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Dragons in our midst: Phyloforensics of illegally traded Southeast Asian monitor lizards



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ABSTRACT

We provide a phylogenetic and population genetic evaluation of the illegal pet and bush meat trade of monitor lizards in the Philippines. We use a molecular dataset assembled from vouchered samples with known localities throughout the country, as a reference for statistical phylogenetic, population genetic, and DNA barcoding analyses of genetic material obtained during a three year survey of the Manila pet trade. Our results provide the first genetic evaluation of a major Southeast Asian city's illegal trade in monitors and allow us to establish several important conclusions regarding actual, versus reported, origins of Manila's black market *Varanus*. Monitor lizards are clearly transported throughout the archipelago for trade; we identified genotypes from areas surrounding Manila, the distinct Bicol faunal subregion of Luzon, Mindanao Island, the Visayan islands, islands of the Romblon Province, the Babuyan islands, and Mindoro Island. Numerous species are involved, including multiple endemic Philippine taxa, the threatened Gray's monitor (*Varanus olivaceus*), and the presumably non-Philippine rough-neck monitor (*Varanus rudicollis*). Our results suggest that traders frequently and deliberately misrepresent the provenance of traded animals, in an apparent effort to increase their perceived market value.

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1. Introduction

The conservation crisis of illegal trade in Southeast Asian wildlife has, by all accounts, reached monumental proportions (Gaulke, 1998; Compton, 2000; Stuart and Timmins, 2000; van Dijk et al., 2000; Schlaepfer et al., 2005; Cheung and Dudgeon, 2006; Shi et al., 2008; Gong et al., 2009). As increasing numbers of vertebrates are removed from their natural habitats, harvested for both legal and illegal trade in skins, bush meat, exotic pets, good luck charms, and traditional medicines (Shine et al., 1996; Shine and Harlow, 1998; Fa et al., 2000; Stuart, 2004; Pernetta, 2009; Welton et al., 2012; Scheffers et al., 2012), the tasks of monitoring trade, seizing and confiscating illegal shipments, apprehending smugglers, and prosecuting dealers have become overwhelmingly com-

plex (Parham et al., 2001; Schlaepfer et al., 2005; Fong et al., 2007). As the smugglers' determination increases in accordance with the commercial value of illegally traded animals (Shine et al., 1996; Pernetta, 2009), the prospect for regulated, sustainable trade has become increasingly unlikely (Shine et al., 1998; Webb and Varadon, 1998; Schlaepfer et al., 2005). Furthermore, as the 'arms race' between illegal dealers and international wildlife law enforcement officials has intensified (Christy, 2008), the sophistication of smuggling operations, illegal wildlife laundering strategies, and methods of detection and substantiation of wildlife origins has likewise increased (Nash, 1997; Yuwono, 1998; Pernetta, 2009).

Trade forensics has come to represent an increasingly diverse and powerful suite of technological, methodological, and analytical tools and resources for identifying trade species and, hopefully, pinpointing their origins (Stuart and Parham, 2007; Fong et al., 2007; Li et al., 2011; Spinks et al., 2012). Although accurate identification of trade animals is accompanied by numerous logistic and biosecurity challenges (for review, see Collins et al., 2012), determining origins of confiscated animals may help identify trade routes and populations at risk from heavy exploitation pressures. Importantly, our ability to identify actual geographic origins of trade animals with molecular

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techniques (and reference databases of densely sampled wild-caught animals from known localities) may eventually prove to be a strong deterrent if illegal traders become aware of these new, sophisticated forensic and law enforcement tools.

Monitor lizards are large-bodied, charismatic, and frequently traded both legally and illegally (Gaulke, 1998; Yuwono, 1998; Cota et al., 2009), where they are harvested for skin (leather), bush meat, and pet markets (Shine et al., 1996; Shine and Harlow, 1998; Fa et al., 2000; Stuart, 2004; Pernetta, 2009; Fidenci and Maran, 2009; Welton et al., 2012). As a heavily exploited vertebrate group (Mace et al., 2007; Schlaepfer et al., 2005) of conservation concern (CITES I, II classification), methods to determine origins of traded animals under intense pressures associated with commercial harvest from wild populations are needed (Gaulke, 1998; Welton et al., 2012).

In this study, we focus on one commercial hub of monitor lizard trade, pet markets in and around metro Manila, Philippines. We use a molecular dataset of *Varanus* sampled from known localities throughout the Philippines, and phylogenetic, population genetic network, and DNA barcoding approaches to identify the provenance of trade animals, and compare our inferences to those reported by traders and dealers. Our results suggest that a phyloforensic approach can reliably pinpoint the origin of trade animals in this island archipelago, and lead us to the conclusion that purveyors of the Manila reptile trade routinely misrepresent the origins of traded animals, presumably to increase their perceived value in the illegal trade. This study demonstrates the need for dense sampling of naturally occurring populations, which is not yet done for many heavily traded taxa, in order to validate identification of source populations of illegally traded animals. With this dataset we hope to establish a baseline resource for monitoring illegal reptile trade and expanding wildlife law enforcement capacity in the Philippines.

