A guide to using GPS-based tracking to study animal societies

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ABSTRACT

GPS-based tracking is a widely used automated data collection method for studying wild animals. Much like traditional observational methods, using GPS devices to study social animals requires making a number of decisions about sampling that can affect the robustness of a study's conclusions. For example, sampling fewer individuals per group across many distinct social groups may not be informative enough for inferring behavioural patterns at a finer social organizational scale, while sampling more individuals per group across fewer groups limits the ability to draw conclusions about populations. Here, we integrate previous insights from animal social network analysis with simulated and empirical data to provide quantitative recommendations when designing GPS-based tracking studies of animal societies. We outline the trade-offs faced by researchers, and how these trade-offs should vary across social organizational scales and social systems in relation to questions of interest, such as those defined within versus among groups, and spanning from cohesive, stable groups through to more open societies. We discuss three fundamental axes of sampling effort requiring consideration when deploying GPS devices to study animal societies: 1) Sampling coverage—the number and allocation of GPS devices among individuals in one or more social groups; 2) Sampling duration— the total amount of time over which devices collect data; 3) Sampling frequency—the temporal resolution at which GPS devices record data. Exploring each axis, we quantify the relationship between sampling effort and sampling error, giving recommendations on GPS sampling design to address research questions across social organizational scales and social systems—from group movement to social network structure and collective decision-making. In doing so, we also highlight practical

limitations on deploying GPS tracking. Our study provides practical advice for empiricists to navigate their decision-making processes when designing GPS-based field studies of animal social behaviours, and highlights the importance of identifying the optimal deployment decisions for drawing informative and robust conclusions.

KEYWORDS

Animal societies | Bio-logging | GPS sampling | GPS tracking | Group and collective behaviours | Group size | Social interactions | Social structure

1. INTRODUCTION

Studying animal societies requires collecting both individual-level (what is the animal doing?) and relational (what is the relationship between animals?) data (Altmann 1974; Krause *et al.* 2013). Prior to data collection, researchers have to make decisions about how to employ finite resources to adequately sample social behaviours. While sampling design is a major consideration across all fields of biology, it is critical when studying social behaviour because the number of possible inter-individual relationships increases exponentially with the study population size (Davis, Crofoot & Farine 2018). Further, social relations can change rapidly over time (Pinter-Wollman *et al.* 2014; Gil *et al.* 2018). Thus, studying social behaviour generally requires sampling individuals simultaneously, frequently, and over large temporal scales. To achieve these requirements, automated sampling methods are increasingly used (Krause *et al.* 2013; Nomano *et al.* 2014; Wilmers *et al.* 2015; Ferreira *et al.* 2020; Gupte *et al.* 2021; Keitt & Abelson 2021; Shizuka *et al.* 2021; Smith & Pinter-Wollman 2021).

One automated method that is becoming increasingly feasible thanks to decreasing costs and better miniaturisation is GPS telemetry. GPS telemetry explicitly captures when and where individual animals go, opening new avenues of research into how animals interact with their social and ecological environment (Cagnacci *et al.* 2010; Tomkiewicz *et al.* 2010; Kays *et al.* 2015; Leu *et al.* 2016). GPS devices can reduce sampling biases and increase the volume and dimension of data collected relative to human observers (Crofoot 2021). Importantly, GPS devices can be deployed on more individuals than could possibly be observed simultaneously, potentially capturing fine-scale social processes such as group

movement and collective decision-making (Strandburg-Peshkin *et al.* 2015). Studies over the last decade have established simultaneous GPS-based tracking as a productive approach for generating new insights into animal social ecology (Dell'Ariccia *et al.* 2008; Nagy *et al.* 2010; Lührs & Kappeler 2013; Strandburg-Peshkin *et al.* 2015; Leu *et al.* 2016; Spiegel *et al.* 2016; Springer *et al.* 2016; Farine *et al.* 2017; Papageorgiou *et al.* 2019; Wielgus *et al.* 2021). Despite its strengths, GPS tracking is far from being a panacea for challenges related to social data collection. The cost of GPS devices (and data transfer), the challenges of deployment, and technological limitations can all constrain study design.

To effectively apply GPS tracking to study social behaviours, researchers need to tailor sampling design to research questions and social systems. Animal social behaviours span various levels of social organization (Wilson 1975; Aureli *et al.* 2008; Prox & Farine 2020), such as how one individual interacts with another, how individuals form groups, how groups themselves interact, and how populations are socially structured (Lukas & Clutton-Brock 2018; He, Maldonado-Chaparro & Farine 2019; Kappeler 2019). Optimal GPS study design strategies will depend on the social organizational level under investigation—for example, tracking all individuals in one social group is useful for sampling interactions among group-mates but not among groups. Another important consideration is that some animals associate almost exclusively with the same set of individuals (e.g., within territory boundaries, Bishop & Groves 1991; Jordan, Cherry & Manser 2007), whereas others form open societies where group membership and size change frequently (Aureli *et al.* 2008; Connor & Krutzen 2015; Farine *et al.* 2015). By influencing how often individuals are found together, these dynamics shape how GPS tracking can be employed to study social behaviours.

In this paper, we first outline the common trade-offs faced by researchers using GPS tracking to study animal societies, focusing on three key axes: sampling coverage, sampling duration, and sampling frequency. We then draw insights from previous studies, two whole-group GPS tracking datasets of vulturine guineafowl (*Acryllium vulturinum*), and simulated data, to provide practical advice for empiricists facing these trade-offs when designing field studies.

2. KEY TRADE-OFFS IN GPS-BASED STUDIES OF SOCIAL BEHAVIOURS

Many factors should be considered when designing GPS-based tracking studies of social behaviours (Fig. S1). Among these are ethical and practical limitations when capturing and tagging animals, and ongoing research and development is aimed at understanding and minimizing these limitations (Portugal & White 2018; Klegarth *et al.* 2021; Portugal & White 2021; Wilson *et al.* 2021). Here, we assume that researchers follow ethical and legal guidelines for deploying GPS devices, and focus on providing guidance on how to deploy devices effectively to optimize data collection for addressing different research questions (Fig. 1).

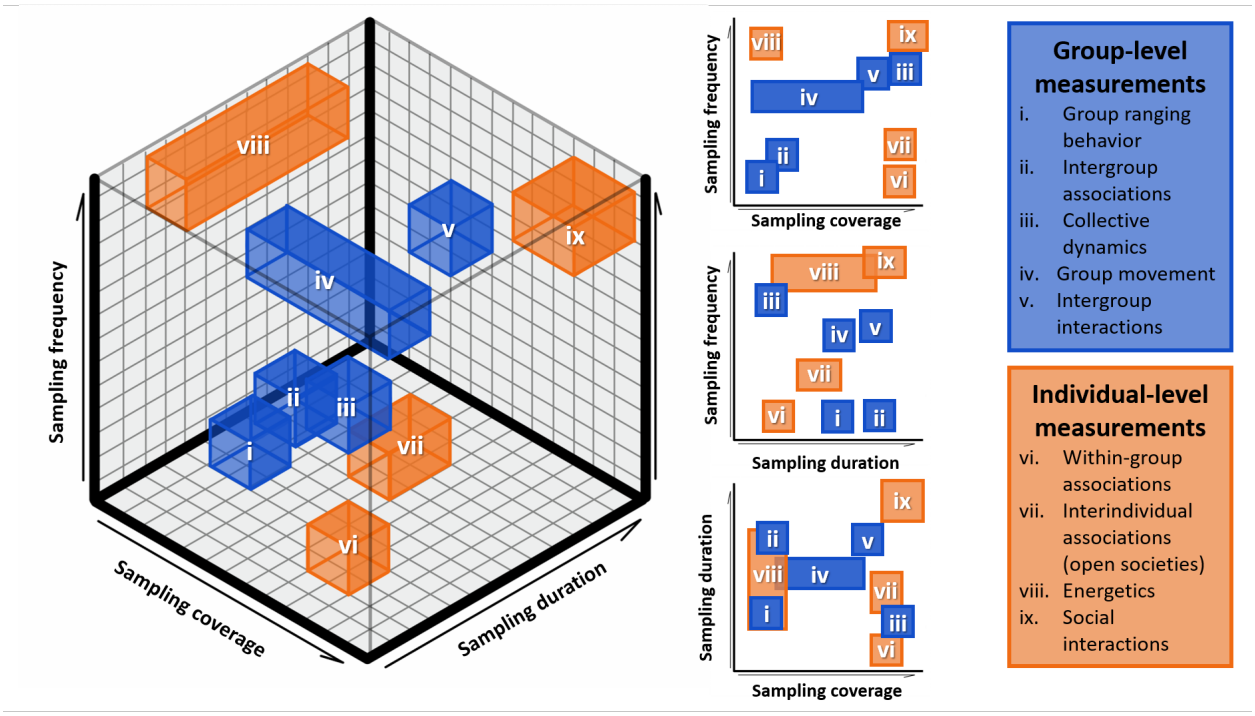

Fig. 1 Three fundamental dimensions of GPS sampling design when studying animal societies. The types of questions that can be answered using GPS tracking are broadly governed by three key axes of study design: sampling coverage—the number and distribution of GPS devices throughout a study population, sampling duration—the total amount of time over which devices collect data, and sampling frequency—the temporal resolution at which devices collect data. Social behaviours can typically be thought of as playing out at group (blue boxes) and individual (orange boxes) levels. Within each level, different measurements (i-ix) require differing levels of investment in each axis, and often face trade-offs across axes to capture specific behaviours of interest. This illustration highlights the relative sampling effort across each dimension for different measurements of social behaviour.

