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Capture-Recapture Reveals Heterogeneity in Habitat-Specific Mongoose Densities and Spatiotemporal Variability in Trapping Success in St. Kitts, West Indies

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ABSTRACT—The small Indian mongoose (*Urva auropunctata*) is a non-native invasive species across the Caribbean and a rabies reservoir on at least four islands in the region. Although previous studies reported mongoose density estimates in their non-native range, the variability in trapping designs, study seasonality, and analytical methods among studies precludes direct comparisons. This study is the first to report mongoose densities for the island of St. Kitts, West Indies. Our objective was to quantify mongoose densities across four habitats characteristic for the island. High capture and recapture rates in this study resulted in detailed estimates of spatial heterogeneity in mongoose densities, ranging from 0.53 (CI95: 0.46–0.61) mongooses/ha in suburban habitat to 5.85 (CI95: 4.42–7.76) mongooses/ha in nearby dry forest. Estimates were robust to the estimation method used (correlation among methods, $r > 0.9$). Female-biased sex ratios estimated from fall season versus mostly unbiased sex ratios estimated from summer season suggests seasonality in capture success resulting from differences in sex-specific activity patterns of mongooses. We found no effect of habitat characteristics, at the scale of trap placements, associated with mongoose capture success.

The small Indian mongoose (*Urva auropunctata* (Hodgson, 1836)) is an opportunistic omnivore that was introduced to the Caribbean region in 1872 to control rodent damage to sugar plantations (Espeut 1882). Mongooses failed at rodent control and are currently established on at least 33 Caribbean islands (Barun et al. 2011), where they are largely considered a non-native, invasive pest species (Berentsen et al. 2018). On Cuba, Puerto Rico, Grenada, and Hispaniola, mongooses are also recognized as the principal wildlife reservoir for rabies virus (Seetahal et al. 2018). Consequently, in their non-native range, mongooses are targeted for management to limit ecological damage and public health risks. Mongoose population and rabies management strategies historically included population reduction by localized lethal trapping or distribution of toxic

baits, whereas modern control methods focus on oral rabies vaccination (ORV) (Berentsen et al. 2018). As a result, most ecology and population biology studies of the small Indian mongoose have been conducted on introduced, insular populations, with a focus on its role as a nuisance species or disease reservoir, rather than on native populations.

Due to their widespread distribution throughout the Caribbean islands, mongooses also represent an interesting model to examine questions related to invasion ecology and island biogeography. A study comparing mongoose population densities on five Caribbean islands investigated area relationships and suggested a strong negative correlation between mongoose densities and the logarithm of island area (Horst et al. 2001). They concluded that this relationship could be

explained by a phenomenon of density compensation, where summed densities of animal species on small islands is comparable to that of mainland or larger islands fauna (i.e., density of animal groups is independent of area; MacArthur and Wilson 1967). Since smaller islands tend to support lower biodiversity, density compensation leads to the conclusion that average population densities of each species should be greater on smaller islands (MacArthur et al. 1972). For density compensation to be observable across similar landscapes, different species sharing the same ecological niches must compete for available resources. Whereas domestic companion animals are widely distributed, wild mammalian carnivores are absent from the Caribbean islands except for eight islands where the raccoon (*Procyon lotor* (Linnaeus, 1758)) has been introduced (Kays et al. 2009; Louppe et al. 2020). While small Indian mongooses are vulnerable to predation by some raptor species in their native range, in most Caribbean habitats, mongoose populations face negligible natural predation or competition risks. It is thus possible that mongoose densities might be driven by local resource availability rather than island biodiversity or area.

A major limitation when comparing mongoose densities estimated on different islands is the variety of sampling (e.g., removal, mark-recapture, distance sampling) and analytical methods used across studies (e.g., Pimentel 1955; Corn and Conroy 1998; Vilella 1998; Horst et al. 2001; Quinn and Whisson 2005; Johnson et al. 2016). The result is great variability among mongoose density estimates (0.19 to 9.0 mongooses/km²; Berentsen et al. 2018) both among and within islands. Moreover, the variability in temporal scale across studies hinders distinction among inter-annual, seasonal and habitat-specific effects on mongoose densities. Although mongoose trapping success is highly variable among studies as well as between individual traps within a trapping array, no research has examined temporal and environmental factors affecting mongoose capture rates and fine-scale trapping success. Identifying temporal windows and environmental variables influencing mongoose foraging behavior to improve bait uptake or capture success could help optimize population and rabies control and management efforts targeting this species. Collecting standardized empirical data on habitat-specific mongoose densities and quantifying habitat features at trap locations to identify factors affecting mongoose fine-scale habitat use represent research pri-

orities to improve our understanding of mongoose ecology in the Caribbean in the context of wildlife rabies management (Johnson et al. 2016; Sauv e et al. 2021).

We conducted our study on St. Kitts, a rabies-free island without active population or disease management interventions (Seetahal et al. 2018). St. Kitts is a 174 km² island located in the West Indies, South of St. Eustatius and North of Nevis (Fig. 1). Mongooses were introduced to St. Kitts from Jamaica during 1884 (Burdon 1920). Mongooses are valued by local communities living on St. Kitts, as they are not perceived as a disease reservoir (Cruz-Martinez et al. 2020) and may have negatively impacted snake populations (Sadjack and Henderson 1991). Although it is locally recognized that mongooses are abundant, no prior study has investigated mongoose densities on St. Kitts.

Our objectives were to 1) estimate mongoose population densities in various representative habitats of St. Kitts, 2) use habitat-specific mongoose density estimations to calculate a weighted average density over the island of St. Kitts, 3) examine factors influencing site- and season-specific capture rates (i.e., mongoose behavior), and 4) evaluate whether fine-scale habitat characteristics at trap locations influence individual trap success.

MATERIALS AND METHODS

Study area

We conducted this study at four sites representative of the dominant habitat types on the Island of St. Kitts, West Indies: grassland, tropical dry forest, suburban habitat, and tropical rainforest (Fig. 2). St. Kitts has a tropical marine climate, with an average annual rainfall of 1,625 mm which falls primarily from August to November (CARICOM et al. 1993).

The grassland, tropical dry forest, and suburban sites were located on the gradually sloping coastal plain expanding seaward from the mountainous central interior of the island, at elevations ranging from 30 to 90 m above sea level. These sites were characterized by an average annual temperature of 27.8  C and minimal seasonal variation (CARICOM et al. 1993). The grassland site was dominated by Guinea grass (*Panicum maximum* Jacq.) and small *Acacia* spp. shrubs, interspersed with small parcels grazed by livestock and occasional residential buildings and dirt roads (Fig. 3). The tropical dry forest was composed primarily of small trees and shrubs, e.g. river tamarind (*Leucaena*

