Commentaries

Home range size and location in relation to reproductive resources in poison frogs (Dendrobatidae): a Monte Carlo approach using GIS data

Jason L. Brown [a,*], Victor Morales [b,1], Kyle Summers [a]

[a] Department of Biology, East Carolina University
[b] La Facultad de Ciencias Biológicas, Universidad Ricardo Palma

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GIS assumes an increasingly prominent role in niche modelling, particularly for those applications that either predict a species' niche or estimate the environmental factors that determine a species' distribution. The use of GIS to model population-level distributions has received considerably less attention. We developed a Monte Carlo method designed to test for statistical associations between population distribution and different types of spatial data. This method examines the spatial distribution between species presence points and distance to key vegetation, comparing the association for the observed data to that of a random data set. Poison frogs (genus *Dendrobates*) display a diverse array of complex parental care strategies, which are linked by an elaborate network of interactions between ecological and social factors. Territorial species vary significantly in their associated reproductive strategies, reproductive resources and size. Species with higher levels of cooperation in parental care have been hypothesized to be more strongly territorial. Here we investigate differences in spatial use patterns between two species of poison frogs, *D. imitator* and *D. variabilis*, that differ in parental care type (uniparental male care versus biparental care, respectively). We predicted that: (1) *D. imitator* would be more closely associated with phytotelmata than would *D. variabilis;* (2) home ranges of *D. imitator* pairs would be more inclusive and overlap more than those of *D. variabilis* pairs; (3) *D. imitator* pairs would maintain smaller home ranges than *D. variabilis* pairs; (4) *D. imitator* pairs would maintain spatially exclusive home ranges. Our results strongly support the prediction that differences in parental care of these two species are reflected in their spatial habitat use, particularly with regard to pool fidelity, territoriality, and home range size and overlap.

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Many factors govern the spatial distribution of organisms, ranging from abiotic (e.g. geography, soil types, rainfall, salinity, temperature and humidity) to biotic (e.g. vegetation, community structure, trophic and reproductive resources). In recent years a great deal of attention has been given to modelling species' niches using geographic information systems, GIS (e.g. Pearce & Ferrier 2000; Anderson et al. 2002; Phillips et al. 2006). Most of these models both predict a species' niche and estimate which environmental factors play a major role in their distribution. These models have greatly increased our understanding of species' distribution ranges, niche composition and taxonomic status (e.g. Raxworthy et al. 2003; Graham et al. 2004; Stockman & Bond 2007). Although the use of GIS to understand the spatial distributions of species has dramatically increased, considerably less attention has been given

to population-level distributions, where factors such as predation risk, competition and resource abundance govern spatial population structure (Fretwell 1977; Werner & Hall 1977; Sih 1982; Resetarits & Wilbur 1989). At the population level, GIS has mainly been used to estimate home ranges and territories (Sinervo et al. 2000; Pröhl & Berke 2001; Pröhl 2002). Currently, there are no GIS methods available to statistically test explicit associations between two types of spatial data at a population level (i.e. vegetation type and species encounter data). Connecting patterns of spatial location to specific resources is not a trivial task, and given the nature of species encounter data, the use of parametric statistics is not valid because the data are nonrandom and dependent.

Here we develop a Monte Carlo method to test for statistical associations between different spatial variables. This method compares the spatial distribution between species' presence points and distance to key vegetation types, by comparing the association of the observed data to that of a random data set. Binary logistic regression or multivariate logistic regression techniques can test for general spatial associations; however, these methods focus on creating models that generate maps representing occurrence probabilities and do not explicitly test the statistical significance of

* Correspondence: J. L. Brown, N312 Howell Science Complex, East Carolina University, Greenville, NC 27858, U.S.A.
E-mail address: jlb0627d2@ecu.edu (J.L. Brown).
[1] V. Morales is at the La Facultad de Ciencias Biológicas, Universidad Ricardo Palma, Lima, Peru.

the association between two factors (Hosmer & Lemeshow 2000; Pearce & Ferrier 2000; Gelfand et al. 2005). The Monte Carlo method is simpler than these methods; it does not rely on complicated models or the use of absence points (points where the species have not been observed), which are problematic at the population level (i.e. given the movement of individuals throughout their habitat, it is not possible to confirm the veracity of absence points).

The ability to test for correlations between spatial data would make an important contribution to ecological, behavioural and evolutionary research. For example, the distribution of reproductive resources has a profound influence on the spatial distribution of organisms, and is likely to affect the nature of the species' reproductive system (Emlen & Oring 1977). A considerable amount of research in passerine birds has focused on the relationships between key resources and mating systems (e.g. Arnold 1999; Hatchwell 2007; Rubenstein 2007). In dunnocks, *Prunella modularis*, the structure and abundance of key resources strongly influence home range sizes, which in turn determine whether the species will be monogamous, polygynous or polyandrous (Davies 1992). Testing for correlations between reproductive resources and individual presence was a key motivation in developing this Monte Carlo method, and its broad application could greatly improve comparative studies for which quantifying associations between resources is important.

