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Using DNA to Identify the Source of Invasive Mongooses, *Herpestes auropunctatus* (Carnivora: Herpestidae) Captured on Kaua‘i, Hawaiian Islands[1]

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Abstract: Two small Indian mongooses (*Herpestes auropunctatus*) were live-captured in 2012 at separate locations on the Hawaiian Island of Kaua‘i, which was previously considered to be free of this invasive species. Genotypes from these two individuals were compared to genotypes of *H. auropunctatus* from the islands of Hawai‘i ($n = 39$), O‘ahu ($n = 91$), Maui ($n = 39$), and Moloka‘i ($n = 19$) to determine the island of origin of the Kaua‘i individuals. Genotypes were generated from each individual using five microsatellite loci. Genetic clustering was estimated by Bayesian inference of spatial clustering of individuals and clustering of groups of individuals. Both analyses separated the samples into three distinct genetic clusters ($K = 3$). Kaua‘i individuals consistently formed a single cluster with individuals from O‘ahu, whereas Hawai‘i and Maui formed a second cluster, and Moloka‘i was the third cluster. Thus, we conclude that the origin of two *H. auropunctatus* captured on Kaua‘i was O‘ahu. All three genetic clusters showed evidence of transportation of mongooses between islands, indicating that sampled islands in the archipelago are capable of acting as both donors and receivers of mongooses.

Keywords: biosecurity, Hawaiian Islands, introduced predator, microsatellite

The small Indian mongoose, *Herpestes auropunctatus* (Hodgson 1836), is an invasive predator in the Hawaiian Islands (Veron et al. 2007, Gilchrist et al. 2009, Bennett et al. 2011, Berentsen et al. 2017). A total of 287 mongooses were introduced to the Hawaiian Islands from Jamaica in 1883–1885 (Bryan 1938, Thulin et al. 2006), and later an unknown number of mongooses from the West Indies were released (Lever 1985, Thulin et al. 2006). While native to Central Asia, this species was introduced to the Hawaiian Islands to control rodent populations in sugarcane fields (Bryan 1938). However, this species was ineffective for rodent biocontrol at the landscape scale, and it quickly became an established threat to native avifauna and invertebrates (Baldwin et al. 1952, Case and Bolger 1991, Hays and Conant 2007). Plantation owners on Kaua‘i, Lāna‘i, and Ni‘ihau refused to accept the importation of mongooses (Baldwin et al. 1952). Established mongoose populations are currently found on many of the Hawaiian Islands, except Kaua‘i and Lāna‘i in the main Hawaiian Islands and several other smaller islands.

In 2012, two individuals were sighted and subsequently trapped near the main port in Lihue, Kaua‘i. With these two individuals captured and euthanized, managers currently believe there is no breeding population of mongoose on Kaua‘i. Identifying the source

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population of these two individuals could allow managers to improve biosecurity plans to stem the tide of invasion before a breeding population is established on a mongoose-free island. The goal of this study was to use microsatellite DNA from mongoose tissue sampled across the Hawaiian Islands, along with population genetic analyses, to identify the source population of the mongoose individuals captured on Kaua‘i. While our study demonstrates how molecular analyses may be used to improve biosecurity practices, we expect the information gained here will also aid efforts to protect natural resources on Kaua‘i from mongoose depredation.

MATERIALS AND METHODS

Sample Collection and Tissue Analyses

Two individual mongooses were captured on opposite sides of Nāwiliwili Harbor, Līhu‘e, Kaua‘i in 2012. The first individual was an adult male that was live captured on 23 May 2012 at Kaua‘i Lagoons. The second individual was a juvenile female that was live captured on 29 June 2012 at Young Brothers shipping dock, which is approximately 2.0 km from the location of the first captured individual (P. Reese, unpublished data). The collection of tissue samples across the Hawaiian Islands included collaboration among several agencies (see acknowledgments). In addition to the two individuals captured on Kaua‘i, 188 mongooses were collected from four other islands (Hawai‘i = 39; Maui = 39; Moloka‘i = 19; O‘ahu = 91). We attempted to obtain individuals from multiple sites across each island so that we could account for potential population structure (Figure 1). Other than the two whole bodies that we obtained from Kaua‘i, the remaining mongooses had approximately 4 mm × 6 mm sections of ear tissue removed with a razorblade sterilized with ethanol and stored in 2.0 mL microcentrifuge tubes containing a DET buffer in a 1:4 volume

