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Tracing the Geographic Origin of a Nonnative Red-banded Snake (Colubridae: *Lycodon rufozonatus*) Found on Jeju Island, Republic of Korea

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ABSTRACT: The rapid growth of global human activities has increased the introductions of nonnative species to an unprecedented level. Among globally documented nonnative species, reptiles and amphibians make up a significant portion. Although the introduction of many nonnative species has been linked to the wildlife trade and stowaways, the origin of introduced individuals often remains unclear. Here, we determined the geographic origin of the second known specimen of Red-banded Snake (*Lycodon rufozonatus*) found in Jeju Island, Republic of Korea, using phylogenetic analyses. In addition, we assessed the establishment potential of the species through ecological niche modeling. Phylogenetic analyses of two mitochondrial genes strongly supported the origin of the specimen from the East or South Central regions of the People's Republic of China, especially Anhui and Zhejiang provinces, suggesting an introduction through anthropogenic activities rather than a natural colonization from mainland Korea. In addition, the ecological niche models had adequate predictive abilities and estimated suitable habitats across the island, suggesting habitat conditions sufficient for establishment and colonization. The potential sources of introduction are legal and illegal trading, as well as accidental transportation as stowaways. The locations of the two *L. rufozonatus* recorded are extremely close, suggesting that the species has potentially established itself in Jeju. The introduction and establishment of *L. rufozonatus* on the island is likely to have negative impacts on the island's native fauna through predation. Therefore, further surveys around the area where the specimens were found and around major ports on the island are required to verify the presence of additional individuals and prevent population establishment.

Key words: Anthropogenic; Ecological niche modeling; MaxEnt; Phylogenetic analyses

RAPID INCREASES in trade, tourism, transportation, and other anthropogenic activities are causing unprecedented increases in the introductions of nonnative species globally (Anderson et al. 2015). Nonnative species can have significant environmental impacts in their introduced ranges, including predation, competition, hybridization and genetic contamination, disease transmission, and alterations of ecosystem functions (Riley et al. 2003; Blackburn et al. 2004; Kraus 2015). Among the documented nonnative species, a significant portion is composed of reptiles and amphibians (Kraus 2015), and some nonnative herpetofauna have caused significant ecological and economic damage (Rodda and Savidge 2007; Shine 2010; Dorcas et al. 2012). In many cases, the introduction routes of these nonnative herpetofauna have been traced back to the pet trade, food and agricultural trades, biological control, and stowaways in cargo (Shine 2010; Engeman et al. 2011; Hoogmoed and Avila-Pires 2015; Groffen et al. 2019; DeVos and Giery 2021).

In the Republic of Korea (R Korea hereafter), more than a dozen species of nonnative reptiles and amphibians have been introduced since the late 1950s (Lee and Park 2016; Groffen et al. 2019; Koo et al. 2020a). Some species of nonnative reptiles and amphibians were introduced into R Korea decades ago from commercial farms, pet trade, and religious ceremonies (Groffen et al. 2019; Koo et al. 2020a). The most notable examples include Red-eared Sliders (*Trachemys scripta elegans*) and American Bullfrogs (*Lithobates catesbeianus*). However, recent reports have raised concerns on the increase of nonnative herpetofauna in R Korea. These include reports on nonnative turtles (Koo et al. 2020a, 2021; Park et al. 2020, 2022), anurans (Borzée et al. 2020), lizards (Kwon et al. 2023), and snakes (Ham et al. 2022). Many of these species were most likely introduced from the rapidly growing reptile and amphibian pet trade in R Korea (Koo et al. 2020b). These studies reported records of species with native ranges outside of R Korea, and the detection and identification of such nonnative individuals could be made relatively easily, as no similar species exist among the native herpetofauna. However, translocations of individuals that are externally similar or conspecific to the native herpetofauna from other parts of the species' range are much more difficult to detect and identify (Othman et al. 2022; Borzée et al. 2023).

Red-banded Snakes (*Lycodon rufozonatus*) are colubrids with a broad geographic distribution encompassing the Korean Peninsula, Japan (the Ryukyu Islands; Uetz et al. 2021), the mainland People's Republic of China (hereafter China), Taiwan Island, the Russian Far East, northern Vietnam, and Laos (Uetz et al. 2021). The species inhabits various habitat types including mountain forests, residential areas adjacent to mountains, rice paddies, and riparian habitats (Lee et al. 2012). The species also has a generalist diet consisting of amphibians, fish, rodents, birds, and other reptiles including other snakes (Lee et al. 2012;

