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Are R. Berentsen

USDA APHIS WS NWRC Colorado, are.r.berentsen@aphis.usda.gov

Caroline C. Sauvé

Université de Montréal

Mel J. Rivera-Rodriguez

USDA APHIS WS NWRC Aalabama

Fabiola B. Torres-Toledo

USDA APHIS WS NWRC Colorado

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Richard B. Chipman

 USDA APHIS WS NRMP New Hampshire

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Authors

Are R. Berentsen, Caroline C. Sauvé, Mel J. Rivera-Rodriguez, Fabiola B. Torres-Toledo, Richard B. Chipman, and Amy T. Gilbert

Population Density of the Small Indian Mongoose (*Urva auropunctata*) Across Multiple Habitat Types and Seasons in Puerto Rico

ARE R. BERENTSEN^{1,*}, CAROLINE C. SAUVÉ², MEL J. RIVERA-RODRIGUEZ³, FABIOLA B. TORRES-TOLEDO¹,
RICHARD B. CHIPMAN⁴, AND AMY T. GILBERT¹

¹United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Fort Collins, Colorado, U. S. A.

²Faculté de Médecine Vétérinaire, Université de Montréal, Saint-Hyacinthe, Québec, Canada

³United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, Auburn, Alabama, U. S. A.

⁴United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Rabies Management Program, Concord, New Hampshire, U. S. A.

*Corresponding author: are.r.berentsen@usda.gov

ABSTRACT—The small Indian mongoose (*Urva auropunctata*) is a rabies reservoir on several Caribbean Islands including Puerto Rico. In the continental United States, oral rabies vaccination (ORV) has been used to control and locally eliminate rabies viruses targeting meso-carnivores including raccoons (*Procyon lotor*), grey foxes (*Urocyon cinereoargenteus*), and coyotes (*Canis latrans*), and has more recently been proposed to mitigate and control mongoose rabies in Puerto Rico. A fundamental understanding of the population density of the target species is an important factor in planning bait application rates prior to ORV operations. In Puerto Rico, most ecological studies on mongooses have been restricted to the rainforest region in the northeastern portion of the island. We calculated population density estimates for mongooses at seven sites representing four habitat types in Puerto Rico. We marked 445 unique mongooses across 593 capture events during 12,530 trap days during 2016–2021. Mean (SE, 95% CI) population densities were greater in closed to open broadleaved evergreen forest habitat (0.79 ± 0.13 , 0.67 – 0.92 mongooses/ha) compared to grasslands (0.43 ± 0.10 ; 0.35 – 0.55 mongooses/ha), rainfed croplands (0.26 ± 0.10 , 0.18 – 0.38 mongooses/ha), and shrub/herbaceous habitat (0.19 ± 0.05 , 0.15 – 0.25 mongooses/ha). We did not detect seasonal variation in mongoose population density (0.48 [0.06; 0.35 – 0.62] and 0.39 [0.06; 0.27 – 0.50] mongooses/ha measured in the wet (May–November) and dry (December–April) seasons, respectively). Multiple ORV applications may be needed annually for adequate population immunity, particularly in habitats with high mongoose population densities and rapid population turnover.

The small Indian mongoose (*Urva auropunctata*) was introduced throughout the Caribbean in the late 19th century, primarily for rodent control in agricultural settings (Hoagland et al. 1989). Initially, rodent damage to agriculture declined, but within ten years scientists were also reporting precipitous declines in native fauna which they attributed to mongooses (Lewis 1953). Ultimately, rodent populations recovered, and the mongoose is now largely considered a pest species throughout most of its introduced range.

Considerable research has been conducted on mongooses throughout the Caribbean on topics ranging from population control (Pimentel 1955a), impacts on native fauna (Vilella and Zwank 1993; Engeman

et al. 2006; Leighton et al. 2008; Lewis et al. 2011), population density (Johnson et al. 2016; Sauvé et al. 2022) and, on some islands, the role as a rabies reservoir (Pimentel 1955b; Zieger et al. 2014; Berentsen et al. 2015, 2023). Early research by Pimentel (1955b) and later by Everard and Everard (1992) discussed mongoose population reduction to control the spread of zoonotic diseases, such as rabies, but that such efforts were unsustainable for long-term disease control. In the continental United States, oral rabies vaccination (ORV) is used to control rabies in several meso-carnivore species, including raccoons (*Procyon lotor*), grey foxes (*Urocyon cinereoargenteus*), and coyotes (*Canis latrans*), through aerial and ground-based distribution

TABLE 1. Proportion of Puerto Rico covered by individual land cover types, based on the GLC Majority Class of the National Land Cover Database. Note: land cover proportions represent Puerto Rico proper and do not include outlying islands.

GLC Majority class	Area (Km ²)	Proportion of Land Cover
Closed to Open Canopy Broadleaved Evergreen Tree Cover	5,408.2	58.94%
Urban Areas	1,292.7	14.09%
Mixed Tree Cover	694.0	7.56%
Grassland	492.0	5.36%
Rainfed Cropland	459.0	5.00%
Mostly Cropland in a Mosaic with Natural Vegetation	209.4	2.28%
Bodies of Water	186.9	2.04%
Undefined	104.4	1.14%
Saline Water Flooded Tree Cover	92.7	1.01%
Mostly Natural Vegetation in a Mosaic with Cropland	82.0	0.89%
Flooded Shrub or Herbaceous Cover	75.0	0.82%
Herbaceous Cropland	42.2	0.46%
Mostly Trees and Shrubs in a Mosaic with Herbaceous Cover	23.0	0.25%
Mostly Herbaceous Cover in a Mosaic with Trees and Shrubs	10.0	0.11%
Closed to Open Canopy Needleleaved Evergreen Tree Cover	4.0	0.04%
Fresh or Brackish Water Flooded Tree Cover	1.0	0.01%

of vaccine baits (Slate et al. 2009; Gilbert and Chipman 2020). Currently, no ORV program for mongooses exists globally, but research suggests ORV may be a potential strategy to control mongoose rabies in the Caribbean region (Vos et al. 2013; Berentsen et al. 2020). Oral baiting programs targeting mongooses in the Caribbean region may also be relevant for population control to protect native fauna as has been suggested for other tropical islands with non-native, invasive mongooses (Sugihara et al. 2018).