2. Methods

2.1. Trade sampling

Genetic samples of Manila trade monitor lizards were obtained non-destructively from skin and muscle biopsies (from tail tips or crests) from 35 animals encountered in Manila pet markets (Cartimar, Arangke, and numerous smaller, and/or temporary market-places), roadside bush meat salespersons, and private pet collections. To protect identities of persons who aided in obtaining selected samples, we simply refer to all of these samples as “Manila area trade samples” and provide no further information on sources.

We conducted interviews with salespersons, traders, or suppliers (Table 1) to establish the origin of the animal in question. Efforts were made to avoid leading these conversations in any way and we asked no additional follow-up questions. Because of the wide variety of information voluntarily provided (varieties of reported origins, numbers of animals reportedly traded from a given source, secondary or tertiary source details of collection or trade route, ancillary information on other animals accompanying monitor lizards, prices paid to original collectors, prices for future transactions, etc.) during these conversations, and because the customary next stage in a discussion with a potential buyer would be to start the process of bargaining, we terminated interviews and sought no other information (nor provided any indication of interest, other than a desire to obtain a tissue biopsy) once an animal's “origin” had been reported to us.

Of the 35 samples we collected, 29 were accompanied by traders' reported origins (Table 1). Reported trade sample origins ranged from general regions (island name only) to very precise areas (small islands or cities). A few samples were accompanied by dual reported origins (i.e., “Camiguin or Batanes;” Table 1), both of which we report.

2.2. Data collection

Molecular sampling included data for 98 individuals, representing all but two of the currently recognized species of *Varanus* from the Philippines (*Varanus bitatawa*, *V. cumingi*, *V. marmoratus*, *V. nuchalis*, *V. olivaceus*, and *V. palawanensis*) as well as vouchered water monitor samples Java, Myanmar, Peninsular Malaysia, Singapore, Sulawesi, and Sumatra (Supporting Information). Outgroup samples were chosen based on Ast (2001), and included 12 species: *V. brevicauda*, *V. dumerilii*, *V. finschi*, *V. flavescens*, *V. griseus*, *V. indicus*, *V. komodensis*, *V. melinus*, *V. niloticus*, *V. nebulosis*, *V. prasinus*, and *V. rudicollis* (Appendix S1). Sequence data were available for the mitochondrial gene NADH dehydrogenase subunit 1 (ND1) and 2 (ND2), and seven surrounding tRNAs (tRNA^{Leu}, tRNA^{Leu}, tRNA^{Gln}, tRNA^{Met}, tRNA^{Trp}, tRNA^{Ala}, tRNA^{Asn}; Ast, 2001). To this dataset, we added sequences of ND1 for 28 pet trade samples, and ND1 and ND2 (plus the seven tRNAs) for 98 vouchered Philippine samples and 7 additional trade samples. Genomic DNA was extracted from tissue (liver, muscle, or scale clippings) stored in 95% ethanol following a guanidine thiocyanate extraction protocol (Esselstyn et al., 2008) Polymerase chain reactions (PCR) and cycle sequencing reactions for the mitochondrial region used the published primers of Ast (2001). We visualized amplified PCR product in 1.5% agarose gels, and purified products with 2 µl of a 20% dilution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ) using a thermal profile of 31 min at 37°, followed by 15 min at 80°. We used ABI Prism BigDye Terminator chemistry (V3.1; Applied Biosystems, Foster City, CA) in cycle sequencing reactions, and purified products with Sephadex Medium (NC9406038, Amersham Biosciences, Piscataway, NJ) in CentriSep 96 spin plates (CS-961; Princeton Separations, Princeton, NJ). Sequencing products were then analyzed with an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Sequencing products were assembled and edited using Geneious (v3.0; Drummond et al., 2011). All novel sequences were deposited in GenBank (accession Nos.: ND1, JX677567–JX677685; ND2, JX677686–JX677774).

2.3. Sequence alignment and phylogenetic analyses

Trade and vouchered samples were aligned to the published dataset of Ast (2001) in Se-AL Sequence Alignment Editor (v2.0a11; Rambaut, 2002). We treated each coding region (ND1, ND2), codon position, and tRNAs (tRNA^{Leu}, tRNA^{Leu}, tRNA^{Gln}, tRNA^{Met}, tRNA^{Trp}, tRNA^{Ala}, and tRNA^{Asn}), as distinct partitions. We used the Akaike information criterion (AIC), as implemented in jModeltest (v0.1.1; Posada, 2008), to select the most appropriate model of nucleotide substitution for each of the partitions. Partitioned maximum likelihood (ML) analyses were conducted in Garli (v2.0.1019; Zwickl, 2006). We performed 10 independent search replicates with starting trees generated using random-order stepwise additions with 100 attachments per taxon. Each replicate was terminated when no topological improvements in log-likelihood were greater than 0.01 for more than 10,000 generations, and no overall improvement in log-likelihood was greater than 0.001 for more than 500 generations. We ran 1000 bootstrap replicates under the same settings to assess clade support, with one tree search per bootstrap replicate. Alignments and resulting topologies are deposited in Dryad (doi:10.5061/dryad.d2f79).

