosa*

1 | INTRODUCTION

Linking individual behaviour with higher level processes has long been a cornerstone of ecological research (Darwin, 1859; DeAngelis & Gross, 1992; Gil et al., 2018; Grimm & Railsback, 2005; Hogeweg & Hesper, 1990; Skellam, 1951; Sutherland, 1996). For motile species, this 'upscaling' is governed by how well any given movement strategy maximizes encounters with positive factors (e.g. food, mates, essential resources) and minimizes encounters with negative factors (e.g. predators and disease; Barraquand & Murrell, 2013; Dougherty et al., 2018; Holling, 1959; Huston et al., 1988; Kareiva & Odell, 1987; Spiegel et al., 2017; Turchin, 1998). Beyond their mechanistic role in driving population/community-level dynamics, encounters are also central to many conservation issues. For instance, an animal's probability of encountering humans and/or human-related activities is a key indicator of the potential for human-wildlife conflict (Meijaard et al., 2011; Poessel et al., 2013), while encounters with vehicles represent a serious source of mortality for many species (Bennett, 1991; Gibbs & Shriver, 2002; Glista & DeVault, 2008). Additionally, emerging zoonotic diseases pose significant and increasing threats to human health and the global economy (e.g. Rothan & Byrareddy, 2020), and locations of risk are simultaneously viewed as 'hotspots' for both conservation and emerging disease (Paige et al., 2015).

Despite the keystone importance of encounter events for a broad range of ecological processes, encounter theory has not kept pace with the developments in animal tracking (Kays et al., 2015; Noonan et al., 2019; Wikelski et al., 2007) or movement modelling (Benhamou, 2014; Fleming et al., 2014a; Gurarie et al., 2009; Hooten et al., 2019; Johnson et al., 2008; Michelot & Blackwell, 2019). Furthermore, existing work has focused primarily on the relationship between animal movement and encounter rates (e.g. Bartumeus et al., 2008; Buchin et al., 2012; Gerritsen & Strickler, 1977; Gurarie & Ovaskainen, 2013; Hutchinson & Waser, 2007; Martinez-Garcia et al., 2020; Visser & Kjørboe, 2006),

while the relationship between individual movement and the spatial locations of encounter events in the environment has remained conspicuously understudied (but see, Hoover et al., 2020; Long et al., 2015; Spiegel et al., 2016). This is a notable limitation as the probability of encountering another individual has well-documented effects on animal behaviour. The landscape of fear hypothesis, for example, is based on the concept that prey species alter their behaviour with respect to spatiotemporal predation risk (Hernández & Laundré, 2005; Kuijper et al., 2013; Laundré et al., 2014; Lima et al., 1985). One prediction of this hypothesis is that individuals can devote more time to foraging in areas where the risk of encountering a predator is low, and should therefore balance predation risk against energetic needs while navigating their environments. Without a method for straightforwardly quantifying how the probability of encountering a predator changes in space, however, empirical work has typically relied on intensive field efforts (e.g. van der Merwe & Brown, 2008) and/or ad hoc proxy measures to quantify the spatial distribution of predation risk (reviewed in Gallagher et al., 2017).

Beyond the importance of encounters in driving predator-prey dynamics, the way in which intraspecific encounter probability varies in space also shapes socio-spatial arrangements. For example, while many species occupy home ranges with undefended boundaries, others maintain actively defended territories (Powell, 2000). In species with intense and potentially lethal intergroup competition, individuals tend to avoid areas near territorial boundaries, where they are likely to encounter neighbouring individuals (Mech & Harper, 2002; Sillero-Zubiri & Macdonald, 1998; Wrangham et al., 2007; Wrangham, Wilson & Hauser, 2007), and are more alert when moving through these locations (Kurihara & Hanya, 2018; Tórrez-Herrera et al., 2020; Wrangham, Wilson, et al., 2007). Indeed, Moorcroft et al. (1999) showed how individual coyotes' (*Canis latrans*) avoidance of areas with a high probability of encountering the scent marks of individuals from neighbouring

packs provided a mechanistic basis for the formation of territorial boundaries (see also Moorcroft, Lewis, et al., 2006). Mechanistic home range approaches, however, require complex, mechanistic models that need to be specifically tailored to each situation (e.g. Giuggioli et al., 2013; Moorcroft, Moorcroft, et al., 2006). The difficulty in quantifying the location, permeability or even existence of territorial borders (Powell, 2000), has meant that researchers often rely on indirect measures such as patterns of home range overlap when studying animal behaviour at and around territorial boundaries (e.g. Bermejo, 2004; Tórriz-Herrera et al., 2020; Vander Wal et al., 2014).

The capacity to leverage information on animal space use to estimate the distribution of encounter locations is beneficial to a wide range of ecological research. Early work by Getty (1981) identified the relationship between location-specific ‘crowding’ and the local potential for encounters, but the empirical nature of Getty’s work limited the generalizability of the approach. More recent studies that have attempted to relate individual movement with encounter locations have used randomization approaches to generate null models (Spiegel et al., 2016, 2018), or used the Bhattacharyya integrand, which is a by-product of home range overlap estimation, as a visual diagnostic tool (French et al., 2019). Here, we build on these studies and develop a formal statistical framework for estimating the spatial distribution of encounter events from animal tracking data. To this end, most analytical work on encounters model animal movement as either bounded ballistic (Gerritsen & Strickler, 1977; Hutchinson & Waser, 2007) or Brownian (Dieker, 2011; Visser, 2008; Visser & Kjørboe, 2006) motion. A key limitation of these models, however, is that they result in uniformly distributed patterns of space use, meaning encounters between individuals also occur uniformly in space. In stark contrast, most real animals exhibit *non-uniform* space use within spatially restricted home ranges (Bowen, 1982; Burt, 1943; Fleming et al., 2014a; Kie et al., 2010; Martinez-Garcia et al., 2020; Moorcroft, Moorcroft, et al., 2006; Noonan, Tucker, et al., 2019; Powell, 2000), and encounters between individuals do not occur uniformly in space, but are instead concentrated at territorial boundaries (Bermejo, 2004; Ellwood et al., 2017; Nievergelt et al., 1998; Wilson et al., 2012), in/around heavily used habitats and/or habitat features (Weckel et al., 2006; Whittington et al., 2011) or at key resources (De Boer et al., 2010; Price-Rees et al., 2013). We therefore base our work on recent analytical work by Martinez-Garcia et al. (2020) incorporating non-uniform movement within home ranges into encounter theory.