2.1 Sampling coverage

All GPS-based studies face financial and practical constraints on the number of devices that can be deployed. Having more devices (relative to the study population size) will naturally provide more data for more-robust inferences of social behaviours. However, deploying more devices is not only financially costlier, it can also introduce a number of logistical challenges in terms of data-recovery (see 2.4). Therefore, researchers need to strategically decide how many devices to deploy, and how broadly to distribute them (i.e., 'sampling coverage').

Sampling coverage requirements will depend on the scale of social organization in relation to research questions and whether a study focuses on social structure (e.g., patterns of association or interactions) or processes (e.g., transmission or collective behaviour). Structure-focused questions, such as whether individuals have preferred or avoided social relationships (e.g., Cantor *et al.* 2012; Best *et al.* 2014; Gero, Gordon & Whitehead 2015), require broad, but not necessarily exhaustive, deployments of devices—it is fine to not capture every single pair of associates, as long as a range of association strengths are represented—with the number of devices to be deployed depending on social scale (e.g., group vs population). In terms of allocation, randomly deploying GPS devices to individuals can effectively test for preferred social relationships. Questions addressing larger population-scale structure, such as whether there are distinct social communities within a population (e.g., Shizuka & Farine 2016), may require distributing GPS devices more broadly to distinguish higher levels of social organisation.

Process-focused questions require thorough coverage of social relationships, which can be very device-intensive. Without a relatively complete representation of social connections, inference may fail (Wild & Hoppitt 2019). For example, observing a pathogen spreading from individual A to B to C, with edges A–B and B–C, would fail to reveal socially-mediated transmission if A and C become infected and B is missing from the study. As such, process-focused questions may need to be studies at smaller scales, where higher proportions of individuals can be tracked, or to focus on interactions among larger social organizational units (e.g., where an entire group can be represented by one device).

2.2 Sampling duration

Sampling duration is fundamentally limited by the battery life of GPS devices (Fig. S1). Power is consumed each time a device switches on to collect a point, leading to a major trade-off between the sampling frequency and the longevity of battery life that determines sampling duration. For example, sampling of GPS collars fitted to wild olive baboons (*Papio anubis*) lasted 15 to 30 days at 1 Hz (Farine *et al.* 2017), whereas those fitted to elephants (*Loxodanta africana*) operate at much lower sampling frequencies but can last many years (Hahn *et al.* 2022). Some GPS devices can partly overcome this challenge by using solar panels to recharge batteries, by applying programming settings such as using geofencing to spatially vary sampling regimes (Sheppard *et al.* 2015), or by using acceleration sensors to switch off/on GPS devices when animals are (in)active (Brown *et al.* 2012). Nevertheless, all studies must strike a balance between sampling frequency and sampling duration. There is increasing awareness that long-term social experiences

can shape fine-scale social behaviours (Biro, Sasaki & Portugal 2016; Strauss & Holekamp 2019). The key consideration is therefore whether a given sampling duration can reveal fine-scale social processes and the long-term factors that govern them.

2.3 Sampling frequency

Sampling frequency impacts both battery life and the inferences that can be made from the resulting data. Animal movement is inferred from sequential fixes, so the more continuously fixes are collected, the more complete the information is about where the individual has been and, potentially, what it has been doing (Wang 2019). In most vertebrates, sampling frequency at 1 Hz (one GPS fix per second) captures complete information about where individuals have moved and how (Ryan *et al.* 2004). However, such high sampling frequencies are energetically demanding, with serious implications for sampling duration. Thus, most studies opt for lower sampling frequencies to save battery life. Studies have collected 10 fixes every 5 minutes (e.g., vulturine guineafowl, Papageorgiou *et al.* 2019), 1 fix every 30 minutes (e.g., swamp wallabies *Wallabia bicolor*, Fischer *et al.* 2018), or 1 fix every hour or more (e.g., African elephants, Wittemyer *et al.* 2008). However, lower sampling frequencies come at a substantial cost in terms of accurately capturing individuals' behaviour. For example, estimates of travel distances are heavily influenced by sampling frequency, often only reaching realistic measures with sub-minute sampling intervals (Rowcliffe *et al.* 2012). In some cases, intermediate locations (i.e., an animal's position in the time between fixes) can be inferred using spatial interpolation (Strandburg-Peshkin *et al.* 2015; Hirakawa *et al.* 2018), smoothing spline models (Whetten 2021), or the dead reckoning technique (Dewhirst *et al.* 2016). It should

also be noted that battery consumption does not scale linearly with increasing sampling frequency. GPS devices use energy each time they (re)boot and search for satellites, which takes longer with sparser sampling regimes, meaning that the same battery charge collects fewer data points at longer sampling intervals. Device typically do not switch off during more intensive regimes. For example, 0.2–0.5 Hz may use as much battery as 1 Hz (but 1 Hz may have greater battery costs for data transfer).

2.4 Further practical considerations

A few other practical issues (Fig. S1) are worth considering. For example, social interactions can take place at small spatial scales (i.e., <1 m, see 3.1), so in such cases GPS accuracy is particularly important. Sampling while consistently keeping GPS devices switched on will typically produce more accurate estimates of positions, because devices can reuse satellite information from previous fixes (eObs GmbH, pers. comm.). Switching off devices between consecutive fixes will generally result in lower accuracy, especially when the gaps are long (e.g., a few hours). Habitat density (e.g., forest canopies vs open savanna) will impact GPS precision because of interference during satellite detection.

Researchers also need to consider data retrieval, which can become cumbersome when deploying many devices simultaneously. Deploying more devices will increase costs if data are retrieved via mobile phone networks, download time if data are retrieved via radio download, or retrapping/relocation effort if data is retrieved by recovering devices. Device data storage capacity may require frequent data retrieval, and missed data

downloads can lead to data loss (e.g., Strandburg-Peshkin *et al.* 2015 retrieved GPS data nightly to avoid data loss; see also Box 1).

3. SOCIAL NETWORK STRUCTURES

Animal social networks are often assembled from social associations or interactions (Whitehead 2008; Farine 2015; Farine & Whitehead 2015; Krause *et al.* 2015), both of which can be inferred from GPS data. In GPS tracking studies, social associations are defined by co-location of individuals, while interactions can be inferred when individuals have a detectable impact on the behaviour of others (e.g., one individual displacing another). Several studies have suggested that social networks are quite robust to sampling subsets of the population, so GPS devices can be strategically deployed to characterize even large social networks. Specifically, Silk *et al.* (2015) estimated that studies sampling 30% or more of a population can generate reliable estimates of individuals' social network positions. Subsequent studies highlighted that repeated sampling and avoiding misidentifications are critical for producing accurate networks (Davis, Crofoot & Farine 2018; Sunga, Webber & Broders 2021)—both are the strengths of GPS tracking data.

3.1 Estimating social associations

Associations can be defined by applying spatiotemporal co-location rules to individuals' GPS fixes. A common approach is to set a distance threshold under which individuals are considered associated. Thresholds should consider the biology of the study organisms

and, particularly for smaller animals, the precision of GPS devices. For example, Godfrey *et al.* (2014) constructed an undirected association network describing the patterns of associations among 60 Australian sleepy lizards (*Tiliqua rugosa*) using synchronous GPS fixes recorded every 10 min and a co-location rule where individuals were assumed to be socially associated when the GPS registered the individuals as within 14 m of each other. This threshold was derived from the observation that lizards within 2 m of each other were likely to make social contact, combined with a median GPS precision of 6 m. Such distance thresholds can be chosen based upon traditional observation of the study organism, through data-driven studies of these thresholds (Haddadi *et al.* 2011), or by using statistical approaches (Papageorgiou *et al.* 2019).