One important consideration when planning bait application rates is the population density of the target species, which may vary across habitat types (Riley et al. 1998; Prange et al. 2003; Slate et al. 2020). Mongoose habitat preferences may vary on different tropical islands (Hoagland et al. 1989). In St. Lucia, Edwards (2006) found mongooses were more likely to be captured in riparian habitats than in scrub or open habitats and Roy et al. (2002) determined mongooses preferred rocky or riparian habitat vs. scrub or grassland habitats in Mauritius. On St. Kitts, Sauv e et al. (2022) reported higher population densities in dry forest habitat when compared with grasslands, rainforests and suburban areas, and with seasonal densities higher in the dry forest

and grasslands during the dry compared to wet season (CARICOM 1993).

The life history of mongooses may also be variable across regions, yet year-round breeding and reproduction has been reported in Puerto Rico (Pimentel 1955b) and may be associated with more uniform densities between wet and dry seasons on the landscape. In Puerto Rico, much of the previous research on mongooses has focused on populations in the rainforest region on the NE portion of the island (Vilella 1998; Quinn and Whisson 2005; Guzm n-Col n and Roloff 2014; Johnson et al. 2016; Guzm n-Col n et al. 2019) with fewer studies in lowland scrub forests (Vilella and Zwank 1993; Johnson et al. 2016). Few data investigating mongoose population biology in other habitats across the island are available. Moreover, the use of different mark-recapture study design and population density estimators in prior studies precludes direct comparisons of results reported from the different studies. The Johnson et al. (2016) study is the most comprehensive in this regard, as it reports density in both dry forest and rainforest habitats and used multiple estimators. The Johnson et al. (2016) study suggested season rather than habitat type was an important factor influenc-

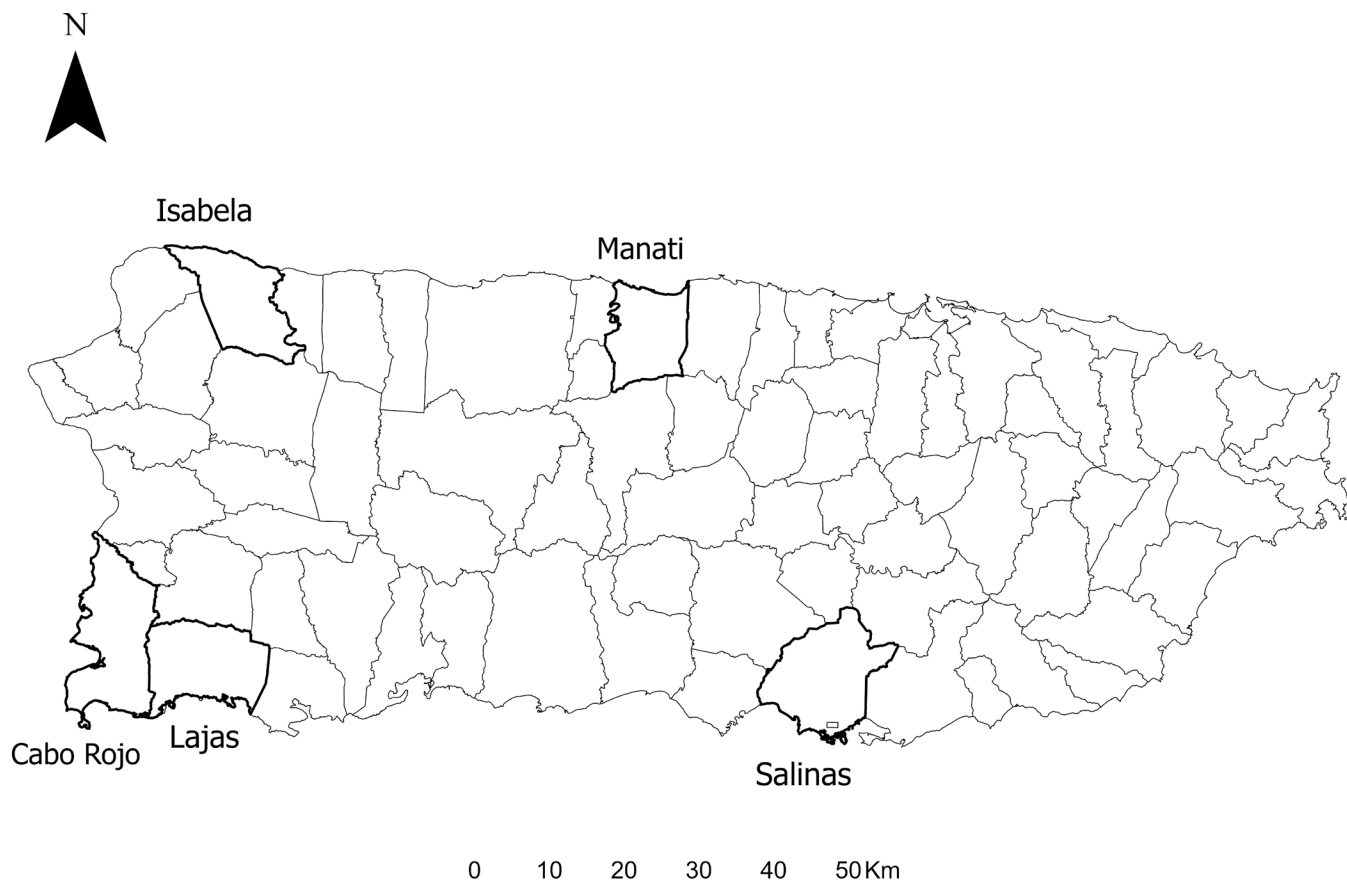


FIG. 1. Location of five municipalities selected for small Indian mongoose (*Urva auropunctata*) population density surveys in Puerto Rico, 2016–2021.

ing population densities between the rainforests and flooded shrub/herbaceous cover habitats (evaluated by Johnson et al. 2016), however these represent 59% and 0.8% of the Puerto Rico Island area, respectively (Table 1), and there is no available information on mongoose population densities for other habitat types. The ideal deployment of ORV to wildlife populations typically occurs at a time of year when natural resources are limited for the target species, when non-target interference is lowest, and when susceptible weaned young of the year may begin foraging independently of adults on the landscape (Elmore et al. 2017).