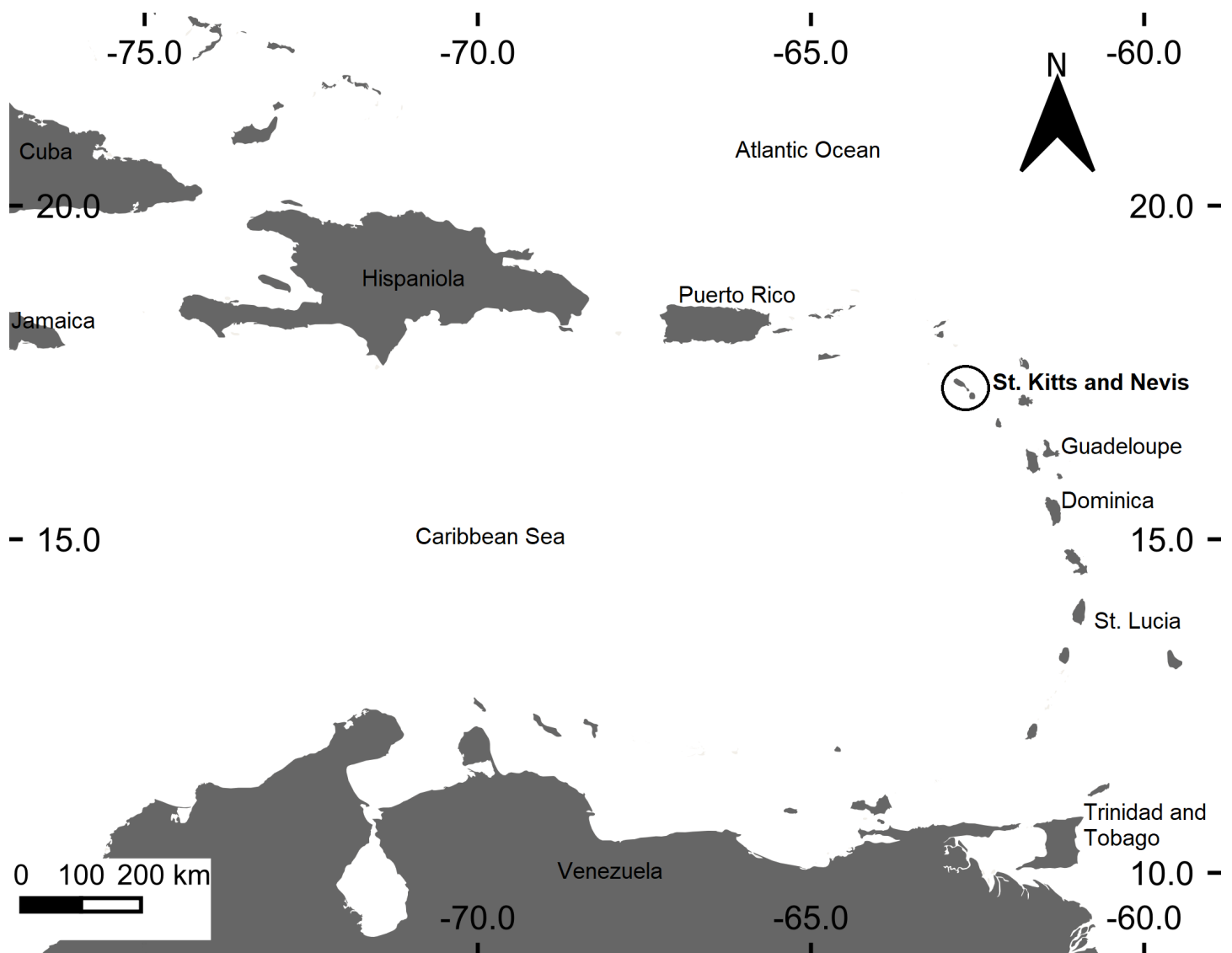
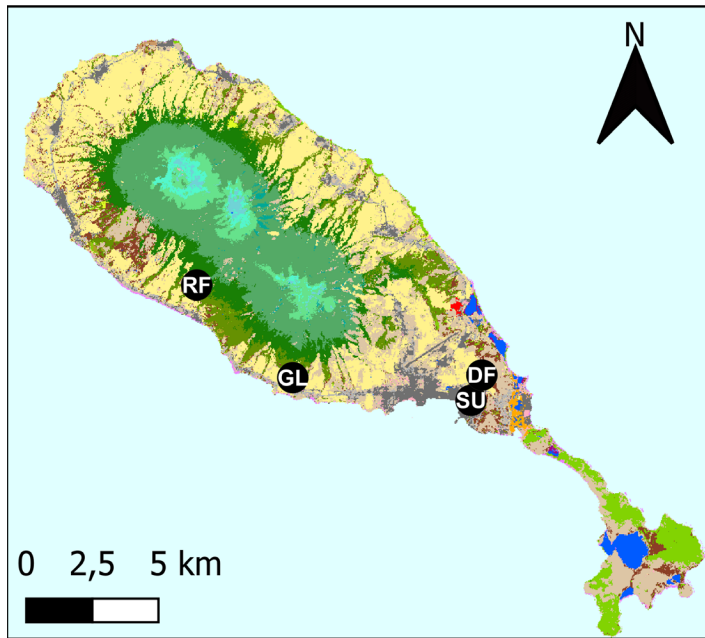


FIG. 1. St. Kitts is part of the Lesser Antilles and its West and East sides border the Caribbean Sea and the Atlantic Ocean, respectively.

leucocephala (Lam.) de Wit), *Croton* spp., and *Acacia* spp., with an understory of herbaceous plants. The understory vegetation at the southern edge of this site was subject to extensive grazing by free-ranging pigs (*Sus scrofa* Linnaeus, 1758). The suburban area was intersected by paved residential roads and was a patchwork of housing lots and vacant land dominated by scrub vegetation. The rainforest site was located approximately 450 m above sea level, with a closed canopy dominated by candlewood (*Dacryodes excelsa* Vahl), *Sloanea* spp., and palm trees (e.g., *Euterpe globosa* C.F.Gaertn.), a dense mid-level understory and abundant terrestrial ferns. Both diurnal and annual temperature variation are minimal at this site, with an average of 24.5° C (Caroline C. Sauvé, personal observation, December, 2021).

Microhabitat characterization

We visually estimated four microhabitat characteristics within a 10 m radius around each trap location during the summer trapping. These included the proportion of soil cover composed of barren soil, leaf litter, dead branches, live vegetation, and buildings; the proportion of vegetation type composed of large trees (approximated > 10 cm diameter at breast height (DBH), small trees (approximated ≤ 10 cm DBH), shrubs, intact herbaceous, and grazed or mowed herbaceous; the estimated topographic slope (≤ 10°, 11–45°, or >45°); and the presence of anthropogenic waste (dichotomous). In addition, we entered trap locations in Google Earth (Google Earth Pro v. 7.3.3.7786), and used the satellite imagery to measure the distance from each trap to the nearest road (either paved or dirt road fragmenting the habitat).



Land Cover and Forest Formation

- Ocean
- High-Medium Density Urban/Built-up
- Low Density Built-up
- Sugar cane (and minor crops)
- Coconut Palm-Pasture
- Pasture, Hay or other Grassy Areas
- Golf Course
- Drought Deciduous Open Woodland
- Montane Non-Forest Vegetation
- Steep Non-Forest Vegetation
- Mixed Forest or Shrubland
- Drought Deciduous Forest/Shrub
- Semi-Deciduous Forest
- Evergreen Forest with Coconut Palm
- Seasonal Evergreen Forest
- Evergreen Forest
- Sierra Palm, Transitional & Tall Cloud Forest
- Elfin and Sierra Palm Cloud Forest
- Emergent Wetland
- Mangrove
- Seasonally Flooded Savannahs & Woodland
- Quarries
- Coastal Sand, Rock, Cliffs or Bare Ground
- Bare Soil
- Water - Permanent

Mongoose capture and handling

We live-captured mongooses using cage traps (Tomahawk live trap, Hazelhurst, WI, U.S.A.) baited with commercial canned tuna in water. At each sampling site, we established a trapping grid of up to 50 traps with 100 m spacing between traps. We baited traps daily in the morning and checked them within 24 hours.

The first trapping session extended from 26 June to 8 August, 2018 (i.e., summer season) and was completed sequentially at each of the four sites. A second trapping session, which we conducted from 29 October to 13 November, 2018 (i.e., fall season), was carried out at the grassland and dry forest sites. Each session consisted of 10 consecutive days of trapping, except for the fall session at the grassland site, which we trapped for eight days due to logistical constraints.

Upon capture, we transferred mongooses into a conical canvas bag for manual restraint, followed by anesthesia via intramuscular injection of tiletamine and zolazepam 1:1 (Telazol®, Zoetis, Florham and Zoletil 100, Virbac, Bury Saint-Edmunds, U.K.) at a dose of 5 mg/kg. Upon initial capture, we determined sex, female reproductive status (pregnant or nursing versus non pregnant nor nursing) based on mammary gland development, and relative age (adult or young of the year [YOY]) based on size and sexual maturity. We inserted a sterile unique Passive Integrated Transponder (PIT) tag (Biomark APT12 FDX_B, Boise, ID) via subcutaneous injection between the shoulder blades. In addition, we visually marked mongooses by either topical application of livestock dye (Weaver Leather Prodye, Mount Hope, OH) or by clipping a stripe of hair using a miniature electric clipper to facilitate identification of recaptures (Fig. 4). Recaptured animals were identified and released without processing.

Mongoose density estimation

We used three methods to estimate mongoose density from trapping data: the mongoose density index (MDI; Johnson et al. 2016), capture-mark-recapture (CMR) models for closed populations using *MARK* (v

← FIG. 2. The St. Kitts island land cover (Helmer et al. 2008), and location of the four sampling sites (DF: Dry forest; RF: Rainforest; SU: Suburban; GL: Grassland) used for estimating mongoose density in the summer and fall of 2018.