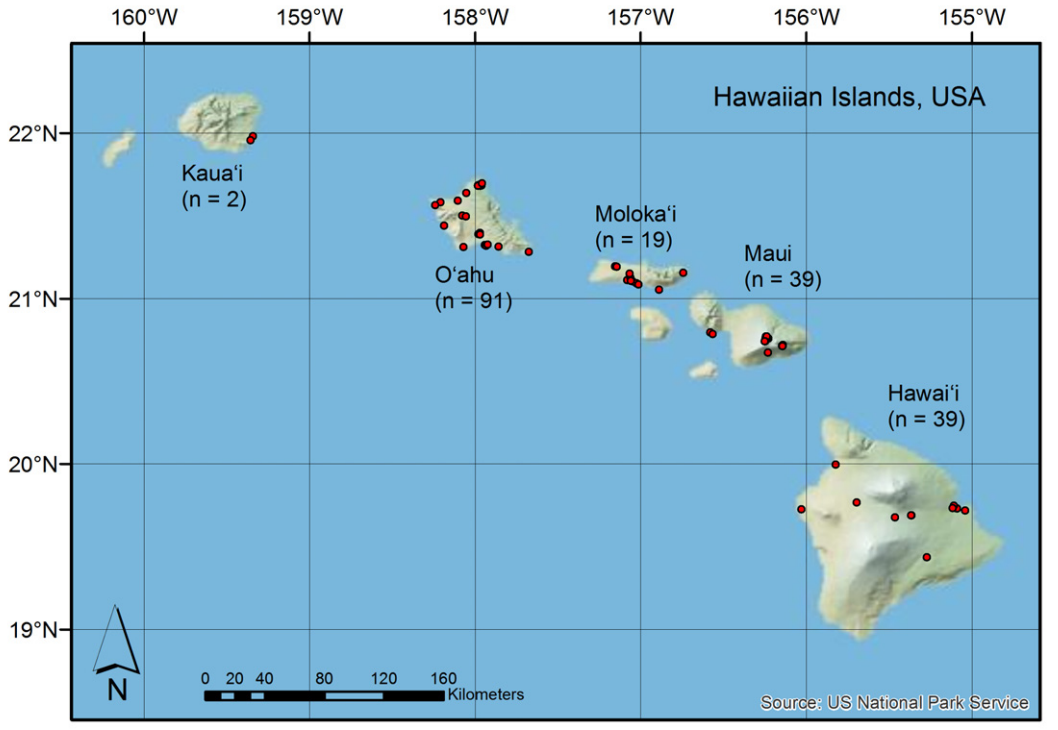

FIGURE 1. Sample locations of small Indian mongooses (*Herpestes auropunctatus*) collected from Hawaiian Islands, USA.

sample to solution ratio (Seutin et al. 1991). The samples were sent to USDA APHIS Wildlife Services National Wildlife Research Center in Fort Collins, Colorado, for laboratory and statistical analyses.