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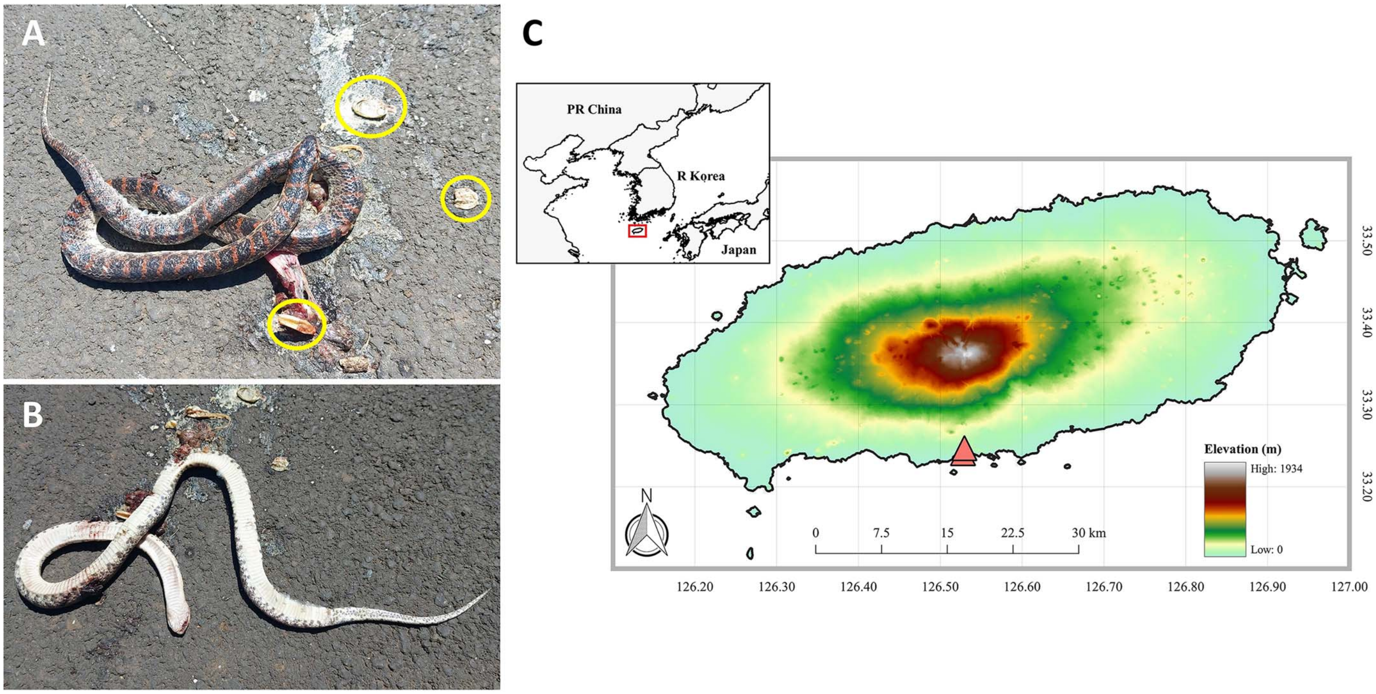

FIG. 1.—The second record of *Lycodon rufozonatus* found as a roadkill in Seogwipo, Jeju Island, Republic of Korea on 28 July 2021. Photographs were taken from the dorsal (A) and ventral (B) angles upon discovery, and the specimen was collected and deposited in Seoul National University (voucher no. MMS11951). The body coloration and patterns provided unambiguous morphological characteristics to identify the specimen at the species level. Several well-developed and calcified eggs were visible (yellow circles in A), indicating the snake to be a gravid female. The observation can be retrieved through iNaturalist (available at https://www.inaturalist.org/observations/88911435). (C) Geographic location and elevation of Jeju Island. The location of Jeju Island within East Asia is highlighted by a red rectangle in the inset map. The 30-m resolution elevation raster used for visualization was generated from the R package microclima (Maclean et al. 2019). The general locations of both *L. rufozonatus* observations recorded in Jeju are shown with two overlapping pink triangles. The map was made in QGIS 3.

Macias et al. 2021). Within the Korean Peninsula, *L. rufozonatus* is found throughout the Democratic People's Republic of Korea (Won 1971; Kim and Han 2009) and is widely distributed across the mainland of R Korea (Song 2007; Jang et al. 2016) and several offshore islands close to the mainland (Jang et al. 2016; Park et al. 2019). The species is, however, conventionally known to be absent from islands further away from the mainland, including the largest island of the Korean Peninsula: Jeju Island (Jang et al. 2016). However, a recent observation recorded a single individual *L. rufozonatus* on the island, observed on 1 March 2020 and subsequently uploaded to iNaturalist (https://www.inaturalist.org/observations/39490505). This was the first record of *L. rufozonatus* on Jeju Island to our knowledge. The individual reported therein was found as a roadkill and the specimen's potential origin has not been investigated.

Here, we report the second confirmed record of *L. rufozonatus* on Jeju Island. As the herpetofauna of the island is generally well described from numerous field surveys (Shim and Park 1998; Ko et al. 2009; Jang et al. 2016), it is unlikely that this specimen represents a previously unknown island population of *L. rufozonatus*. Therefore, we considered the possibility of anthropogenic introduction from two potential geographic origins, either from the mainland R Korea (especially southern R Korea) or from regions outside of R Korea. We test our hypotheses using phylogenetic analyses of two mitochondrial genes and assess the potential for establishment of nonnative *L. rufozonatus* on Jeju Island through ecological niche modeling.

MATERIALS AND METHODS

Specimen Collection

The specimen reported in this study was found as a roadkill on 28 July 2021, in Seogwipo, Jeju Island (33.241007°N, 126.527766°E; ca 29 m above sea level [asl]; datum = WGS84; Fig. 1). The general morphological characteristics and physical conditions of the specimen were observed and photographed upon discovery (Fig. 1). The whole specimen was collected and temporarily fixed in 20% ethanol and then subsequently transferred to 95% ethanol for long-term preservation. The preserved specimen was deposited in the Research Institute for Veterinary Science, Seoul National University, Korea, under voucher number MMS11951. As comparative specimens, we also added tissue samples collected from three fresh roadkills of *L. rufozonatus* distributed in northern R Korea (Table 1). These samples were stored in 95% ethanol prior to DNA extraction.

Laboratory Protocols

We extracted genomic DNA from preserved tissues using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Germany), following the manufacturer's protocols. We amplified two mitochondrial genes, cytochrome *c* oxidase subunit I (COI) and cytochrome *b* (Cytb), using polymerase chain reactions (PCR). We used the primers LCO1490 (5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′) and HCO2198 (5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′) for COI (Folmer et al. 1994) and the primers L14919 (5′-AAC CAC

TABLE 1.—Taxon sampling, specimen voucher numbers, locality, and GenBank accession numbers for the two mitochondrial genes (COI and Cytb) used for phylogenetic analyses. Accession numbers of newly generated sequences are in bold.