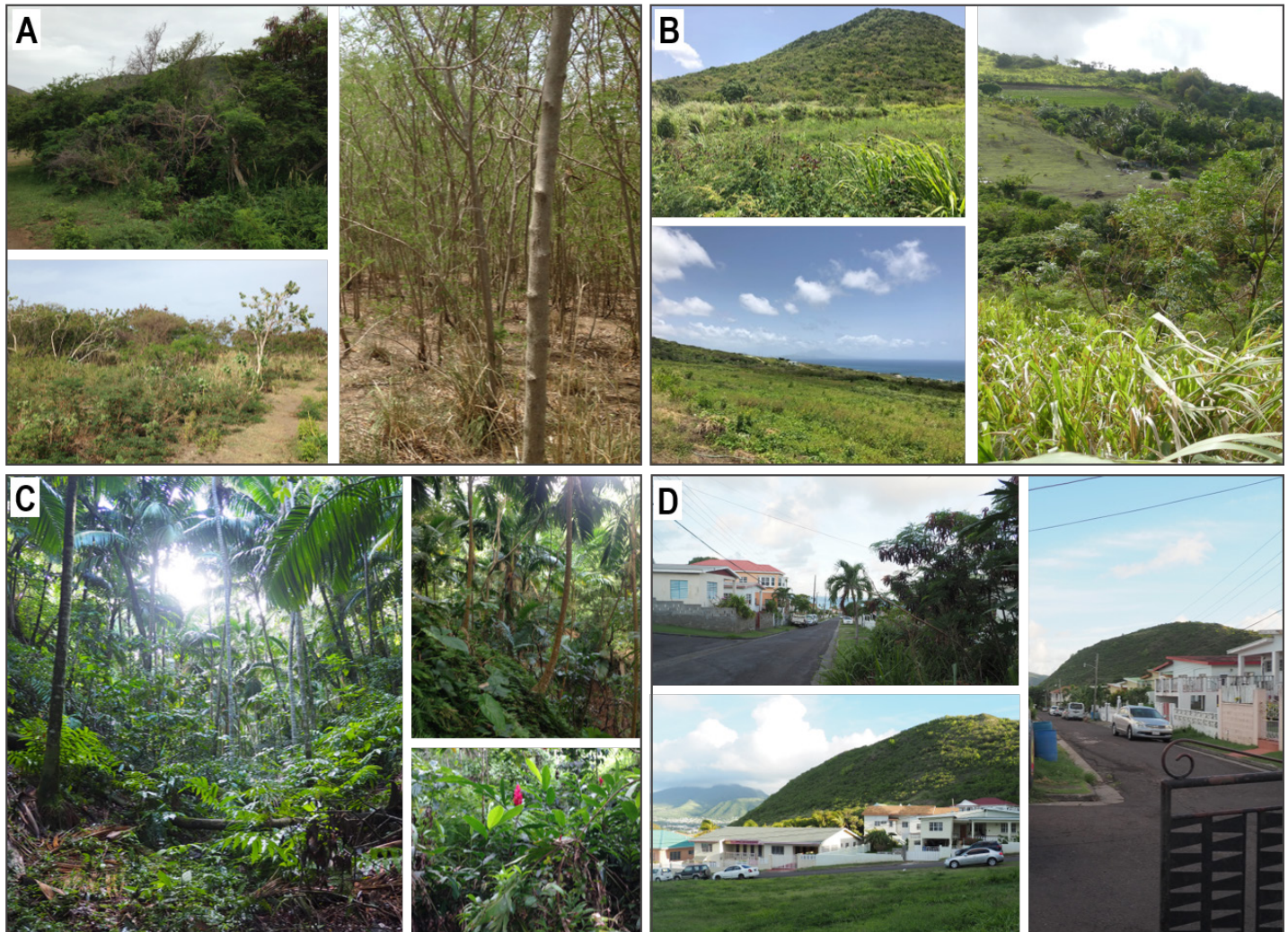


FIG. 3. Sites sampled for mongoose density on St. Kitts, West Indies in the summer and fall of 2018. A. Tropical dry forest; B. Grassland; C. Tropical rainforest; and D. Suburban area (Birdrock neighborhood). All pictures were taken during the dry season, between 26 June and 08 August, 2018 by C. C. Sauvé.

9.0; White and Burnham 1999), and spatially explicit capture-recapture (SECR). We chose these estimators based on the validity of their assumptions for our system, and to facilitate comparisons between our mongoose density estimates and those reported in recent studies (Johnson et al. 2016).

The Mongoose Density Index (MDI) uses minimum number known alive (MNKA) as an abundance index to calculate population density by the equation:

$$\hat{D}_{MDI} = \hat{N}_{MDI} / \hat{A}_{MDI} \text{ (Equation 1)}$$

Where \hat{N}_{MDI} = the number of unique individuals captured within a single session and \hat{A}_{MDI} = the effective trapping area (km²) calculated by creating concave hulls around all trap locations within individual sites.

Capture mark recapture

We used the *RMark* interface (Laake 2013) and the program *MARK* to generate a series of Huggins closed

population capture models with mongoose sex and relative age (adult or YOY) as groups. We allowed for a difference based on behaviour where age, sex, time (as a discrete variable with one level for each trapping occasion, as well as a continuous variable), or any combination of these variables could affect capture (p) and recapture (c) rates differently. The fall trapping session at the grassland site was two days shorter than the other sessions, impeding its inclusion in the same capture history dataset for CMR modelling. Moreover, preliminary models revealed important variation in the effects of covariates on capture rates across seasons. Therefore, we fit separate models for each trapping session, as well as different models for the grassland and dry forest sites during the fall session. We assessed model goodness of fit by using Fletcher \hat{c} (Fletcher 2012) as a measure of over-dispersion (e.g. Cooch and White

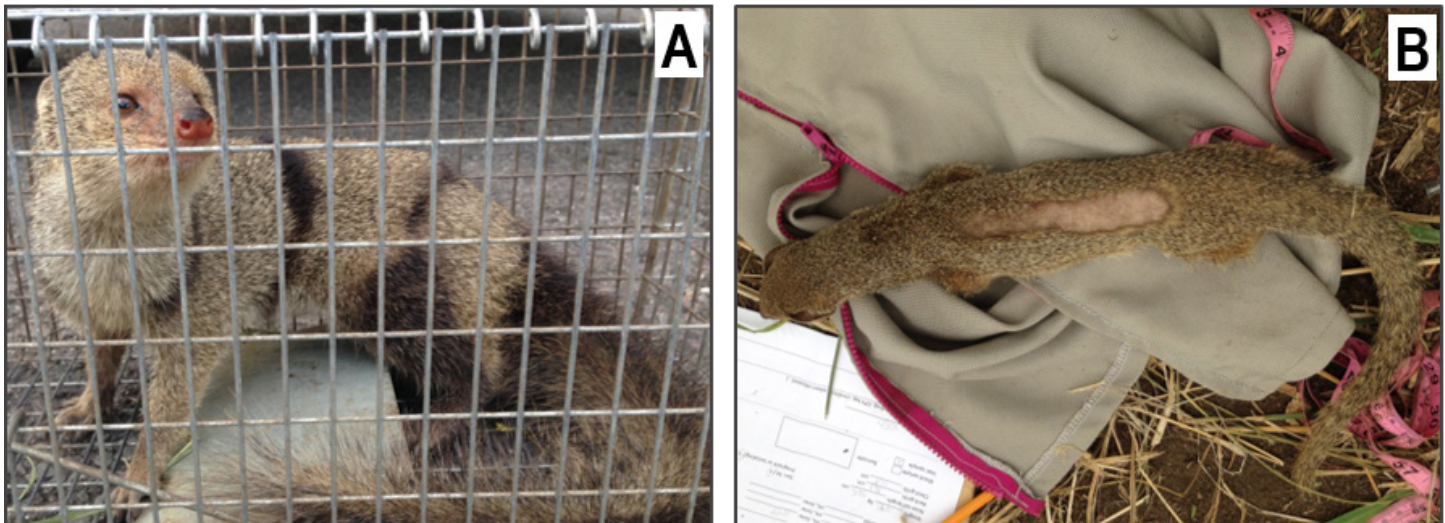


FIG. 4. Mongoose visual marking used in St. Kitts to facilitate recapture identification. Mongooses were primarily identified using A) stripe pattern allowing individual identification by topical application of livestock black dye (Weaver Leather Prodyne, Mount Hope, OH). Alternatively (e.g., rainy days when dye would not dry on animal's fur upon release), mongooses were visually identified by clipping a stripe of hair using a miniature electric clipper. In addition, all mongooses were individually tagged by inserting a unique Passive Integrated Transponder (PIT) tag (Biomark APT12 FDX_B, Boise, ID) via subcutaneous injection between the shoulder blades.

2018). We ranked models using Akaike's Information Criterion corrected for finite sample size (AICc; Burnham and Anderson 2002), and effects of covariates on capture rates were considered supported when their inclusion in a model induced a drop in the AICc of at least two points compared to a simpler model excluding the variable (Arnold 2010). Models generated in MARK produce population abundance (\hat{N}_{MARK}) and capture and recapture rate (p and c) estimates. We estimated the effective sampling area (\hat{A}_{MARK}) used to calculate density as detailed in Johnson et al. (2016). Briefly, we calculated site- and session-specific mean maximum distances moved (MMDM; Wilson, and Anderson 1985) using trap recapture data from a same session. We generated a 0.5 MMDM buffer around each trap and computed the area formed by merging buffers from a same site using QGIS (v3.16.4; QGIS.org 2021). Again, we estimated density by $\hat{N}_{MARK} \setminus \hat{A}_{MARK}$.