Our objective was to estimate mongoose population densities in multiple habitat types across Puerto Rico during both the wet and dry seasons. We hypothesized mongoose population densities would vary by habitat type with higher densities in forested habitats compared to other (open cover) habitat types such as grasslands or agricultural areas. Based on recent comparable studies in Puerto Rico and St. Kitts, we also expected mongoose population density estimates to vary by wet or dry season.

MATERIALS AND METHODS

Study area

We conducted this study at seven 0.5–1.0 km² sites on Federal, Commonwealth, and private land in five municipalities across Puerto Rico during 2016–2021: Aguirre (Salinas municipality), Escabi (Lajas Municipality), Refuge and Salt Flats (Cabo Rojo municipality), Isabela (Isabela municipality), and Manati North/South (Manati municipality) (Fig. 1). We initially selected these sites as broad representatives of mixed forest, dry forest, and agricultural habitats. We further refined the site-specific habitat types using land class data from the National Land Cover Database (NLCD; Multi-Resolution Land Characteristics Consortium, <https://www.mrlc.gov/>). We used ArcGIS Pro (ESRI, Redlands, CA) to extract the NLCD land class data associated with our study sites and calculated the proportion of the site occupied by each dominant habitat class as defined by the GLC Majority designation. Each site fell into one of the following four habitat classes: 1) Closed to Open Canopy Broadleaved Evergreen Tree Cover (hereafter

TABLE 2. Habitat class categories for seven sites across Puerto Rico, October 2016–September 2021, as determined by the GLC dominant land class category in the National Land Cover Database, and the proportion of each study site occupied by each habitat class.

Site name	Trapping plot size (km ²)	GLC dominant land class	Proportion of trapping plot
Refuge	1.0	Grassland	100%
Escabi	1.0	Grassland	79.7%
Aguirre	0.5	Closed to Open Canopy Broadleaved Evergreen Tree Cover	62.4%
Manati South	1.0	Closed to Open Canopy Broadleaved Evergreen Tree Cover	91.2%
Manati North	0.5	Closed to Open Canopy Broadleaved Evergreen Tree Cover	100.0%
Salt Flats	0.5–1.0	Flooded Shrub or Herbaceous Cover	98.6%
Isabela	0.5	Rainfed Cropland	79.9%

Broadleaved evergreen forest); 2) Flooded Shrub or Herbaceous Cover; 3) Grassland; and 4) Rainfed Cropland (Table 2). We defined the trapping seasons as wet (May–November) or dry (December–April) based on island-specific rainfall patterns (Miller and Lugo 2009). Exact date ranges for trapping activity at each study site are found in Fig. 2.

Capture and handling

We live-captured mongooses in cage traps (Tomahawk Trap Company, Hazelhurst, Wisconsin, U. S. A.) baited with commercial canned tuna (Quinn and Whisson 2005). We arranged traps in a grid with traps placed 100 m apart, with perimeter traps 50 m from the edge of the designated trapping area, for a densi-

ty of 100 traps/km². We set traps in the morning and checked them every 24 hours for 10 days, rebaiting as necessary. The only exception was at one site during winter 2018, where trapping was suspended after five days for reasons unrelated to the study. We anesthetized captured mongooses with an intramuscular injection of 5 mg/kg tiletamine/zolazepam (Telazol[®], Zoetis Inc., Kalamazoo, Michigan, U. S. A.; Kreeger and Arnemo 2012). We injected a sterile passive integrated transponder (PIT) tag (Avid Identification Systems, Inc., Norco, California, U. S. A.) subcutaneously between the shoulder blades for individual mongoose identification. We also recorded weight, sex, reproductive status (e.g., pregnant and/or lactating), and relative age from each unique mongoose prior to releasing animals at the location of capture following arousal from anesthesia. Mongooses re-captured within a 10-day session were released without processing. Mongooses re-captured across different trapping sessions were anesthetized and processed as previously described except for the PIT tagging. Nontarget animals were immediately released from traps at the location of capture.

Population density estimation

We used three methods to estimate mongoose density from trapping data: 1) the mongoose density index (MDI; Johnson et al. 2016); 2) capture-mark-recapture (CMR) models for closed populations using program MARK (v 9.0; White and Burnham 1999) and/or the RMark interface (Laake 2013); and 3) spatially explicit CMR (SECR) models.

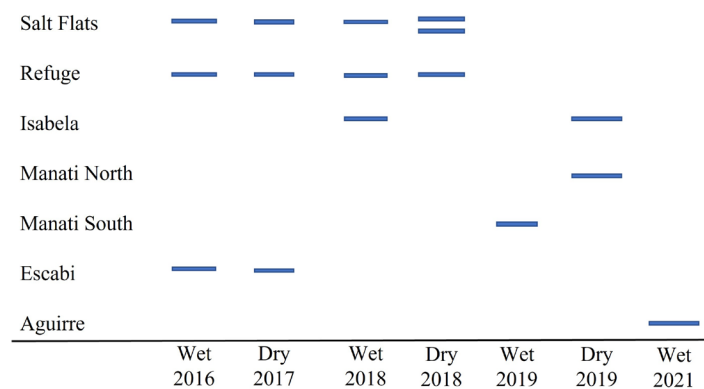


FIG. 2. Mongoose sampling frequency across seven sites during the wet and dry seasons in Puerto Rico, 2016–2021.