We first demonstrate the general utility of this method for three simulation-based scenarios that occur routinely in biological systems: (a) a population of individuals that occupy relatively distinct home ranges, but with some degree of spatial overlap with neighbours at the edges of their ranges (e.g. Mertl-Millhollen, 1988; Wronski, 2005); (b) a pair of individuals with a hard territorial border between their home ranges (e.g. Henschel & Skinner, 1991; Moorcroft, Lewis, et al., 2006) and (c) a predator with a large home range that encompassed the home ranges of multiple prey (e.g. Herfindal et al., 2005; Loveridge et al., 2009). We next highlight the real-world applicability of our

method on GPS data from white-faced capuchins *Cebus capucinus* tracked on Barro Colorado Island, Panama, and sleepy lizards *Tiliqua rugosa* tracked in Bunday, South Australia. We show here how the spatial distribution of encounters can provide an estimate of the location of territorial borders, and demonstrate the possibility of gaining insights into species’ ecology by comparing changes in movement patterns against the CDEs. We conclude with a discussion of the potential applications of this distribution for better understanding the dynamics of populations of interacting individuals.

2 | MATERIALS AND METHODS

2.1 | The conditional distribution of encounters

Before describing the details of our conditional distribution of encounter (CDE) estimator, it is important to note at the outset that although we rely on assumptions in deriving our estimator, the spatial distribution of encounter locations is a target distribution that exists even if the assumptions of the present estimator may not be met by every dataset. Our framework for estimating the spatial distribution of encounter events in the environment is based on the assumption that the mean instantaneous encounter rate $\tilde{\mathcal{E}}_{ij}(t)$ at time t between individuals indexed i and j with location vectors $\mathbf{r}_i(t)$ and $\mathbf{r}_j(t)$ is given by

$$\tilde{\mathcal{E}}_{ij}(t) = \gamma_{ij} \int d\mathbf{r}_{ij}(t) \Phi(r_{ij}(t)) p(r_{ij}(t)), \quad (1)$$

where γ_{ij} is a proportionality constant that governs encounter risk, also termed the encounter parameter (Gurarie & Ovaskainen, 2013), $r_{ij} = |\mathbf{r}_i - \mathbf{r}_j|$ is the distance between individuals i and j , $\Phi(r_{ij})$ is a relative measure of the probability of an encounter occurring when the two individuals are some distance apart (termed the ‘encounter kernel’) and $p(r_{ij})$ is the probability density of separation distance r_{ij} (Martinez-Garcia et al., 2020). Under the assumptions of stationarity (i.e. no change in the means or variances over time), local encounters (i.e. two individuals occurring at the same place at the same time) and uncorrelated movement between individuals, and conditional on an encounter event between individuals i and j taking place, Equation 1 can be reduced to the normalized product of the individual home range estimates $p_i(\mathbf{r})$ and $p_j(\mathbf{r})$

$$\text{CDE}_{ij}(\mathbf{r}) = \frac{p_i(\mathbf{r})p_j(\mathbf{r})}{\iint d^2\mathbf{r}' p_i(\mathbf{r}')p_j(\mathbf{r}')}. \quad (2)$$

The assumption that movement is uncorrelated across individuals is valid even with cross-correlation-inducing encounters, so long as the individuals’ movement is uncorrelated with one another outside of the encounter event, and the duration of encounters is relatively short compared to the home-range crossing time-scales. While the work by Martinez-Garcia et al. (2020), which formed the basis of our work, derived encounters for Ornstein–Uhlenbeck (OU)

processes (Uhlenbeck & Ornstein, 1930), the estimator described by Equation 2 is not constrained to OU processes, and full derivations are presented in Appendix S1. In Figure 1, we provide a visualization of the relationship between movement within home ranges, encounter events and the CDE for a pair of simulated trajectories generated from uncorrelated Ornstein–Uhlenbeck Foraging (OUF) processes (Fleming et al., 2014a, 2014b), which features autocorrelated positions and velocities, and a defined home range.

For some biological systems, it may be more informative to consider encounters between more than two individuals or between groups of interest (e.g. males and females, predators and prey, individuals from one group encountering individuals from another) as opposed to the unstructured distribution of encounters between all individuals in a population. Here we expand beyond individuals i and j to consider two groups I and J , all with otherwise similarly interacting individuals (i.e. no individuals interact more or less than any others), though this latter approximation can be relaxed by the modification of a proportionality constant (see Appendix S1). Making the same assumptions as before, the group-level CDE between individuals in group I and those in group J is given by the normalized density

$$\text{CDE}_{IJ}(\mathbf{r}) = \frac{\sum_{i \in I} \sum_{j \in J} p_i(\mathbf{r}) p_j(\mathbf{r})}{\iint d^2 \mathbf{r}' \sum_{i \in I} \sum_{j \in J} p_i(\mathbf{r}') p_j(\mathbf{r}')}. \quad (3)$$

The limited number of methods available for estimating the spatial distribution of encounter events has meant that, to date, researchers have often relied on describing patterns of home range overlap as an indirect proxy (e.g. Bermejo, 2004; Tórrrez-Herrera et al., 2020; Vander Wal et al., 2014). A number of different metrics are routinely used to compare trajectories, including the Bhattacharyya Coefficient (BC; Fieberg & Kochanny, 2005; Winner et al., 2018), Kullback–Leibler divergences (Hooten et al., 2014) or earth mover's distances (Kranstauber et al., 2016). To place this approach in context with the present work, in Appendix S1, we derive an expression for the individual-level CDE in terms of home range overlap via the BC for OU movement processes. The BC is a measure of similarity between a pair of distributions that ranges from 0 to 1, 1 if the two distributions are identical, and 0 if there is no shared support (Bhattacharyya, 1943). We find that the denominator of the individual-level CDE in Equation 2 is given by,

$$\iint d^2 \mathbf{r}' p_i(\mathbf{r}') p_j(\mathbf{r}') = \frac{\text{BC}_{ij}^2}{8\pi\sigma_{ij}}, \quad \sigma_{ij} = \frac{\sigma_i\sigma_j}{\sigma_i + \sigma_j}, \quad (4)$$

where σ_i and σ_j are the variances of the probability density functions for the position of each individual (both in the x and y coordinates because movement is assumed isotropic).

Importantly, the CDE is calculated from individual home range estimates, $p_i(\mathbf{r})$, which are themselves estimates derived from data. Point estimates on the CDE contours (e.g. 95% or 50% isopleths) should, therefore, be accompanied by a measure of the confidence (Pawitan, 2001). To this end, we propagate uncertainty in the home range estimates into each CDE via a combination of Gaussian reference function (GRF) approximation to the individual home range estimates, followed by the delta approximation (Cox, 2005, see Appendix S2). This estimator and, accompanying confidence intervals, is fully implemented in the `encounter()` function in the `ctmm` R package (ver. 0.5.11 and later). In Appendix S3, we provide details on a simulation study aimed at exploring the statistical performance of our CDE estimator, and the code necessary to reproduce these simulations is provided in Appendix S4.

The CDE bears qualitative resemblance with the Bhattacharyya integrand (e.g. French et al., 2019), although the latter does not have a probabilistic interpretation. In Appendix S3, we also provide a side-by-side comparison of the statistical performance of the CDE and the Bhattacharyya integrand in terms of capturing the spatial distribution of encounter events.