Spatially explicit capture recapture

We calculated mongoose density by SECR using the *secr* package (Efford 2020). We used capture history data, site-specific trap layout and trap usage as input observations. Although we baited and checked all traps daily, there were some instances of traps stolen or moved. The SECR method accounts for the null probability of capturing an animal in a trap that was temporarily not operational using the trap 'usage' spec-

ification. Model specification in SECR also requires the specification of a distance beyond the traps where capture probability is negligible. We used a buffer of 4σ (Efford 2021a) and estimated σ from the capture history data using the root pooled spatial variance (RPSV) function from the *secr* package. We used the maximal 4σ value obtained among all sessions and sites as a buffer value in each model. Capture history data from each session and site were modelled separately. We generated hybrid mixture models in which animal sex was included as a covariate. We considered the following effects: sex, learned response to capture (detection probability at first capture different from subsequent captures), transient response to capture (detection different only if the individual was captured on the last occasion), time (as detailed above). In SECR, density is derived from detectability, defined as a half-normal function of distance using two parameters: magnitude (g_0) and sigma (σ) (Efford 2020). We considered candidate models in which effects altered detectability either via g_0 and σ , or via g_0 only. Moreover, we tested for spatial heterogeneity in densities over the sampling grid by modelling density as either a homogenous flat surface, a linear trend surface, or a quadratic trend surface (Efford 2021b). We generated a candidate model list comprising all possible combinations of these effects on detection parameters and density. We used the same AICc model selection criteria for SECR and MARK models.

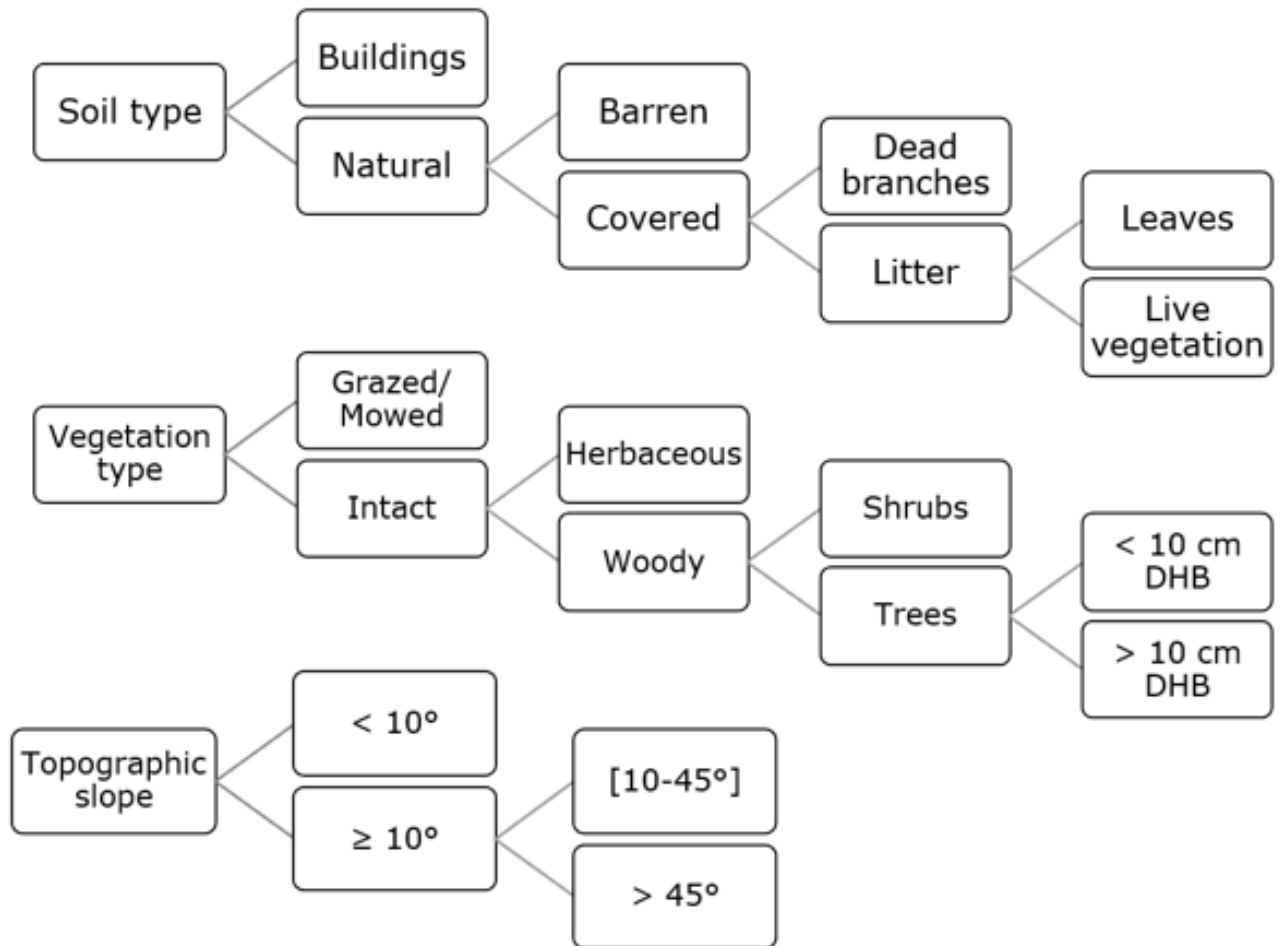


FIG. 5. Compositional data hierarchy used to defined sequential binary partitions in the isometric log-ratio transformation generating orthogonal variables entered as fixed effects in generalized linear models investigating the influence of microhabitat at trap location on capture success.

For SECR analyses, we randomly discarded one of the two captures from the capture history for animals captured in a same trap on a given date.

Factors influencing trapping success

We investigated factors influencing mongoose trapping success by interpretation of covariates affecting capture rates in CMR models, and modelling trapping success as a function of local microhabitat characteristics. We calculated the total number of captures obtained in each trap (N_{capture}) during the summer trapping period and performed goodness of fit tests to assess whether site-specific N_{capture} counts were Poisson-distributed (*vcd* package; Meyer et al. 2020). We fit Poisson or negative-binomial generalized linear models (GLM) to site-specific N_{capture} using microhabitat characteristics (soil cover, vegetation type, topographic slope, presence of anthropogenic waste, and distance to nearest road) as fixed effects. Because soil cover, vegetation type, and topographic slope represented compositional data (i.e., mutually dependent categories summing to

one), we transformed these variables using the isometric log-ratio transformation (Egozcue et al. 2003). We defined the hierarchy among variables using sequential binary partitions (Fig. 5) specified using the compositions package (van den Boogaart et al. 2021). We used the balances resulting from this transformation as fixed effects in our GLMs.

In the first step, we identified covariates exerting influence on site-specific N_{capture} using the null hypothesis testing approach. Each fixed effect variable was used to generate univariate GLMs. Non-informative covariates (i.e., those having coefficient P -values > 0.2) were dropped from the fixed effect list for further steps (Grosbois et al. 2008). In step two, we generated a candidate set of model formulas including all possible first-order combinations of retained fixed effects. We calculated Pearson correlation coefficients for each pairwise combination of fixed effects to ensure no correlated variables (defined as $r > 0.6$) were included together in the multivariate models. We performed model selection

TABLE 1. Capture success and female reproductive status for mongoose trapping conducted on the island of St. Kitts at four sites representative of different habitat types and during up to two sampling occasions during June through November, 2018.

	Grassland		Dry forest		Suburban	Rainforest
	Summer	Fall	Summer	Fall	Summer	Summer
Total no. captures	142	60	245	184	35	113
No. traps	36	36	46	45	49	37
Trapping session duration (days)	10	8	10	10	10	10
Captures per unit effort (No. captures/trap·day)	0.39	0.21	0.53	0.41	0.07	0.31
Unique no. males	23 (26%)	13 (28%)	86 (49%)	54 (35%)	13 (45%)	31 (46%)
Unique no. females	66 (74%)	33 (72%)	91 (51%)	100 (65%)	16 (55%)	36 (54%)
Unique no. juveniles	5 (5%)	2 (4%)	7 (4%)	2 (1%)	2 (7%)	6 (9%)
% females pregnant or nursing	38.3%	14.3%	60.1%	35.4%	66.7%	76.5%

based on AICc. We considered that a fixed term significantly improved a model when its inclusion reduced the AICc by at least two points compared to the simpler model excluding this variable (Burnham and Anderson 2002). We averaged the models with a $\Delta AICc \leq 2$ and in which all covariates significantly improved the fit (Arnold 2010). We standardised model coefficients by standard deviation (package *MuMIn*; Barton 2020) to ensure their comparability (Rosenthal et al. 1994). Coefficient estimates and associated *P*-values represent conditional model averages (Barton 2020). Because traps form a grid over the trapping site, we tested for spatial autocorrelation by performing a permutation test for the Moran's I statistic using the spatial weights from the 8 nearest neighbors (package *spdep*, Bivand and Wong 2018) on all models retained.

Statistical analyses

We performed all statistical analyses within the R environment (R Core Team 2021). Unless stated otherwise, we present means with their standard error (*SE*), we compared means using pairwise two-sided *t*-tests adjusted for multiple comparisons using the Holm correction (Holm 1979), and statistical significance is set to $\alpha = 0.05$.

Ethics statement

Animal capture and handling was approved by the Animal Use Ethics Committee of University of Montreal (CÉUA 19-Rech-1993) and by the Ross University School of Veterinary Medicine Institutional Animal Care and Use Committee (IACUC 18.06.21).