Poison frogs of the genus *Dendrobates* (sensu Silverstone 1975) display a diverse array of parental care strategies, from male parental care to biparental care (Summers & Amos 1997; Summers & Earn 1999; Summers & McKeon 2004). In all species in this genus, egg clutches are attended by a parent, and tadpoles are transported after hatching by one parent to a suitable water source. Most tadpoles are cannibalistic and are typically placed individually in pools. The most common parental care strategy is uniparental male care, in which clutch attendance and tadpole transportation are done by the male. In some species, these duties are split by both sexes (asymmetrical biparental care or biparental care), or taken over by the female entirely (uniparental female care). Species with female parental care, asymmetrical biparental care and biparental care have evolved novel behaviours, such as the use of very small phytotelmata (e.g. bromeliad axils); for example, in many species, adult females provide trophic eggs to their larvae (Weygoldt 1980; Brust 1993; Caldwell & de Oliveira 1999). These complex reproductive strategies are linked in an elaborate network of interactions between ecological and social factors. Variation occurs among species in many traits, including the type of reproductive resources utilized (e.g. the type of pool used for tadpole deposition), mating system, and home range and territory size (Caldwell & de Oliveira 1999; Pröhl & Berke 2001; Pröhl 2005). Species with high levels of cooperative parental care have been hypothesized to be more aggressively territorial (Caldwell & de Oliveira 1999; Pröhl & Berke 2001), although this has not been tested explicitly.

In a previous study we described differences in territoriality, reproductive resource utilized, parental care type, mating system and site fidelity between two sympatric species of Peruvian poison frogs, *D. variabilis* and *D. imitator* (Brown et al. 2008). The aim of the present study was to investigate differences in space use between these same two species of poison frogs, one of which has uniparental male care (*D. variabilis*) and one of which has biparental care (*D. imitator*). *Dendrobates imitator* uses small phytotelmata, has biparental care (with trophic egg-feeding) and a socially monogamous mating system. In contrast, *D. variabilis* uses large phytotelmata, has uniparental male care and a highly promiscuous mating system (Brown et al. 2008). We tested the following hypotheses in the context of these two parental care types.

(1) *Dendrobates imitator* is more closely associated with phytotelmata than is *D. variabilis*. Given the increased offspring investment and reduced number of offspring in biparental care species, the fitness costs of competition and cannibalism are much higher. Therefore, *D. imitator* should maintain exclusive use of pools, spending more time in close proximity to pools, monitoring them, and returning frequently to feed tadpoles with trophic eggs (Brown et al. 2008).

(2) The home ranges of males and females in *D. imitator* breeding pairs are more strictly overlapping than those of *D. variabilis* breeding pairs. Species with biparental care may form pair bonds, remaining together for extended periods. Furthermore, when providing trophic eggs for multiple tadpoles, pair members often interact daily (Caldwell & de Oliveira 1999; Brown et al. 2008). These interactions should result in largely overlapping home ranges.

(3) *Dendrobates imitator* breeding pairs maintain smaller home ranges than *D. variabilis* breeding pairs. Biparental care species should maintain smaller home ranges, allowing them to monitor phytotelmata within their ranges more effectively and defend range boundaries with greater diligence.

(4) *Dendrobates imitator* breeding pairs should maintain exclusive home ranges. Exclusive pool use is critical for biparental care species (see above); hence, adjacent home ranges should not overlap.

To our knowledge this is the first study to investigate the spatial association between reproductive resources and the spatial distribution of an animal using a statistically rigorous GIS method.

METHODS

Study Sites

The first study area was located in the Cainarachi valley, northeast of Tarapoto, Departamento San Martín, Perú, on the road to Yurimaguas (kilometre marker 34). In May 2005 we established two field sites in the Cainarachi valley that we monitored daily from 19 May to 28 July 2005, 15 May to 27 July 2006, and 25 May to 1 August 2007. Site A was located to the east of Rio Cainarachi (6°25′25.60′ S, 76°18′25.52′ W) at 597 m above sea level. The area surveyed was 36 × 26 m (940 m²). Site B was located to the west of Rio Cainarachi (6°24′57.74′ S, 76°17′41.05′ W) at 612 m above sea level, approximately 4 km northwest of Site A. The area surveyed at Site B was 24 × 40 m (960 m²). Both sites contained populations of *D. imitator* and *D. variabilis*. The understory of Site A was predominately *Heliconia* plants but also contained large populations of *Dieffenbachia*, Marantacae, Melastomataceae and *Socratea*. The understory of Site B was predominately Marantaceae but contained localized patches of Bromeliaceae, *Dieffenbachia* and *Heliconia*.

A second study area (Site C, 6°32′31.48′ S, 76°6′30.21′ W) was established in March 2007 in the Huallaga Canyon, 7 km northeast of Chazuta, off Rio Tunumtunumba, 1 km downstream from Catarata Tunumtunumba. Site C was 180 m above sea level and approximately 30 km southeast of Sites A and B. We monitored Site C daily from 30 March to 21 May 2007. The area surveyed was 18 × 26 m (468 m²). Although only *D. imitator* was observed at this site, populations of *D. variabilis* were observed nearby, within 0.5 km. The understory of this site was predominately *Dieffenbachia*, but it also contained patches of Marantaceae.

Transects and 2 × 2 m grids were established at each site. At the Cainarachi valley study area, we selected two plots for transect surveys: one 'natural' plot and one 'artificial' plot. The natural plot (Site A), contained no artificial phytotelmata, whereas the 'artificial' plot (Site B) contained a high density of artificial phytotelmata (plastic bottles fixed to trees ca. 1–2 m high). The combination of sites with natural and artificial phytotelmata allowed us to obtain more data but also ensured that the data from the site that included artificial pools was comparable to that from a natural site. Each site was marked with flagging to form a rectangular grid with numbered flags at 2 m intervals. Capture points were recorded at 0.5 m

resolution; this was done by visually subdividing each 2 m^2 grid into four 1 m^2 squares, which were further subdivided into four 0.5 m^2 squares. Between 19 May 2005 and 1 August 2007, we walked transects ($N = 206$, Site A = 65, Site B = 113, Site C = 28; totalling 8717 min) on an average eight times per week at varying hours.