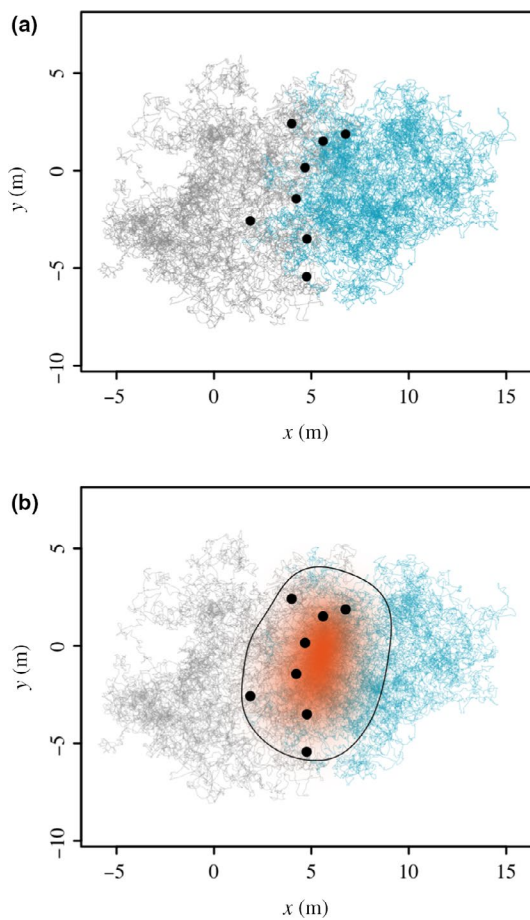


FIGURE 1 Panel (a) depicts the encounter locations (black points) for a pair of trajectories simulated from Ornstein–Uhlenbeck Foraging (OUF) processes. In (b) the resulting CDE estimate (orange shading) and 95% contour are shown. For illustrative purposes, we identified encounter locations as places where the two simulated tracks were <1 m apart

2.2 | Workflow for estimating the CDE

Our framework allows researchers to use animal movement data to generate a probabilistic representation of the spatial locations of

encounter events in the environment. It does so by incorporating information on individual patterns of home range use into a spatial distribution of encounter events (i.e. the CDE). While the minimum requirement for CDE estimation is a pair of home range estimates, we built our framework around autocorrelated kernel density estimation (AKDE; Fleming, Fagan, et al., 2015) as modern tracking data are almost invariably autocorrelated (Noonan et al., 2020; Noonan, Tucker, et al., 2019). AKDE also benefits from having quantified uncertainty that can be propagated to the CDE. We refer readers interested in the statistical efficiency of AKDE to Fleming and Calabrese (2017) and those interested in a comparison of AKDE to other commonly used home range estimators to recent work by Noonan, Tucker, et al. (2019).

With a prepared movement dataset in hand, the first step in the workflow is ensuring that the individuals of interest are range resident as the CDE is a long-term estimate of encounter location probabilities for movement within home ranges. When the data do not show evidence of range-residency, home range estimation, and therefore CDE estimation, is not appropriate (Calabrese et al., 2016; Fleming & Calabrese, 2017). We therefore strongly recommend starting with visual verification of range-residency via variogram analysis (Fleming et al., 2014a). Once range-residency has been verified, the next step is to fit a series of range-resident continuous-time movement models to the data, such as the Independent and Identically Distributed (IID), OU and OUF processes. Model selection should then be employed to identify the most appropriate model for the data (Fleming et al., 2014b; Fleming, Subaşı, et al., 2015; Fleming et al., 2019). With a fitted, selected movement model in hand, AKDE home range estimates can then be estimated (Fleming & Calabrese, 2017; Fleming, Fagan, et al., 2015; Fleming et al., 2018), and these can be used to obtain CDEs.

While the CDE can be informative on its own, it is also a probability density that has contours just like a home range estimate. Placing contours on the CDE permits the identification of areas where a specified quantile (e.g. 95% or 50%) of encounters will occur, while the error propagation techniques described above enable CIs to be placed on these contours. These CDE estimates may either be the final product of the analysis, or be used in subsequent analyses such as estimating territorial boundaries, identifying changes in behaviour within the 95% CDE area or habitat features associating with high/low density regions of the CDE. The workflow we describe involves several steps. The *ctmm* package, however, streamlines this procedure, and a full example of the workflow is shown in Appendix S5.

2.2.1 | Ecologically guided case studies

To demonstrate the ecological significance of the CDE, we generated simulated datasets for three scenarios that routinely occur in biological systems: (i) a population of individuals that occupy relatively distinct home ranges, but with some degree of spatial overlap with neighbours at the edges of their ranges (e.g. *Lemur catta*

Mertl-Millhollen, 1988; *Tragelaphus scriptus* Wronski, 2005; *Tiliqua rugosa* Kerr & Bull, 2006a); (ii) a pair of individuals with a hard/defended territorial border between their home ranges (e.g. *Crocuta crocuta* Henschel & Skinner, 1991; *C. latrans* Moorcroft, Lewis, et al., 2006); and (iii) a predator with a large home range that overlaps the home ranges of multiple prey individuals (e.g. *Lynx lynx* Herfindal et al., 2005; *Panthera leo* Loveridge et al., 2009). Details for these scenarios are presented in turn.

Scenario (i): Overlapping home ranges with permeable borders. In our first scenario, we simulated tracking data for a population of seven individuals with equally sized, regularly spaced home ranges. Individuals were arranged hexagonally. For each individual, we sampled 1×10^7 locations from an isotropic, IID process with a spatial variance of 6,500 m². We then estimated individual home range areas and the 95% CDE using the workflow described above.

Scenario (ii): Exclusive home ranges with hard borders. In our second scenario, we simulated tracking data for a pair of individuals with a hard territorial border between mutually exclusive home ranges. For each individual, we sampled 5,000 locations from IID processes that were Gaussian along the y-axis, but half normal along the x-axis (i.e. reflected along $x = 0$), and with a spatial variance of 2000 m². As above, we then estimated individual home range areas and the 95% CDE.

Scenario (iii): Predator-prey encounters. In our third scenario, we simulated tracking data for a predator with a large home range that encompassed a population of 30 prey individuals. Notably, this scenario would also be appropriate for species where large male home ranges overlap numerous smaller female ranges (Calabrese et al., 2021; Clutton-Brock, 1989). For each individual, we sampled 500 locations from an isotropic, IID process. The home range centre of the predator was set to (0, 0) and the spatial variance to 1×10^7 m², while the home range centres of the prey were drawn from a bivariate Poisson distribution with spatial variances of 2000 m². We then estimated individual home range areas as above, but here excluded all prey-prey encounters when estimating the CDE, so that this represented only the spatial distribution of predator-prey encounters.