RESULTS

We tagged 561 individual mongooses across 781 captures (Table 1). There were seven instances where two mongooses were found in a single trap and three instances where mongooses did not recover from anesthesia. The proportion of adult females pregnant or nursing differed between the summer (57.1%) and the fall (31.6%, $P = 0.002$). Summer pregnancy or nursing proportions were also lower at the grassland site (38.3%) compared to other sites (65.6%, $P < 0.001$). The sex ratio of captured animals was consistently biased towards females at each site and during both trapping sessions, but the effect was particularly marked at the grassland site and during the fall session at the dry forest site (Table 1). Average mongoose captures per unit effort were highest in the dry forest (0.53 captures/trap·day), followed by the grassland (0.39 captures/trap·day), the rainforest (0.31 captures/trap·day), and lowest in the suburban site (0.07 captures/trap day). Capture rates were higher during the summer than in the fall at both sites that were sampled twice (Table 1).

Mongoose density estimation

Density estimates obtained from the three methods were highly correlated among sites and seasons (all Pearson correlation coefficients ≥ 0.92 , with $r = 0.99$ between MARK and SECR estimates), and most confidence intervals for site- and season-specific densities calculated by the different estimators overlapped. MARK models systematically provided the lowest density estimates (range: 0.53–3.33 mongooses/ha),

TABLE 2. Mongoose abundance, area sampled (ha), sex-ratio (%♀), and density (no. mongooses/ha) estimated using three different methods based on capture-mark-recapture data. The 95% confidence intervals of each estimate are shown in brackets, where applicable. Mongooses were trapped at four different sites during summer (i.e., between late June and early August) and two of the same sites were also sampled during fall (i.e., between late October and early November).

Method	Grassland		Dry forest		Suburban	Rainforest
	Summer	Fall	Summer	Fall	Summer	Summer
MDI						
Abundance (MNKA)	87	46	170	149	29	67
Density	2.82	1.49	4.88	4.35	0.80	2.40
Area	30.8	30.8	34.8	34.2	36.4	27.9
Sex-ratio (%♀)	0.74 (0.64–0.83)	0.72 (0.59–0.85)	0.51 (0.44–0.59)	0.64 (0.57–0.72)	0.55 (0.37–0.74)	0.54 (0.42–0.66)
MARK						
Abundance	98 (90–107)	58 (44–78)	191 (178–206)	163 (154–172)	33 (29–38)	76 (69–84)
Density	1.81 (1.65–1.98)	1.57 (1.17–2.10)	2.82 (2.62–3.03)	3.33 (3.15–3.52)	0.53 (0.46–0.61)	1.26 (1.15–1.39)
Area	54.14	37.1	67.8	48.8	62.4	60.5
Sex-ratio (%♀)	0.73	0.72	0.51	0.64	0.55	0.54
SECR						
Density	2.56 (1.92–3.29)	2.06 (1.28–3.31)	5.01 (3.99–6.28)	5.85 (4.42–7.76)	0.62 (0.11–3.63)	1.42 (1.07–1.87)
Area	35.0	22.4	33.6	24.6	24.1	45.9
Sex-ratio (%♀)	0.73 (0.63–0.82)	0.72 (0.57–0.83)	0.51 (0.44–0.59)	0.63 (0.56–0.71)	0.45 (0.28–0.63)	0.52 (0.40–0.64)

while the SECR models generated the highest estimates (range: 0.62–5.85 mongooses/ha), except for the rainforest site for which the MDI estimate was higher (2.40 mongooses/ha, compared to 1.26 and 1.42 mongooses/ha derived from the MARK and SECR models, respectively). SECR has been shown to generate estimates closer to true abundance values in large populations but to overestimate abundance in smaller populations ($n \leq 50$; Blanc et al. 2013). Since summer MNKA are > 50 at each site except the suburban site (Table 2), hereafter we report SECR density values for the dry forest, grassland and rainforest sites, and MARK density values for the suburban site unless specified otherwise.

Summer mongoose densities were highest for the dry forest (95% confidence interval [CI95] = 3.99–6.28 mongooses/ha), followed by the grassland (CI95 = 1.92–3.29 mongooses/ha), the rainforest (CI95 = 1.07–1.87 mongooses/ha) and lastly the suburban site (CI95

= 0.46–0.61 mongooses/ha; Table 2). All summer density estimates differed among habitats, while density confidence intervals overlapped across seasons for both sites sampled twice (fall estimate CI95 = 4.42–7.76 and 1.28–3.31 mongooses/ha for the dry forest and grassland, respectively).

We observed seasonal differences in sampled areas used to compute MARK density estimates (Table 2). These differences were the result of a noticeable change in mongoose mean maximal distances moved (MMDM; used in trapping area estimation). The MMDM by mongooses captured at the grassland site decreased from 198 ± 114 m during the summer trapping session to 122 ± 47 m during the fall sampling. Similarly, MMDM in the dry forest site decreased from 238 ± 153 m during the summer to 134 ± 60 m in the fall. Although effective sampling area (ESA) estimated by SECR differed from the areas estimated using MMDMs, SECR ESAs

TABLE 3. Top ranked models generated in MARK for mongoose density estimation at four sites representative of the St. Kitts landscape (grassland [GL], dry forest [DF], suburban area [SU] and rainforest [RF]). Covariates included in the candidate model sets were sex, time (discrete), Time (continuous) and site for the summer trapping session.

Session	Sites	No. capture histories in model (n)	Parameters affecting capture rate (p) and p estimates	Parameters affecting recapture rate (c) and c estimates	No. parameters estimated	Fletcher \hat{c}
Summer	GL, DF, SU, RF	354	None (p(.) retained) p = 0.190	Sex ($c_{\delta} > c_{\varphi}$) Time (c decreases over session) Site ($c_{RF} > c_{GL} > c_{DF} > c_{SU}$) Range = 0.010-0.193, \bar{x} = 0.077 \pm 0.006	7	0.993
Fall	DF	147	None (p(.) retained) p = 0.209	Sex ($c_{\delta} = 0.07$, $c_{\varphi} = 0.03$)	3	0.949
Fall	GL	46	None (p(.) retained) p = 0.176	None (c(.) retained) c = 0.068	2	0.999

also decreased between the summer and fall sessions for all sites sampled on both occasions (35.0 to 22.4 ha, and 33.6 to 24.6 ha for the grassland and dry forest sites, respectively).

Island-wide weighted average mongoose population density

A simple average including all sites and trapping sessions resulted in a mean SECR density for St. Kitts of 2.92 ± 0.84 mongooses/ha. When resampling over a St. Kitts land cover database (Helmer et al. 2008; Appendix 1) and using summer site-specific SECR densities, we estimate island-wide mongoose density at 2.28 ± 0.68 mongooses/ha.

Factors affecting capture rates

Top-ranked models retained for density estimation using MARK differed by season and site (Table 3). Initial capture rates tended to be constant and systematically greater than recapture rates. Recapture rates varied among sites and between sexes (except for the fall trapping session at the grassland site). During the summer, recapture rates decreased from the first to the tenth trapping days. In contrast, recapture rates were uniform during the fall trapping sessions at both sites sampled.

For all session-site combinations, the top-ranked SECR model used to estimate density did not include any covariate affecting detection parameters, suggesting that mongoose detection probability did not significantly change over the trapping periods, was not affect-

ed by any behavioral reaction to past trapping history (i.e., trap avoidance or seeking), and was equal between sexes. Mongoose densities were spatially homogeneous over all sites, except the suburban area which displayed a quadratic trend in mongoose densities (Fig. 6). The best model accounting for the spatial heterogeneity in mongoose density over the suburban site resulted in an estimated average density of 0.62 ± 0.70 mongooses/ha, while the same model with homogeneous density over the site estimated density at 1.39 ± 0.66 mongooses/ha.

Factors influencing trapping success

We observed variability in individual trap capture rates, with some trap locations consistently yielding captures, while other trap locations were less frequented (Fig. 7a). This variability was not simply a result of the same individual mongoose consistently entering the same trap, as the number of unique captures also substantially varied among traps within the grid (Fig. 7b).

Soil type, vegetation type and topographic slopes varied among sites (Fig. 8) and among trap locations within sites. However, we found no spatial autocorrelation in trapping success over the sites, and therefore used non-spatial GLMs to investigate the effects of microhabitat features on trapping success. Although sites differed in the microhabitat features that were retained in the best models describing trap success, none of the coefficients from the regression models were statistically significant (Table 4).