2.4. Phylogenetic networks and sequence-matching assignment of trade samples

We employed the NeighborNet algorithm (Bryant and Moulton, 2004) in the program SplitsTree (v4.10; Huson and Bryant, 2006) to generate phylogenetic networks for the ND1 dataset for each major clade recovered to include trade samples (Fig. 1). To assess the

Table 1

Summary of trade samples used in this study, with faunal regions shown in parentheses and figure identifications corresponding to Figs. 2 and 3.

Figure ID	Trader reported locality	Putative taxonomic ID	Identified locality	Phylogenetic ID
a	Palawan Island (Palawan)	<i>V. palawanensis</i>	Southeastern Luzon, Catanduanes, or Polillo islands (Luzon)	<i>V. olivaceus</i>
b	Municipality of Nara, Palawan Island (Palawan)	<i>V. palawanensis</i>	Unknown (see Discussion)	<i>V. rudicollis</i>
c	Palawan Island (Palawan)	<i>V. palawanensis</i>	Unknown (see Discussion)	<i>V. rudicollis</i>
d	Iwahig, Palawan Island (Palawan)	<i>V. palawanensis</i>	Unknown (see Discussion)	<i>V. rudicollis</i>
e	Irawan, Palawan Island (Palawan)	<i>V. palawanensis</i>	Unknown (see Discussion)	<i>V. rudicollis</i>
f	No locality reported	–	Central or northeastern Mindanao, Dinagat, or Camiguin Sur islands (Mindanao)	<i>V. cumingi</i>
g	No locality reported	–	Luzon Island (Luzon)	<i>V. marmoratus</i>
h	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>	Southwestern Luzon Island (Luzon)	<i>V. marmoratus</i>
i	Municipality of Coron, Busuanga Island (Palawan)	<i>V. palawanensis</i>	Luzon Island (Luzon)	<i>V. marmoratus</i>
j	Palawan Island (Palawan)	<i>V. palawanensis</i>	Luzon Island (Luzon)	<i>V. marmoratus</i>
k	Bulacan Province, southern Luzon Island (Luzon)	<i>V. marmoratus</i>	Luzon Island (Luzon)	<i>V. marmoratus</i>
l	Bulacan Province, southern Luzon Island (Luzon)	<i>V. marmoratus</i>	Luzon Island (Luzon)	<i>V. marmoratus</i>
m	Davao, southern Mindanao Island (Mindanao)	<i>V. cumingi</i>	Luzon Island (Luzon)	<i>V. marmoratus</i>
n	Laguna Province, southern Luzon Island (Luzon)	<i>V. marmoratus</i>	Babuyan Island (Babuyan Island Group) or Luzon Island (Luzon)	<i>V. marmoratus</i>
o	Laguna Province, southern Luzon Island (Luzon)	<i>V. marmoratus</i>	Babuyan Island (Babuyan Island Group) or Luzon Island (Luzon)	<i>V. marmoratus</i>
p	No locality reported	–	Babuyan Island (Babuyan Island Group) or Luzon Island (Luzon)	<i>V. marmoratus</i>
q	Municipality of Baguio, central Luzon Island (Luzon)	<i>V. marmoratus</i>	Aurora Province, northeastern Luzon Island (Luzon)	<i>V. marmoratus</i>
r	Tarlac Province, central Luzon Island (Luzon)	<i>V. marmoratus</i>	Aurora Province, northeastern Luzon Island (Luzon)	<i>V. marmoratus</i>
s	Tarlac Province, central Luzon Island (Luzon)	<i>V. marmoratus</i>	Aurora Province, northeastern Luzon Island (Luzon)	<i>V. marmoratus</i>
t	Itbayat or Batanes islands (Batanes Island Group)	<i>V. marmoratus</i>	Likely Mindoro Island (Mindoro)	<i>V. cf. marmoratus</i>
u	Camiguin Island (Babuyan Island Group) or Batanes Island (Batanes Island Group)	<i>V. marmoratus</i>	Likely Mindoro Island (Mindoro)	<i>V. cf. marmoratus</i>
v	Busuanga Island (Palawan)	<i>V. palawanensis</i>	Likely Mindoro Island (Mindoro)	<i>V. cf. marmoratus</i>
w	Cavite Province, southern Luzon Island (Luzon)	<i>V. marmoratus</i>	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>
x	Batangas Province, southern Luzon Island (Luzon)	<i>V. marmoratus</i>	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>
y	Negros Island (Visayan)	<i>V. nuchalis</i>	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>
z	Batangas Province, southern Luzon Island (Luzon)	<i>V. marmoratus</i>	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>
aa	Tagaytay City, Luzon Island (Luzon) or Palawan Island (Palawan)	<i>V. palawanensis</i>	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>
bb	Calamba City, southern Luzon Island (Luzon)	<i>V. marmoratus</i>	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>
cc	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>	Bicol Peninsula, Luzon Island (Luzon)	<i>V. cf. marmoratus</i>
dd	No locality reported	–	Masbate Island (Visayan)	<i>V. nuchalis</i>
ee	No locality reported	–	Southeastern Negros Island (Visayan)	<i>V. nuchalis</i>
ff	No locality reported	–	Southeastern Negros Island (Visayan)	<i>V. nuchalis</i>
gg	Municipality of Baco, Mindoro Island (Mindoro)	<i>V. cf. marmoratus</i>	Southwestern Negros Island (Visayan)	<i>V. nuchalis</i>
hh	Mindoro Island (Mindoro)	<i>V. cf. marmoratus</i>	Sibuyan Island (Romblon Island Group)	<i>V. nuchalis</i>
ii	Mindoro Island (Mindoro)	<i>V. cf. marmoratus</i>	Sibuyan Island (Romblon Island Group)	<i>V. nuchalis</i>