A simple approach to defining an association threshold is to interrogate the distribution of inter-individual distances and extract the first mode, which likely represents individuals that are socially associating. In larger groups, associations can be defined following a chain rule, where all individuals that form part of a connected component are considered as being associated (e.g., if A–B and B–C, then A–C even if A and C are beyond the threshold). There are also tools (Ansari *et al.* 2020) for identifying clusters of GPS fixes to infer behavioural events or states (e.g., kills by predators or behavioural activity states). However, few have been extended to detect clustered social associations (i.e., inferring the presence of social aggregations) across time (but see Kalnis, Mamoulis & Bakiras 2005).

3.2 Inferring social interactions

An emerging application of GPS tracking is to infer social interactions among individuals. Unlike associations, which are readily characterised at low sampling frequencies, interactions require simultaneous high-frequency data (e.g., 1 Hz). This is because inference is drawn from relative movements at fine spatiotemporal scales, rather than proximity alone. For example, dominance interactions can be detected from approach-avoid interactions (A approaches B and B moves away) and chases (Strandburg-Peshkin *et al.* 2015). Thus, studying social interactions requires sequential detections collected simultaneously across individuals. The ability to detect interactions from GPS tracking data will also depend on the spatial scale over which they occur relative to GPS error. For example, a GPS error within 1 m allows for detections of displacements that occur over tens of meters in baboons (e.g., Strandburg-Peshkin *et al.* 2015), but make it more challenging to detect those that take place within a meter or less, as in the vulturine guineafowl (Dehnen *et al.* 2022). Furthermore, GPS tracking is perhaps best-suited to detecting extreme interactions (e.g., chases), while many other interactions (e.g., vocal interactions, allogrooming) cannot be detected from spatial positions alone. If extreme interactions are non-randomly distributed among individuals (e.g., Dehnen *et al.* 2022), the resulting networks may be biased. These issues aside, detecting interactions is achievable. Finally, we note that inferred interactions should be verified by traditional observations (e.g., by making videos of the GPS data), while it should be feasible to extend machine learning approaches for detecting patterns in temporal data to extract interactions from GPS trajectories.

3.3 Constructing social networks

Whereas association events or interactions can be inferred from singular snapshots of spatial positions, social relationships between individuals are typically quantified from the tendency for individuals to associate or interact over (observation) time. The simple ratio index (SRI) defined as the number of observations of two individuals together divided by the total number of observations involving either of them (Hoppitt & Farine 2018), is commonly used to calculate relationship strength. However, this SRI formula needs to be modified for GPS data, as an observation of individual A without individual B is only informative if B is confirmed elsewhere (i.e. both A and B have a data point, either together or apart). Therefore, the denominator of the formula should only include observations where GPS data are simultaneously available for both individuals.

The trade-off between sampling frequency and sampling duration is critical in GPS-based social network studies. High sampling frequencies (e.g., 1 Hz) are robust in capturing how association events or interactions change from one time point to the next (Hobson, Avery & Wright 2013; Farine 2018). However, substantial data under high sampling frequency in short periods can create a false sense of certainty when defining relationships, which play out over months or years (e.g., spanning inter-reproductive periods). Lower sampling frequencies (e.g., every hour) will fail to capture the moment-by-moment dynamics of social associations or interactions, but may be better at capturing how relationships change (or not) over time. Both the changes in associations or interactions and the changes in relationship strengths can be studied using dynamic networks, but represent different dimensions of social behaviours.

4. SOCIAL BEHAVIOURS WITHIN GROUPS

In cohesive groups, the spatial behaviours of group members are typically shaped by those of others (Farine *et al.* 2017). However, it remains unclear how GPS coverage within a social group (which is often the foremost consideration when designing a study) affects the inferences made about individuals' spatial position in their group and the spatial properties of groups (Fig. 2). To address this gap, we evaluated how sub-sampling influences inferences of individual and group spatial behaviours (see 4.1 and 5.1, respectively), using GPS tracking and simulated data (see Box 1 for methods).

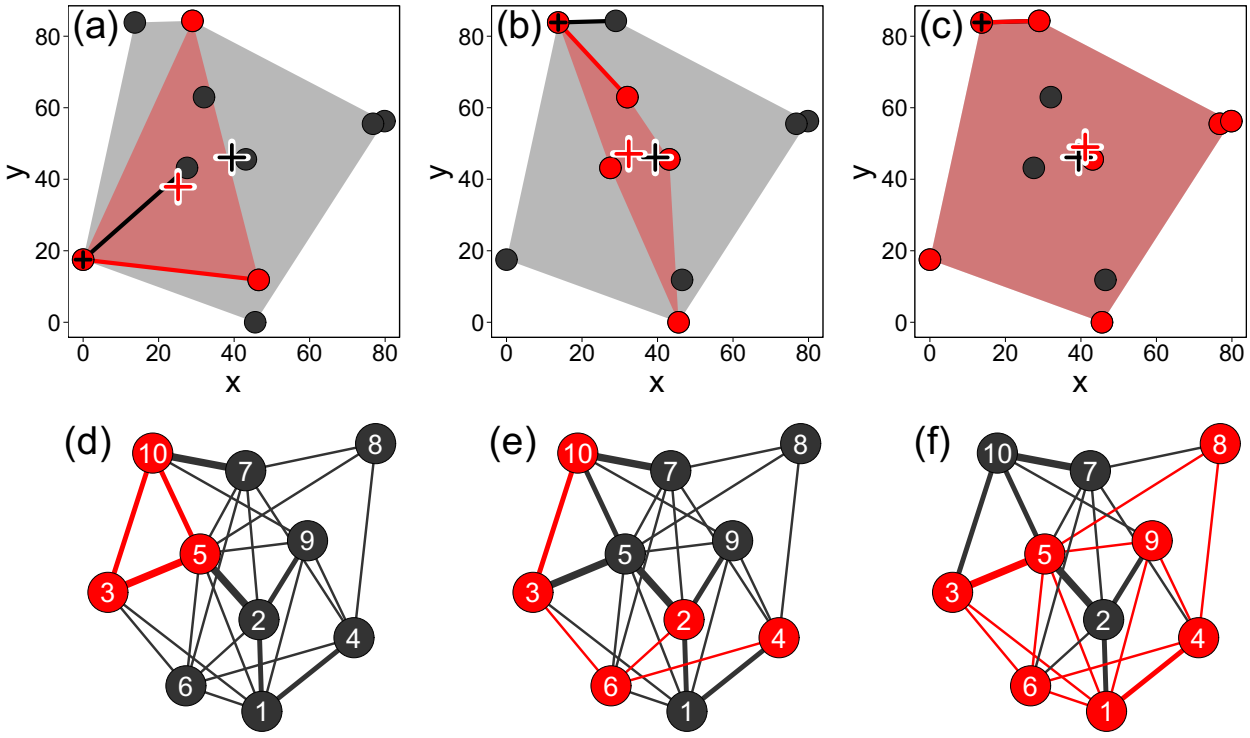

Fig. 2 An illustration of the effects sub-sampling on estimates of individual- and group-level properties. Deploying GPS devices on a subset of group members

305 (black=all group members, red=sampled individuals) can impact behavioural measures.
306 At the individual-level, subsampling influences the accuracy of estimates in the identity of,
307 and distance to, the nearest neighbours (e.g., red focal individuals marked with a cross
308 in a–c as members in smaller subsamples have different nearest neighbours and larger
309 nearest neighbour distances); at the group-level, subsampling influences the accuracy of
310 estimates in group spatial coverage (i.e., MCP, the minimum convex polygons, a–c) and
311 the geometric centroid of the spatial positions of individuals (large bold crosses, a–c).
312 Subsampling can eventually influence inferences on social association network structures
313 (d–f, corresponding to a–c).

314 **4.1 Estimating individuals' spatial positions within groups**

315 Individuals' spatial positions relative to other group members can influence vulnerability
316 to predation (Barta, Flynn & Giraldeau 1997), foraging competition with group-mates (Gall
317 & Manser 2018), or availability to receive information from social partners (Rosenthal *et*
318 *al.* 2015). When inferring such positions, there is a trade-off between the accuracy of
319 estimates and sampling coverage. Increasing the proportion of tracked individuals results
320 in exponential decreases in error of estimates of distance to nearest neighbour and spatial
321 centrality (surroundedness) (Fig. 3). Both empirical and simulated data suggest that,
322 regardless of group sizes, studies can miss up to half of the individuals in a group while
323 still being able to make accurate estimates of nearest-neighbour distances (i.e., median
324 error <1 m when 50% tracked, Fig. 3-a, i-iii). While error sizes are generally small, it is
325 worth noting that any non-zero error would also result in mis-assignment of the identities
326 of such neighbours (Fig. 2; the chance of mis-assignment is the same as the proportion

of non-tracked individuals in groups). For surroundedness (Fig. 3-b, i-iii), reliably accurate estimates require a larger proportion (≥60%) of a group to be GPS-tracked, especially in smaller groups (Fig. 3-b i,iii). The relationship between GPS coverage and error is well captured by an exponential curve (see Table S1). In all cases, lower GPS coverage is necessary in larger groups.