Mongoose Density Index (MDI)

The MDI uses the minimum number known alive (MNKA; the number of unique individuals captured within a single capture session) as an abundance index to calculate population density by the equation: $\hat{D}_{MDI} = MNKA/\hat{A}_{MDI}$ where \hat{A}_{MDI} = the effective trapping area (km²) calculated by creating concave hulls around all trap locations within capture sites. We calculated confidence intervals around the MNKA count estimates using the *poisson.test* function in R (R-Core Team 2021).

Capture Mark Recapture

We generated a series of Huggins closed population capture models using mongoose sex and relative age (adult or juvenile) as group factors. We considered age, sex, time (as a discrete variable with one level for each trapping session, and as a continuous variable) as covariates potentially affecting capture (p) and recapture (c) rates. We fit separate models for each trapping season-site and considered a null (intercept only) model and all combinations of the covariates as candidate models but lacked power within the capture data to evaluate models including parameter interactions. We assessed model goodness of fit using Fletcher \hat{c} (Fletcher 2012) as a measure of over-dispersion (e.g., Cooch and White 2018) and ranked models using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). We considered covariates supported when their inclusion in a model induced a $\Delta > 2$ AICc compared to a nested model excluding the variable (Arnold 2010). We estimated the effective sampling area (\hat{A}_{MARK}) used to calculate density using mean maximum distance moved (MMDM; Wilson and Anderson 1985; Johnson et al. 2016; Sauvé et al. 2022).

Spatially Explicit Capture-Recapture

We calculated mongoose density by SECR methods using the *secr* package in R (Efford 2022a). We used capture history data, site-specific trap layout and trap usage as input observations (Sauvé et al. 2022). We modelled capture history data from each season-site separately using hybrid mixture models using sex as a covariate. We considered the following effects on estimated detection parameters and density: 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), and time (Sauvé et al.

2022). 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 quadratic trend surface (Efford 2022b). We generated a candidate model list comprising all possible combinations of these effects and used the same AICc model selection criteria for SECR and MARK models.

Seasonal and habitat class effects on mongoose density

To test the effect of habitat and season on mongoose densities, we modelled MARK density estimates as a function of the dominant habitat class assigned to the site (Table 2) and the season when trapping took place. In these models, the independent variable (mongoose density) is an estimate (i.e., derived from a first-step CMR model) characterized by a sampling error. This represents a case of the 'generated regressor' problem, where second-step regressions generate underestimated standard errors if not properly addressed (Pagan 1984). To address this, we used bootstrapped standard errors (Greene 2017; Chen et al. 2022). For each trapping season, we generated 500 bootstrap samples by resampling capture histories with replacement. We derived site- and season specific mongoose density using the best MARK model for each bootstrap sample to generate a series of first-step regression outputs. We used these regression outputs to estimate the second-step regression, consisting of two univariate generalized linear models (GLM) with normally distributed errors and identity link function. Fixed effects tested were habitat class (4 levels) and season (2 levels). We used standard deviations from the coefficient estimates as the bootstrapped standard errors.

We performed all statistical analyses within the R environment (R Core Team 2021). Unless stated otherwise we present means with their standard error (SE) and 95% confidence interval.

Ethics statement

Animal capture and handling followed the guidelines of the USDA APHIS WS National Wildlife Research Center's Institutional Animal Care and Use Committee under research protocols QA-2888 and QA-2573. Additional authorizations were provided by the Puerto Rico Department of Natural and Environmental Resources (scientific collection permits 2014-IC-014, 2015-IC-088, 2016-IC-149, 2021-IC-035) and the US Fish and Wildlife Service (special use permits 41521-2016-17 and 41521-2017-09).

RESULTS

We marked 445 individual mongooses across 593 capture events (Table 3; 12,530 trap days). There was one instance where two mongooses were found in a single trap, and one mongoose mortality (animal that did not recover from anesthesia). The sex ratio of captured animals generally did not differ from 1:1, except during the dry season 2017 at the Salt Flats and Escabi where it was male-biased (Table 4). There was substantial variability in average mongoose captures per unit effort (CPUE) observed in our study. Captures per unit effort were highest in Aguirre (0.194 captures/trap·day) and Manati North (0.159 /trap·day) and lowest during the wet seasons at the Refuge (0.008 captures/trap·day) and the Salt Flats (0.006 captures/trap·day) (Table 5). The three trapping sessions with CPUE < 0.02 had insufficient capture histories for MARK and SECR models to converge, while the trapping history from one season with CPUE = 0.024 allowed the MARK model to converge but not the SECR model.

Mongoose density estimation

Density estimates obtained from the MNKA and MARK methods were highly correlated ($r = 0.90$), but correlations between MNKA and SECR ($r = 0.38$) and between SECR and MARK estimates ($r = 0.49$) were lower (Fig. 3). Most confidence intervals for site- and session-specific densities calculated by the different methods overlapped. MARK models generally provided the lowest density estimates (range: 0.06–0.97 mongooses/ha), while the SECR models generated the highest estimates (range: 0.21–1.84 mongooses/ha). SECR is known to generate estimates closer to true abundance values in large populations but to overestimate abundance in smaller populations (i.e., when $n \leq 50$; Blanc et al. 2013). Since MNKA estimates are < 50 at most sites (Table 5), hereafter we report MARK density values for all sampling seasons, except for Manati north (Dry 2019), Manati south (Wet 2019) and the Refuge (Dry 2017) for which SECR values are also reported (Table 3). For sessions for which CMR models did not converge, MNKA estimates are reported (Table 3). Mean (SE; 95% CI) population densities were 79 (13; 67–92) mongooses/km² for the broadleaved evergreen forest habitat, 19 (5; 15–25) mongooses/km² for the flooded shrub/herbaceous cover habitat, 43 (10; 35–55) mongooses/km² for grasslands and 26 (10; 18–38) mongooses/km² for rainfed cropland.

Factors affecting capture rates

Top-ranked models retained for density estimation using MARK were primarily the constant rates (p(.) and c(.)) models, but covariates were retained for some site-season combinations (Table 5). For three of 16 trapping sessions, first capture rates increased from the first to the last trapping days within a session and were greater for adults than for juveniles in two instances. Recapture rates varied by sex for one trapping of 16 trapping sessions, with the male recapture rate being greater than the female recapture rate. Capture rates were systematically greater than recapture rates across all trapping sessions analyzed.