support for inferred splits in the network, a bootstrap analysis was conducted with 1000 replicates. We created a BLAST database of known-locality *Varanus* collected throughout the Philippines for the mitochondrial data partition using the BLAST+ toolkit (Camacho et al., 2009). The BLAST algorithm (Altschul et al., 1990) was used to compare trade sequences against the local BLAST database. To increase the specificity of matching a particular set of haplotypes the setting for word size was increased to 100 and the mismatch cost was increased to negative four.

3. Results

3.1. Identification and assignment of trade samples

Although the mitochondrial data collected for all trade samples and the available dataset (Ast, 2001) allow for the phylogenetic placement of individuals from the Manila pet trade among vouchered samples, the resolution of phylogenetic relationships remains coarse (Fig. 1). For most major clades observed to contain

samples from the pet trade, our analyses infer close relationships between trade and voucher samples within an island, or at least a faunal region, but were not able to resolve fine-scale relationships among vouchered and non-vouchered samples (Fig. 1).

Trade samples are recovered among seven major clades representing five species: *V. cumingi*, *V. marmoratus*, *V. nuchalis*, *V. olivaceus*, and *V. rudicollis* (Fig. 1). However, trade samples are disproportionately identified as the widespread species *V. marmoratus* (66% or 23/35 individuals; Tables 1 and 2). Far fewer samples collected in the black markets represent the other four species: *V. cumingi* (3%), *V. nuchalis* (17%), *V. olivaceus* (3%), and *V. rudicollis* (11%). No individuals sampled from the pet trade are, as of yet, inferred to be *V. palawanensis* (Fig. 1).

Although most trade samples are *V. marmoratus*, we were surprised by the phylogenetic assignment of other individuals from the pet trade. Phylogenetic analyses support the identification of four trade samples (reportedly from Palawan) as *V. rudicollis*, a species with a documented natural range on the southern Asian mainland, Borneo, and Sumatra, but currently not the Philippines (Bayless and Adragna, 1997; Grismer, 2011; Fig. 1). Additionally,