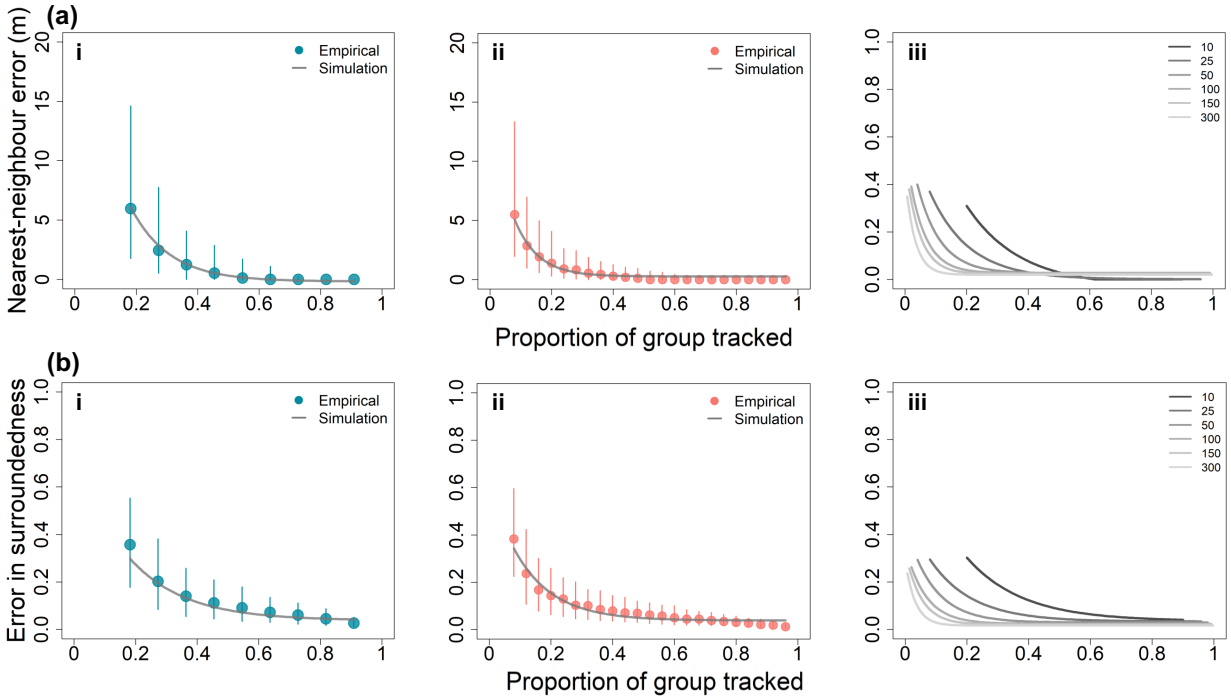

Fig. 3 Error in estimates of the nearest-neighbour distance (a) and surroundness (b) decrease exponentially with increasing GPS coverage. (i-ii) Tracking data from two vulturine guineafowl groups (i: N = 11; ii: N = 25) randomly subsampled to explore the effects of GPS coverage on estimates of individuals' spatial positions in groups. Points represent the median error of estimates from the subsampled empirical data, with vertical bars showing the 1st and 3rd quartiles of errors. Curves represent the predicted median error of estimates from exponential models (Table S1) fitted to simulated data matching

the spatial extents and group sizes in empirical data. (iii) Curves showing the exponential relationship between GPS coverage and error drawn from simulated data with varying group sizes (Table S2).

4.2 Collective movement and decision-making

A typical characteristic of group-living animals is the emergence of collective behaviours (Sumpter 2006). For instance, groups of fish engage in collective schooling behaviour to reduce predation risk to any individual (Herbert-Read *et al.* 2017), whereas griffon vultures (*Gyps fulvus*) forage in a 'sky network' where individuals learn about available food sources by observing the behaviour of their neighbours (Cortés-Avizanda *et al.* 2014). Studying collective behaviours requires perhaps the greatest observational effort (Strandburg-Peshkin *et al.* 2015; Hughey *et al.* 2018), comprising high-spatiotemporal-resolution movement data (high sampling frequency) and high GPS coverage in order to capture the transient socio-spatial dynamics that produce collective outcomes. To date, most studies have been conducted in semi-wild systems, such as homing pigeons (Pettit *et al.* 2013; Sankey *et al.* 2021), where individuals can be easily recaptured to apply and remove GPS devices. However, the limitations of sampling frequency can be overcome by focussing sampling effort to discrete periods to maximize the collection of simultaneous high-resolution data. For example, solar-powered GPS devices on vulturine guineafowl are given three days to recharge so that all devices have full batteries to collect high-resolution at the same time every fourth day (Box 2).

5. BEHAVIORS AMONG GROUPS

Assessing behaviours at the group level can reveal inter-group behavioural variability and the influences that groups exert on each other. One prominent way in which groups vary is in their movement characteristics—for instance, meerkat groups emerge from their burrows at different times of day (Thornton, Samson & Clutton-Brock 2010), and vulturine guineafowl groups differ in home range size and daily travel distance (Papageorgiou & Farine 2020a). Most simply, the behaviour of a group (or groups) can be inferred from a GPS-tracked group member (Papageorgiou & Farine 2020a; Papageorgiou *et al.* 2021). This can, for example, capture how groups interact with each other, for instance via inter-group social interactions (Crofoot *et al.* 2008; Papageorgiou *et al.* 2019) or dispersing individuals (Alberts & Altmann 1995; Armansin *et al.* 2020; Klarevas-Irby, Wikelski & Farine 2021). However, there is currently little guidance on how many GPS-tracked individuals are required to characterise other group-level properties. Metrics such as the precise location of the group (e.g., for habitat selection of groups) or the level of spatial dispersion of group members (e.g., as an indirect measure of risks) will be more precise as more individuals are tracked. Further, studying behaviours such as inter-group interactions or associations—which are substantially rarer than within-group interactions (e.g., when only a small proportion of individuals in each group infrequently interact or associate with others from different groups)—will generally require deploying more GPS devices per group (Box 2) and increasing GPS sampling duration.

380 **5.1 Behavioural characteristics of groups**

381 Group location (i.e., the geometric centroid of all individuals) and spatial dispersion (i.e.,
382 the total area covered by a group) are fundamental metrics characterizing group-level
383 behavioural patterns. Using both empirical and simulated data (Box 1), we find that
384 estimating the precise location of cohesive groups is relatively robust to low GPS
385 coverage. In vulturine guineafowl, as few as two tagged individuals can estimate a group's
386 centroid with <5 m of error (Fig. 4-a, i-ii), which is small given that groups can travel up to
387 10kms per day (Papageorgiou *et al.* 2021). For both simulated and empirical data, the
388 relationship between GPS coverage and centroid estimation error follows a negative
389 exponential relationship (Fig. 4a). As such, unless extremely precise locational
390 information is needed, the spatial location of groups can be sufficiently estimated with as
391 few as 1-3 devices per group, regardless of group size. By contrast, estimating a group's
392 spatial dispersion [e.g., the area of a minimum convex polygon (MCP) containing all group
393 members] requires the majority of the group to be marked, especially in smaller groups
394 (Fig. 4-b, i-iii). Even with very high GPS coverage (e.g., >80%), measures often
395 underestimated the dispersion of the group by 20% or more. The relationship between
396 GPS coverage and spatial dispersion error is well captured by a negative exponential
397 function (Fig. 4b).