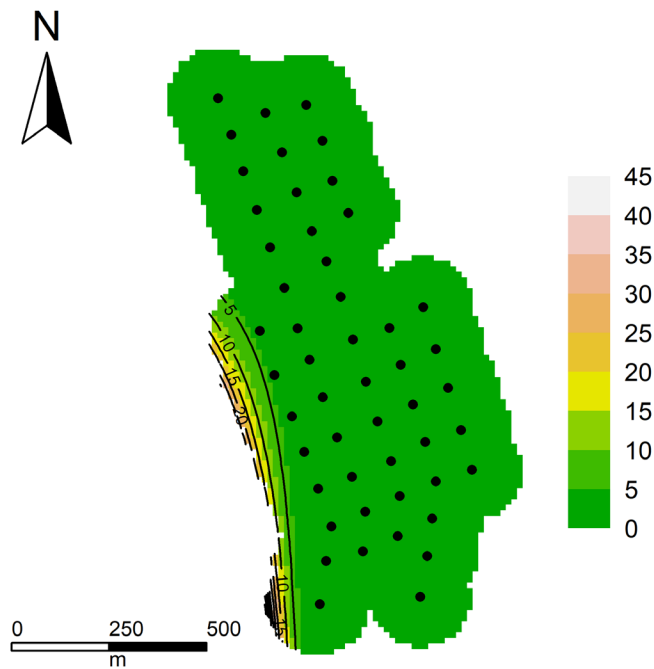


FIG. 6. Mongoose density over the suburban site estimated using a quadratic trend surface in secr (Efford 2020). Black dots illustrate trap location over the sampling area.

DISCUSSION

We provide the first mongoose density estimations for the island of St. Kitts, as well as robust evidence that mongoose densities vary considerably among habitat types across the island. This questions the way average island densities have been calculated in previous studies and the density-area relationship derived thereof (e.g., Horst et al. 2001), with important implications for the design of management interventions targeting this species. Our data suggest sex- and season-specific effects on trapping success, which affects apparent sex ratios derived from CMR estimates. Differential catchability between males and females and across seasons may result from variation in foraging activity, with potential consequences for interventions targeting the small Indian mongoose in the Caribbean islands (e.g., oral rabies vaccination or toxicant bait uptake rates).

Habitat-specific mongoose densities

Few other studies have investigated inter-habitat variation in mongoose densities in the Caribbean. Johnson et al. (2016) estimated mongoose densities in Puerto Rico in a rainforest and in a dry forest during the fall and spring seasons and found no significant differences in mongoose densities among sites and seasons. However, their capture (0.10 ± 0.01 captures per trap-

day) and recapture rates (0.012 ± 0.004 captures per trap·day) were considerably lower than those observed in our study (total captures: 0.31 ± 0.06 captures per trap·day; recaptures: 0.09 ± 0.02 captures per trap·day), resulting in large confidence intervals in the Puerto Rico density estimates (Johnson et al. 2016). Moreover, the Johnson et al. (2016) study was conducted across two years, and inter-annual effects on mongoose densities cannot be excluded. Similarly, mongoose densities estimated in a variety of habitats ranged from 0.6–6.8 and 2.0–13.7 mongooses/ha in Jamaica and St. Croix, respectively (Hoagland et al. 1989; Horst et al. 2001). However, no standard error or confidence interval is reported with the Jamaica and St. Croix density estimates and trapping efforts on St. Croix were conducted over a period of eight years, without clear identification of seasonal variation in survey timing (Hoagland et al. 1989; Horst et al. 2001). As a result, inter-annual, seasonal and habitat-specific differences in mongoose densities are unclear from these studies. The timing of our CMR surveys controls for inter-annual and seasonal variability in mongoose densities, thus ensuring that observed habitat-specific differences in mongoose density are associated with site-specific characteristics. Because mongooses have few to no predators and are not subject to any form of population control or management in St. Kitts, the observed densities in our study likely represent varying habitat carrying capacities associated with local resource availability. We found eight-fold differences between mongoose densities measured at our least and most populated sites, with sites sorted by increasing densities: suburban neighborhood < rainforest < grassland < dry forest. This ordering was consistent upon resampling of the grassland and dry forest sites in the fall.

Our observed relative differences in mongoose population density estimates among sites were also robust to the density estimation method used, although our MARK estimates were systematically lower than our SECR estimates (differences mostly non-significant). SECR estimators account for spatial heterogeneity in animal densities over the survey area and consider individual home range proximity to the site (Borchers and Efford 2008), generating more accurate density estimates when sample size is sufficient (i.e., abundance > 50) for model parameter estimation. In this study, mongoose densities were homogeneous over sampling

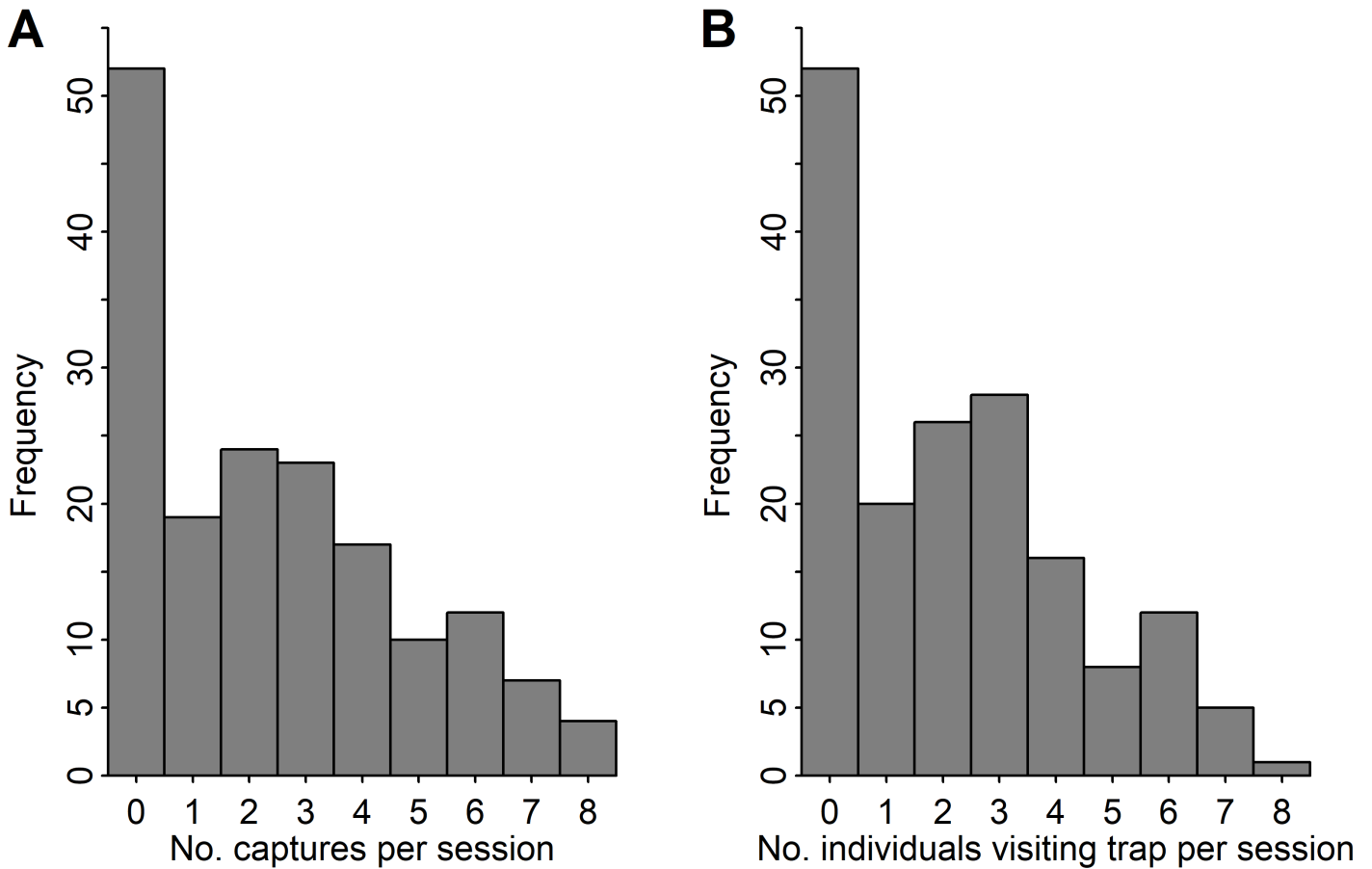


FIG. 7. Distribution of the total number of captures (A) and the number of unique mongooses captured (B) in each trap ($n = 169$) operated during the summer 2018 session, all four sites combined. While a considerable number of traps yielded zero captures, others captured a mongoose nine out of ten trap days.

arrays, except at the suburban site. Although the landscape was relatively homogeneous across the suburban trapping array, the higher mongoose density area at the southwestern quadrant of the site (Fig. 7) might be explained by local habitat similar to the grassland site, where mongooses were estimated to be more abundant. The greater than two-fold difference in mongoose suburban densities estimated by the spatially homogenous versus heterogeneous SECR models stresses the importance of accounting for spatial heterogeneity over the survey area when present.