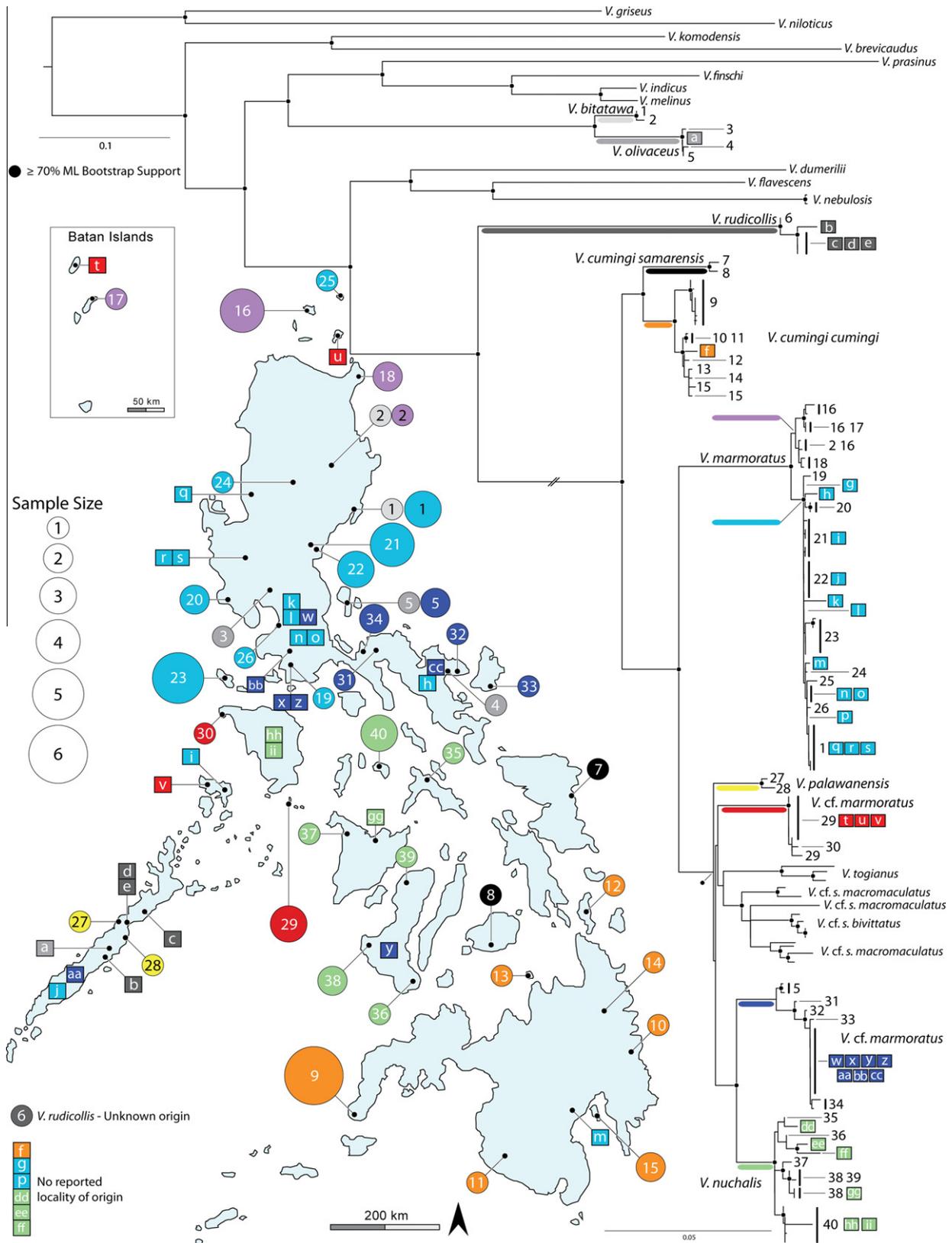


Fig. 1. Hypothesized relationships of Philippine species of *Varanus* and phylogenetic placement of black market trade samples illustrated by the maximum likelihood (ML) bootstrap consensus tree (darkened circles denote nodes with high bootstrap support; $\geq 70\%$). Colors correspond to major clades identified on the phylogeny. Trade samples represented by alphabetic labels within squares, with circle diameter corresponding to sample size. Location of trade samples corresponds to the reported origin by traders. Scale bar represents number of nucleotide substitutions per site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a single trade sample (also reportedly from Palawan) was identified as the rare, endemic frugivorous monitor *V. olivaceus*. Another sample, with no reported origin, was identified as the southern Philippines water monitor *V. cumingi*. Interestingly, analyses resulted in strong support for two trade samples being closely related to vouchered populations of *V. nuchalis* from Sibuyan Island in the Romblon Island Group (Fig. 1). This isolated, deep-ocean island is not only difficult to reach, but most remaining habitat is contained within the protected landscape of Mt. Guiting-Guiting Natural Park.

3.2. Network analyses

Fifty-two unique haplotypes were represented among the seven major clades observed to possess trade samples (Fig. 1), with 19% (or 10 samples) coming from the illegal pet trade. Results of haplotype network analyses corroborate major results observed from phylogenetic analyses (Fig. 2); however, several networks provide finer resolution among vouchered and trade samples. First, the haplotype of the trade sample of *V. olivaceus* is identical to a vouchered sample from the Caramoan Peninsula (Figs. 1 and 2; Welton et al., 2012). Second, three trade samples of *V. cf. marmoratus* share identical haplotypes with vouchered specimens from Semirara Island (part of the Mindoro faunal region). However, as Semirara is difficult to access, these samples could have been illegally collected on the large, easily accessed, and geographically proximate island of Mindoro (Figs. 1 and 2). Third, the single trade sample assigned to *V. cumingi* occurring in the southern Philippines shares identical haplotypes with vouchered populations on Mindanao Island.

Table 2

Summary of trade samples used in this study compared to vouchered species using BLAST.

Figure ID	Putative taxonomic ID	Taxon ID with highest score	% Identity	E score
a	<i>V. palawanensis</i>	<i>V. olivaceus</i>	100	0
b	<i>V. palawanensis</i>	<i>V. rudicollis</i>	98	0
c	<i>V. palawanensis</i>	<i>V. rudicollis</i>	99	0
d	<i>V. palawanensis</i>	<i>V. rudicollis</i>	99	0
e	<i>V. palawanensis</i>	<i>V. rudicollis</i>	99	0
f	–	<i>V. cumingi</i>	100	0
g	–	<i>V. marmoratus</i>	100	0
h	<i>V. cf. marmoratus</i>	<i>V. marmoratus</i>	100	0
i	<i>V. palawanensis</i>	<i>V. marmoratus</i>	100	0
j	<i>V. palawanensis</i>	<i>V. marmoratus</i>	100	0
k	<i>V. marmoratus</i>	<i>V. marmoratus</i>	99	0
l	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
m	<i>V. cumingi</i>	<i>V. marmoratus</i>	100	0
n	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
o	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
p	–	<i>V. marmoratus</i>	100	0
q	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
r	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
s	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
t	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
u	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
v	<i>V. palawanensis</i>	<i>V. marmoratus</i>	100	0
w	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
x	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
y	<i>V. nuchalis</i>	<i>V. marmoratus</i>	100	0
z	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
aa	<i>V. palawanensis</i>	<i>V. marmoratus</i>	100	0
bb	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
cc	<i>V. marmoratus</i>	<i>V. marmoratus</i>	100	0
dd	–	<i>V. nuchalis</i>	100	0
ee	–	<i>V. nuchalis</i>	99	0
ff	–	<i>V. nuchalis</i>	98	0
gg	<i>V. marmoratus</i>	<i>V. nuchalis</i>	100	0
hh	<i>V. marmoratus</i>	<i>V. nuchalis</i>	99	0
ii	<i>V. marmoratus</i>	<i>V. nuchalis</i>	100	0

Unfortunately, the distance between vouchered locations on Mindanao precludes more fine-scale inferences of this sample's exact origin (Figs. 1 and 2). Fourth, many trade samples identified as true *V. marmoratus* from Luzon Island share the closest haplotype similarity to vouchered populations in the regions surrounding the capital city of Manila in central Luzon (Figs. 1 and 2). Finally, haplotypes of trade samples of *V. cf. marmoratus* from the Bicol faunal region are identical to vouchered populations on the Bicol Peninsula (Figs. 1 and 2).