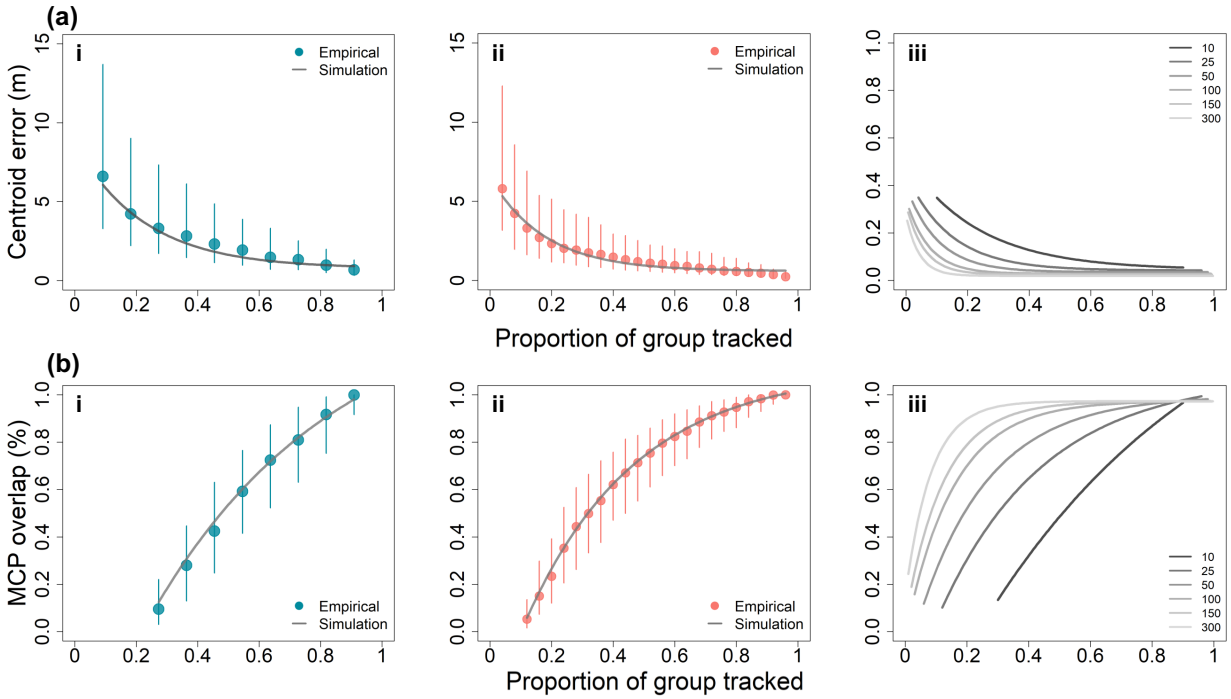

Fig. 4 Error in estimates of group centroid (a) and spatial dispersion (b) decrease exponentially with GPS coverage. (i-ii) Tracking data from two vulturine guineafowl groups (i: N = 11; i: N = 25) and simulated data randomly subsampled to explore the effects of GPS coverage on estimates of group position and dispersion. Points represent the median error of estimates from the subsampled empirical data, with vertical bars showing the 1st and 3rd quartiles of errors. Curves represent the predicted median error of estimates from exponential models (Table S1) fitted to simulated data matching the spatial extents and group sizes in empirical data. (iii) Curves showing the exponential relationship between GPS coverage and error drawn from simulated data with varying group sizes (Table S2).

409 **5.2 Inter-group relationships**

410 Groups influence each other through the dispersal of individuals (Alberts & Altmann 1995;
411 Bond *et al.* 2021), associations between groups (Qi *et al.* 2014; Papageorgiou *et al.* 2019;
412 Henriquez *et al.* 2021), or agonistic interactions (Thompson *et al.* 2017; Dyble *et al.* 2019).
413 Studying dispersal requires deploying GPS devices to both dispersers and to the groups
414 that these dispersers might move between. In such cases, a single tagged resident
415 individual in each group is likely to be sufficiently informative if group membership is highly
416 stable. Studying intergroup associations follows the same principles as studying
417 associations among individuals (see 3.1), where the unit of focus (i.e., groups) can be
418 meaningfully represented by a single individual if the scale over which groups are spread
419 is small relative to the space over which groups move. Finally, while studying agonistic
420 interactions among groups broadly follows the same principles as studying interactions
421 among individuals, there may be additional challenges. Groups may detect each other
422 over large distances and be more likely to passively avoid interactions (e.g., through scent
423 marking; Christensen *et al.* 2016), leaving the spatial scale at which groups interact
424 unclear. Further, not all individuals might contribute equally to inter-group interactions,
425 meaning that consideration should be put regarding who to deploy GPS devices onto.

6. SOME STRATEGIC CONSIDERATIONS

Besides the constraints outlined above, several other factors should be considered when deploying GPS devices to study social behaviour. Below we list and discuss a few of these, and in Box 2 we outline how we deployed GPS devices and programmed these to achieve the multiple aims of our vulturine guineafowl project.

6.1 Redundancy

In most cases, studies should consider tracking extra individuals in each group beyond the minimum required for the study design. For example, while the locations of each cohesive social group might be captured by a single group member, its GPS device could fail or the individual could die. Further, when using mixed GPS sampling strategies (see 6.3), having multiple individuals in each group can maximise the probability of at least one individual collecting higher resolution data.

6.2 Partitioning sampling effort in time

It can be useful to vary GPS sampling across time to focus data collection on certain time windows over others. For example, diurnal species are largely inactive at night (Isbell *et al.* 2017; but see Loftus *et al.* 2021), meaning that GPS devices are often switched off at night to conserve battery. It can also be worthwhile to program devices to increase sampling frequency during periods when animals are more active (e.g., morning and/or evening), or decrease sampling frequency during seasons when conditions are less optimal for data collection (e.g., during breeding seasons, Box 2). However, when doing

so, it is worth considering whether partitioning sampling in time could introduce biases or result in incorrect inferences.

6.3 Mixed GPS sampling frequencies

The major trade-off is between sampling frequency and sampling duration. Even with solar-powered GPS devices, the capacity to collect high-resolution data across entire days is limited (Box 2). A solution to this is to use a mixture of sampling regimes—having some individuals deployed to prioritise shorter bursts of higher sampling frequencies and some individuals prioritised to capture long-term sampling. With solar-powered devices, it is often possible to programme devices to switch from low– to high-resolution as the battery charges (Box 2). Such an approach can allow devices to work in a collaborative way.

6.4 Supplementing GPS tracking with other observational data

A key limitation of GPS tracking data for inferring social behaviours is that observers are blind to the absence/presence of untracked individuals in close spatial proximity. GPS tracking studies can therefore benefit from supplementary observational data (Smith & Pinter-Wollman 2021). Behavioural patterns revealed by observational data can be the ground-truth to those inferred with GPS tracking data, and can be used to evaluate the extent to which data derived from a given deployment of GPS sampling are able to capture true behavioural patterns in animal societies. However, integrating GPS and non-

465 GPS data into the same analysis introduces data compatibility challenges, and
466 approaches for harmonizing such datasets warrant further development.

467 **6.5 Combining GPS data with other sensors**

468 Modern GPS tracking studies use additional sensors (Williams *et al.* 2020), such as
469 accelerometers, gyrometers (Marin 2020), heart rate monitors, or body temperature
470 loggers (e.g., Linek *et al.* 2021). Such data can substantially increase the dimensions of
471 information researchers can retrieve about animals' behaviours (e.g., Harel, Loftus &
472 Crofoot 2021). Movement-related sensors can improve data on trajectories by allowing
473 tracks between GPS fixes to be reconstructed using dead reckoning (Wensveen, Thomas
474 & Miller 2015). This can effectively increase sampling frequency with minimal additional
475 battery consumption.

476 In a social context, acceleration data could be useful when inferring dyadic social
477 interactions such as inter-individual displacements (Strandburg-Peshkin *et al.* 2015),
478 individual behavioural states (Chimienti *et al.* 2016), or behavioural synchrony among
479 individuals (Strauss *et al.* 2021). Further, information about environmental contexts social
480 animals experience could also be inferred from the GPS devices themselves, such as
481 measuring solar exposure (e.g., whether an animal is under cover or not) from changes
482 in GPS battery voltage in solar-powered devices. However, additional sensors increase
483 battery consumption (albeit often a lot less than the GPS sensor itself), and can
484 substantially increase the cost of data storage, retrieval, and management, especially in
485 large-scale studies (Box 2). Furthermore, although some devices come with multiple
486 sensors onboard (e.g., combined GPS sensor and accelerometer), others might require

integrating a separate device along with the GPS device. This can be physically challenging (e.g., there may not be room for a second sensor or device, or exceed weight limits), and for studies requiring synchronization between data streams, communication must be established between the devices or sensors.

7. CONCLUDING REMARKS

GPS tracking is a powerful tool for studying social behaviour, but studies face many trade-offs. Drawing from previous studies, and new empirical and simulated data, we have illustrated how sampling coverage, sampling duration, and sampling frequency can be optimised to address different research questions. For example, many social measures—of individuals within groups (e.g., spatial position) or of groups themselves (e.g., centroids)—can be reliably estimated by tracking relatively few group members. Other measures, such as social interactions among individuals, social processes, or the spatial dispersion of groups, require more intensive sampling frequencies or greater coverage of individuals. We caution against aiming to sample at the highest frequency possible at the cost of sampling duration, and instead suggest that most studies of social behaviour will benefit from prioritising stratified sampling over a longer duration. A good rule of thumb is to sample at the lowest frequency possible that still captures the behaviours under study (e.g., the majority of GPS devices deployed to guineafowl are programmed with the population regime, Box 2). Although our discussion here has focused on cohesive groups, such rules may also apply in non-cohesive groups. However, open societies with fluctuating group membership and size present a different challenge for GPS-based

research, as the pool of individuals from which to sample is often unclear and our findings at the group level are likely to be relevant for whole populations. In general, while there are multiple trade-offs involved at the same time when designing GPS-based studies, there are likely to be optimal sampling strategies to suit most research questions.