The top ranked SECR model differed by site (Table 6). The covariates retained in the models for the Manati site were time as a continuous trend, where the σ parameters of detection function curves increased over the trapping season while $g(0)$ decreased, and sex, with σ being greater for males than females. At the Refuge site, a learned response to capture was retained, with $g(0)$ decreasing between first and subsequent captures. All three season-sites displayed spatial trends in mongoose densities, with one or two site edges hosting higher densities than the core of the sites (Fig. 4). While the Refuge and Manati South sites displayed a linear gradient in mongoose density, the Manati North site was characterised by a quadratic density surface (Table 6).

Seasonal and habitat class effects on mongoose density

On average, higher mongoose densities were estimated for the broadleaved evergreen forest habitat compared to all other habitat classes (Table 7). Mongoose densities estimated in grasslands, flooded shrub or herbaceous habitat, and rainfed cropland were lower and not different in pairwise contrasts. Lastly, mongoose density estimates were generally higher during the wet season for sites that were sampled across multiple seasons, though not statistically different between wet and dry seasons (Table 8).

Of female mongooses where pregnancy/lactation data were recorded, we found 21/27 (44%) and 17/34 (50%) of female mongooses were either pregnant and/or lactating in January–February and March–April, respectively. For July–August and September–October 25/50 (50%) and 5/18 (22%), respectively, of female mongooses were pregnant and/or lactating.

TABLE 3. Small Indian mongoose (*Urva auropunctata*) capture success, abundance and population density estimates using Minimum Number Known Alive (MNKA), MARK, and Spatially Explicit Capture-Recapture (SECR) models in Puerto Rico at six sites representing four habitat types during multiple sampling occasions, October 2016 - September 2021. The 95% confidence intervals for each estimate are shown in brackets, where applicable. Dashes indicate models did not converge due to low sample size and/or recapture rates.

Site/session	Aguire		Manati		Isabela		Refuge		Salt Flats		Escabi					
	Wet 2021	Dry 2019	Wet 2019	Wet 2018	Dry 2019	Wet 2018	Dry 2017	Dry 2018	Dry 2017	Dry 2018	Wet 2018	Dry 2017				
Total captures	70	73	85	13	9	42	59	38	8	42	54	12	13	3	23	49
Trapping session duration (days)	9	10	10	10	10	10	10	10	10	10	10	5	10	10	10	10
Capture per unit effort (No. captures/trap-day)	0.194	0.159	0.092	0.027	0.018	0.042	0.059	0.038	0.008	0.042	0.054	0.024	0.013	0.006	0.026	0.054
MNKA Abundance	45 (32.8–60.2)	57 (43.2–73.9)	70 (54.6–88.4)	12 (6.2–21.0)	8 (3.5–15.8)	35 (24.4–48.7)	53 (39.7–69.3)	36 (25.2–49.8)	7 (2.8–14.4)	37 (26.1–51.0)	42 (30.3–56.8)	12 (6.2–21.0)	13 (6.9–22.2)	3 (0.6–8.8)	22 (13.8–33.3)	43 (31.1–57.9)
MNKA Density	1.75 (1.27–2.33)	1.80 (1.36–2.33)	0.98 (0.76–1.23)	0.33 (0.17–0.58)	0.22 (0.10–0.44)	0.43 (0.30–0.60)	0.65 (0.49–0.86)	0.44 (0.31–0.62)	0.09 (0.03–0.18)	0.46 (0.32–0.63)	0.52 (0.37–0.70)	0.15 (0.08–0.26)	0.16 (0.09–0.27)	0.08 (0.02–0.24)	0.43 (0.27–0.65)	0.84 (0.61–1.13)
Area (ha) used in MNKA estimate	25.8	31.6	71.8	36.0	36.0	81.0	81.0	81.0	81.0	81.0	81.0	81.0	81.0	36.0	51.0	51.0
MARK Abundance	49 (43–56)	65 (54–79)	81 (69–94)	15 (9–24)	8 (8–9)	35 (34–36)	59 (52–68)	37 (34–40)	—	47 (34–66)	52 (40–68)	12 (12–12)	—	—	23 (21–25)	61 (37–102)
MARK Density	0.97 (0.85–1.10)	0.86 (0.71–1.04)	0.53 (0.45–0.62)	0.39 (0.24–0.62)	0.13 (0.12–0.14)	0.29 (0.29–0.30)	0.56 (0.49–0.65)	0.30 (0.28–0.32)	—	0.40 (0.29–0.56)	0.06 (0.05–0.08)	0.10 (0.10–0.11)	—	—	0.32 (0.29–0.35)	0.67 (0.41–1.11)
Area (ha) used in MARK estimate	50.7	76.2	152.4	37.9	61.9	119.5	105.4	124.9	—	117.3	811.7	115.3	—	—	71.3	91.5
SECR Density	1.00 (0.62–1.60)	1.07 (0.22–5.21)	1.84 (0.84–3.90)	1.08 (0.16–7.05)	0.26 (0.05–1.45)	1.09 (0.23–5.22)	0.60 (0.35–1.04)	0.23 (0.16–0.34)	—	0.32 (0.21–0.51)	0.21 (0.11–0.39)	—	—	—	1.25 (0.34–4.65)	1.40 (0.21–9.3)
Area (ha) used in SECR estimate	56.6	86.3	35.6	11.1	31.2	64.9	88.3	192.0	—	116.9	209.6	—	—	—	16.77	22.7