3.3. DNA barcoding

As shown in the haplotype and phylogenetic analyses, sequence similarity is high within and among populations of *Varanus* species. Sequence-matching with the BLAST algorithm resulted in all trade samples having E-scores of zero for all Philippine *Varanus* species and *V. rudicollis* indicating trade samples are more likely to be any Philippine species or *V. rudicollis* than a random sample. Known-locality samples with highest sequence-matching score and percent sequence-matching identity result in the same identification of trade samples as phylogenetic and haplotype analyses (Table 2). Most trade sample sequences were 100% identical to a known-locality sequence, and some were identical to multiple samples. Due to a lack of statistical significance between most matched sequences, which location sampled within a species is the source of a particular trade sample is difficult to ascertain. For instance, trade samples g–s are 99–100% identical to all samples in the *V. marmoratus* clade (Luzon proper), making it impossible to specify which location the trade samples come from (Table 2).

4. Discussion

4.1. Phyloforensics and origins of Manila's black market pet trade

With 35 samples from illegal pet markets in Manila, bush markets, and private collectors, we are able to provide a preliminary forensic evaluation of the black market trade of Philippine monitor lizards and evaluate the accuracy of reported harvest localities. Interviews with local dealers resulted in 29 samples with reported localities throughout the archipelago, 25 of which appear to be Philippine species (Tables 1 and 2). Of these samples (excluding *V. rudicollis*, see below), we tested the accuracy of reported localities for 25 individuals. We found 44–56% (11–14/25) of the reported harvest localities accurate to the reported faunal region as well as the reported island (three of the reports consisted of two possible collection regions; Table 1). Accounting for variation resulting from dual-region reports, the percentage of trade samples originating in the major faunal regions and island groups are as follows: 58–68% Luzon faunal region; 3% Mindanao faunal region; 10% Mindoro faunal region; 13% Visayan faunal region; 6% Romblon Island Group; and 0–10% Babuyan Island Group (Table 1). Among trade samples genetically identified as originating from the Luzon faunal region, 52–68% (16–21 individuals) are confirmed to have originated on Luzon proper, with 33% (seven individuals) originating in the Bicol Peninsula (Table 1). Clearly, the Manila black market pet trade has the capacity to obtain animals from throughout the archipelago (and possibly beyond; see below).

4.2. Accuracy of traders' reported origins

Approximately half of our Manila pet trade sampling was misreported as originating on islands that differed from the inferred location based on genotype (Table 1). Although the rate of misidentification is high, deliberate misrepresentation of species