Box 1. Our empirical data is drawn from two social groups of vulturine guineafowl (N = 11 and N = 25) in which all members were simultaneously tracked. We randomly selected 100 time stamps from the tracking data, spanning several months, from each group. At each time stamp, the data were subsampled by randomly removing group members [producing groups of size 1 to (N-1)], with each level of sub-sampling repeated 10 times (i.e., producing 10 combinations of subsampled individuals for each time stamp). We then extracted four spatial measures describing individual positions and group properties: the distance from some focal individual to its nearest neighbour (a common measure of social association), the spatial centrality of a focal individual within the group (i.e., 'surroundedness', or 1 – CV, where CV is the circular variance of the vectors pointing to the focal individual; see Christman & Lewis 2005 for CV), the spatial position of the entire group (the geometric centroid of all sampled individuals' positions), and the spatial spread of the group [represented by the area of the minimal convex polygon (MCP) containing all sampled individuals]. The effect of sub-sampling on each measure was quantified as the error between the "true" value derived from the full group data and the "observed" value derived from the subsampled individuals only. For nearest-neighbour distance and centroid, the error was defined as the point-to-point distance from the true position (of the spatially-nearest neighbour or the original centroid, respectively) to the observed position (of the nearest remaining neighbour or the new centroid). Error in surroundedness was defined as the difference between the true and observed circular variance for some focal individual included in the subsampled group. Error in group spread was defined as the percent overlap between the MCPs of the subsampled and original group.

We then simulated data to confirm the relationships between GPS coverage and error. First, for each time stamp in the empirical data, we simulated empirically derived groups (N=11 and N=25), where simulated individuals' X and Y coordinates were drawn from a uniform distribution with the same spatial boundaries as the empirical snapshot. We simulated 100 empirically derived group observations to match each time stamp in the empirical data, and subsampled and measured these following the same procedure as empirical groups.

Second, to examine the general effects of GPS coverage on the accuracy of individual- and group-level behavioural estimates, we complemented our empirical dataset and empirically-informed simulations with purely simulated groups varying in size from 10 to 300. Here, X and Y coordinates were drawn from uniform distributions between 0 and 1. We simulated 100 group observations for each group size, which were subsampled and measured following the same procedure as empirical groups.

Box 2. The GPS-based vulturine guineafowl project was established at Mpala Research Centre in central Kenya in 2016 to study social dynamics within and across groups, at timescales spanning from moment-by-moment movement to lifetime ranging. A pilot study on group membership of a small number of colour-banded individuals and five GPS-tracked birds (15 g, solar-powered devices, e-obs Digital Telemetry, Grünwald, Germany) showed that group compositions and sizes were highly consistent. The study also confirmed the advantages of using solar-powered GPS devices in an equatorial savannah environment—solar conditions there allow for consistent GPS sampling throughout the year from 06:00 to 19:00. Subsequently, more solar-powered GPS devices were deployed to individuals both within and across groups. Specifically, we tracked 2-3 birds per group but distributing sampling effort across as many groups as possible (eventually with a coverage of an entire population consisting of >20 groups). GPS sampling effort was designed to prioritise population-level behavioural patterns, by programming the devices to switch on for a 10-second sampling window every 5 minutes (i.e., the 'Population regime', Table 1). A burst of 10 fixes optimizes accuracy of GPS fixes as the battery costs per fix are minimal, and later fixes in each burst are generally more accurate because satellite coverage (i.e., the number of satellites communicating with the device) increases over the time the devices remain on. To take advantage of solar power, devices were programmed to sample at high frequency (i.e., 1 Hz sampling for 15 minutes at a time) when battery charge was high. Every bird in each group was also colour-banded to facilitate visual identification, regardless of whether they were GPS tagged or not. Combining twice-weekly observations field observations of group membership and size with our population-level GPS data shed light on the underlying patterns of social

associations among individuals (both within and across groups), revealing the multilevel social structure of the whole population (Papageorgiou *et al.* 2019). Over time, continued measurements further revealed how group size affects movement and ranging (Papageorgiou & Farine, 2020a) and how groups use the landscape across seasons (Papageorgiou *et al.* 2021).

Under the population-level sampling regime (Table 1), devices collect data at high sampling frequency approximately 25% of the time, suggesting that it is feasible to collect extensive movement data with high temporal resolution. However, variation in battery charge can lead to asynchrony across devices. To study within-group social dynamics (e.g., how groups make decisions), every bird in each of two focal groups (Box 1) was GPS-tracked and devices were programmed to collect data on the same day, every fourth day, spending the intervening days recharging (except for two birds in each group with devices programmed with the population regime to track daily ranging). This 'high-res' regime (Table 1) ensures that all devices collect >6 h of synchronous, fine-temporal-scale movement data of all individuals on each operating day. Such data have supplemented observational data to infer how individuals respond to group decisions (Papageorgiou & Farine 2020b), and to characterise other aspects of group behaviour, as in this study.

Field observations revealed that males are philopatric while females disperse. Thus, devices were primarily deployed onto males for long-term data collection. As some adult females bred, GPS devices were also deployed to these females for opportunities to find nests and to study incubation behaviours. However, the batteries of devices deployed on these breeding females often struggled to maintain an adequate charge due to poor solar

conditions—incubating birds can stay under dense vegetation for up to 25 days at a time (Nyaguthii 2021). We benefited from the ability to remotely program devices—reducing sampling frequency to one fix per 15 minutes ensured the capacity of batteries to cover the whole incubation period. To study dispersal behaviours, subadult females were GPS-tracked (Klarevas-Irby, Wikelski & Farine 2021). In this case, new devices were deployed to ensure maximum battery power (sampling at high frequency covering ca. 30% of the time in a day). Comparing fine-scale movements of dispersers with residents relied heavily on the ability to have at least one device in each group sampling at high frequency at any time (facilitated by having multiple tagged individuals per group).

Overall, the project has had as many as 121 simultaneously GPS-tracked birds, and many challenges have arisen in project maintenance and data management. For example, each device produces ca. 500 MB of tracking data approximately every 10 days, that requires up to 4 h of downloading time every second day. This is in addition to extensive effort and time needed to regularly check and maintain deployed devices, and to recover devices when individuals are predated. To partially address these challenges, the accelerometer sensors integrated into our devices have been turned off, as the resulting data streams would prove infeasibly large for our current download regime (but the devices can be re-programmed for collecting acceleration data if desired).

	Population	Group	Individual
Sampling coverage	1–6 individuals per group, averaging 1 device per 10 group members	All individuals in a group	Individuals of interest (e.g., subadult females, incubating females)
Sampling duration	Prioritise long-term (lifetime of individuals)	Medium-term (seasonal)	Focused (e.g., breeding season, dispersal period)
Sampling frequency	Population regime (every day): *Highest battery charge*: 1 Hz *Medium battery charge*: 10 fixes every 5th minute *Low battery charge*: 1 fix every 15th minute	High-res regime (every 4th day): 1 Hz from 06:00 until battery depletes, and 2 birds per group following the population regime	Specific regimes, e.g.: *Dispersal*: population regime *Breeding*: 1 fix every 15th minute

614 **Table 1. Overview of GPS sampling strategies for the vulturine guineafowl project.**

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AUTHORS' CONTRIBUTIONS

PH, JAKI and DRF conceptualized the study. PH and JAKI conducted the analyses. PH drafted the manuscript and all authors contributed critically to the revisions and gave approval for publication.