We opted to simulate from IID processes for these case studies as the lack of autocorrelation allowed for more rapid convergence of the estimated home range areas and CDEs (Noonan, Tucker, et al., 2019). Here again, however, we do not expect any qualitatively different behaviour for data from autocorrelated movement processes when using a home-range estimator that accounts for said autocorrelation. We also note that the amount of data we simulated for each scenario were based on a case-specific trade-off between computation time, accuracy and visual clarity of the results.

2.3 | Empirical studies

2.3.1 | White-faced capuchins

White-faced capuchins (*C. capucinus*; henceforth capuchins) are New World primates that feed primarily on fruit and invertebrates

(Chapman & Fedigan, 1990). They are group-living, with intense (Crofoot, 2007) and potentially lethal (Gros-Louis et al., 2003) inter-group competition. Previous work on this species has found that they have home range areas of $c. 8 \times 10^5$ – 1.5×10^6 m² (Tórréz-Herrera et al., 2020). Although the perceptual range of *C. capucinus* has not been assessed under field conditions, work on the closely related brown capuchin (*Sapajus apella*) found visual perceptual ranges of $c. 8 \times 10^3$ m² (Janson & Di Bitetti, 1997), satisfying the assumption of perceptual ranges \ll home ranges. Encounter probability plays an important role in governing capuchin behaviour, and previous work has shown that capuchins tend to avoid areas where they are likely to encounter animals from neighbouring groups (Tórréz-Herrera et al., 2020; Wrangham, Lundy, et al., 2007), and the location at which neighbouring individuals encounter one another can shape the patterns of individual participation in cooperative defence and, ultimately, conflict outcome (Crofoot & Gilby, 2012; Crofoot et al., 2008). We applied our CDE estimation framework to tracking data from five individuals belonging to separate, neighbouring social groups on Barro Colorado Island, Panama.

Locations for these five individuals were collected every 4 min during daylight hours (6–18 hr) between December 2016 and February 2017, using GPS tracking devices (e-obs GmbH, Gruenwald, Germany). Visual inspection of the tracking data and empirical variograms suggested these individuals occupied fixed (i.e. stationary), effectively distinct home ranges, though with narrow contact zones where home ranges overlapped at inter-group boundaries. Following the workflow described above, we estimated the CDE between these neighbouring groups. We then applied ridge estimation to the estimated CDE using the R package *KS* (ver. 1.11.7; Duong et al., 2007). Ridge estimation extends the problem of estimating the mode of a unimodal probability density function to higher dimensions (Chen et al., 2015). The resulting 'density ridges' are paths that follow the high-density regions of a probability distribution. In the present context, ridges represent locations where encounters are more probable and are therefore likely to be territorial edges. To understand whether the spatial distribution of encounters influenced capuchin behaviour, we subset each individual dataset into movement that occurred inside and outside of the 95% CDE, fit movement models to each of these two subsets and estimate movement speeds following Noonan, Fleming, et al. (2019). We then compared the movement speeds of animals inside and outside of the 95% CDE using the meta-regression model implemented in the R package *METAFOR* (ver. 2.1-0 Viechtbauer, 2010). This approach allowed uncertainty in each individual speed estimate to be propagated into the population-level estimate when making comparisons. To compare the CDE to the locations of encounter events, we identified the locations of 62 instances where GPS-tracked individuals were within 200m of one another. As a further demonstration of the ecological relevance of the 95% CDE area, we compared the locations of 12 field-observed inter-group encounters, which were not used to estimate the CDE, with the estimated territory

boundary and 95% encounter area. To collect these observations, a team of observers conducted on-the-ground observations of the capuchin groups from 1 January 2017 through 28 February 2017. Observations lasted between 5 and 9 hr per day, where observers followed one capuchin group on foot and documented a variety of behaviours. Each of the five capuchin groups were observed at least three times during the study period; however, two of the groups were observed at a higher frequency (minimum 2 days per week for each of these two groups). Inter-group encounters between capuchin groups that occurred during the observational time period were documented on an all-occurrence basis and the GPS location of the encounter was recorded using a handheld Garmin GPS unit.

2.3.2 | Sleepy lizards

We further applied our workflow to GPS data from three sleepy lizards (*T. rugosa*) tracked in Bunday, South Australia at a field site near Bunday Bore Station (33°88'82.40"S, 139°31'07.18"E). The sleepy lizard is a large, long-lived, primarily herbivorous, skink from temperate regions of Australia (Kerr & Bull, 2006b). Previous work on this species has found that they have home range areas of $c. 4 \times 10^4$ m² (Bull & Freake, 1999), and perceptual ranges of $c. 1.3 \times 10^3$ m² (Auburn et al., 2009), again satisfying the assumption of perceptual ranges \ll home ranges. Visual inspection of the tracking data and empirical variograms suggested these individuals occupied fixed home ranges, satisfying the assumption of stationarity. In contrast to the capuchin example detailed above, sleepy lizard home ranges often overlap extensively with conspecifics (Kerr & Bull, 2006a), but do exhibit some level of territorial defence (Spiegel et al., 2018). GPS locations for these three individuals were collected every 2 min over a ~2.5-month period in Austral spring 2017 (October–December). We estimated the CDE for these three animals following the general workflow described above. The CDE in this case was the renormalized sum of all pairwise products (excluding self-encounters) estimated using the group encounter relations. Because the outer parts of sleepy lizard home ranges overlap extensively with conspecifics, CDE areas with high probabilities may therefore relate more to the location of valuable resources than to territorial boundaries (Leu & Bull, 2016; Sih et al., 2018). To understand how the CDE's capacity to identify key habitat features compared to more conventional approaches, we contrasted it with the area where the 95% and 50% home range contours of all three individuals intersected.

3 | RESULTS

3.1 | Ecologically guided simulations

In our first scenario of overlapping home ranges with permeable borders (Figure 2a), we found that this type of socio-spatial