DNA Extraction and Amplification

Genomic DNA was extracted from tissue samples using the DNeasy Blood and Tissue Kit, automated on a QIAcube (Qiagen, Hilden, Germany) with the Animal Tissues and Rodent Tails protocol with default settings, and then stored at −20.0 °C. We used primers developed to amplify five microsatellite loci from small Indian mongoose (Thulin et al. 2002). PCR reactions were performed using the Multiplex PCR Kit (Qiagen) and primer concentrations of 10.0 μM in two 19.0 μL multiplex reactions (Table 1). PCR cycling conditions were as follows: initial denaturation at 95 °C for 15 min, 20 cycles of 94 °C for 30 s, touchdown annealing temperature decreasing 0.5 °C per cycle for 90 s (panel A T_a = 60–50 °C, panel B T_a = 55–45 °C), and extension at 72 °C for 45 s, followed by five cycles of 94 °C for 30 s, annealing temperature for 90 s (panel A T_a = 50 °C, panel B T_a = 45 °C), and extension at 72 °C for 45 s (Table 1). We used a final extension of 60 °C for 30 min. PCR products were added to a mixture of HiDi Formamide (Life Technologies, Carlsbad, California, USA) and GeneScan 400HD ROX Size Standard (Life Technologies). All loci were run on an ABI 3130 or 3500 Genetic Analyzers (Life Technologies) following standard protocols. Alleles were binned and scoring was manually checked using GeneMapper v.5.0 (Life Technologies). Complete scored genotypes for each individual were exported to GMconvert v.0.32 (Faircloth 2006) to generate Genepop input files.

DNA Data Analysis

Microsatellite genotypes were checked for the presence of null alleles and genotyping errors using Micro-Checker (Van Oosterhout et al. 2004). Assumptions of Hardy-Weinberg Equilibrium (HWE) and linkage disequilibria (LD) were tested using Arlequin v.3.5.2.2 (Excoffier and Lischer 2010). The significance of the tests were assessed at $P = .05$, which was Bonferroni corrected for multiple comparisons (Rice 1989). Total number of alleles (N_A) and number of private alleles (alleles found only on one island, A_{PR}) per locus by island were compiled by Convert v.1.31 (Glaubitz 2004; Table 2).

The microsatellite data were analyzed using a Bayesian clustering program BAPS v.6.0 (Corander et al. 2006, Corander et al. 2008a), to identify the source population for the Kaua'i individuals. This approach tests a range of defined number of genetic clusters

TABLE 1

Microsatellite Multiplex Panels Used in this Study Based on Loci Developed for the Small Indian Mongoose (*Herpestes auropunctatus*) (Thulin et al. 2002)

Panel	Locus	Primer Sequence (5′–3′) F, forward; R, reverse	Dye	T_a (°C)	n	Size Range (bp)	N_A	H_O	H_E
A	Hj15	F: CAGGGCTGAGACAATATCCACTA R: GTAACCGCCTTTTTCTTTCCTCTG	NED	50	190	231–239	2	0.42	0.47
	Hj34	F: TACAGGCAGTTAGAAGTCACATTT R: GAGTTCAAGCCCCACATCAGAG	FAM	50	190	183–201	6	0.59	0.68
	Hj45	F: TCAATTTGCCGTCCTTTACA R: GGGCTTTTGGGTTACTTTTG	HEX	50	190	223–235	5	0.50	0.58
B	Hj40	F: AATGGACAGAAAGTGGGAGGAATA R: ATCAGGCCACCAATCAGTCATC	HEX	45	190	235–245	4	0.37	0.50
	Hj56	F: AGCCCCAAATCAGACTC R: GAACTGGGCTGGAATCT	NED	45	190	208–232	8	0.69	0.77

T_a, annealing temperature; n, number of samples; N_A, number of alleles; H_O, observed heterozygosity; H_E, expected heterozygosity.