			Accession no.	
Species	Specimen ID/Voucher no.	Locality	COI	Cytb
Lycodon rufozonatus	MMS11951	Jeju Island, R Korea	**OQ200136**	**OQ200119**
Lycodon rufozonatus	21LRCC001	Chuncheon, R Korea	**OQ200345**	**OQ200120**
Lycodon rufozonatus	21LRCC002	Chuncheon, R Korea	**OQ200344**	**OQ200121**
Lycodon rufozonatus	21LYCC009a	Chuncheon, R Korea	**OQ200162**	**OQ200122**
Lycodon rufozonatus	NIBRRP0000100358	Goheung, R Korea	JQ798868	JQ798786
Lycodon rufozonatus	NIBRRP0000100254	Uiseong, R Korea	JQ798869	JQ798787
Lycodon rufozonatus	NIBRRP0000000117	Namwon, R Korea	–	JQ798788
Lycodon rufozonatus	SR1	Jiangxi, China	KR045865	–
Lycodon rufozonatus	SR143	Zhejiang, China	KR045999	–
Lycodon rufozonatus	SR144	Zhejiang, China	KR046000	–
Lycodon rufozonatus	SR145	Zhejiang, China	KR046001	–
Lycodon rufozonatus	SR146	Zhejiang, China	KR046002	–
Lycodon rufozonatus	SR147	Zhejiang, China	KR046003	–
Lycodon rufozonatus	SR158	Zhejiang, China	KR046010	–
Lycodon rufozonatus	SR160	Zhejiang, China	KR046011	–
Lycodon rufozonatus	SR161	Zhejiang, China	KR046012	–
Lycodon rufozonatus	SR162	Zhejiang, China	KR046013	–
Lycodon rufozonatus	SR163	Zhejiang, China	KR046014	–
Lycodon rufozonatus	SR164	Zhejiang, China	KR046015	–
Lycodon rufozonatus	CLS1	Zhejiang, China	MH153669	–
Lycodon rufozonatus	CLS2	Zhejiang, China	MH153670	–
Lycodon rufozonatus	CLS3	Zhejiang, China	MH153671	–
Lycodon rufozonatus	CLS4	Zhejiang, China	MH153672	–
Lycodon rufozonatus	CHS163	Xian, China	MK064659	MK201306
Lycodon rufozonatus	CHS164	Anhui, China	–	MK201307
Lycodon rufozonatus	CHS601	Anhui, China	MK064768	–
Lycodon rufozonatus	BS06	Hunan. China	MZ031435	–
Lycodon rufozonatus	BS28	Hunan. China	MZ031457	–
Lycodon rufozonatus	BS29	Hunan. China	MZ031458	–
Lycodon rufozonatus	ZS-3	Guangdong, China	JN833598	–
Lycodon rufozonatus	ZS-4	Guangdong, China	JN833599	–
Lycodon rufozonatus	ZS-5	Guangdong, China	JN833600	–
Lycodon rufozonatus	S-87	Jiangxi, China	KF698933	–
Lycodon rufozonatus	S-88	Jiangxi, China	KF698934	–
Lycodon rufozonatus	S-90	Anhui, China	KF698937	–
Lycodon rufozonatus	S-104	Guangxi, China	KF698935	–
Lycodon rufozonatus	S-105	Guangxi, China	KF698936	–
Lycodon rufozonatus	SYSr000909	Anhui, China	–	MK201427
Lycodon rufozonatus	SYSr001365	Hunan. China	MK064829	MK201482
Lycodon rufozonatus	SYSr001770	Zhejiang, China	–	MT625858
Lycodon rufozonatus	SYSr002061	Jiangxi, China	–	MT625860
Lycodon rufozonatus	GP133	Sichuan, China	–	KC733194
Lycodon rufozonatus	GP625	Liaoning, China	–	KC733196
Lycodon rufozonatus	CIB101	China	–	KF732924
Lycodon rufozonatus		China	–	JF827672
Lycodon albofuscus			–	KX660501
Lycodon aulicus			–	KC010350
Lycodon bibonius			–	KC010351
Lycodon chrysoprateros			MH274407	–
Lycodon laoensis			LC105619	–
Lycodon muelleri			MH274410	–
Lycodon stormi			–	KC010380
Lycodon subcinctus			MK064885	MK844536
Boiga dendrophila			MG935446	LC105639

CGT TGT TAT TCA ACT-3′) and H16064 (5′-CTT TGG TTT ACA AGA ACA ATG CTT TA-3′) for Cytb (Burbrink et al. 2000). The PCR reactions were prepared in a total volume of 20 μl with final concentration of PCR reagents containing 50 ng/μl of template DNA, 0.125 μM of each forward and reverse primer, 0.1 unit/μl of Ex Taq (Takara; Shiga, Japan), 1× Ex Taq buffer (Takara Bio Inc., Japan), 0.2 mM of dNTPs mix (Takara Bio Inc.), 1.875 mM of $MgCl_2$ and double distilled water. For COI, the PCR was conducted with an initial denaturation at 94°C for 5 min followed by 35 cycles at 94°C for 30 s, annealing at 55°C for 1 min, extension at 72°C for 1 min, followed by a final extension at 72°C for 10 min (Folmer et al. 1994). The PCR for Cytb was conducted with an initial denaturation at 94°C for 3 min followed by 30 cycles at 94°C for 1 min, annealing at 46°C for 1 min, extension at 72°C for 1 min, followed by a final extension at 72°C for 5 min (Burbrink et al. 2000). The PCR products were purified and sequenced using the ABI 3730xl DNA Analyzer (Applied Biosystems, USA) at Cosmogenetech (Seoul, R Korea). We deposited all newly generated sequences in GenBank (available at https://www.ncbi.nlm.nih.gov/genbank/) under accession numbers OQ200136, OQ200162, OQ200344, and OQ200345 for COI sequences and OQ200119–OQ200122 for Cytb sequences (Table 1).