Collecting and Mapping Data into a GIS

At each site, visible host plants (primarily Bromeliaceae, *Heliconia*, *Dieffenbachia*, Marantaceae, *Xanthosoma*), tree holes, *Socratea* palms, artificial pools, fallen logs and plants taller than 0.5 m were mapped and identified to family or genus; however, given their high diversity, trees were classified into one group. Although we recognize that certain species of trees contain more phytotelmata (i.e. tree holes and bromeliads), trees are generally used indiscriminately by poison frogs (unpublished data). Furthermore, we mapped the phytotelmata, which circumvents potential problems associated with this generalization. Mapped vegetation data were converted to polygons and points on a map using ArcGIS 9.2 (ArcInfo, ESRI, Redlands, CA, U.S.A.). Transect capture data were converted to points on a map using ArcGIS 9.2.

Calculation of Home Ranges

Home range (defined as total area occupied by an individual) analyses were carried out using the Animal Movement Analysis extension (Hooge & Eichenlaub 1998) in ArcView GIS (version 3.2a) (ESRI, Redlands, CA, U.S.A.) and were calculated for individuals with a minimum of three captures. Because the extent of territoriality between the two species differs, our comparisons focused on home range sizes. We calculated home ranges using both 100% minimum convex polygon (MCP) and fixed kernel estimates; given the different strengths of these methods (detailed below), we elected to use both. MCP were used to estimate the area occupied by an individual, but this technique frequently overestimates territory sizes and provides no indication of visit frequency (Worton 1987; Boulanger & White 1990). Kernel estimates (KHRs) provide a more accurate estimate of space use, accounting for capture density; however the estimation of the smoothing parameter (h) can be difficult and, if used injudiciously, can also result in erroneous ranges (Row & Blouin-Demers 2006). Kernel ranges were calculated for two probabilities: 95% and 50%. We estimated h using least-square cross-validation (LSCV).

Home Range Overlap

We used ArcInfo GIS 9.2 to compare home range overlap and distance between home ranges. We used KHR 50% estimates because they reflect the core area occupied by each individual, accounting for capture density (as described above). We calculated the distance between home ranges by calculating the centroid, or centre, of the KHR 50% estimate and measuring the distance between paired
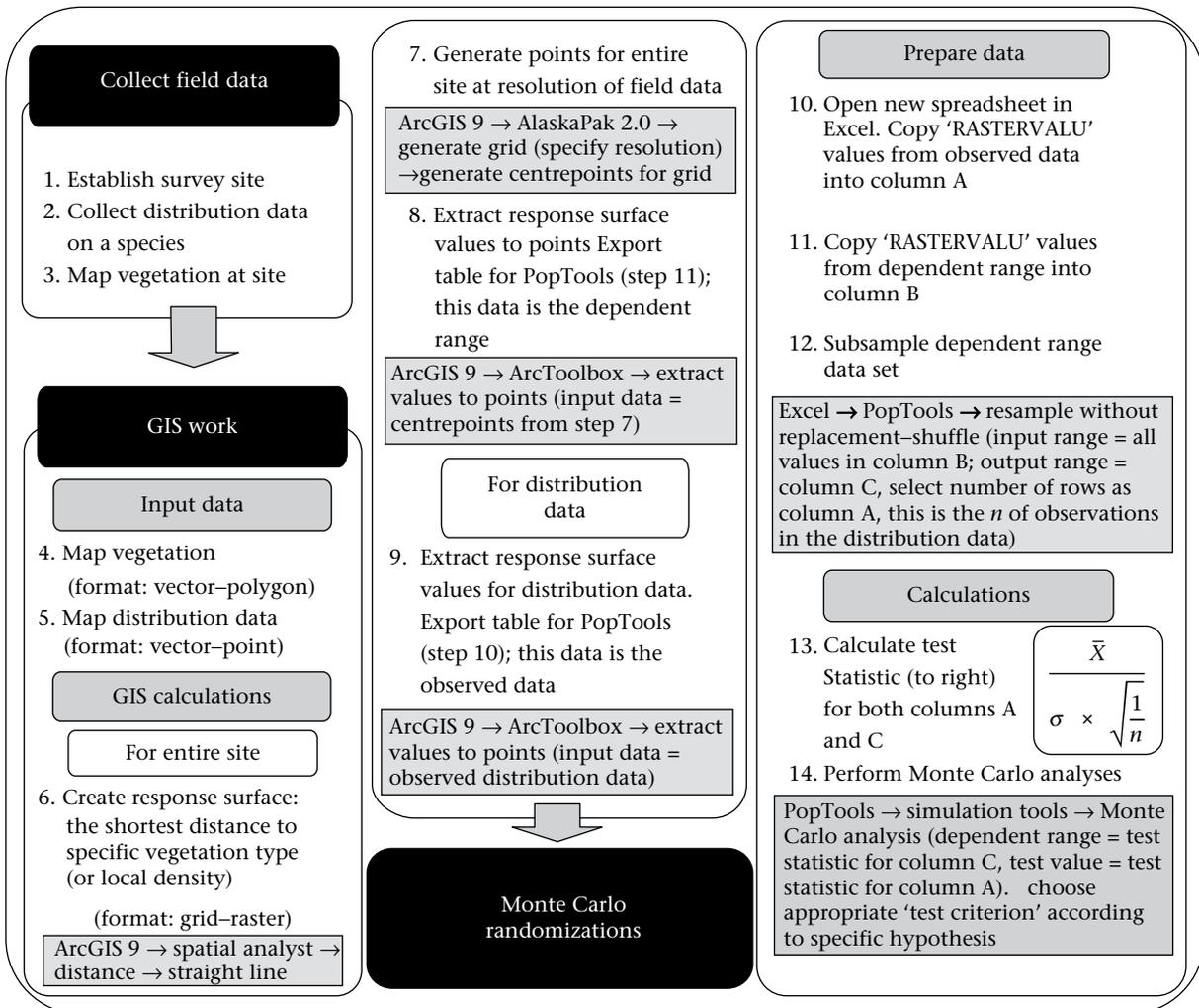