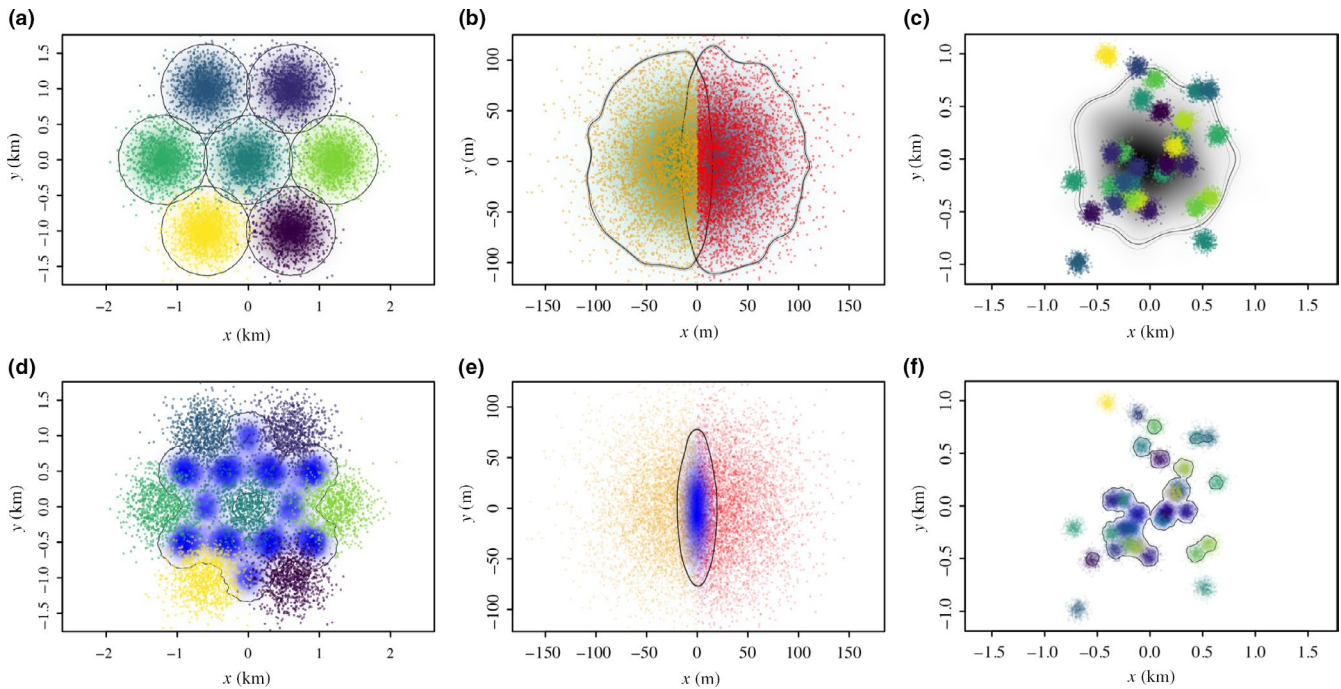


FIGURE 2 The top row depicts simulated tracking data and home range estimates for: (a) a population of individuals that occupy primarily exclusive home ranges but with overlapping boundaries; (b) a pair of individuals with a hard territorial boundary between their ranges at $x = 0$; and (c) a predator (black density and contours) with a large home range that encompasses multiple smaller prey home ranges (coloured points). In the lower row, panels (d), (e) and (f), the resulting conditional distributions of encounters (CDEs) are shown in blue (darker shadings of blue represent greater probabilities)

arrangement resulted in the 95% CDE area predicting encounters as being more likely to occur in boundary regions and lower probabilities towards home range centres (Figure 2d). Notably, while the bulk of the probability density was centred on the area of intersection of neighbours' 95% home ranges, there was support for encounters occurring well beyond these areas and closer to the core of individuals' home ranges. This highlights how the area of home range intersection can underestimate the area over which encounters are likely to occur, especially when overlap is low (see also Appendix S1). In our second scenario for a pair of individuals with a hard territorial border between mutually exclusive home ranges (Figure 2b), we found that the CDE was correctly distributed along the territorial boundary, but with a spillover that was proportional to the bandwidth of the home range estimates (Figure 2e). Unsurprisingly, in our predator-prey scenario, 95% of the predator-prey encounters were predicted to occur near the centre of the predator's home range, and the home ranges of prey located near the centre of the predator's home range were entirely within the 95% CDE (Figure 2c,f). For prey near the periphery of the predator's home range, however, there were still locations within their home range that were within the 95% CDE, but only in heavily used areas. In other words, predation risk for these individuals was greatest not where they are closest to the predator's home range centre, but where they spent most of their time relative to where the predator went. This highlights the importance of accounting for non-uniform space use when determining the spatial distribution of predation risk.