Phylogenetic Analyses

In addition to the newly generated sequences, we aligned the sequences of *L. rufozonatus* with their homologous sequences retrieved from GenBank (see Table 1). These sequences were mostly composed of *L. rufozonatus* originating from R Korea (Jeong et al. 2013) and China. For outgroup taxa, we included congenerics *L. albofuscus*, *L. aulicus*, *L. bibonius*, *L. chrysoprateros*, *L. laoensis*, *L. muelleri*, *L. stormi*, *L. subcinctus*, and a colubrid *Boiga dendrophila,* based on previous studies on the phylogeny of *Lycodon* and broader colubrid relationships (Guo et al. 2013; Pyron et al. 2013; Siler et al. 2013). Because of the limitation in availability of sequences for each mitochondrial gene fragment and each taxon in GenBank, we used the COI and Cytb gene fragments as two independent data sets. For both data sets, we aligned the sequences using the MUSCLE algorithm (Edgar 2004) embedded in Geneious Prime (v2022.2.2; Biomatters Ltd., Auckland, New Zealand). The final data sets contained 41 sequences of 572–base pair (bp) –long fragments for COI and 23 sequences of 585-bp-long fragments for Cytb.

We determined the best partitioning schemes and best-fit nucleotide substitution models for our data sets using the software PartitionFinder v2.1.1 (Lanfear et al. 2017). We ran the analyses with greedy search algorithm (Lanfear et al. 2012) and unlinked branch lengths parameter, and determined the best-fit nucleotide substitution models based on the Bayesian information criterion (BIC). Using the strategy of three codon positions for both data sets, we recovered a single partition for COI with the HKY model with gamma distributed rates (HKY + G) as the best fit substitution model. For Cytb, we recovered two partitions based on (1) the first and second codon positions and (2) the third codon position. For the first Cytb partition, the best-fit model was HKY with a proportion of invariant sites and gamma distributed rates (HKY + I + G), and for the second Cytb partition, the best-fit model was GTR with gamma distributed rates (GTR + G). Next, we used both Bayesian inference (BI) and maximum likelihood (ML) methods to conduct phylogenetic analyses. We constructed the BI tree using the software MrBayes v3.2.7 (Ronquist et al. 2012). For both genes, we conducted two independent runs of Markov chain Monte Carlo (MCMC) consisting of three heated chains and one cold chain, estimated for 20 million generations and sampled every 1000 generations. The first 25% of the samples were discarded as burn-in. Parameter stationarity was confirmed by determining that the average standard deviation of split frequencies had reached a value below 0.005 at the end of the run. In addition, parameter convergence was assessed by confirming effective sample size (ESS) > 200, using Tracer v1.7.1 (Rambaut et al. 2018). The resulting trees after burn-in were summarized into a 50% majority-rule consensus tree. Next, we constructed the ML tree on W-IQ-TREE (Trifinopoulos et al. 2016) using 1000 ultrafast bootstrap replicates. The resulting trees from both BI and ML were visualized in FigTree v1.4.4 (Rambaut 2018). We considered phylogenetic relationships with ultrafast bootstrap values (UFboot) $\geq$ 95% and posterior probabilities (pp) ≥ 0.95 to be strongly supported.

Ecological Niche Modeling

We used ecological niche models (ENMs) to assess the establishment potential of *L. rufozonatus* on Jeju Island. To do so, we implemented the maximum entropy method (MaxEnt; Phillips et al. 2017) at broad and narrow spatial scales. At the broad spatial scale, the ENM was calibrated on a spatial extent covering the entire range of *L. rufozonatus* occurrence points. Jeju Island falls within this extent and the output prediction was cropped to the spatial extent of the island. We considered this approach to be adequate considering the generalist ecology of *L. rufozonatus* and the overall climatic conditions across its geographic distribution (Lee et al. 2012; Macias et al. 2021; Uetz et al. 2021). At the narrow spatial scale, we calibrated the ENM on a focal area of potential geographic origin approximated from the results of phylogenetic analyses (see the following and Figs. 2, 3). We implemented this approach to constrain the environmental conditions used for model calibration to the potential area of origin.

For broad-scale modeling, we collected georeferenced occurrence points of *L. rufozonatus* using the R package megaSDM (Shipley et al. 2022), resulting in 2898 occurrence points across R Korea, mainland China, Taiwan Island, Japan, and northern Vietnam, broadly representing the geographic distribution of the species (see Uetz et al. 2021 for the geographic distribution of *L. rufozonatus*). The two occurrence points recorded in Jeju were excluded from the data set. Next, considering the dense spatial clustering of occurrence points in Taiwan Island and R Korea, we spatially thinned the initial occurrence data set using the R package spThin (Aiello-Lammens et al. 2015). This procedure reduced the number of occurrences down to 398 and ensured that each occurrence point was at least 15 km apart from other occurrence points (Supplementary Fig. S1; Data S1, available online). In addition, we sampled 10,000 bias-corrected background points to compensate the spatial bias of occurrence data further (Phillips et al. 2009; Merow et al. 2013; Barber et al. 2022), following the general method outlined in Shin et al. (2021). For environmental variables, we used 19 bioclimatic variables and elevation raster downloaded from WorldClim 2.1 (available at https://www.worldclim.org/; Fick and Hijmans 2017), a slope raster calculated from the WorldClim elevation raster using ArcMap v10.8.2 (ESRI, Redlands, CA), and land cover variables obtained from EarthEnv (available at http://www.earthenv.org/; Tuanmu and Jetz 2014). The land cover variables included cultivated landscape cover, herbaceous vegetation cover, shrub cover, and forest cover, thus broadly representing the known habitat types of *L. rufozonatus* (Lee et al. 2012). All environmental data layers were obtained at the 30–arc-second (~1 km) spatial resolution and cropped to the spatial extent representing the geographic distribution of *L. rufozonatus*. To reduce multicollinearity between environmental layers, we removed the variables with the Pearson's $|r| > 0.7$. Thus, the following nine variables were retained for downstream modeling processes: annual mean temperature