Figure 1. Data flow diagram for GIS Monte Carlo method. The GIS Monte Carlo method consists of three stages: Collect field data, GIS work and Monte Carlo randomizations. Grey boxes represent the computational steps taken to execute each calculation.

individuals' centroids. These values were standardized to account for differences in home range sizes by using the following equation: Distance between centroids$/\sqrt{(\text{MCP}\male + \text{MCP}\female/2)}$. We calculated the proportion of home range overlap for the KHR 50% estimates by dividing the range overlap by the smaller of the pair's home range area. The resulting data were log-transformed to meet the assumption of homogeneity of variance and analysed using independent samples *t* tests performed in SPSS 15.00 (SPSS 2007).

GIS Monte Carlo Method

The GIS Monte Carlo method (GMCM) utilizes field data from transects sites (i.e. key vegetation types, locations of artificial pools) and incorporates them into a GIS. Once the data are incorporated, simple calculations are used to create a 'response surface'. For example, after plotting the distribution of 'host plants', we created a response surface representing the shortest distance to a particular host plant from any location within the survey site. The resolution of the 'response surface' corresponds to the resolution of the field data, and in this study, it was a 0.5 m^2 pixel resolution. We can use the generated response surface to test the spatial correlations of individual distributions in the two species to the nearest environmental variables (i.e. host plants). GMCM does this by randomly sampling points from the response surface and calculating the frequency with which the randomly sampled points are greater (or less) than the observed data (depending on the hypothesis). Point sampling is repeated thousands of times, creating a distribution that allows us to estimate a *P* value. We can also create response
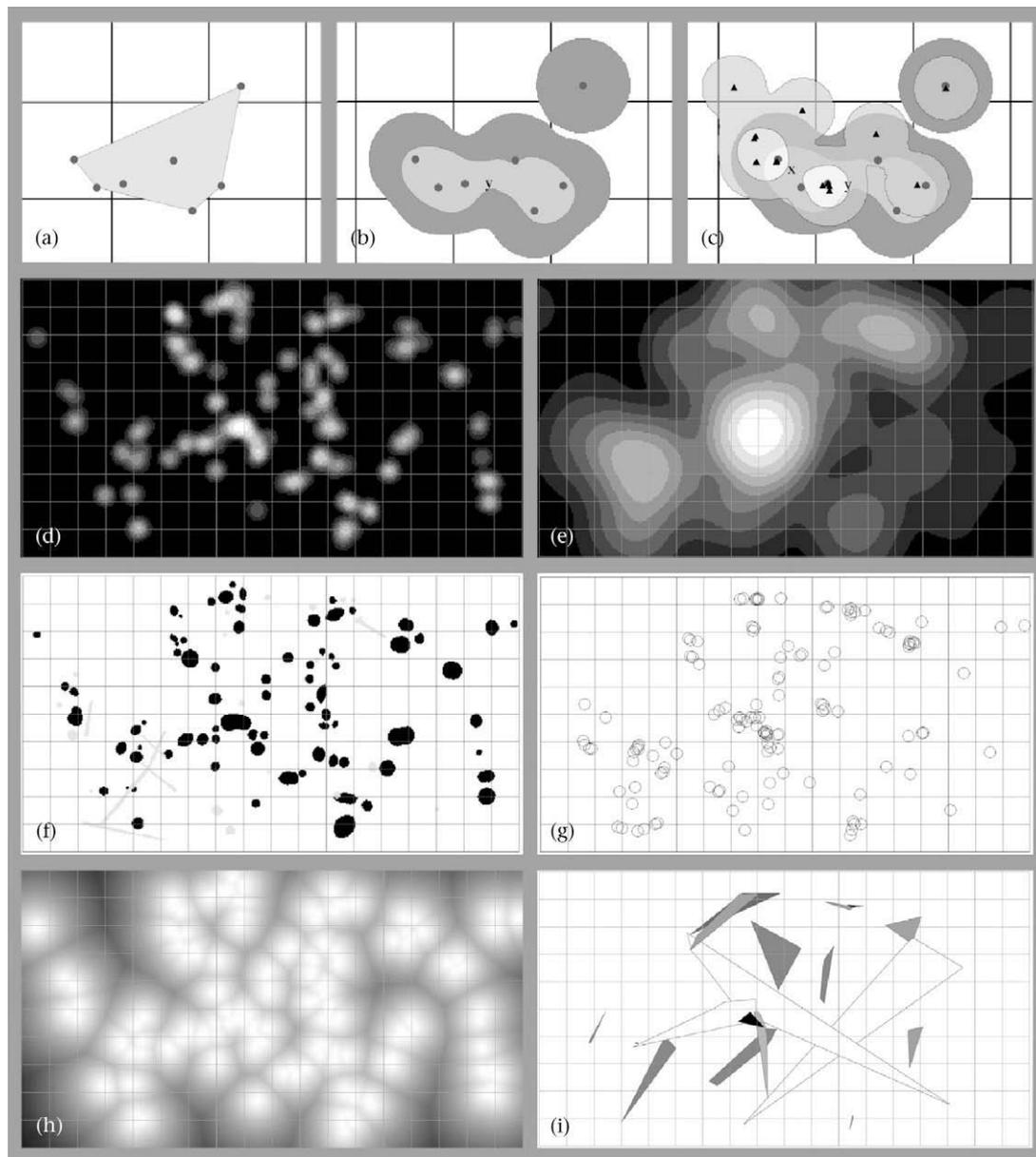
Figure 2. GIS Calculations. (a) Minimum convex polygon home range calculated for an individual with seven capture points (grey dots). (b) Kernel home range estimate calculated from the same capture points. The darker, outer circle represents a 95% probability of an area containing that individual during our study period. The lighter inner circle represents a 50% capture probability. The 'y' depicts the centroid of KHR 50%. (c) Two overlapping kernel home ranges of a pair. Note the restricted 50% capture probability for the female's home range, depicted in lighter shades; capture points are depicted by triangles and the centroid of KHR 50% by 'x'. Kernel methods account for density of capture points. (d) Density of *Heliconia* at Site A using a 1 m search radius (lighter values depict higher densities). (e) Density of *Heliconia* at Site A using a 5 m search radius (lighter values depict higher densities). (f) Vegetation plotted at Site A; *Heliconia* are plotted in black, all other types are plotted in light grey. (g) *Dendrobates imitator* capture points at Site A. (h) Shortest distance to a *Heliconia* at Site A (lighter values depict shorter distances). (i) Minimum convex polygon (MCP) home ranges for all individuals at Site A. Transient individuals are shown in white. All panels contain a 2 m^2 grid.
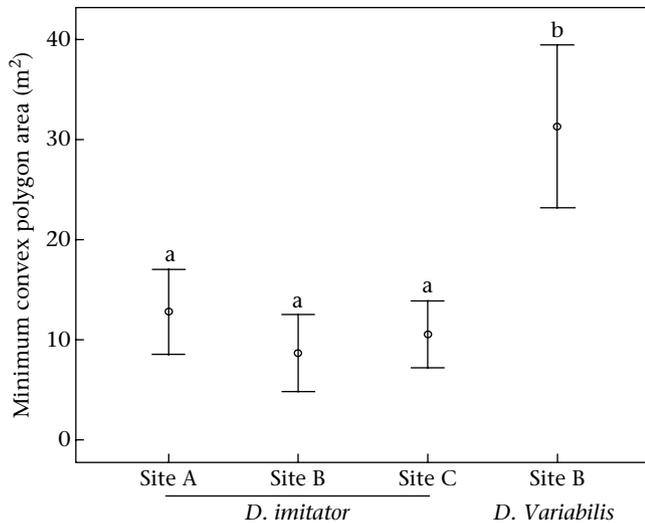
Figure 3. Mean ± SE minimum convex polygon (MCP) home range sizes of D. imitator and D. variabilis at each site. Different superscript letters denote significant differences between sites.