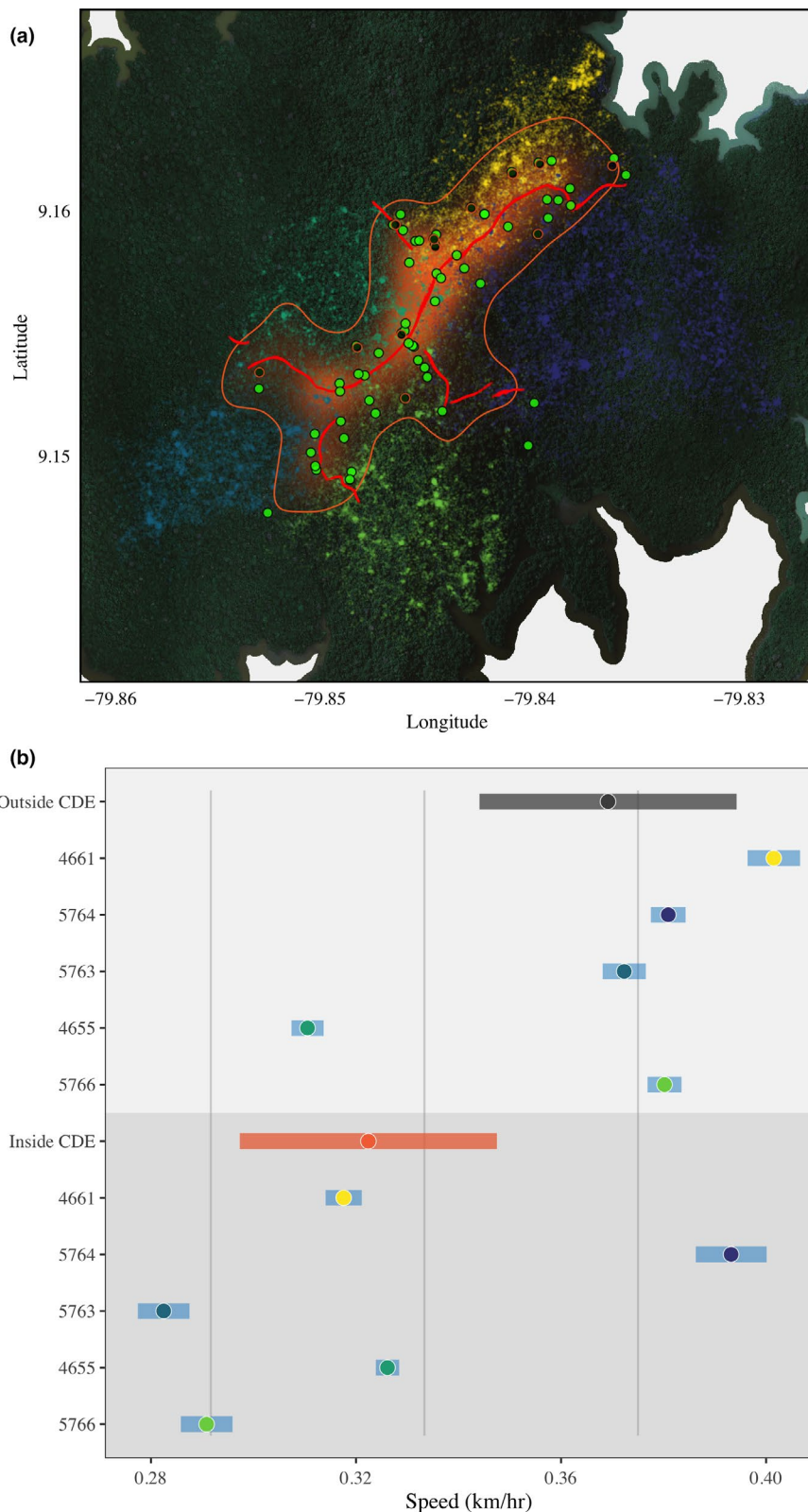
3.2 | Empirical case studies

3.2.1 | White-faced capuchins

As would be expected for a species with intense inter-group competition, we found that spatial overlap between capuchin home ranges was low (median BC: 0.13, range: <0.01–0.28; Figure 3). Mirroring our simulation-based results above (Figure 2d), the resulting CDE was centred along the boundaries between the individuals' tracking data, highlighting how most of the inter-group encounters are likely to occur at, or close to, the edges of the individuals' home ranges. Ridge estimation on the CDE resulted in estimates of the territorial boundaries that mapped onto the edges of each animal's home range (Figure 3a). In addition, we found that all 12 directly observed (i.e. by researchers in the field) encounters, and 58 of the 62 GPS observed encounters (i.e. 94.6%) fell within the 95% contours of the CDE. These were within 193.6 m of the estimated territorial boundaries (median 52.6 m; range: 1.1 m–193.6 m). These findings demonstrate the direct correspondence between the 95% CDE and capuchin ecology.

Interestingly, we also found that the capuchins we analysed modified their movement behaviour in relation to the local probability of encountering a neighbouring individual. While there was no evidence for a general relationship between movement speed and distance from home range centre ($R^2 = <0.001$, $p = 0.83$),

FIGURE 3 GPS data from five white-faced capuchins *Cebus capucinus* from five neighbouring social groups tracked on Barro Colorado Island, Panama. In panel (a) the conditional distribution of encounters (CDEs) are depicted in orange shading, while the orange line delineates the 95% contour. The red lines depict the territorial borders estimated via ridge estimation on the CDEs, and the large black points represent the locations of field-observed encounters between neighbouring individuals from these five social groups, the green dots depict encounters observed from the tracking data. Note how 94.6% of the encounters occurred within the 95% contour of the CDEs. In panel (b), mean individual and population-level speed estimates for movement inside and outside of the 95% CDE are depicted, showing how, on average, animals moved significantly more slowly when in the 95% CDE



we found that when moving within their home ranges, but not within the 95% CDE, capuchins moved with a mean speed of 0.37 km/hr (95% CIs: 0.34–0.40). In contrast, animals moved significantly more slowly ($p = 0.036$) when moving through the 95% CDE, with a mean speed of only 0.32 km/hr (95% CIs: 0.30–0.35; Figure 3b).

3.2.2 | Sleepy lizards

Although the three sleepy lizards we analysed occupied relatively distinct home ranges with low spatial overlap (median BC: 0.23, range: 0.13–0.39), there was a focal point around the only source of standing water in the area where the home ranges of all three

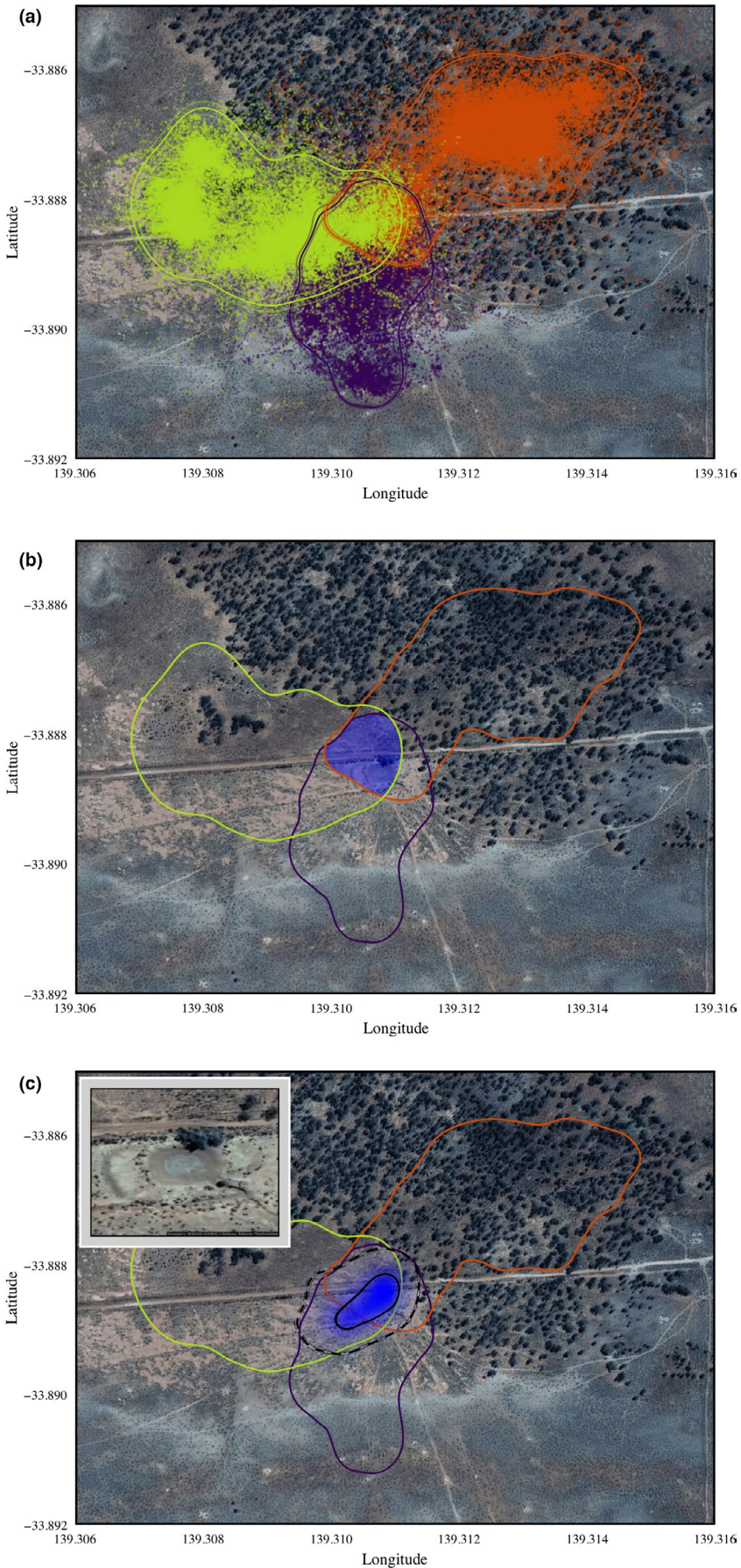


FIGURE 4 In panel (a), GPS data from three sleepy lizards (*Tiliqua rugosa*) tracked in Bundery, South Australia are depicted. The contours depict the estimated 95% home range areas $\pm 95\%$ confidence intervals. Panel (b) shows the 95% home range contours, as well as the area where all three 95% home ranges intersect (blue shading). In c), the conditional distribution of encounters (CDEs) for these animals are shown in orange while the solid black line delineates the 50% contour and the dashed black line delineates the 95% contour. Note how the CDE is centred on the only watering hole in the surrounding area (inset in panel c), while the area of intersection covers space well beyond the watering hole at the 95% level