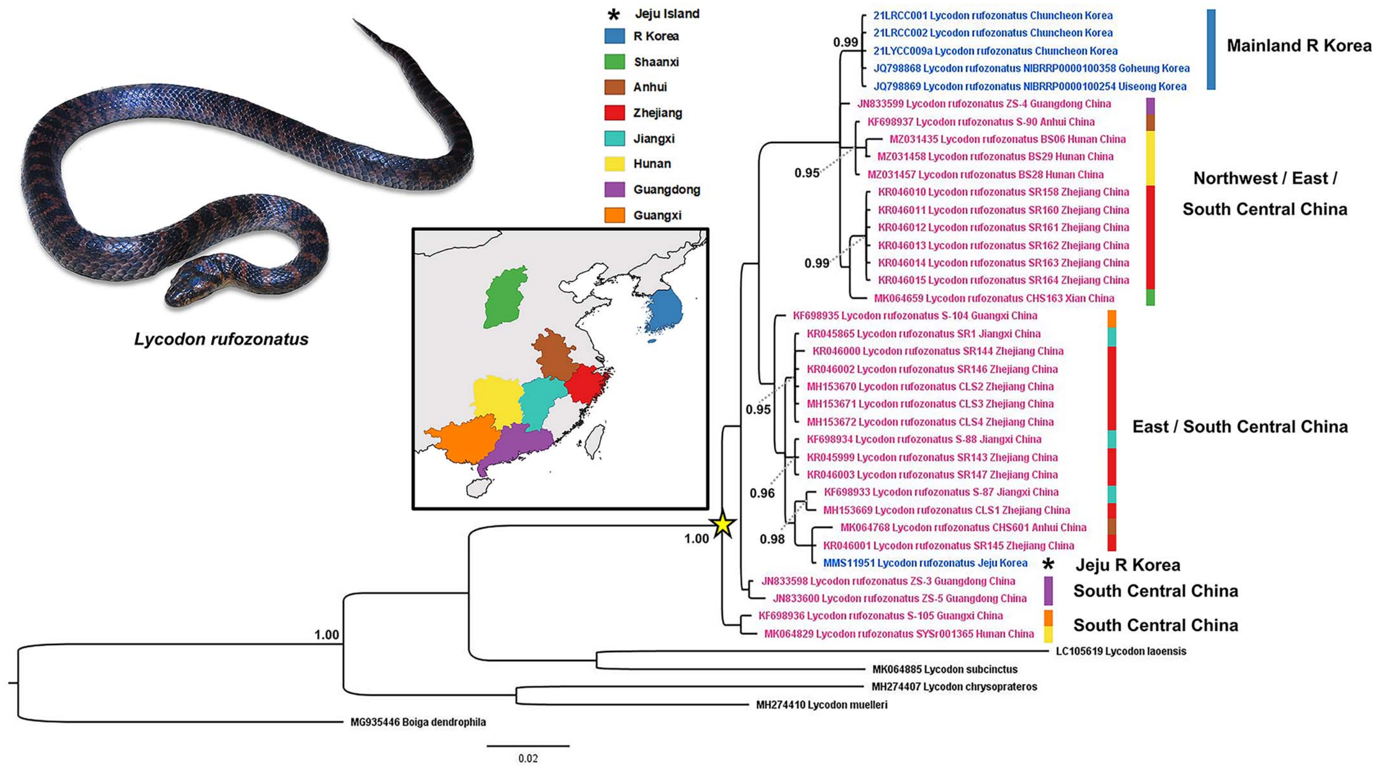

FIG. 2.—BI phylogeny of *Lycodon rufozonatus* based on the 572-bp alignment of the mitochondrial cytochrome *c* oxidase subunit I gene (COI). The node for the *L. rufozonatus* clade is highlighted with a yellow star. The samples originating from R Korea are colored in blue, and the samples originating from China are colored in red. Each vertical bar on the right side of the phylogenetic tree indicates major geographic groupings, with colors matching the general (province-level) geographic origin of samples shown in the inset map. The sample collected from Jeju (voucher MMS11951; highlighted with an asterisk) is nested within a clade composed of samples from East and South Central China, and is widely separated from a strongly supported clade composed of mainland Korean samples. The node values indicate pp $\geq$ 0.95. The inset photograph of *L. rufozonatus* was taken by YS.

(bio1), isothermality (bio3), maximum temperature of warmest month (bio5), annual precipitation (bio12), precipitation of driest month (bio14), cultivated landscape cover, herbaceous vegetation cover, shrub cover, and slope. The variable selection step was conducted using the R package ntbox (Osorio-Olvera et al. 2020). Next, we tuned the MaxEnt model parameters using the gridSearch function of the R package SDMtune (Vignali et al. 2020). We tested the combinations of 13 different feature classes (L, Q, H, P, LQ, LP, QH, QP, HP, LQH, LQP, LQHP, LQHPT) and 10 regularization multipliers (from 0.5 to 5 in 0.5 increments) and evaluated candidate models using fourfold spatial block cross-validation. The spatial blocks were generated with the ENMeval package (v2.0.4; Muscarella et al. 2014; Kass et al. 2021). From the 130 MaxEnt candidate models thus generated (Data S2, available online), we determined the optimal parameters to be the LP feature classes and a regularization multiplier of 0.5, based on the highest test AUC (area under the receiver operating characteristic curve). To statistically evaluate the ENMs, we used the AUC, the True Skill Statistic (TSS; Allouche et al. 2006), and $\mathrm{AUC_{DIFF}}$; the first two metrics evaluating the predictive performance of models and the third metric evaluating the degree of model overfitting (Warren and Seifert 2011).