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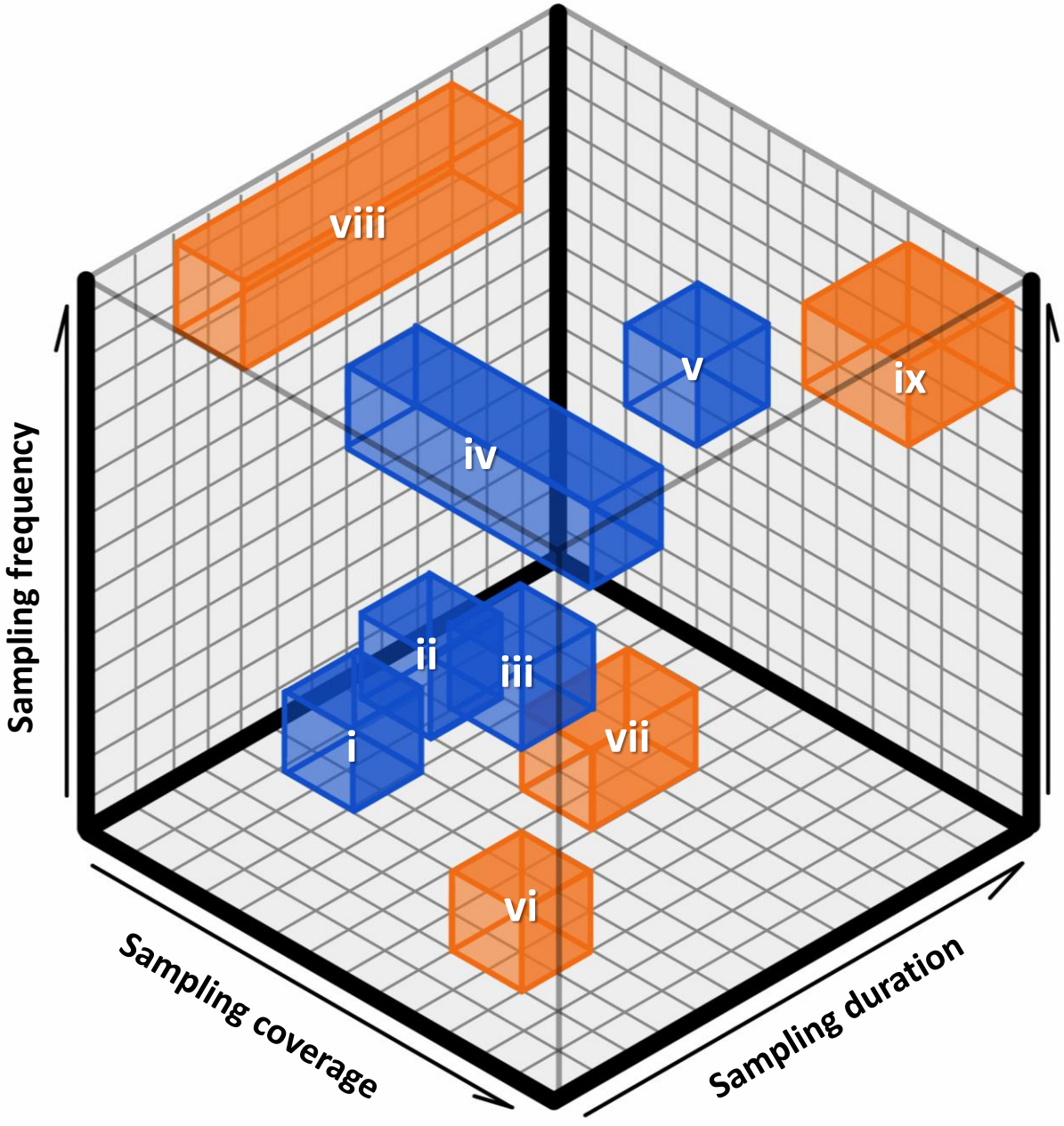
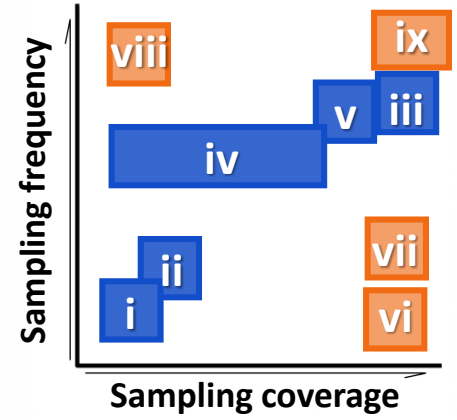
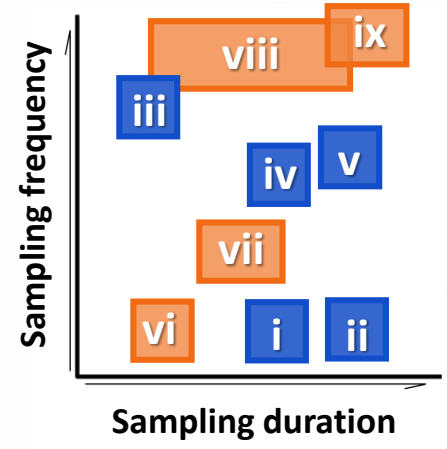
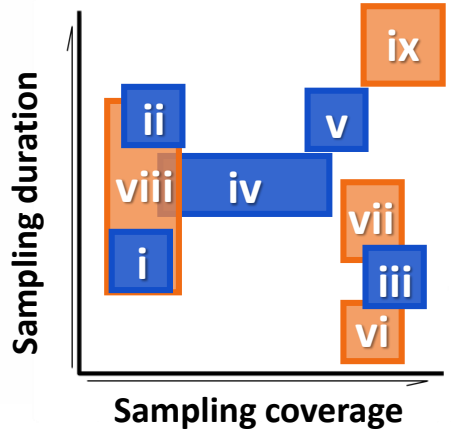






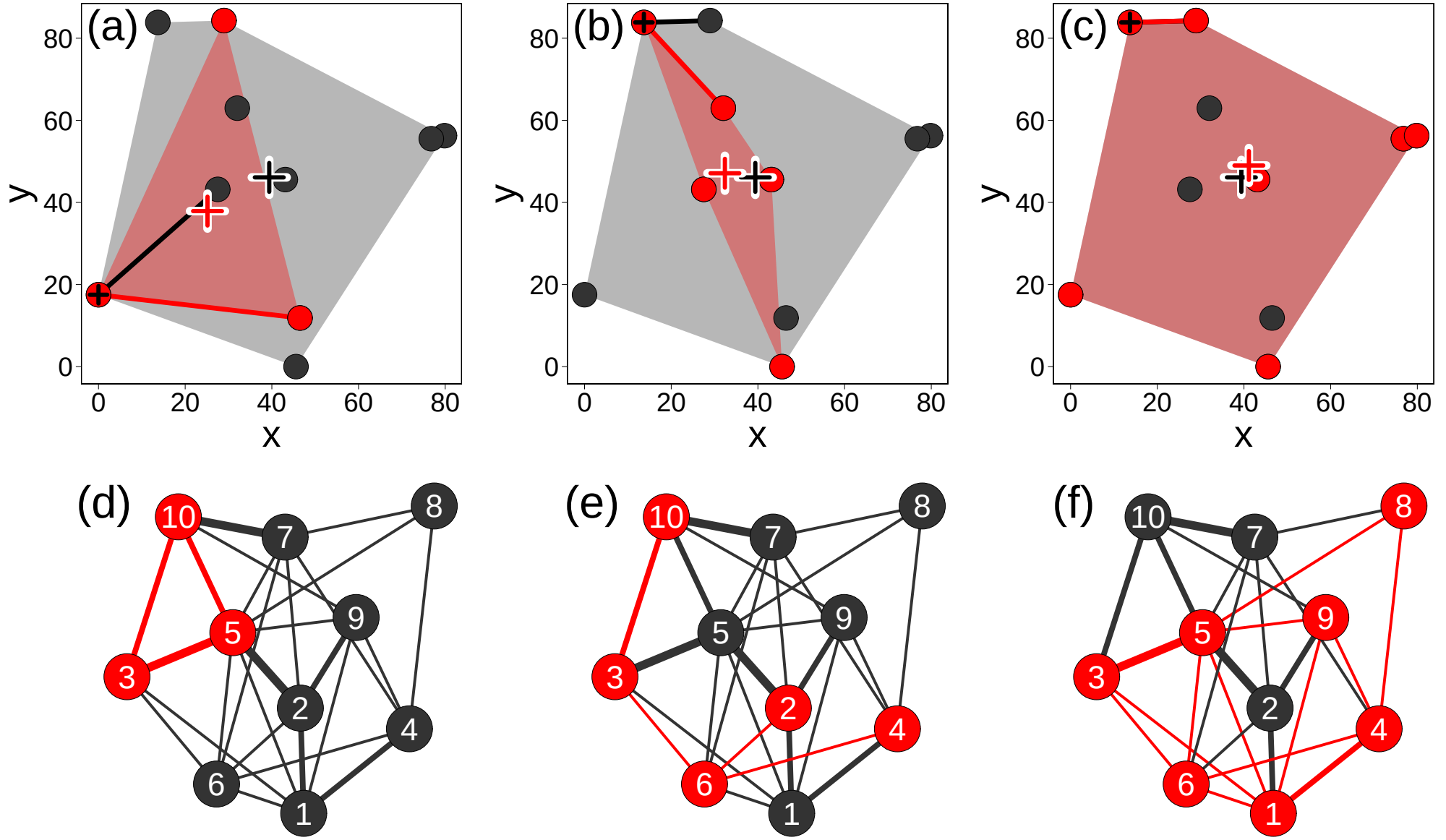


Group-level measurements

i. Group ranging behavior
ii. Intergroup associations
iii. Collective dynamics
iv. Group movement
v. Intergroup interactions