individuals intersected (Figure 4a). For these animals, the bulk of the CDE's probability density was centred on this water source, suggesting that the majority of encounters are likely to occur at or around this valuable resource (Figure 4c). If we had applied the conventional approach of describing patterns of home range overlap, however, the area where all three home ranges intersected covered space well beyond the watering hole at the 95% level (Figure 4b), and there was no location where the 50% contours of all three animals overlap (results not shown).

4 | DISCUSSION

Intra- and inter-specific encounters are keystone ecological events that govern the dynamics of many higher level processes (Barraquand & Murrell, 2013; Dougherty et al., 2018; Holling, 1959; Huston et al., 1988; Kareiva & Odell, 1987; Spiegel et al., 2017; Turchin, 1998). Despite this, the relationship between individual movement strategies and encounter processes has remained conspicuously understudied. Furthermore, previous work has focused almost exclusively on relating animal movement to encounter rates (e.g. Bartumeus et al., 2008; Gerritsen & Strickler, 1977; Gurarie & Ovaskainen, 2013; Hutchinson & Waser, 2007; Martinez-Garcia et al., 2020; Visser & Kjørboe, 2006). This has left researchers interested in understanding the spatial dynamics of encounter processes with only empirically based null models (Spiegel et al., 2016, 2018) or informal measures of the spatial distribution of encounters (e.g. French et al., 2019). In response, we have derived an estimator of the spatial distribution of encounter events that builds straightforwardly off of one of the most ubiquitous analyses in movement ecology—home-range estimation.

4.1 | Properties and assumptions of the CDE

Before discussing the properties of the CDE estimator described in the present work, it is crucial to note that the spatial distribution of encounter locations exists even if the assumptions of our estimator are not met by the data. In other words, although the assumptions of the present estimator may not be met by every dataset, it does not negate the existence of the CDE. In deriving our CDE estimator, we relied on three key assumptions to maintain analytical tractability: (a) stationarity in the movement processes; (b) that encounters are local events; and (c) that movement is uncorrelated across individuals. Stationarity in this context refers to the fact that we are assuming the individuals of interest are range resident, and do not exhibit a range shift, or major change in home-range behaviour over time. While large-scale analyses suggest that this assumption holds true for many animal tracking datasets (Noonan et al., 2020; Noonan, Tucker, et al., 2019), we recommend verification prior to analysis, as significant changes in movement behaviour (e.g. range shifts, migrations, dispersals, etc.) will clearly influence the area over which encounters occur. In terms of encounters being local events, we anticipate this

assumption holding for many species as encounters tend to occur over much shorter distances than the radii of their home range areas (e.g. Middleton et al., 2013; Muirhead & Sprules, 2003). For species with large perceptual ranges, however, the encounter kernel in Equation 1 can be carried through in the derivations and modified to account for the greater area over which an encounter can be considered to happen. Perhaps the most important assumption of the present framework is that movement is uncorrelated across individuals. As noted above, the assumption of uncorrelated movement is still valid with cross-correlation-inducing encounters, so long as the individuals' movement is uncorrelated outside of the encounter event, and the duration of encounters is relatively short compared to the home-range crossing time-scales (e.g. encounters on the order of minutes vs. range crossing times of days). Nonetheless, correlated movement is a well-documented phenomenon that is likely to occur in a wide range of species (Calabrese et al., 2018; Couzin et al., 2005; Strandburg-Peshkin et al., 2015). While expanding the current framework to account for cross-correlated movement was beyond the scope of the present study, future work on this topic is clearly warranted.

In terms of accuracy, our simulation study revealed how, because the CDE is estimated conditionally on multiple home-range estimates, any biases in these will be propagated into CDE estimates. Accurate home-range estimates are therefore critical for the CDE to accurately reflect the spatial distribution of encounters between tracked individuals (see also Winner et al., 2018). For a discussion on how to obtain accurate home-range estimates, we refer readers to Noonan, Tucker, et al. (2019). In addition, more effort remains to derive bias corrections for both the Gaussian and kernel estimates. As a further limitation, it is crucial to note that the CDE requires multiple individuals, of potentially different species, to be tracked in the same place at the same time, and provides no information on encounters with unmonitored animals. In other words, if the CDE has a low location-specific probability, this does not necessarily mean an encounter is unlikely if an individual is moving through an area that is regularly visited by untracked animals. Good coverage of the local population is therefore necessary for the CDE to fully capture the spatial distribution of encounters. Importantly, while data density can be a limiting factor in practical applications, this fundamental limitation also exists for any method that quantifies encounter processes, including randomizing paths to generate null models (Spiegel et al., 2016, 2018), comparing home range overlap (e.g. Bermejo, 2004; Tórréz-Herrera et al., 2020; Vander Wal et al., 2014), or applying mechanistic home range analysis (Moorcroft et al., 1999). We therefore recommend that researchers interested in understanding encounter dynamics focus their data collection on good coverage of a localized population.

4.2 | The ecological importance of encounter distributions

Our empirical case studies show how the CDE can be used to straightforwardly quantify key aspects of population/community dynamics. For instance, while many truly territorial species actively

defend borders (Powell, 2000; Stamps & Buechner, 1985) for other species, borders tend not to be rigid territorial boundaries, but permeable contact zones (Anich et al., 2009; Ellwood et al., 2017; Stewart et al., 1997). Understanding behaviour at and around territorial boundaries, however, is a deceptively challenging question that, to date, has relied on labour-intensive field efforts (e.g. Delahay et al., 2000; Kilshaw et al., 2009; Kruuk, 1972) or modelling species-specific mechanistic processes (Giuggioli et al., 2013; Moorcroft et al., 1999). In the capuchin data we analysed, we showed how the 95% CDE provided an accurate predictor of 12 inter-group encounters that were field-observed independent of the tracking data, as well as how application of ridge estimation on the CDE yielded an objective estimate of the territorial boundaries. Additionally, the CDE can be used to identify any changes in movement behaviour that directly result from location-specific encounter probability. For instance, despite a lack of evidence for a general relationship between movement speed and distance from home range centre, we found that when the capuchins we analysed moved through the area contained within the 95% CDE, they did so at a significantly slower speed than when moving through areas where encounters with neighbours were low. While the mechanisms behind this difference in movement for these individuals were not explored in the present study, this agrees with previous work which found that capuchins exploit resources in inter-group boundary areas more thoroughly and spend longer feeding in each patch they encounter (Tórriz-Herrera et al., 2020).