TABLE 2

Number of Samples (n), Number of Alleles (N_A), and Number of Private Alleles (A_{PR}) for Each Locus Tested in the Small Indian Mongoose (*Herpestes auropunctatus*) Summarized by Island in Hawai'i, USA

Locus	Hawai'i			Maui			Moloka'i			O'ahu			Kaua'i			Total		
	n	N_A	A_{PR}	n	N_A	A_{PR}	n	N_A	A_{PR}	n	N_A	A_{PR}	n	N_A	A_{PR}	n	N_A	A_{PR}
Hj15	39	2	–	39	2	–	19	2	–	91	2	–	2	1	–	190	2	–
Hj34	39	4	–	39	5	1	19	3	–	91	4	1	2	2	–	190	6	2
Hj40	39	4	–	39	3	–	19	2	–	91	3	–	2	2	–	190	4	–
Hj45	39	4	–	39	4	–	19	2	–	91	5	1	2	1	–	190	5	1
Hj56	39	7	1	39	5	–	19	4	–	91	4	1	2	3	–	190	8	2

(K) based on Bayesian posterior probabilities. The highest posterior probability determines the most likely number of genetic clusters found within the genotypes provided. We identified the origin of the Kaua'i individuals based on the cluster(s) they were assigned to. We used capture locality (latitude and longitude coordinates of capture site) as an informative prior probability distribution in the Bayesian analysis with each individual being considered iteratively for cluster membership (spatial clustering of individuals; Corander et al. 2008b, Cheng et al. 2013). The inclusion of capture location information allowed the spatial genetic structure to be depicted as a map (Voronoi tessellation) of the genetic clusters (Corander et al. 2008b). The uncertainty associated with genetic cluster assignment was calculated by one minus the posterior probability of the cluster assignment and graphed as a third axis applied to the previously mentioned Voronoi tessellation (Corander et al. 2008b). We also analyzed the data without precise capture locality but used an informative prior probability that groups individuals by capture island ($n = 5$) (clustering of groups of individuals; Corander et al. 2006, Corander et al. 2008a). A preliminary run of $K = 1$–10 with 10 iterations for each K was used to approximate the value of K. After the preliminary run we ran $K = 1$–5 with 20 iterations for each K to confirm the value of K. Once we identified the number of genetic clusters, we estimated differentiation with pairwise F_{ST} through 10,000 permutations in Arlequin (Excoffier and Lischer 2010).

RESULTS

Each microsatellite produced between two and eight alleles across all samples ($n = 190$). Each locus was polymorphic across all islands sampled except Kaua'i where two loci each had a single allele due to the small sample size ($n = 2$; Table 2). Alleles unique to a particular island were observed in three of the five loci tested on three of the five islands sampled. The islands of Hawai'i and Maui each had a single private allele for a single locus (Hj56 and Hj34, respectively), while private alleles were observed in three loci on O'ahu (Hj34, Hj45, and Hj56). After Bonferroni corrections, there was no evidence of deviation from HWE and no evidence of linkage disequilibrium. The presence of null alleles was detected at locus Hj34; however, we included this locus in the analyses as it was not expected to bias our estimates because it occurred at a frequency of <0.20 (Dakin and Avise 2004).

The genetic clustering analyses, based on groups of individuals and precise geographic locality, identified three genetic clusters ($K = 3$). The first cluster included samples from Hawai'i and Maui, the second cluster included samples from Moloka'i, and the third cluster included samples from O'ahu and the two Kaua'i samples (Figure 2). There were five exceptions to this pattern; two samples from Hawai'i fell into the third cluster, a single sample from Hawai'i fell into the second cluster, and a single O'ahu and single Moloka'i sample grouped into the first