Individual-level measurements

vi. Within-group associations
vii. Interindividual associations (open societies)
viii. Energetics
ix. Social interactions


(a)
(b)
(c)
(d)
(e)
(f)
x
y
0
20
40
60
80
1
2
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6
7
8
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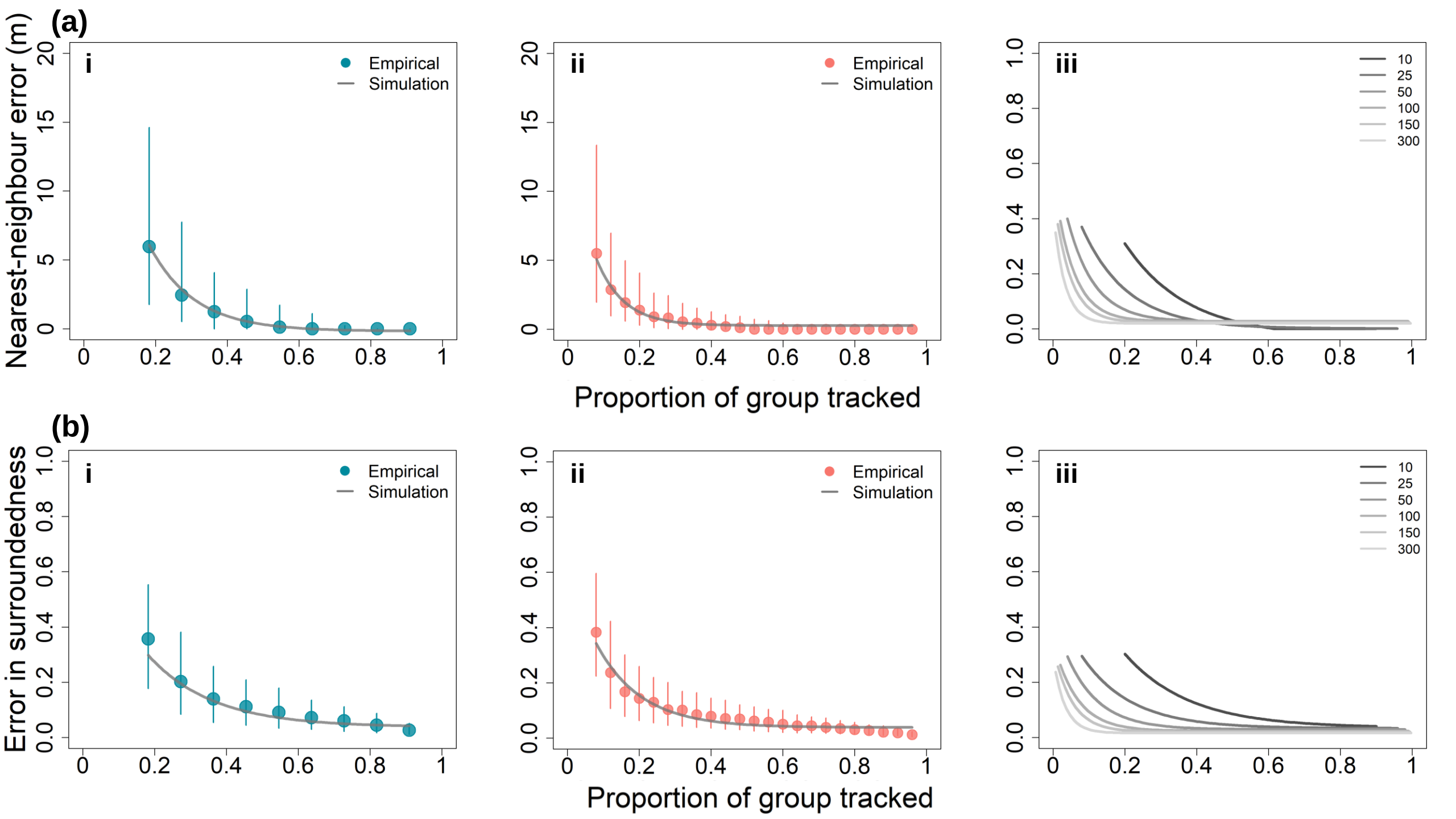
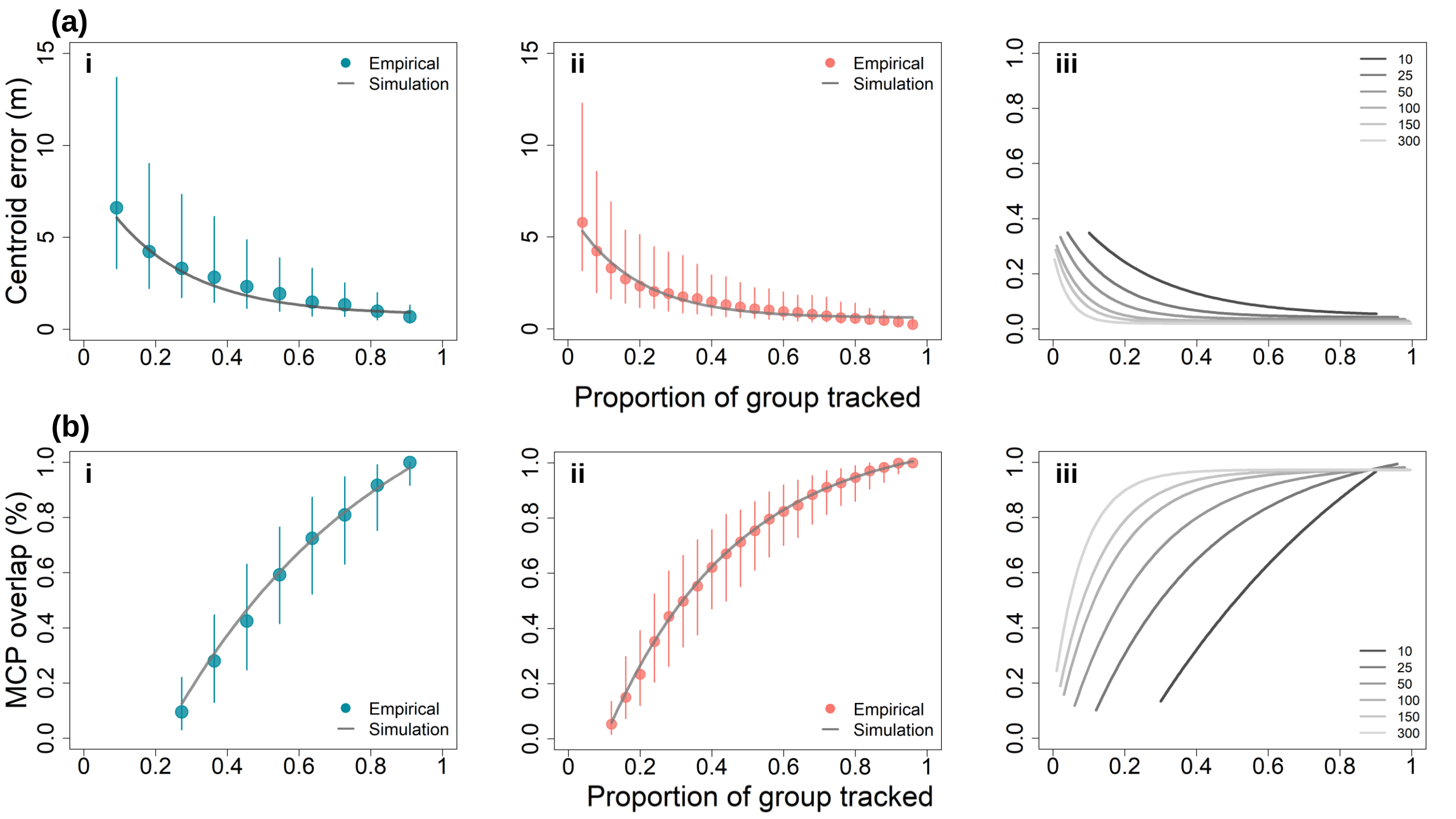
10


(a)
Nearest-neighbour error (m)
i
Empirical
Simulation
ii
Empirical
Simulation
iii
10
25
50
100
150
300
Proportion of group tracked
(b)
Error in surroundedness
i
Empirical
Simulation
ii
Empirical
Simulation
iii
10
25
50
100
150
300
Proportion of group tracked


(a)
i
ii
iii
Empirical
Simulation
Centroid error (m)
Proportion of group tracked
10
25
50
100
150
300
(b)
MCP overlap (%)