In our study, the high number of mongooses marked and recaptured resulted in rich capture histories for each site and trapping season, and MNKA values indicated population sizes ≥ 50 , except for the suburban site. Therefore, our estimates from non-spatial CMR may be slightly biased toward lower numbers for three of the four sites sampled. The absolute differences in densities estimated using the different CMR models highlighted in our study stresses that to compare mongoose

densities across the insular range of the species, methods should be standardized across studies. Mongoose population densities reported throughout the Caribbean islands are highly variable (0.19–9.0 mongooses/ha; Berentsen et al. 2018), and although this might result from differences in habitats sampled and island-specific differences in mongoose populations, part of this variation can be attributed to differential experimental design and estimation methods. For instance, while mongoose densities of 2.5 mongooses/ha were reported at Cabo Rojo, Puerto Rico (Horst et al. 2001) using the Lincoln estimate (known to overestimate density when recapture rates are low; Lynn 2009), densities ranging between 0.75–1.85 were reported for the same area using a SECR estimation model (Johnson et al. 2016). We recommend the use of SECR models, because they are well-adapted to mongoose trapping data and yield unbiased and meaningful precision of estimates, given good quality capture histories.

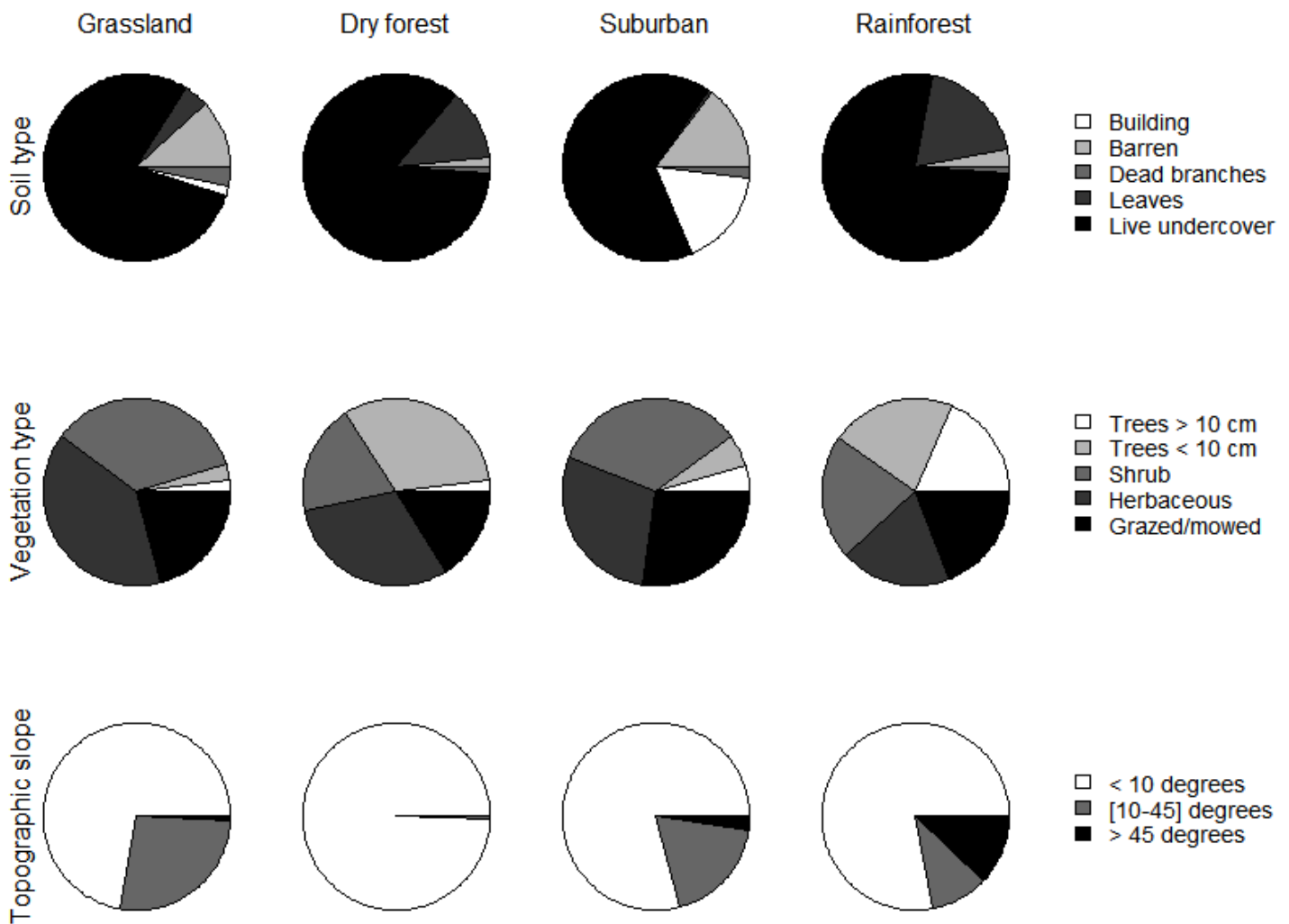


FIG. 8. Microhabitat characterisation. Average microhabitat characteristics at trap locations estimated at four sites representing different St. Kitts habitats. Trap sites from all habitat types were dominated by live undercover, small trees and shrubs, and low topographic slopes. As expected, the suburban site had a greater proportion of soil occupied by buildings (all pairwise $P < 0.001$) and a lower proportion covered by live vegetation (pairwise P ranging from < 0.001 to 0.019) compared to other sites. The proportion of barren soil was similar between the grassland (12.5 ± 0.9) and the suburban sites (14.8 ± 1.4 ; $P = 0.51$) due to the presence of paved and dirt roads, respectively, while the rainforest (3.3 ± 0.9) and dry forest (1.8 ± 0.8) had low proportions of barren soil ($P = 0.51$). Dominant vegetation type varied among sites. The proportion of large trees was higher in the rainforest (18.8 ± 0.8) than in all other sites (3.0 ± 0.5 ; all pairwise $P < 0.001$). The dry forest site was flatter (proportion of slopes $< 10^\circ = 99.5 \pm 0.8$ versus 85.1 ± 1.9 , $P < 0.001$), while the rainforest was characterized by more extreme topography (proportion of slopes $> 45^\circ = 12.1 \pm 0.9$ versus 1.1 ± 0.5 ; $P < 0.001$).

Island-wide weighted average mongoose population density

The substantial inter-habitat differences in mongoose densities observed in this study have important implications for the validity of island-specific mongoose densities reported in the literature, and the theories derived thereof. Island-wide mongoose densities have been calculated by simply averaging estimates

from surveys conducted at different times and sites over an island (e.g., Hoagland et al. 1989; Horst et al. 2001). These estimates have been used to suggest that observed average mongoose densities across islands are highly correlated with the log of island size (correlation coefficient: -0.98 ; Horst et al. 2001), in accordance with the density compensation theory (MacArthur et al. 1972).

TABLE 4. Top models explaining trapping success using trap-site microhabitat characteristics as fixed effects. Model coefficients are standardized, weighted-averaged among models with a $\Delta AICc \leq 2$ and in which all covariates significantly improved the fit.

Habitat type	Variable in model(s) retained	Coefficient in conditional averaged model \pm SE	P-value (averaged model)	Models used in averaging (AICc; weight)
Grassland	Presence of anthropogenic waste (PAW)	-0.065 \pm 0.047	0.180	$N_{\text{capture}} \sim \text{PAW}$ (159.06; 0.40)
	Vegetation: Trees/shrubs (TvsS)	-0.078 \pm 0.044	0.084	$N_{\text{capture}} \sim \text{DistRoad}$ (160.14; 0.23)
	Soil: Covered/barren (CvsB)	0.054 \pm 0.039	0.182	$N_{\text{capture}} \sim \text{CvsB}$ (160.62; 0.18)
	Distance to nearest road (DistRoad)	0.062 \pm 0.036	0.100	$N_{\text{capture}} \sim \text{TvsS}$ (161.39; 0.12)
				$N_{\text{capture}} \sim \text{PAW} + \text{DistRoad} + \text{CvsB} + \text{TvsS}$ (162.83; 0.06)
Dry forest	Vegetation: Trees/shrubs (TvsS)	0.040 \pm 0.033	0.235	$N_{\text{capture}} \sim \text{OvsB}$ (195.43; 0.42)
	Soil: Open vs buildings (OvsB)	0.047 \pm 0.035	0.191	$N_{\text{capture}} \sim \text{TvsS}$ (195.79; 0.35)
				$N_{\text{capture}} \sim \text{OvsB} + \text{TvsS}$ (196.73; 0.22)
Suburban	Soil: Covered/barren (CvsB)	-0.300 \pm 0.212	0.168	$N_{\text{capture}} \sim \text{CvsB} + \text{TvsS}$ (112.09; 0.41)
	Vegetation: Trees/shrubs (TvsS)	0.413 \pm 0.211	0.056	$N_{\text{capture}} \sim \text{TvsS}$ (112.28; 0.37)
				$N_{\text{capture}} \sim \text{CvsB}$ (113.33; 0.22)
Rainforest	Soil: Leaves/live vegetation (LeavesvsLive)	-0.090 \pm 0.055	0.114	$N_{\text{capture}} \sim \text{LeavesvsLive}$ (147.26; 0.38)
	Topography: $> 10^\circ / < 10^\circ$ (InfvsSup10)	0.078 \pm 0.053	0.160	$N_{\text{capture}} \sim \text{InfvsSup10}$ (147.40; 0.36)
				$N_{\text{capture}} \sim \text{LeavesvsLive} + \text{InfvsSup10}$ (148.00; 0.26)

Although using data from this study, habitat-weighted and raw island averages do not differ statistically ($P=0.57$), changes in the proportion of the island's land cover made up of the different habitat-types considered could have led to substantially different results. This highlights the fact that although conducting mongoose density estimation studies in habitats suitable for the species optimizes capture rates, sampling all primary habitat types is essential to obtain appropriate overall island population density estimates.