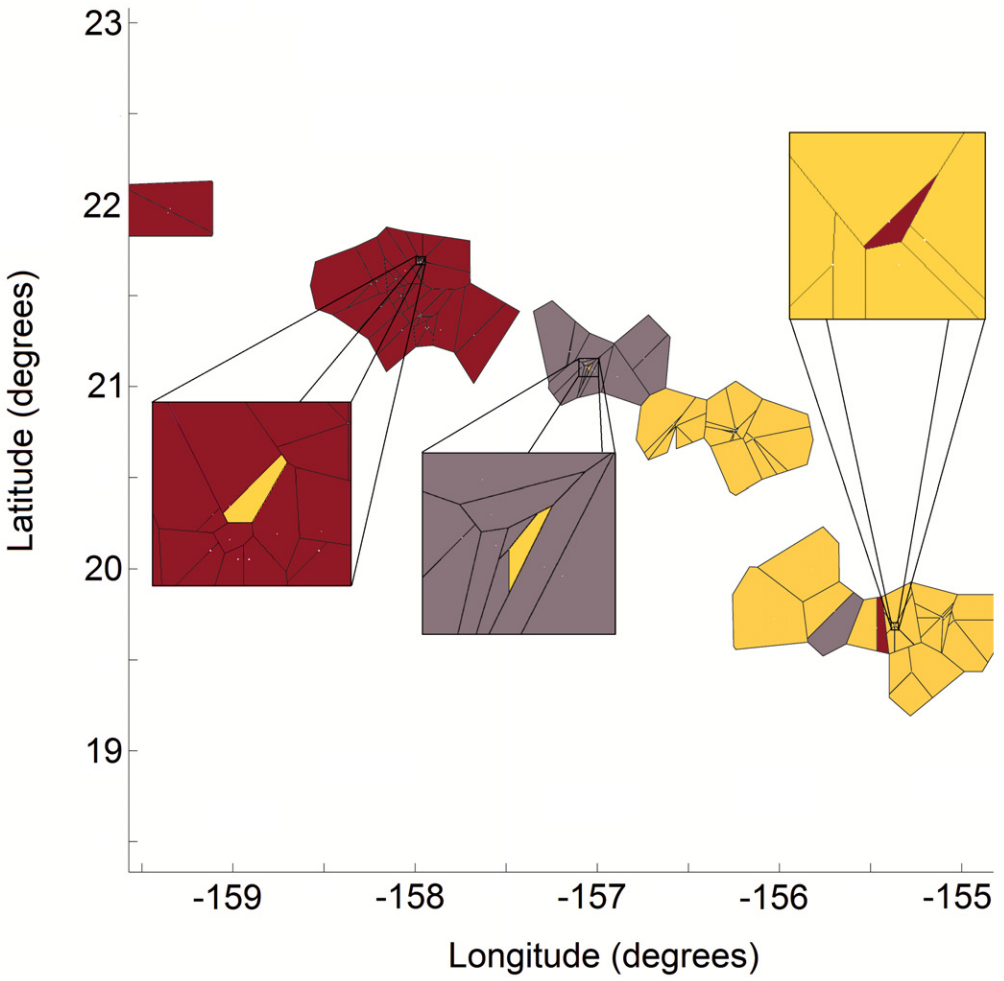

FIGURE 2. Voronoi tessellation depicting spatial structure of the observed genetic clusters ($K = 3$) of small Indian mongoose (*Herpestes auropunctatus*) samples collected from Hawaiian Islands, USA. Each cell within an island represents a sample collected in this study. The shape and size of each cell is based on the proximity of each sample to surrounding samples. Insets amplify detail of indicated areas. The color of each cell identifies which genetic cluster the sample is assigned to. The O'ahu genetic cluster is predominantly shaded red (including the two samples from Kaua'i in the upper left portion of the figure), the Moloka'i genetic cluster is predominantly shaded gray, and the Hawai'i/Maui genetic cluster is predominantly shaded yellow.

cluster (Figure 2). The local uncertainty of assigning a sample to a genetic cluster ranged from 0.0 to 0.52 (Figure 3).

Pairwise comparisons of F_{ST} between genetic clusters ranged from 0.112 to 0.195. Among pairwise comparisons, the smallest F_{ST} value was between the Hawai'i/Maui cluster and O'ahu cluster (0.112, $P < .001$), then the Hawai'i/Maui cluster and Moloka'i cluster (0.191, $P < .001$), and the largest F_{ST} value was between the O'ahu cluster and the Moloka'i cluster (0.195, $P < .001$).