The narrow-scale model was calibrated on a combined area of Anhui, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shanghai, and Zhejiang provinces, with 54 occurrence points and 10,000 bias-corrected background points sampled within the calibration area. As the modeling extent and the number of occurrence points differed from that of the broad-scale modeling, we selected the following set of eight variables for narrow-scale modeling, applying the same collinearity cutoff as the broad-scale modeling: annual mean temperature (bio1), mean temperature of driest quarter (bio9), annual precipitation (bio12), precipitation seasonality (bio15), cultivated landscape cover, herbaceous vegetation cover, shrub cover, and elevation. We then conducted a separate model tuning process using the SDMtune package, testing the same number of feature classes and regularizations as the broad-scale model. We evaluated the candidate models with fourfold spatial cross-validation and used the highest test AUC to select optimal parameter combinations, which was the P feature combined with a regularization value of 5 (Data S3, available online). The final model was statistically evaluated using the same criteria as the broad-scale model. For the spatial projection of the narrow-scale model, we additionally estimated the extrapolation risk by calculating the multivariate environmental similarity surface (MESS; Elith et al. 2010) using the dismo package (Hijmans et al. 2020). For both broad- and narrow-scale models, the outputs were in the cloglog format (Phillips et al. 2017). We assessed variable importance using permutation importance, and calculated the 10% presence threshold to produce binary presence/absence maps. All modeling procedures were conducted in R v4.2.2 (R Core Team 2022) and we used the WGS84 coordinate reference system for spatial data projections.

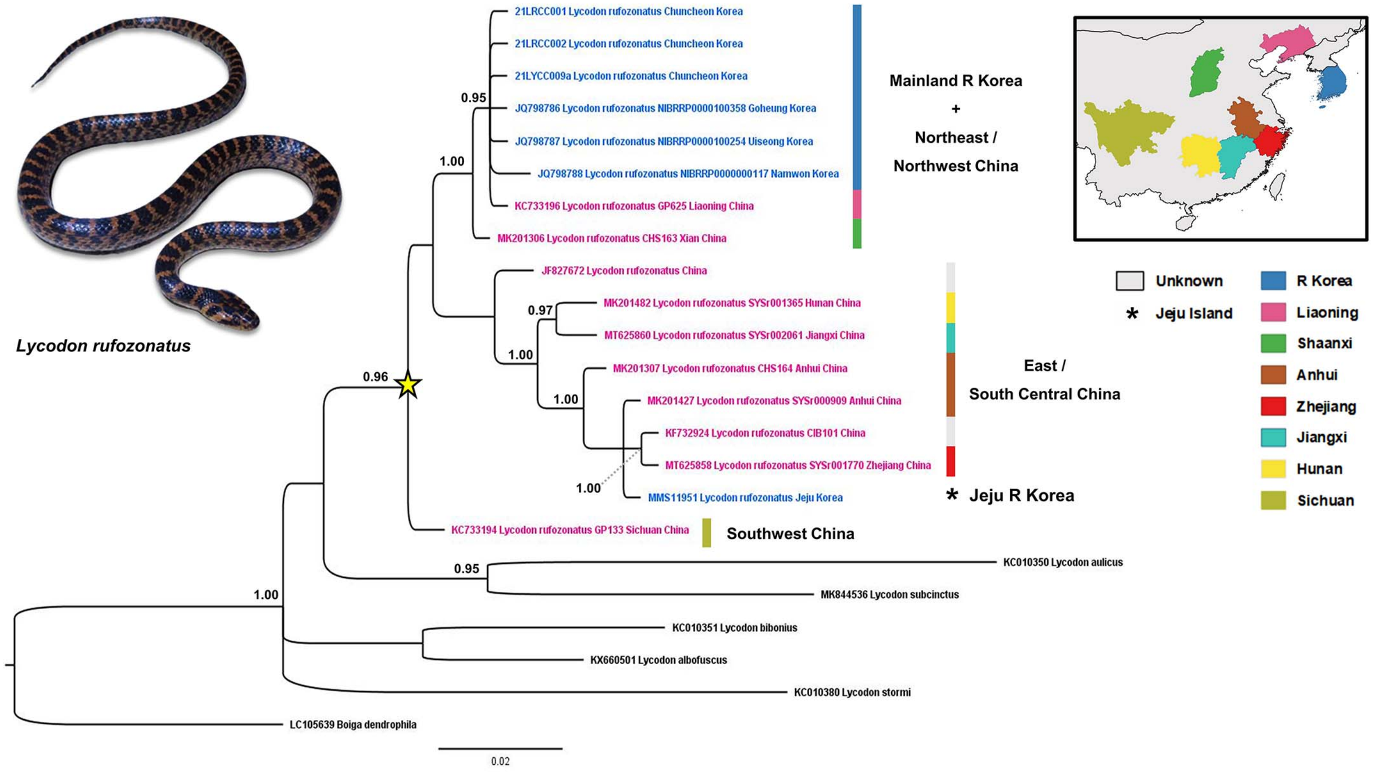

FIG. 3.—BI phylogeny of *Lycodon rufozonatus* based on the 585-bp alignment of the mitochondrial cytochrome *b* (Cytb) gene. The node for *L. rufozonatus* clade is highlighted with a yellow star. The samples originating from R Korea are colored in blue, and the samples originating from China are colored in red. Each vertical bar on the right side of the phylogenetic tree indicates major geographic groupings of samples, with colors matching the general (province-level) geographic origin of samples shown in the inset map. The sample collected from Jeju (Voucher MMS11951; highlighted with an asterisk) is nested within a strongly supported clade composed of samples from East and South Central China, and is widely separated from a strongly supported clade composed of samples from mainland R Korea, Northeast China, and Northwest China. The node values indicate pp $\geq$ 0.95. The inset photograph of *L. rufozonatus* was taken by YS.

RESULTS

Description of the Specimen from Jeju

The red dorsal body coloration, white ventral coloration, and black crossband patterns of the specimen are diagnostic characteristics of *L. rufozonatus* and enabled us to make unambiguous identification at the species level. At least three well-developed and fully calcified eggs were visible around and within the body cavity upon discovery (Fig. 1A), confirming the specimen to be a sexually mature female. The observation was uploaded on iNaturalist (available at https://www.inaturalist.org/observations/88911435).