Application of our CDE framework can also be used to identify key resources and quantify location-specific potential for competition. In species with high spatial overlap, areas where encounters are more likely to occur probably relate more to valuable resources than territorial boundary dynamics. For example, in our analysis of the sleepy lizard data, instead of reflecting patterns of territoriality, the CDE was localized around the only source of standing water in the three animals' home ranges. This finding agrees with previous work in this study system that found that this water source was a valuable resource that influences the population's spatial ecology (Leu & Bull, 2016). Notably, in this respect, neither the area of intersection of the 95% nor the 50% home ranges for these animals adequately identified this aspect of these sleepy lizard's space use. This highlights how the CDE directly captures ecologically relevant information. In contrast, describing patterns of home range overlap can require researchers to make some level of subjective judgement in their analyses, due in large part to the fact that this approach fails to account for non-uniform patterns in space use and encounter probability. Beyond the utility of the CDE in our empirical case studies, this framework can be used to investigate a wide range of intra- and interspecific relationships such as predator-prey and/or community dynamics, understanding how encounter rates vary in corridors, along key migration routes, in larger versus smaller reserves, etc. At the intraspecific level, the relationship between individual-level heterogeneity, personality and movement is currently active area of research (Barry et al., 2020; Harris et al., 2020; Harrison et al., 2019; Hertel et al., 2020; Spiegel et al., 2017). Assuming differences in

phenotypic traits (e.g. age, sex or personality) manifest as variation in movement and space use, the method developed here provides a simple tool for translating individual-level variation in sociability into hot/coldspots of encounters. We anticipate that this could augment many social network studies that focus on individual heterogeneity and neglect the spatial component of social interactions (see also Spiegel et al., 2016). Finally, future work could also extend this framework to explorations of the movement and behaviour of a single individual over time (e.g. quantifying site fidelity or revisitations) as an alternative to over overlap indices or grid cell-based methods (e.g. Vázquez Diosdado et al., 2018). Given the growing interest in individual variation in movement patterns (e.g. Spiegel et al., 2017), this is a promising direction to formally quantify such differences.

4.3 | The CDE as a conservation tool

Although the case studies presented here were focused on demonstrating the utility of the CDE for understanding basic ecological processes, understanding where key types of encounters happen is also valuable from a conservation perspective. Human-wildlife conflict represents a major conservation concern which, over the past 20 years, has gone from a barely recognized issue to a major conservation focus (Dickman, 2010; Distefano, 2005; Ravenelle & Nyhus, 2017). The probability of encountering humans and human-related activities is a key indicator of the potential for human-wildlife conflict. Here, the CDE can be extended to model and estimate the distribution of conflict events and help focus management actions and interventions where they will have maximum effect. Road traffic incidents, for instance, where an animal encounters and is potentially hit by a car, represent a serious source of mortality for many species (Bennett, 1991; Gibbs & Shriver, 2002; Glista & DeVault, 2008), and carry an economic cost of ~\$1 billion/year in Europe (Bruinderink & Hazebroek, 1996) and ~\$8 billion/year in the United States (Huijser et al., 2017). Given that researchers routinely use tracking data to study interactions between animals and vehicles (Murray & St. Clair, 2015; Neumann et al., 2012; Zimmermann et al., 2014), application of the CDE in this context would aid in better understanding how variation in traffic volume and animal movement affects road traffic incidents risk, and would provide crucial baseline information for developing effective mitigation strategies. In practice, this would involve pairing individual home range estimates with distributions of traffic volume in Equation 2 to identify areas where animal-vehicle encounters are more likely. If traffic volume is perfectly uniform across the roads the animal crosses, then the encounter locations would be concentrated on areas where the animal's home range overlaps the road, for non-uniform traffic volume, however, encounter locations would be informed both by animal and vehicle movement. Much like our animal-animal findings (e.g. Figure 4), we anticipate that this approach would provide insights that are beyond the ability of simple intersections with the home range polygon and the road line. Additionally, emerging zoonotic and anthroponotic diseases pose significant and increasing

threats to both human and animal health, respectively (Estrada et al., 2017; Rothan & Byrareddy, 2020), and locations of risk are simultaneously viewed as 'hotspots' for both conservation and emerging disease (Paige et al., 2015). Given the importance of accounting for animal movement when modelling disease dynamics (Dougherty et al., 2018), the CDE represents a potentially fruitful tool for identifying disease transmission hotspots.

4.4 | Concluding remarks

In this study we have developed methods for estimating the conditional distribution of encounter events. Conceptually, the CDE describes how encounters change in space for movement within home ranges, and solidifies what has heretofore only abstractly been defined. Furthermore, we have derived this distribution and confidence interval, implemented its statistical estimator for empirical movement data and demonstrated the broad ecological relevance of the CDE. Notably, the general estimation framework developed in this work builds straightforwardly off of home range estimation, and, as such, requires no specialized data collection protocols. CDE estimation thus allows researchers to quantify hitherto intractable aspects of population/community dynamics without the need for intensive field efforts, complex data collection or relying on ad hoc indices. This method is now openly available via command line interface through the *ctmm* R package (Calabrese et al., 2016; CTMM Initiative et al., 2019) or through the web-based graphical user interface available at ctmm.shinyapps.io/ctmmweb/ (Calabrese et al., 2021; Dong et al., 2017). Future extensions of this framework focused on relaxing some of the current assumptions (i.e. stationarity, local encounters and uncorrelated movement across individuals) are clearly warranted.

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AUTHORS' CONTRIBUTIONS

M.J.N., R.M.-G., C.H.F. and J.M.C. conceived the study; C.H.F. developed the methods and open-source code; R.M.-G. derived the underlying analytical framework and provided the Spanish translation

of the abstract; M.J.N. conducted the analyses and drafted the manuscript; G.H.D., M.C.C., R.K., B.T.H., D.C., E.P., A.S., D.S. and O.S. carried out the fieldwork and collected the tracking data. All the authors contributed to study concepts and writing.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13597>.

DATA AVAILABILITY STATEMENT

The white-faced capuchin *Cebus capucinus* and sleepy lizard *Tiliqua rugosa* data are openly available through the Dryad Data Repository <https://doi.org/10.5061/dryad.sf7m0cg5d> (Noonan et al., 2021). The *ctmm* code is openly available on CRAN via <https://cran.r-project.org/package=ctmm>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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