surfaces of host plant densities (as opposed to nearest linear distance), allowing us to test the effect of 'host plant' density on the spatial distribution of individuals. Since density depends on the unit of area used to measure it, we can calculate density using a variety of areas to ask different questions. For example, do 'host plant' densities more strongly affect individual distributions over a large area or a small area? We can investigate this issue by changing the search radius used to calculate densities, for example, from 5 m to 1 m, and compare the estimated P values. We could also reduce (or increase) the search radius until there is no significant effect, which would allow us to tease apart the function of 'host plant' density on individuals' distributions for a poison frog species. For examples of the GIS calculations (mentioned above) see Fig. 2.

Monte Carlo randomizations were done using PopTools 2.75 (Hood 2000) in Microsoft Excel 2007. Data sets were generated in ArcGIS 9.2 using a raster file (the response surface) generated from each vegetation type (or artificial pool), calculating linear distance to vegetation or vegetation density. Resulting raster data set values were extracted to points generated at the resolution of the original transect grid (0.5 m^2) using ArcGIS extension AlaskaPak 2.0 (NPS 2008, Spatial Analyst's Toolbox), and those values were exported into PopTools and categorized as the dependent range (DR). This data set represents all the values of the sample site (i.e. shortest distance to host plants from every location within the site), from which dependent values were randomly selected. The observed values for occurrence data were imported into ArcGIS 9.2. Only one randomly selected point from each individual captured was used to avoid pseudoreplication. The corresponding raster values (from the same raster file used to generate the DR) were extracted to the points and those values were imported into PopTools as our 'test' values. The subsampling of the dependent range was performed in PopTools 2.75 (see Fig. 1), which randomly selected a subset of

numbers from the entire data set. The number of dependent values selected at each iteration corresponded to the number of occurrence points. Each observed data set was compared to the randomly selected values from the dependent data set (10 000 replicates) using a test statistic, $\overline{X}_0/\sigma_0 \times \sqrt{1/n_0} - \overline{X}_d/\sigma_d \times \sqrt{1/n_d}$, which compares the frequency with which the test value of the dependent data set is greater (or less) than the observed data set (depending on the hypothesis). This compares the frequency that random points are more closely associated with key types of vegetation than are the observed individual locations.