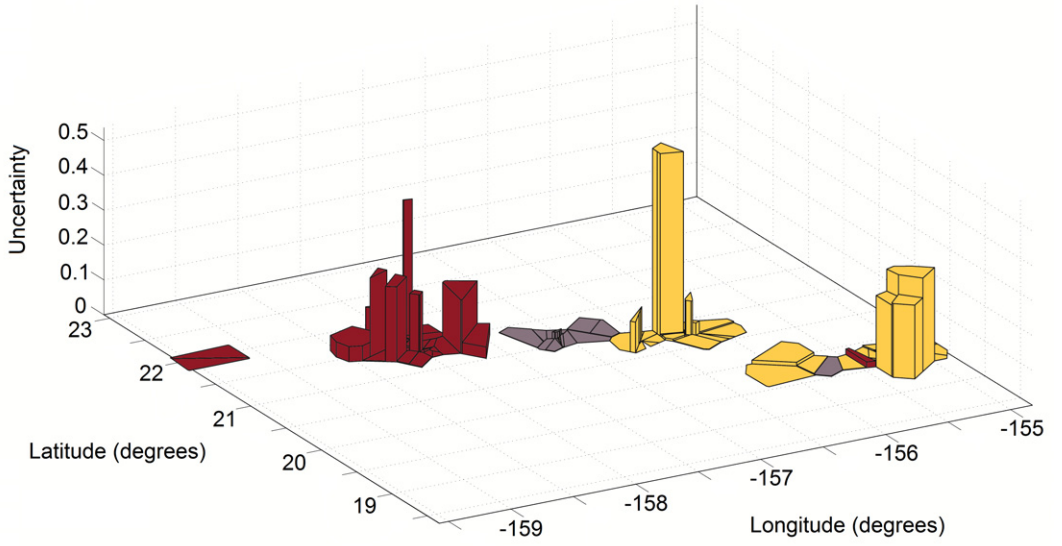

FIGURE 3. Graph of local uncertainty associated with genetic cluster assignment (Figure 2) of small Indian mongoose (*Herpestes auropunctatus*) samples collected from the Hawaiian Islands, USA. The uncertainty values associated with the assignment of the two Kaua'i samples to the O'ahu genetic cluster were 2.63×10^{-4} and 7.23×10^{-5}. The uncertainty value was calculated as one minus the conditional posterior probability. The O'ahu genetic cluster is predominantly shaded red (including the two Kaua'i samples), the Moloka'i genetic cluster is predominantly shaded gray, and the Hawai'i/Maui genetic cluster is predominantly shaded yellow.

DISCUSSION

The goal of our study was to identify the source of two invasive mongooses captured on Kaua'i in 2012. We detected genetic structure within the dataset from only five microsatellite loci to identify a total of three genetic clusters across the Hawaiian Islands: (1) Hawai'i and Maui, (2) O'ahu, and (3) Moloka'i. Our analyses of genetic clustering among individual genotypes demonstrated a close genetic association between the Kaua'i and O'ahu samples. Therefore it is likely that the two mongooses captured on Kaua'i were introduced from O'ahu. The uncertainty associated with the assignment of the two Kaua'i samples to a genetic cluster with O'ahu individuals was very low (2.63×10^{-4} and 7.23×10^{-5}), as indicated by the flat cells representing the Kaua'i samples (Figure 3).

When genetic clustering included a prior probability that assumes individuals originated from island of capture, the algorithm consistently identified the same three clusters as without this prior probability, and these included the same individuals. Thus two clusters each contained individuals from multiple islands (five groups assigned to three clusters), which suggests recent gene flow among islands.