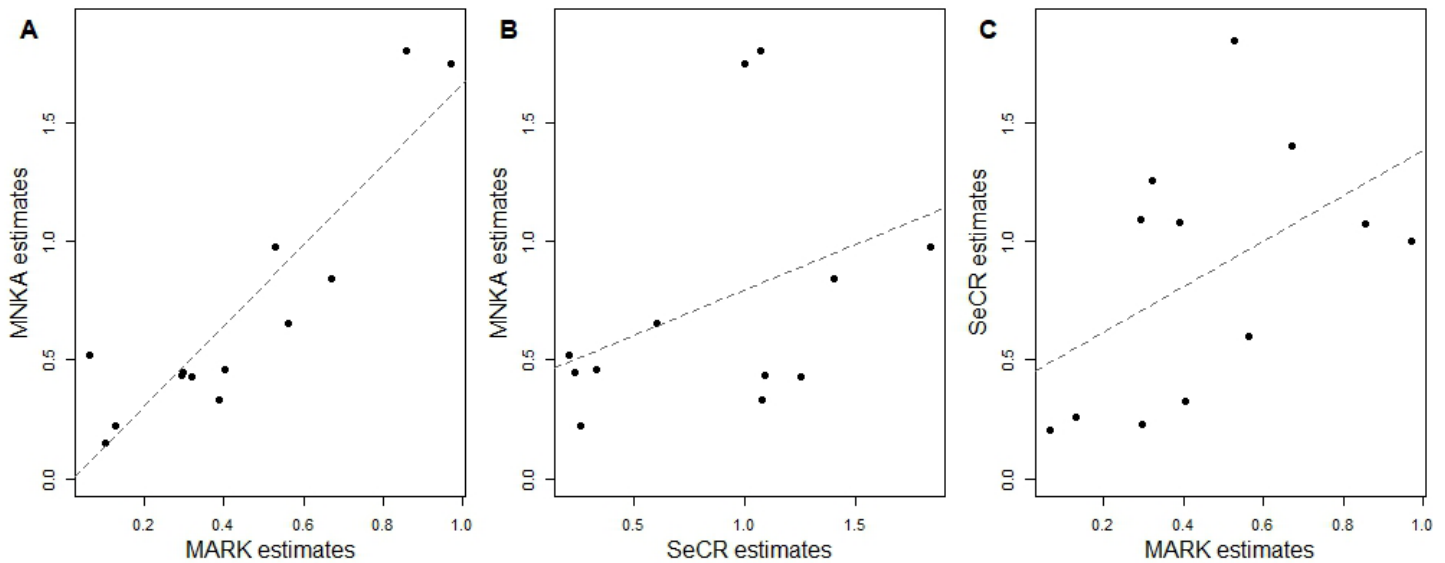


FIG. 3. Correlation matrices showing a high level of correlation ($r = 0.90$) between small Indian mongoose (*Urva auropunctata*) population density estimates obtained from the MNKA and MARK methods and lower correlation ($r = 0.49$) between the SECR and MARK estimates across seven sites and two seasons (wet and dry) in Puerto Rico, 2016–2021.

DISCUSSION

This study provides the first comprehensive evaluation of mongoose population densities using standardized sampling methods and multiple estimators across four distinct habitat types in Puerto Rico. Habitat-based population density may have implications for understanding rabies virus transmission dynamics in Puerto Rico, as well as for planning disease or population mitigation or control measures on this or other Caribbean islands. Epidemiological models by Sauvé et al. (2022) found landscape heterogeneity in habitat-specific carrying capacities and average carrying capacities over the island were among the major drivers of mongoose rabies dynamics in Puerto Rico. While the carrying capacities of mongooses in various habitats in Puerto Rico are unknown, identifying habitats supporting higher mongoose population densities may provide opportunities for local mitigation measures to control the spread of rabies virus, bites to humans, and reduce ecological damage associated with this non-native, invasive species. Overall, we found higher mongoose population densities in the broadleaved evergreen forest habitat than in open cover habitats evaluated in this study, supporting our hypothesis of higher population densities in habitats with greater forest and canopy cover. Our results contrast slightly with those reported by Johnson et al. (2016) who found no significant difference in mongoose density between a rainforest habitat

(also classified as broadleaved evergreen tree cover, the same habitat class as three sites in our study) and a dry forest (the flooded shrub/herbaceous cover habitat in our study and the same study location as in Johnson et al. 2016). However, findings from our study are consistent with those reported in St. Kitts, where mongoose densities were higher in a dry forest than in grassland and suburban habitats (Sauvé et al. 2022). Oral rabies vaccine bait application rates (baits/km²) may need to be greater when targeting populations in broadleaved evergreen forest habitats, while lower application rates may be appropriate for populations in grasslands, flooded shrub/herbaceous cover or rainfed cropland habitats (Berentsen et al. 2020).

We observed no statistical differences in mean density estimates between seasons, similar to previous studies in Puerto Rico (Johnson et al. 2016). Nevertheless, estimates tended to be generally higher during the wet rather than dry seasons. Moreover, sites with seasonal population density estimates within a single year (2018 for the Salt Flats and Refuge) showed higher population density estimates in the wet season compared to the dry season. Seasonal effects on mongoose density estimates over a site may be attributable to 1) animals moving to other habitats due to life history or habitat-specific seasonal effects on resource availability (i.e., habitat:season interactions), 2) inter-annual variations in densities may be confounded as seasonal

TABLE 4. Number of male, female and juvenile mongooses captured in Puerto Rico at six sites representing four habitat types during multiple sampling occasions, October 2016–September 2021.