Statistical Analysis

One way ANOVAs were performed in SPSS 15 (SPSS Inc. 2007) to test differences in home ranges. Tukey's post hoc tests were used for pairwise comparisons because sample sizes were unbalanced. All data were log-transformed to meet the assumption of homogeneity of variance. Home range data collected during 2005 and 2006 from Site B were not statistically different (Mann–Whitney U test: D. variabilis: MCP: $U = 7$, $N_{2005} = 7$, $N_{2006} = 9$, $P = 0.230$; KHR 50%: $U = 14$, $N_{2005} = 7$, $N_{2006} = 9$, $P = 1.000$; D. imitator: MCP: $U = 9$, $N_{2005} = 4$, $N_{2006} = 5$, $P = 0.136$; KHR 50%: $U = 11$, $N_{2005} = 4$, $N_{2006} = 5$, $P = 0.166$) and were combined into one data set for each species. We collected data from Sites A and C only in 1 year. Mann–Whitney U tests and independent sample t tests were performed in SPSS 15, and Monte Carlo two-sample randomization tests were performed in Excel 2007 using PopTools 2.75.

RESULTS

Home Ranges

Home range sizes calculated for D. imitator did not differ between sites, but did differ from home range sizes for D. variabilis (ANOVA: MCP: $F_{3,57} = 2.982$, $P = 0.019$; KHR 50%: $F_{3,57} = 8.011$, $P < 0.001$; Tukey HSD reported that only pairwise differences between species were significant: $P < 0.05$; Fig. 3, Table 1). There were no differences in home range sizes between the sexes at any site (unpublished data).

Home Range Overlap

The home ranges of D. imitator pairs had a higher proportion of overlap than those of D. variabilis pairs (independent samples t test: $t_{13} = 3.955$, $P = 0.034$; Table 1). Additionally, the core ranges of pairs were closer together for D. imitator pairs compared to those of D. variabilis pairs (independent samples t test: $t_{13} = 2.901$, $P = 0.007$; Table 2). The two species also displayed differences in conspecific range overlap, and paired D. imitator had significantly fewer ranges intersecting their combined territories (independent samples t test: $t_{13} = 7.592$, $P < 0.001$; Table 2). The mean ± SD number of days between first and last capture at all sites was 38.97 ± 15.55, averaging 5.18 ± 2.93 captures per individual. Dendrobates variabilis individuals were less likely to be recaptured than were D. imitator individuals (mean ± SD = 3.56 ± 0.73 and

Table 1
Mean ± SD (range) home range estimates for each study site

	MCP (m^2)	KHR 95% (m^2)	KHR 50% (m^2)	Days between first and last capture	N captures	N individuals
Site A: D. imitator	13.51±18.31 (53.42–0.07)	109.83±190.77 (762.13–5.10)	22.82±40.39 (143.19–1.19)	46.41±13.76 (65–24)	4.76±1.71 (8–3)	17
Site B: D. imitator	8.67±10.92 (31.74–0.43)	110.36±130.29 (329.72–6.64)	30.56±41.43 (102.19–1.15)	43.22±16.43 (65–13)	6.00±4.27 (16–3)	9
Site C: D. imitator	10.53±13.72 (52.70–0.15)	43.37±41.61 (137.94–0.26)	9.89±10.75 (41.92–0.04)	35.06±14.13 (54–10)	6.88±3.60 (16–3)	17
Site B: D. variabilis	31.32±32.59 (90.97–0.640)	423.45±480.53 (1617.21–10.30)	113.36±137.17 (526.9–4.51)	33.94±16.66 (62–7)	3.56±0.72 (5–3)	16

Table 2
Mean ± SD (range, N) or mean ± SD (N) individual home ranges for *Dendrobates imitator* and *D. variabilis* breeding pairs

	Mean MCP (m²)	Mean KHR 50% (m²)	Proportion of range overlap	Distance between centroids	Conspecific range overlap (N)
D. imitator	4.64±4.32 (17.31–0.15, 18)	4.13±3.52 (10.19–0.40, 18)	82.5±14.5 (9)	0.79±0.65 (9)	0.75±0.88 (9)
D. variabilis	38.9±39.76 (90.97–6.30, 9)	163.2±212.08 (526.90–13.06, 9)	65.9±20.9 (6)	11.21±7.79 (6)	4.0±0.71 (6)
P			0.04	0.01	<0.001

5.76 ± 3.29, respectively; Mann–Whitney *U* test: $U = 187$, $N_{imitator} = 43$ $N_{variabilis} = 16$, $P = 0.003$).

GIS Monte Carlo Method

The home ranges of *D. variabilis* were not significantly associated with any vegetation or artificial pools (Table 3); however, at each site the distribution of *D. imitator* was correlated with the presence of the most abundant host plant (Monte Carlo estimates: Site A: *Heliconia*: $N = 47$, $P < 0.001$; Site B: artificial pools: $N = 22$, $P \sim 0.044$; Site C: *Dieffenbachia*: $N = 29$, $P < 0.001$; Table 3). In addition, the distribution of *D. imitator* at Site B was more closely associated with artificial pools than was that of *D. variabilis* (Monte Carlo two-sample randomization test: $N_{imitator} = 22$, $N_{variabilis} = 16$, $P \sim 0.033$). The correlation to host plant density varied for each site (Table 4). At Site A, *Heliconia* densities calculated for smaller areas (0.5 m² and 1 m²) and for larger areas (5 m²) were significantly correlated to the observed distributions of *D. imitator* (Monte Carlo estimate: $N = 47$, $P < 0.001$; Fig. 2d, e). At Site B, the densities of artificial pools calculated for very small areas (0.5 m²) were not correlated with the observed distributions of *D. imitator*; however, densities of artificial pools calculated for larger areas (1 m² and 5 m²) were significantly correlated (Monte Carlo estimate: $N = 22$, $P < 0.001$). Lastly, at Site C, the *Dieffenbachia* densities calculated for smaller areas (0.5 m², 1 m², 4 m²) were significantly correlated with the distribution of *D. imitator* (Monte Carlo estimate: $N = 29$, $P < 0.001$), but larger areas (5 m²) were not (Monte Carlo estimate: $N = 29$, $P \sim 0.665$).