Phylogenetic Analyses

We recovered a strongly supported clade for *L. rufozonatus* in both COI and Cytb trees and found that the phylogeny inferred from both gene fragments were sufficiently informative to determine the genetic relationship and potential geographic origin of the specimen sampled in Jeju Island. Both BI (Figs. 2, 3) and ML trees (Figs. S2, S3, available online) for COI and Cytb produced nearly identical topology with a notable difference in the position of a single sample from Western China (Sichuan Province) for the Cytb tree (see below). Therefore, we focus primarily on the results of the BI trees. The clades of *L. rufozonatus* were geographically structured in both trees; however the sample collected from Jeju Island was within the clade composed of samples from East and South Central China (Anhui and Zhejiang provinces), instead of clustering with geographically proximate samples from mainland R Korea (Figs. 2, 3).

For the COI tree based on the BI analysis, the *L. rufozonatus* clade was further divided into four subclades (Fig. 2). From the top to the bottom of the tree, the regional composition of each clade is as follows: (1) a subclade composed of samples restricted to the Korean Peninsula, Northwest China, East China, and South Central China, (2) a subclade containing our Jeju sample and the samples limited to East and South Central China, (3) a subclade composed of samples from South Central China, and (4) another subclade consisting of samples from South Central China (Fig. 2).

The Cytb tree based on the BI analysis resolved two subclades, with a sample from Southwest China (Sichuan Province) recovered as the basal node (Fig. 3). The first subclade consisted of all samples from the Korean Peninsula, Northeast China (Liaoning Province), and Northwest China (Shaanxi Province) whereas the second subclade clustered our Jeju sample with *L. rufozonatus* from East and South Central China (especially Anhui and Zhejiang provinces; Fig. 3). One major difference between the BI and ML trees based on the Cytb fragment was the placement of a *L. rufozonatus* sample from Southwest China (Sichuan Province). Although the BI tree recovered this sample as the basal node of the two major subclades of *L. rufozonatus* with relatively high support (pp = 0.73), the ML tree recovered this sample as the basal node to other *Lycodon* species used as

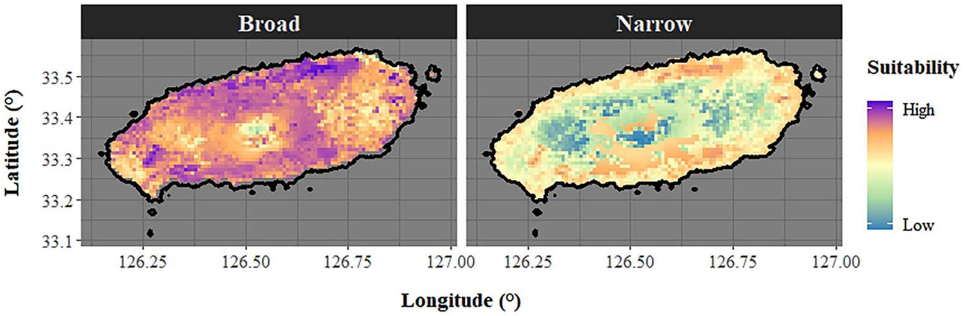

FIG. 4.—MaxEnt ecological niche models for *Lycodon rufozonatus* predicted for Jeju Island. The broad-scale model (left panel; AUC = 0.690; TSS = 0.192; AUC_{DIFF} = 0.082) was cropped from a model calibrated on the full geographic range of *L. rufozonatus*, whereas the narrow-scale model (right panel; AUC = 0.746; TSS = 0.362; AUC_{DIFF} = 0.095) was first calibrated on an area of potential geographic origin estimated from phylogenetic analyses and then projected on to Jeju Island. A total of 398 occurrence points were used to calibrate the broad-scale model, and 54 occurrence points were used to calibrate the narrow-scale model. The model visualization was done in R using the packages rasterVis (Lamigueiro and Hijmans 2021) and ggplot2 (Wickham 2016).

outgroup, thus rendering *L. rufozonatus* polyphyletic (Fig. S3). However, this placement was poorly supported (UFboot < 0.5) and did not affect the consistency in phylogenetic placements of *L. rufozonatus* originating from Jeju Island within both Cytb trees.

Ecological Niche Modeling

Both broad-scale (AUC = 0.690; TSS = 0.192; AUC_{DIFF} = 0.082; Fig. 4; Fig. S4, available online) and narrow-scale (AUC = 0.746; TSS = 0.362; AUC_{DIFF} = 0.095; Fig. 4; Fig. S5, available online) modeling produced ENMs with adequate predictive performances based on the evaluation metrics used, although the values of evaluation metrics were higher for the narrow-scale model. For the broad-scale model, annual mean temperature (bio1) was the most important variable, followed by isothermality (bio3), annual precipitation (bio12), cultivated landscape cover, maximum temperature of warmest month (bio5), slope, precipitation of driest month (bio14), shrub cover, and herbaceous vegetation cover (Table S1, available online.). Regarding the narrow-scale model, the most important variable was cultivated landscape cover, followed by elevation, mean temperature of driest quarter (bio9), precipitation seasonality (bio15), annual precipitation (bio12), annual mean temperature (bio1), shrub cover, and herbaceous vegetation cover (Table S2, available online).

Response curves for the broad-scale model show suitable habitat conditions at annual mean temperature (bio1) above approximately 8°C, isothermality (bio3) below 30, annual precipitation (bio12) below 2000 mm, and herbaceous vegetation cover lower than approximately 37% (Figs. S6, S7, available online). The response curves estimated for maximum temperature of warmest month (bio5), precipitation of driest month (bio14), cultivated landscape cover, shrub cover, and slope were above the presence threshold. However, habitat suitability showed increase with decreasing maximum temperature of warmest month, increasing precipitation of driest month, decreasing cultivated landscape cover, increasing shrub cover, and increasing slope (Fig. S6). Response curves for the narrow-scale model show suitable habitat conditions at mean temperature of driest quarter (bio9) below approximately 8°C, precipitation seasonality (bio15) below about 98, cultivated landscape cover below 62%, and elevation below approximately 200 m. The response curves for annual mean temperature (bio1), annual precipitation (bio12), herbaceous vegetation cover, and shrub cover were above the presence threshold. However, habitat suitability showed an increasing trend with the decrease of annual precipitation, herbaceous vegetation cover, and shrub cover, and annual mean temperature showed a flat response above the presence threshold (Fig. S7).