Site/session	Aguirre		Manati		Isabela		Refuge		Salt Flats		Escabi			
	Wet 2021	Dry 2019	Wet 2019	Dry 2019	Wet 2018	Dry 2018	Wet 2016	Dry 2017	Dry 2018	Dry 2018	Wet 2016	Dry 2017		
No. traps	40	46	92	49	49	100	100	100	100	100	50	90		
No. unique traps visited	35 (88%)	30 (65%)	43 (47%)	11 (22%)	4 (8%)	31 (31%)	37 (37%)	26 (26%)	7 (7%)	31 (31%)	35 (35%)	9 (9%)	18 (20%)	29 (32%)
No. unique males	21 (46%)	36 (63%)	42 (60%)	6 (50%)	7 (88%)	15 (42%)	28 (53%)	12 (33%)	3 (43%)	10 (27%)	28 (67%)	4 (33%)	9 (69%)	10 (45%)
No. unique females	25 (54%)	21 (37%)	28 (40%)	6 (50%)	1 (12%)	21 (58%)	25 (47%)	24 (67%)	4 (57%)	27 (73%)	14 (33%)	8 (67%)	4 (31%)	2 (12%)
No. unique juveniles	5 (11%)	1 (2%)	10 (14%)	0 (0%)	1 (13%)	7 (19%)	9 (17%)	0 (0%)	0 (0%)	4 (11%)	1 (2%)	3 (25%)	0 (0%)	2 (10%)

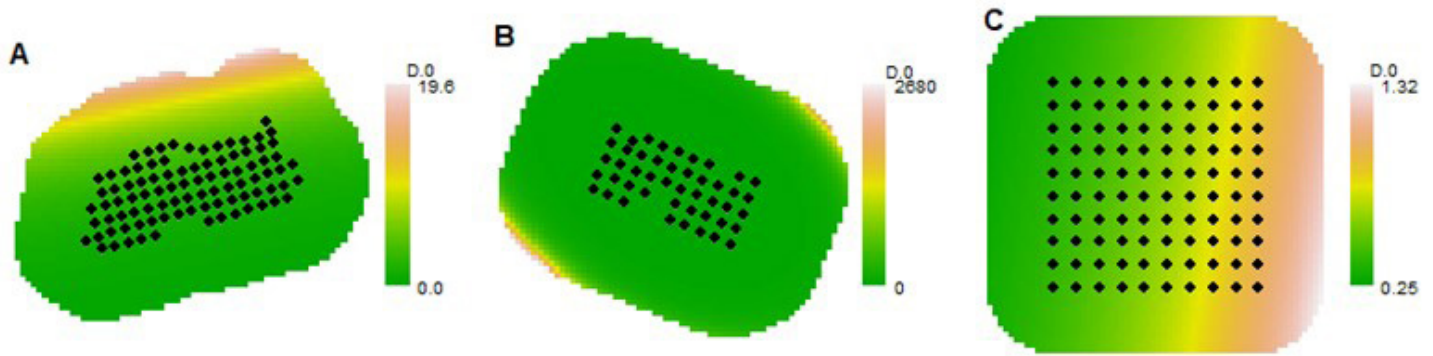


FIG. 4. Estimated mongoose population density over the site-seasons displaying significant surface trends in SECR (Effort 2020). Black dots illustrate trap locations over sampling areas in Puerto Rico. (A) Manati South, wet season 2019; (B) Manati North, dry season 2019; (C) Refuge, dry season 2017.

effects because all sites were not sampled during both seasons within a given year, or 3) an artifact of the CMR method. Because our density estimates were based on capture data, any seasonal effect influencing individual motivation to forage, consume bait, and enter traps may result in apparent seasonal trends in derived population densities. Oral rabies vaccination and vertebrate population control programs, including population reduction using toxicant baits, rely on bait uptake by the target species. Thus, the efficiency of such programs could be affected by similar factors as those influencing mongoose trapping success. We acknowledge sampling was not conducted evenly across seasons or sites, impeding the assessment of season:site interactions.

At the Salt Flats and Refuge sites, inter-annual density estimates showed a drop in population density from 2017 to 2018. The precise reason for this apparent decline remains unknown, but during autumn 2017 Hurricanes Irma and Maria had a significant island-wide impact on Puerto Rico and hurricane-related damage to these sites cannot be excluded as a contributing factor. Severe weather events have impacted small mammal populations elsewhere in the Caribbean (Shiels et al. 2020).

Both mongoose population density estimates and captures per unit effort (CPUE) in Puerto Rico (range: 0.006–0.194 captures/trap·day) were lower than those reported in comparable habitats (range: 0.53–0.21 captures/trap·day) but were comparable to the lowest CPUE reported from St. Kitts (suburban habitat; 0.07 captures/trap·day; Sauvé et al. 2022). Population densities in comparable habitats in St. Kitts were all higher than the matched habitat in Puerto Rico based on this study, despite the same capture methods and analytical

methods used. For example, at the grassland habitat on St. Kitts, MNKA population densities were estimated at 1.29–3.31 mongooses/ha compared with a range of 0.03–1.13 mongooses/ha from a comparable habitat in Puerto Rico during this study. Why these differences exist remain unclear, yet one possible explanation is that St. Kitts is free from rabies virus, whereas in Puerto Rico rabies virus circulates within the mongoose population and may result in additional mortality for mongoose populations where the disease is enzootic (Berentsen et al. 2015, 2023). Moreover, predation by raptors or snakes (both of which are absent on St. Kitts) may represent an additional source of natural mortality in Puerto Rico (Santana and Temple 1988; Berentsen et al. 2016).

Wildlife rabies control and vertebrate population management are complex processes that require careful consideration of population ecology of the target species. An integrated strategy that may include population management, ORV and public health messaging regarding the risk of wildlife-mediated rabies may be required to achieve management objectives. For some rabies reservoir species (e.g., raccoons) inhabiting temperate regions with synchronized life history patterns, a single annual vaccination strategy may be appropriate, but more frequent applications of ORV may be needed where life history of the target species is not highly synchronized. In Puerto Rico, mongooses typically breed twice a year with birth pulses reported during March–April and July–August (Pimentel 1955b), but our data from January–February and September–October suggests pregnant and/or lactating mongooses can be found throughout the year. Given their important role in epidemiology of mongoose rabies, multiple ORV applica-

TABLE 5. Top ranked models generated in MARK for small Indian mongoose (*Urva auropunctata*) density estimation in Puerto Rico at five sites representing four habitat types and during up to three sampling occasions during October 2016 through September 2021. Covariates included in the candidate model sets were sex, age (adult versus juvenile), time (discrete), and time (continuous).