DISCUSSION

GIS Monte Carlo Method

GMCM provides novel opportunities to test geographical associations between the distribution of individuals and environmental factors at a population level. For example, one could use this method to test for correlations between abiotic factors such as soil type, light or moisture, and a plant's distribution. Furthermore, it could be used in conservation biology to evaluate key associations between the distribution of an animal or plant at a scale much more specific than niche modelling, demonstrating exact correlations. It

could also be used at a larger scale to test for associations between specific habitat features. This method provides a novel approach to investigating processes functioning at a population level, such as competition. For example, a researcher could perform a comparative study evaluating the association of an inferior competitor's distribution with a key resource in the absence or presence of a superior competitor. It also is possible to test major hypotheses in habitat selection theory (such as the ideal despotic and ideal free distributions; see Fretwell 1972) using this method to compare observed distributions to weighted response surfaces (reflecting the suitable habitat) and species densities.

There are limitations to the GMCM method; in particular, the scope of inference is limited to the study site or very similar sites. For example, we cannot claim that *D. imitator* will always be associated with *Dieffenbachia* plants, even though individuals' distributions were tightly correlated with *Dieffenbachia* at Site C. Observations suggest that *D. imitator* prefers *Heliconia* over *Dieffenbachia*, and, if given the choice, would probably choose *Heliconia* (Brown et al. 2008). However, because *Dieffenbachia* were abundant at Site C but *Heliconia* were not, most frogs used *Dieffenbachia*. This is important because when testing for relationships to key resources, researchers need to ask questions that pertain to the function of the resources, not to the individual resources themselves. In situations where different things that serve the same function are equally abundant, such as phytotelmata, a correlation may not be detected to an individual resource but rather to a resource category. Finally, the Monte Carlo test statistic is very conservative and may be prone to type II errors. This is especially true when an observed data set has a very tight correlation to a key factor, resulting in a small variance, and the points sampled at random from the dependent data set have a large variance. Even if the means were considerably smaller for the observed data set, because of the small variance, the resulting test value could be larger (see Methods, GIS Monte Carlo Method) than that from the random data set and, therefore, the association would be rejected.

Poison Frog Home Ranges

We previously described differences in territoriality, reproductive resources utilized, parental care type and site fidelity between *D. imitator* and *D. variabilis* (Brown et al. 2008). Based on mating

Table 3
GIS Monte Carlo distance associations (mean ± SD, range, N) and Monte Carlo test values

	Feature	Observed distance (m)	Average site distance (m)	MC test values		Estimated *P*
				Observed	Randomized: mean (CI)	
Site A: *D. imitator*	*Heliconia*	0.59±0.71 (3.36–0.05, 47)	2.72±1.87 (8.56–0, 4335)	6.08	15.89 (17.79–14.21)	**<0.001**
Site B: *D. imitator*	Trees	0.69±0.42 (1.49–0, 22)	1.56±1.20 (6.29–0, 4032)	7.78	6.28 (8.38–4.70)	0.89
	Marantacae	1.18±1.11 (5.01–0, 22)	1.15±1.21 (6.38–0, 4032)	4.99	6.58 (8.97–4.89)	0.72
	Artifical pools	0.69±0.63 (1.79–0.29, 22)	2.03±1.45 (7.41–0, 4032)	5.16	6.77 (8.94–5.20)	**0.04**
	All phytotelmata	0.49±0.43 (1.75–0, 22)	1.54±1.14 (6.36–0, 4032)	5.42	6.58 (9.01–4.86)	0.12
Site C: *D. imitator*	Trees	1.18±0.52 (2.22–0.31, 29)	1.19±0.67 (3.65–0, 1581)	11.39	6.14 (8.22–4.55)	1
	Dieffenbachia	0.29±0.23 (0.83–0.00, 29)	1.66±1.16 (6.06–0, 1581)	6.96	21.16 (34.10–11.32)	**<0.001**
Site B: *D. variabilis*	Trees	0.80±0.64 (2.61–0, 46)	1.56±1.20 (6.29–0, 4032)	8.54	8.96 (10.98–7.315)	0.35
	Marantacae	1.23±1.16 (4.31–0, 46)	1.15±1.21 (6.38–0, 4032)	7.27	6.57 (8.27–5.20)	0.82
	Artifical pools	0.92±0.61 (2.57–0.15, 46)	2.03±1.45 (7.41–0, 4032)	10.15	9.67 (8.04–11.64)	0.8
	All phytotelmata	0.78±0.58 (2.46–0.09, 46)	1.54±1.14 (6.36–0, 4032)	9.22	9.27 (11.24–7.49)	0.46

Significant values are shown in bold.