When predicted for the environmental conditions of Jeju Island, both broad- and narrow-scale models predicted suitable habitats for *L. rufozonatus* on the island, although the predicted area was somewhat different between the two models. The broad-scale model predicted the entire area of Jeju Island to be suitable for *L. rufozonatus* (Fig. 4; see Fig. S8, available online, for the presence/absence map). Although the narrow-scale model also predicted a broad area of the island to be suitable for the species, the predicted suitable habitats were mostly located around the lowland coastal regions and midelevation area further inland (Fig. 4; see Fig. S8 for the presence/absence map). The MESS calculated across the island showed that the extrapolation risk is generally low across the projection range (Fig. S9, available online).

DISCUSSION

In this study, we determined the potential geographic origin of a second known *L. rufozonatus* specimen from Jeju Island of R Korea, a region where the species is known to be absent. The results of our phylogenetic analyses strongly supported the origin of the examined specimen from East or South Central China, rather than from the geographically proximate mainland R Korea. Also, the ENM results showed that the environmental conditions of Jeju Island are suitable for the species. Therefore, our study demonstrates the introduction of a snake species from a nonnative source and suggests the potential for population establishment.

While pinpointing the exact location of origin of this specimen within China was not possible, three potential routes of translocation can be considered. The first scenario is the introduction through stowaways in cargo. Globally, the origins of various nonnative reptiles and amphibians have been traced back to accidental transportation (Rodda et al. 1992; Bassett et al. 2021; DeVos and Giery 2021; Montes et al. 2022). Small species of snakes and lizards have spread globally through the trade of potted plants and other products (Chapple et al. 2013; Bassett et al. 2021; DeVos and Giery 2021). Medium to large species of snakes can also be transported accidentally as stowaways, as in the notorious example of Brown Treesnakes (*Boiga irregularis*) on the island of Guam, USA (Rodda and Savidge 2007). The locations of the two *L. rufozonatus* records on Jeju Island are extremely close to each other (less than 800 m apart in straight-line distance), suggesting the potential for similar or even the same geographic origins. The second scenario includes the legal and illegal trade for human consumption. Capture and consumption of wild snakes are strictly prohibited in R Korea. However, legal capture for captive breeding in commercial snake farms and importation are possible for some species under valid permits, including *L. rufozonatus* (Korean Law Information Center 2017). In addition, the illegal trade of snakes from China to R Korea for human consumption has been reported previously (Park 2004). Therefore, both legal and illegal trades are likely sources of origin for nonnative snakes. The third possibility is the introduction from the pet trade, which is one of the key sources of introduced nonnative herpetofauna globally (Lockwood et al. 2019). Although reported introductions of nonnative herpetofauna into R Korea from the pet trade have been increasing (Koo et al. 2020c, 2021; Park et al. 2020; Ham et al. 2022), the introduction of nonnative *L. rufozonatus* from the pet trade is unlikely, as the species is not traded nor is it popular within the reptile pet trade of R Korea. Therefore, introduction through stowaway and/or trade for human consumption is more likely than introduction from the pet trade.

The two records of *L. rufozonatus* from Jeju Island highlight the recent arrival of the species on the island, and the second confirmed record could point to a recurring accidental introduction of the species. We cannot confirm the establishment of a nonnative *L. rufozonatus* population on Jeju Island, nor can we assess the consequences of introduction at this point. However, two roadkills recorded 1 yr apart from each other in two extremely close locations suggest that at least several individuals could have been introduced already. Moreover, a record of a sexually mature and gravid female examined in this study further suggests potential establishment, although it is possible that it was a stowaway or introduced through the food trade.

The results of ENMs also demonstrate that the environmental conditions of Jeju Island are largely suitable for *L. rufozonatus*. Although the range of predicted suitable habitats was somewhat different based on the model calibration extents, such a difference is expected, as the narrow-scale model was calibrated on a subset of species' distribution characterized by low elevation. Given the generalist habitat preferences and broad diet of *L. rufozonatus* (Lee et al. 2012; Macias et al. 2021), the species is likely to be highly flexible in its ecological requirements. In addition, the environmental conditions of Jeju Island are likely to fall within the fundamental niche of the species, given its broad geographic distribution encompassing both temperate and subtropical climates (Uetz et al. 2021). Consequently, the habitat suitability of *L. rufozonatus* on Jeju Island predicted from the narrow-scale model is likely to be an underestimation, and the habitat suitability of nonnative *L. rufozonatus* on Jeju Island is likely to be sufficient to allow the establishment and further colonization.

The introduction and establishment of *L. rufozonatus* on Jeju Island can have negative impacts on the native fauna of the island, as the species is known to prey upon various types of terrestrial and aquatic vertebrates, including other snakes (Lee et al. 2012). For example, Jeju Island is the only known range of Chinese Many-toothed Snakes (*Sibynophis chinensis*) within R Korea (National Institute of Biological Resources [NIBR] 2019). *Sibynophis chinensis* is protected under the highest conservation priority within R Korea because of its restricted distribution within the country and low population density (Endangered Species Class I, listed Endangered in the National Red List; NIBR 2019). Thus, the introduction of a nonnative predator can add further pressure on a species that is already threatened by habitat loss (NIBR 2019; Macias et al. 2021). Therefore, further efforts are needed to determine whether additional individuals of nonnative *L. rufozonatus* are present on the island. Surveys can target the area where the two specimens were found and around the major ports of Jeju Island. However, the generally cryptic ecology of snakes, combined with the nocturnal habits of the species and the likely low density for a population at an early stage of introduction, greatly increase the survey efforts required for effective monitoring. Thus, such surveys can additionally benefit from citizen participation as it can greatly increase survey efforts with minimal resource inputs and time constraints (Shin et al. 2022).

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SUPPLEMENTAL MATERIAL

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