Site	Session	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}
Escabi	Wet 2016	22	None (p(.) retained) p = 0.280	None (c(.) retained) c = 0.013	2	1.00
	Dry 2017	41	None (p(.) retained) p = 0.104	None (c(.) retained) c = 0.036	2	0.90
Salt Flats	Wet 2016	38	None (p(.) retained) p = 0.140	None (c(.) retained) c = 0.019	2	0.93
	Dry 2017	43	None (p(.) retained) p = 0.153 Age + Time	None (c(.) retained) c = 0.045	2	0.95
	Dry 2018	7	(p increases over session and $P_{adult} > P_{YOY}$; range = 0.007-0.999) Time	None (c(.) retained) c < 0.001	4	0.93
Refuge	Wet 2016	38	(p increases over session; range = 0.119-0.701)	Sex ($c_{\delta} = 0.054 > c_{\text{♀}} = 0.008$)	4	0.99
	Dry 2018	36	None (p(.) retained) p = 0.298	None (c(.) retained) c = 0.008	2	0.98
Isabela	Wet 2018	12	None (p(.) retained) p = 0.156 Age + Time + Sex	None (c(.) retained) c = 0.014	2	1.00
	Dry 2019	8	(p increases over session, $p_{\delta} < P_{\text{♀}}, P_{adult} > P_{YOY}$; range = 0.00-1.00)	None (c(.) retained) c = 0.023	5	0.93
Aguirre	Wet 2021	49	None (p(.) retained) p = 0.240	None (c(.) retained) c = 0.090	2	1.02

tions may be needed to target susceptible young of the year as they begin to forage and move independently from adults, given that infection of this cohort is a key driver of rabies virus perpetuation at landscape scales. Our results suggest mongoose population densities are habitat-dependent, and that there may be weak seasonal variation in population abundance. This study used the same sampling methods and density estimators as described for a recent mongoose density study in St. Kitts (Sauvé et al. 2022), providing a framework to compare mongoose habitat- and season-specific density across Caribbean islands with and without mongoose rabies. We acknowledge that this study was limited to a few

habitat types represented across Puerto Rico. Future research into mongoose population densities in urban/suburban habitats, mountainous regions and coastal forests would provide more complete habitat representation with respect to mongoose population density across key habitats of the island. Similarly, conducting similar studies on other Caribbean islands could provide data necessary to address the hypothesis considering additional mortality pressure in mongoose populations impacted by rabies virus and/or different (mongoose) predator communities across the Caribbean region, as well as ecological hypotheses linking mongoose population densities with island size (e.g., Horst et al. 2001).

TABLE 6. Top ranked models generated in SECR for small Indian mongoose (*Urva auropunctata*) density estimation in Puerto Rico at three sites representative of five different habitat types during March 2017 through August 2019. Covariates for the detection function parameters (g_0 and σ) included in the candidate model sets were sex, age (adult versus juvenile), time (discrete), Time (continuous), behavior (discrete), Behavior (continuous), while a flat surface ($D \sim 1$), a linear trend surface ($D \sim x+y$) and quadratic trend surface ($D \sim x + y + x^2 + y^2 + xy$) were considered for the density parameter. Parameter coefficients are presented along with their 95% confidence interval in parentheses.

Site	Session	N detections	Parameters affecting detection function parameters (g_0 and σ) behavior	Density surface	No. parameters estimated
Refuge	Dry 2017	59	$\sigma = 3.37$ (2.48–4.26)	Linear	8
			$\sigma.b = 1.20$ (0.15–2.24)	$D.x = 0.41$ (0.02–0.81)	
			$g_0 = -0.478$ (-2.78–1.82)	$D.y = -0.07$ (-0.46–0.31)	
Manati North	Dry 2019	73	$g_0.b = -5.12$ (-7.80– -2.44)	Quadratic	13
			Time + Sex	$D.x = 0.02$ (-0.27–0.32)	
			$\sigma = 3.93$ (3.16–4.69)	$D.y = -0.28$ (-0.75–0.19)	
			$\sigma_{\delta} = 1.60$ (0.82–2.38)	$D.x^2 = 1.52$ (0.52–2.51)	
			$\sigma.T = 0.03$ (-0.04–0.10)	$D.y^2 = 1.50$ (0.07–2.92)	
			$g_0 = -3.50$ (-5.67– -1.32)	$D.xy = 1.36$ (0.3–2.40)	
Manati South	Wet 2019	85	$g_0_{\delta} = 1.33$ (-1.00–3.66)	Linear	10
			$g_0.T = -0.25$ (-0.55–0.04)	$D.x = -0.36$ (-0.77–0.05)	
			Time + Sex	$D.y = 1.24$ (0.67–1.81)	
			$\sigma = 2.71$ (2.17–3.26)		
			$\sigma_{\delta} = 1.18$ (0.54–1.83)		
		$g_0 = -0.95$ (-2.2–0.72)			
		$g_0_{\delta} = -1.16$ (-2.79–0.46)			
		$g_0.T = -0.61$ (-0.86– -0.36)			

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TABLE 7. Small Indian mongoose (*Urva auropunctata*) density (no. mongooses/ha) estimated using MARK Huggins closed population models grouped by habitat class, based on capture data across seven sites in Puerto Rico, 2016–2021. We calculated standard errors by bootstrap resampling of capture histories with replacement.

Habitat class	Average density (mongooses/ha) \pm SE	95% CI
Closed to Open Canopy Broadleaved Evergreen Tree Cover	0.79 \pm 0.05	0.68–0.89
Grassland	0.43 \pm 0.08	0.28–0.58
Rainfed cropland	0.26 \pm 0.20	0.14–0.66
Flooded Shrub or Herbaceous Cover	0.19 \pm 0.06	0.07–0.32

TABLE 8. Small Indian mongoose (*Urva auropunctata*) density (no. mongooses/ha) estimated using MARK Huggins closed population models grouped by season, based on capture data across seven sites in Puerto Rico, 2016–2021. We calculated standard errors by bootstrap to account for the fact that density represents a generated regressor.

Season	Average density (mongooses/ha) \pm SE	95% CI
Dry	0.39 \pm 0.06	0.27–0.50
Wet	0.48 \pm 0.07	0.35–0.62

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