St. Kitts is smaller than any island considered in

the Horst et al. (2001) analysis, yet the habitat-specific weighted average density estimated in our study is lower than any average density reported in the former study (range: 2.5–6.6 mongooses/ha). We tentatively explain this divergence by two factors: differential density estimation methods and the influence of sampling locations. Comparing our St. Kitts density estimates with densities calculated with the same methods (SECR) and in similar habitats in Puerto Rico suggests that St. Kitts (area: 174 km²) mongoose densities are higher than those found in similar habitats on a larger

island (Puerto Rico area: 8900 km²). Indeed, our average estimate for the dry forest site on St. Kitts was 5.43 ± 0.42 mongooses/ha, while the Puerto Rico estimate for a similar habitat (Cabo Rojo) was 1.3 ± 0.55 mongooses/ha (Johnson et al. 2016). Similarly, our rainforest estimate on St. Kitts was 1.42 (IC95 = 1.07–1.87) mongooses/ha, whereas the Puerto Rico estimate at El Yunque was 0.96 ± 0.02 mongooses/ha (Johnson et al. 2016). To determine whether this density-area relationship is consistent across the Caribbean islands, additional density studies conducted in comparable habitat types across different islands and using standardized trapping designs and capture history analysis methods are needed.

Factors influencing mongoose trapping success

Although mongoose capture has been reported to be challenging in some circumstances (e.g., Coolman 2006), very few studies quantified the factors favoring mongoose capture success. We investigated local characteristics of the habitat that might influence mongoose trapping success on a fine spatial scale (resolution: 100 m²), but found no significant relationship between individual trap success and soil cover, vegetation type, surrounding topography and presence of anthropogenic waste or buildings despite high variability in capture rates among the different traps. This suggests a lack of microhabitat specialization and that the home range of mongooses might be more important for determining local resource selection compared to fine-scale site and trap microhabitat.

In addition to providing density estimates, our MARK model selection allows us to interpret factors that affected mongoose catchability in our study. We observed a strong behavioral effect, with first capture rates being on average 2.8 ± 0.07 times higher than recapture rates. This suggests that mongooses generally develop trap aversion following initial capture. Moreover, first and subsequent capture rates were differentially influenced by covariates in MARK models. While first capture rates were temporally constant throughout the trapping sessions, summer recapture rates decreased by a factor of 1.8 over the course of the 10-day trapping session. This suggests that in our system, increasing the duration of trapping efforts would not substantially increase the number of mongooses recaptured.

In addition, our estimated sex-ratios were significantly biased toward females at both sites sampled

in the fall, and at the grassland in the summer. This is consistent with Johnson et al. (2016) who reported a female-biased sex ratio in the fall, as opposed to a male-biased sex ratio in the spring in a dry forest site. Yet, mongoose sex ratios in the Caribbean islands are generally considered unbiased, and deviations from a 1:1 ratio in some studies are thought to result from differential sex-specific catchability or other biases in trapping techniques (Horst et al. 2001). In particular, trap-removal studies generally yield apparent male-biased sex ratios in early phases of the study (e.g., Nellis and Everard 1983; Coblenz and Coblenz 1985; Vilella 1998), which may be attributable to larger male home ranges and greater mobility compared to females (Horst et al. 2001). In contrast, mark-recapture trapping generally results in sex ratios closer to 1:1, although deviations in both directions and seasonal variations have been reported (Pitt et al. 2015; Johnson et al. 2016). While our SECR models suggested constant and equal detectability between the sexes, most recapture rates estimated in MARK models were higher for males than females. Although including sex-based heterogeneity in CMR models is expected to correct for differential capture rates, a simulation study suggested that resulting sex ratio estimates might nevertheless be skewed toward the sex displaying higher catchability (McKnight and Ligon 2017). Our CMR models might thus underestimate female catchability in the fall and at the grassland.

While mongooses can breed year-round, they are considered seasonal breeders in the Caribbean islands, with a birth peak occurring between May and August followed by a six to eight weeks nursing period (Pearson and Baldwin 1953; Pimentel, 1955; Gorman 1976; Nellis and Everard, 1983; Coblenz and Coblenz 1985). The observed season-specific proportions of females either pregnant or actively nursing reported in this study further suggests that our summer survey thus took place during the birthing season, while we conducted our fall survey during females' post-lactation period. It is conceivable that females were overrepresented in captures due to sex-specific behaviours. Pregnancy and particularly nursing pose high energy demands for females, which reflects in female body weight and condition. Females reach their minimal body weight and fat stores between August and September (Coblenz and Coblenz 1985), while they are still caring for their

offspring (Nellis and Everard 1983; Hays and Conant 2007). Sex-specific seasonal variation in mongoose body conditions likely influence individuals' motivational state to forage, consume baits, and enter traps.

The persistent female-biased sex ratio at the grassland site likely reflects poorer resource availability, which is supported by significantly lower summer female body weight (difference in means = 57.6 g, $P = 0.006$; no difference in male body weights, $P = 0.96$) and reproductive rates at this site compared with other sites. In the fall, when female-biased sex ratios were observed at both sites surveyed, there was no difference in female body weight ($P = 0.92$) and reproductive rates ($P = 0.50$) between the grassland and the dry forest.

Our results suggest that sex- and site-specific factors including breeding, maternal care, movements and habitat quality may have seasonal effects on male and female capture rates. Additional trapping efforts on St. Kitts in the winter and spring are needed to determine whether apparent biased sex ratios are inversed during the mating season, when males actively search for mates. Although the apparent female-biased sex ratio observed in this study is most likely an artefact of the trapping process, it nevertheless has noteworthy implications. Population control programs targeting this invasive species would have a greater impact on mongoose population dynamics if conducted when females are most susceptible to trapping. Similarly, ORV or toxicant bait uptake may be greatest during the post-weaning period, when females are actively foraging with young of the year.

In conclusion, this study reports the first mongoose population density estimate conducted on the island of St. Kitts. We found important differences in mongoose densities among the four habitat types surveyed and recommend that land cover be taken in consideration when inferring average island mongoose densities from mark-recapture estimates. We also found apparent site- and season-dependent female-biased sex-ratios, which are most likely attributable to differential behavior associated with mongoose breeding cycle and habitat quality. Understanding spatial heterogeneity in mongoose densities and temporal variation in sex-specific capture rates may inform actions and/or programs to control damage to native fauna by mongooses and rabies virus circulation in mongoose populations. We recommend sampling representative habitats across islands, and the

adoption of standardized study design and density estimation methods for comparability across the Caribbean region. This would allow for a more rigorous assessment of the density-area relationship in insular mongoose populations.

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APPENDIX 1. Habitat type definitions for the St. Kitts landscape based on thematic resolution simplification of the landcover raster (Helmer et al. 2008). Thematic resolution simplification down to six categories was conducted by reassigning pixel codes to either one of the four Caribbean terrestrial habitat types considered in this study, habitats deemed inhospitable for mongooses, or unsampled habitat types. Unsampled habitat areas were excluded from the weighted island-wide mongoose density estimate, since no information on mongoose density in these habitats was available.

Habitat type	Pixel codes used in resampling	Proportion of St. Kitts island area (%)
Suburban	High-medium density urban or built-up land Low density built-up land (rural or residential)	7.3
Grassland	Sugar cane (and minor crops) Coconut palm-pasture Pasture, hay or other grassy areas (e.g. soccer fields) Golf course	45.1
Rainforest	Evergreen forest with coconut palm Seasonal evergreen forest Evergreen forest (including Sierra palm forest) Sierra palm, transitional and tall cloud forest Elfin and sierra palm cloud forest	12.3
Dry forest	Drought deciduous open woodland Deciduous, evergreen coastal or mixed forest or shrubland, with or without succulents Drought deciduous forest/shrub Semi-deciduous forest (includes semi-evergreen forest)	31.0
Inhospitable habitat	Quarries Coastal sand, rocks, cliffs or bare ground Bare soil (included bulldozed land)	3.1
Unsampled habitat	Water-permanent Emergent wetland Mangrove Montane non-forest vegetation Steep non-forest vegetation Seasonally flooded savannahs and woodland	1.1