In addition to identifying the source island of the Kaua'i individuals, our analyses also indicated that mongooses may have been transported among other islands in the archipelago recently. Five individuals were assigned to clusters that were different from the island where the sample was collected. Two individuals from Hawai'i possessed an allele at locus Hj40 that was otherwise limited to individuals from the O'ahu cluster. One individual from Hawai'i possessed an allele at locus Hj56 that was limited to individuals from the Moloka'i genetic cluster. One heterozygous individual from Moloka'i possessed an allele at locus Hj40 that was otherwise not observed on that island but had a high frequency in the Hawai'i/Maui cluster. Finally, one individual from O'ahu was heterozygous for an allele at locus Hj45, which was otherwise not observed on that

island. Three of these cases (two individuals from Hawai'i belonging to the O'ahu cluster and one individual from O'ahu belonging to the Hawai'i/Maui cluster) may be explained by a single motif mutation as an insertion or deletion of a dinucleotide repeat, but the remaining two cases cannot be explained so easily given the observed allele frequencies (one individual from Hawai'i belonging to the Moloka'i cluster and one individual from Moloka'i belonging to the Hawai'i/Maui cluster). It is thus most likely that individuals have been transported between islands and thus poses an ongoing challenge to stemming exchange of this invasive species among islands.

DNA methodologies have been used to identify non-native species arrivals to islands and their associated source populations (e.g., mice, Hardouin et al. 2010; Argentine ant, Corin et al. 2007). One important use of genetic tools is determining if island-wide eradications of vertebrates have been successful. For example, Abdelkrim et al. (2007) and Savidge et al. (2012) used genetic evidence to determine whether rats observed after an eradication campaign were survivors of the eradication attempt or recent immigrants. Population genetics are often the only means of establishing non-native species introduction routes, and these methods and technologies can be used to inform island communities of management/eradication units and biosecurity strategies. (e.g., separating islands into eradication units, Savidge et al. 2012). However, the utility of genetic analyses may be limited in island communities due to gene flow and time required for genetic differentiation (Manel et al. 2005, Fitzpatrick et al. 2012). Genetic surveys should be performed prior to eradication events to estimate genetic differentiation among target populations and to later evaluate the success of eradication campaigns (Savidge et al. 2012).

Early detection and elimination of invasive species on islands is fundamental to the protection of island resources. Despite early reasoning that favored mongoose as a biocontrol agent, mongoose are a threat to island ecosystems by causing native species declines, transmission of zoonotic pathogens, and damaging the economy (Hays and Conant 2007). Prior to the two individual mongooses found near the harbor on Kaua'i in 2012, the biosecurity that was implemented for mongoose introductions to Kaua'i was minimal. Mongoose surveillance methods are limited to the use of tracking tunnels (inked and baited cards placed in tunnels to reveal foot tracks of animal visitors) near the main port in Kaua'i with a rapid-response team ready to trap, and general public education covering how mongooses are unwanted pest species on Kaua'i (P. Reese, pers. comm.). Relative to the efforts to maintain Kaua'i mongoose-free, there are examples of very extensive biosecurity actions occurring to prevent unwanted vertebrate pest species from arriving on islands. For example, Guam practices extensive biosecurity for preventing brown tree snakes (*Boiga irregularis*) from leaving Guam in cargo. The security measures utilize an integrative pest management plan that includes the use of detection dogs to survey cargo for snakes, trapping and use of poison baits around ports, and spotlighting fence lines for hand-removal (Engeman et al. 2018). New Zealand is known for their strong stance on island biosecurity, which includes the prevention of pest species introductions into the country, rapid-response for invasive species removal following detection (Broome 2007), and keeping off-shore islands predator free (Russell et al. 2008). Part of what makes these biosecurity efforts attractive and effective is that the various techniques and methodologies that are used are periodically tested and validated (Russell et al. 2008, Engeman et al. 2018). DNA analyses can help elucidate invasion pathways and thus direct managers to increase biosecurity at weak links. In this case, daily ship traffic to and from Kaua'i establishes the strong possibility of mongoose or other vertebrate pest transport, and preventing such arrival and establishment will require more robust biosecurity measures between O'ahu and Kaua'i ports, continued public education about this issue, and effective and on-going surveillance efforts.

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