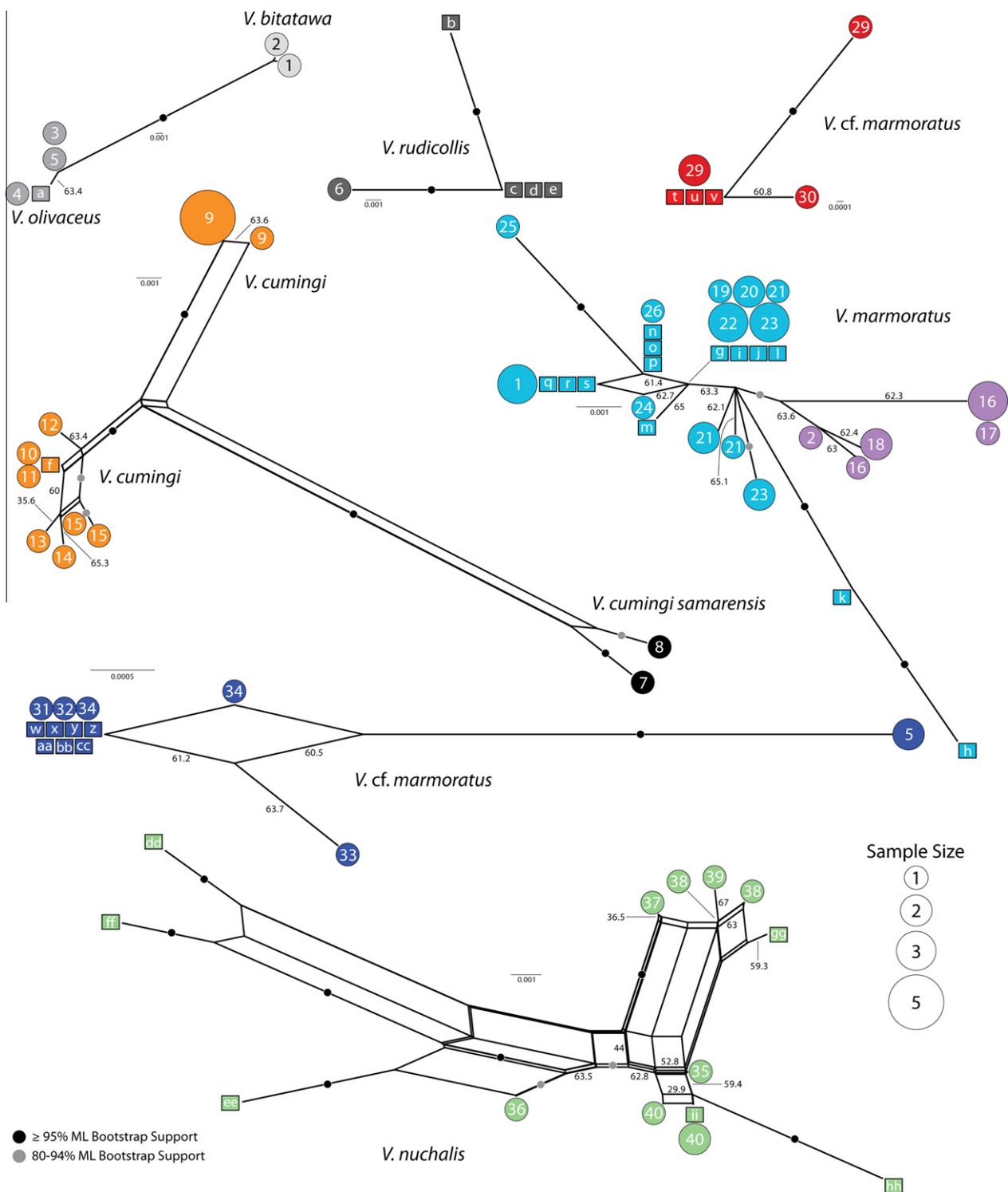


Fig. 2. Mitochondrial haplotype networks inferred by SplitsTree (Huson and Bryant, 2006). Alphabetic and numerical labeled haplotypes correspond to identifications of vouchered (Supporting Information) and trade (Tables 1 and 2) samples.

identification to command higher prices in the trade has been well documented elsewhere (Jacquet and Pauly, 2007; Ogden, 2008; Buck, 2009; Cawthorn et al., 2012).

Some of these misleading reports are not surprising. For example, in our experience while conducting this and other studies (interview data from market surveys for turtles, other lizards, snakes, mammals and birds; RMB, CDS, ES, unpublished data), we frequently observed Manila pet traders reporting a Palawan origin

for animals, presumably in hopes of obtaining higher prices from Manila customers. Not only does the Palawan faunal region have a unique, highly endemic faunal assemblage (Diesmos et al., 2004; Esselstyn et al., 2010; Blackburn et al., 2010), but the entirety of the island is considered a protected area (Diesmos and Palomar, 2004; La Viña, 1997) and the collection of any wild vertebrates is highly restricted and heavily monitored by the Palawan Council for Sustainable Development (Republic Act No. 7611),

under Resolution No. 07-332. As a result, exotic pets from Palawan command a particular allure in Manila's black market pet trade (Gavino and Schoppe, 2004; Cruz et al., 2007). Although we expected many false Palawan reports, no Palawan endemic monitors (*V. palawanensis*) were confirmed in the Manila trade, as has been observed for other reptiles (Gavino and Schoppe, 2004; Diesmos et al., 2004; Fidenci and Maran, 2009).

4.3. *V. rudicollis* on Palawan?

The reporting of specific Palawan localities (Iwahig and Nara; Table 1) for genetic samples determined to be *V. rudicollis* warrants comment. Although four samples identified as *V. rudicollis* were reported by traders as having originated on Palawan, no substantiated or vouchered (corresponding to an accessible preserved museum specimen) genetic data are available for this species from a known locality on Palawan. Our inference of *V. rudicollis* in the Manila trade is based on the high degree of shared sequence identity (98–99%) between trade samples. Sequence-matching shows that trade samples b–e match to *V. rudicollis* and no other sampled species. This species is well documented from Thailand, throughout the Malaysian Peninsula, and on Borneo and Sumatra (Grismer, 2011), but its original description was based on a specimen reportedly from the Philippines (Gray, 1845). However, in more than 150 years since its original description, no additional substantiated Philippine records have been forthcoming (Bayless and Adragna, 1997). Among *Varanus* biologists, the general assumption has been that the Philippine type locality for this species is in error (e.g., Bayless, 1997; Bayless and Adragna, 1997; Pianka et al., 2004). Although the close proximity and biogeographical relationship between Borneo and Palawan (Esselstyn et al., 2010; Blackburn et al., 2010; Siler et al., 2012) lends credence to the argument that *V. rudicollis* may naturally occur on this island, our genetic corroboration of this species' identity in the Manila pet trade is neutral with respect to whether it naturally exists in wild populations in the archipelago. The reference sequence consists of genbank data collected from a salvaged pet trade sample obtained in Lawrence, Kansas, phenotypically identified as *V. rudicollis* (Grismer, 2011; L. Welton, *personal observation*). Therefore, our findings cannot discriminate between the possibility of a natural population of *V. rudicollis* on Palawan versus trade samples originating from a non-Philippine part of the species' range, and then either smuggled through Palawan dealers to Manila or simply smuggled to Manila and misrepresented as having originated on Palawan. However, given bureaucratic and logistical obstacles to conducting biodiversity surveys on Palawan, and the fact that its forests remain so poorly studied, we acknowledge that a large bodied, semi-arboreal species of *Varanus* could escape detection by biologists in the same way that the now heavily traded, conspicuous Philippine forest turtle avoided positive identification until just this last decade (Diesmos et al., 2004). Highly distinctive, undescribed species of arboreal monitor lizards continue to be discovered elsewhere in the archipelago (Gaulke and Curio, 2001; Welton et al., 2010).