Table 4
Mean ± SD (range) GIS Monte Carlo density associations

	Feature	Search radius (m)	Observed density (m²)	Average site density (m²)	Estimated P
Site A: *D. imitator*	*Heliconia*	0.5	2.22±2.25 (7.75–0)	0.16±0.75 (9.37–0)	**<0.001**
	Heliconia	1	1.19±0.99 (3.38–0)	0.16±0.48 (5.36–0)	**<0.001**
	Heliconia	5	0.33±0.17 (0.83–0.04)	0.16±0.19 (0.90–0)	**<0.001**
Site B: *D. imitator*	Artifical pools	0.5	0.92±1.47 (4.42–0)	0.15±0.63 (9.25–0)	0.131
	Artifical pools	1	0.56±0.51 (1.67–0)	0.14±0.37 (5.00–0)	**<0.001**
	Artifical pools	5	0.20±0.08 (0.34–0.09)	0.13±0.11 (0.72–0)	**<0.001**
Site C: *D. imitator*	*Dieffenbachia*	0.5	2.40±1.52 (4.37–0)	0.84±1.45 (11.28–0)	**<0.001**
	Dieffenbachia	1	1.60±0.79 (3.19–0)	0.84±0.84 (4.79–0)	**<0.001**
	Dieffenbachia	4	0.94±0.31 (1.72–0.46)	0.78±0.37 (1.79–0.04)	**<0.001**
	Dieffenbachia	5	0.86±0.26 (1.44–0.50)	0.76±0.33 (1.54–0.09)	0.67

Significant values are shown in bold.

systems theory (Clutton-Brock 1991) and our observations, we predicted that: (1) *D. imitator* would be more closely associated with phytotelmata than would *D. variabilis*; (2) home ranges for *D. imitator* pairs would be more strictly overlapping than those for *D. variabilis* pairs; (3) *D. imitator* pairs would maintain smaller home ranges than *D. variabilis* pairs; and (4) *D. imitator* pairs would maintain exclusive home ranges.

In this study we have shown that the distribution of reproductive resources is correlated with home range distribution of *D. imitator*, but not of *D. variabilis* (supporting prediction 1). Although phytotelmata are also important for *D. variabilis* (since they use them for reproduction), phytotelmata were only loosely linked to the distribution of *D. variabilis*. Many *D. variabilis* individuals were observed far from pools, probably either foraging or searching for new mates or phytotelmata.

The home ranges of known paired individuals were more tightly linked, showing significantly higher overlap than those of *D. variabilis* (Table 2, supporting prediction 2). We found that home ranges of *D. imitator* were, on average, three to five times smaller than those of *D. variabilis*, supporting prediction 3. Lastly, the home ranges of *D. imitator* were more exclusive and showedd little overlap with the home ranges of congeneric individuals (supporting prediction 4). In all but two cases, home range overlap in *D. imitator* was the result of transient individuals 'passing by', not due to actual territory overlap. These differences in range overlap are probably associated with *D. imitator*'s necessity to monopolize the use of pools to provide exclusive areas for courtship (associated with pair bonding in this species), tadpole deposition and (most importantly) tadpole feeding.

The occurrence of *D. imitator* was tightly linked to phytotelmata density at multiple scales. This species chose habitats (large areas) with high densities of host plants and smaller localized areas within that habitat where host plants were concentrated. The preference for habitats with a high density of phytotelmata is not surprising for a phytotelm-breeder. However, for species with high levels of territoriality, there is probably some trade-off within high-density habitats: these habitats provide a large array of territory choices (groups of pools), but the probability of negative species interactions is higher (i.e. territorial disputes, calling bouts, mate competition). The observed association between small localized groups of phytotelmata probably reflects the preference of *D. imitator* for high-quality sites to establish territories. Sites that contain many phytotelmata within a small area are more feasibly defended and monitored. Furthermore, in smaller territories, each sex is able to monitor the activities of the other sex with increased diligence, reducing the risk of extrapair mating.

Our results for *D. imitator* are similar to those from a previous study of *D. vanzolinii*, a closely related species that also shows biparental care (Caldwell & de Oliveira 1999). Pairs in both of these species have exclusive, largely overlapping ranges. Territories of both species also seem to be associated with phytotelmata. However, the observed home range size for *D. vanzolinii* in Caldwell

& de Oliveira's study (mean ± SD: 31.50 ± 23.05 m², range 75.09–7.23 m²) differed from that of *D. imitator* in our study, being on average three times larger than that of *D. imitator*. This difference probably reflects variance in the abundance of phytotelmata at these study sites (phytotelmata density at the *D. vanzolinii* site was estimated at 1/70 m² versus 1/5 m² for Sites A–C in our study).

Previous studies on *D. ventrimaculatus*, a species with male parental care that is closely related to *D. variabilis*, support our results (Summers & Amos 1997; Poelman & Dicke 2008). A study of *D. ventrimaculatus* sensu lato (for details on classification see Brown et al. 2006) by Poelman & Dicke (2008) estimated that the home range sizes for these two species are very similar (range 1.2–129 m² MCP).

In conclusion, the GMCM provides a novel opportunity to test fine-scale spatial associations between the distributions of poison frogs and of phytotelmata at a population level. These results strongly support the prediction that differences in parental care and mating system are reflected in spatial habitat use, in particular, pool fidelity, territoriality, home range size and home range overlap. Poison frog species with biparental care and social monogamy should show increased phytotelm fidelity and territoriality, smaller home ranges and greater home range overlap for pairs, and minimal home range overlap between pairs.

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