4.4. Current limitations and future prospects for forensic studies of manila's trade

This study has allowed assignment of trade samples to islands or biogeographical subregions within large islands (Table 1); however, current limitations of available data (L. Welton et al., unpublished data; this study) do not allow us to identify origins of many animals with greater accuracy. We recommend two approaches to ameliorate this limitation. First, additional sampling from vouchered, natural populations throughout the Philippines should be undertaken and added to this dataset. As *Varanus* are commonly encountered throughout the archipelago (*personal observations*), it

would not be difficult to sample animals on every major island (and numerous locations within larger islands) with a concerted effort, and develop a comprehensive genetic reference database for the country. More importantly, however, we recommend the use of numerous, rapidly evolving nuclear loci (next-generation sequencing technology, microsatellites, SNPs, etc.); these genetic resources are now routinely employed and readily available (Morin et al., 2004; Ogden et al., 2008, 2009; Ogden, 2011; Garvin et al., 2010). As vouchered population sampling increases, the limiting factor for applying cutting-edge trade forensic methods will simply become the need for more variable nuclear loci and access to genetic samples from animals in the trade. With the addition of these types of data, phyloforensic methods will be able to pinpoint, with significantly improved accuracy, specific origins of illegally poached animals.

This study represents the first test case of a phyloforensic method in the Philippines. Numerous additional, unrelated taxa should now be similarly studied; the Manila pet trade regularly deals in a wide variety of amphibians, reptiles, birds, mammals, and marine fish (CDS, ES, *personal observations*). Additionally, phyloforensic monitoring of the illegal Philippine pet trade should focus on the numerous well-developed trade centers we are aware of on Palawan (Puerto Princesa City), Cebu (Cebu City), and Mindanao (Davao City) islands, as well as many smaller cities on Luzon Island (*personal observations*). Many of these clearly are the conduits through which animals enter the Philippines from other countries, as well as sources for illegal smuggling of animals to regions outside of the Philippines. Finally, in many rural provinces in the Philippines, thriving local bush meat markets deal in wild caught forest species (Welton et al., 2012; Fig. 3). We anticipate that most of these will be found to deal in species from areas in close proximity to these smaller local markets, but this speculation remains to be tested. In addition to the necessity of widespread geographic and taxonomic sampling to combat illegal trade in the Philippines, such efforts should be extended to countries where illegal trade in animals is of similar concern. Much of Southeast Asia, central Africa, Australia, and northern South America have been plagued by circumstances similar to those found in the Philippines. These regions are home to species which are highly sought after in the pet, traditional medicine, and skin trades (Shine et al., 1996; Shine and Harlow, 1998; Fa et al., 2000; Stuart, 2004; Pernetta, 2009), and should be targeted for widespread sampling of natural populations in order to assess those populations most at risk and severely threatened by illegal exploitation.

4.5. Importance of consumer education and genetic monitoring of trade

Our intent has been to arrive at an initial understanding of the geographical extent of monitor lizard trade in the Philippines, numbers of taxa involved, and degree of misrepresentation of origins employed by traders. Although we aspire to develop a genetic database with additional geographic and genetic sampling to provide wildlife enforcement officials with a powerful conservation tool for future use, one additional motive should be addressed. As the middle class civil society demographically expands in the Philippines, consumer education efforts are becoming an increasingly important component of conservation (Posa et al., 2008). Informed consumer choices become possible as sustainable use of natural resources becomes increasingly important in the daily lives of environmentally aware consumers, and information regarding the origins of wildlife products becomes increasingly available. Previous studies have shown that if consumers can be informed as to the true origins of exploited natural populations, they may choose to avoid the purchase of non-sustainably harvested, or non-local, animal products (Kaiser and Edward-Jones,



Fig. 3. (Top, Middle) photographs of Philippine monitor lizards for sale in illegal black market trade centers in the Philippines. Photographs by LJW and RMB. (Bottom) Agta hunter (and daughter) cleaning hunting catch (*Varanus bitatawa*; see Welton et al., 2012) in Isabela Province, Luzon Island, northern Philippines. Photograph courtesy of T. Minter.

2006; Logan et al., 2008; von der Heyden et al., 2009; Cawthorn et al., 2012; Huxley-Jones et al., 2012). We hope that this study will contribute to the growing environmental awareness and increasing concern for sustainable natural resource use in Philippine society (Leefers and Castillo, 1998; Briones, 2005; Posa et al., 2008; Sodhi et al., 2009), and that herpetoculturists, legal animal traders, and the Manila public will hold bush meat dealers, zoological parks, and pet market traders accountable for the source of animals they sell, trade, breed, and maintain in captivity.

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Appendix A. Supplementary material

Detailed locality information of vouchered specimens used in this study (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.10.013>.

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