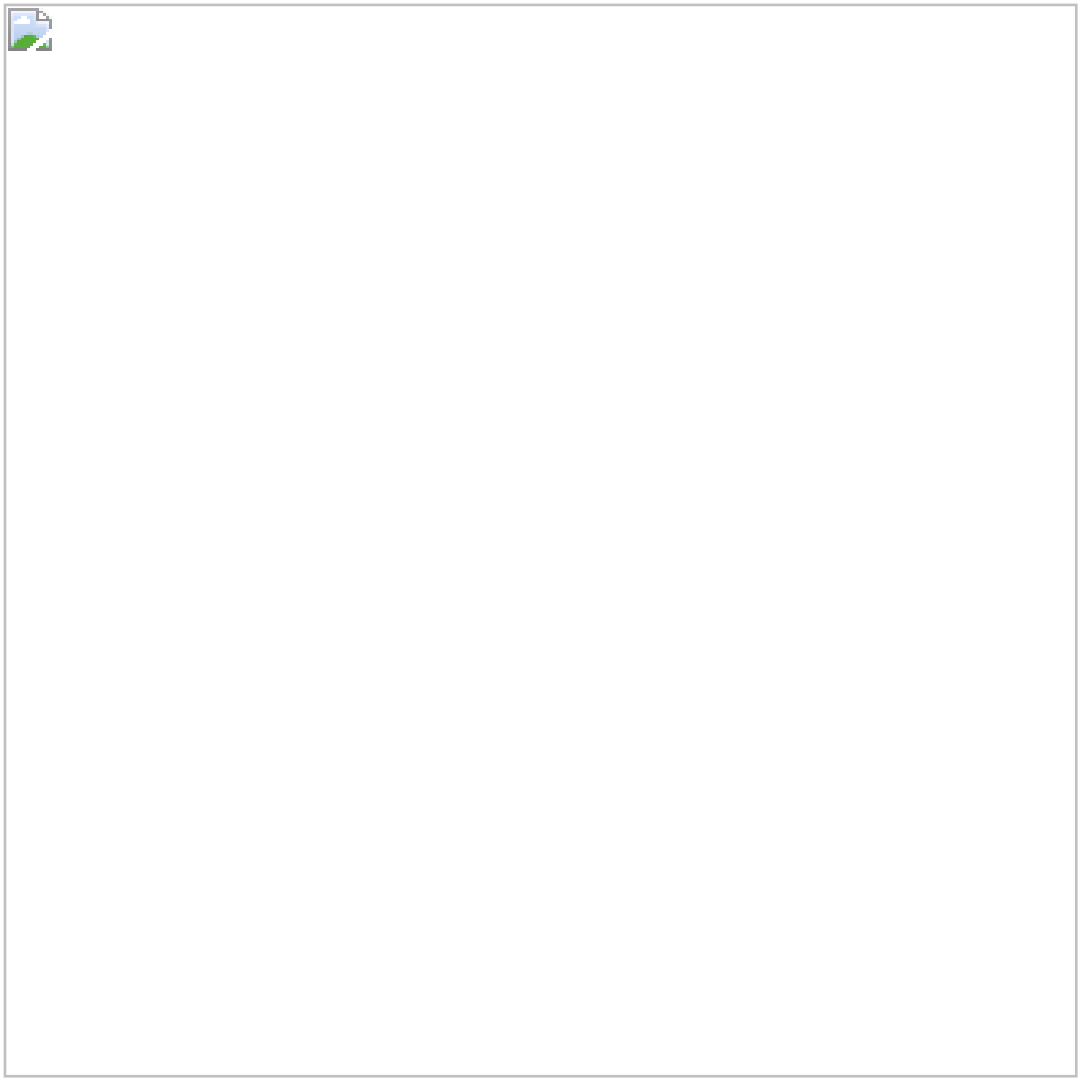

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Genetic Relationship Between Founders of a Threatened Freshwater Turtle in a Mexican Wildlife Management Unit. A Conservation Strategy

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Abstract

Management Units for Wildlife Conservation (UMAs according to its Spanish acronym), are used for the ex-situ reproduction of freshwater turtles. These areas, often administered by local communities, are dedicated to conservation and sustainable management. The critically endangered freshwater turtle *Dermatemys mawii* has been successfully reproduced in several UMAs; however, no genetic management plan has been developed to maintain offspring genetic variability. Therefore, this study aims to determine the kinship relationship and homozygosity through the loci index of founder individuals in three UMAs devoted to the reproduction of *D. mawii* for the establishment of breeding groups. We collected skin samples of *D. mawii* in 2017 from 117 founder individuals from three UMAs located in the state of Tabasco, southeast Mexico. Ten specific *D. mawii* microsatellite markers were used for genotyping the founder individuals. We estimated the pedigree relationship between founders and proposed the formation of three breeding groups to optimize the use of related and non-related individuals to meet UMA-specific objectives and evaluated the genetic diversity retention of the breeding groups. The breeding groups were integrated as follows: 1) conservation breeding group consisting of 16 unrelated females and 7 unrelated males that presented a lower level of homozygosity (< 0.4); 2) research breeding group consisting of 45 females and 16 males that were unrelated or presented a half-sibling relationship and with a medium level of homozygosity (<0.6); and 3) a sustainable breeding group comprising 29 females and 4 males that were not necessarily unrelated and with a high level of homozygosity (> 0.6). Genetic diversity retention (Ho, He) was highest for the conservation breeder group and research breeder group. UMAs can create 3 breeding groups with different objectives: 1) species conservation, 2) research, and 3) sustainable use of species. All breeding groups can retain genetic diversity. Our proposal can enrich conservation actions and sustainable use for *D. mawii* at both national and international levels, specifically within the Mesoamerican corridor.

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Keywords
genetic diversity, genetic relatedness, *Dermatemys mawii*, captive breeding, breeding groups, conservation

Introduction

Captive breeding programs are widely used to increase populations of endangered species and reduce the impact of anthropogenic threats which are difficult to address directly (Spencer et al., 2017). These conservation programs aim to conserve maximum genetic diversity and increase the population size in captivity while at the same time preventing threatened species from adapting to the captive environment. This will ensure that they remain representative of wild population sources with the final goal of reintroducing individuals and establishing self-sustaining populations in the wild (Witzenberg & Hochkirch, 2011; Miller et al., 2018; Farquharson et al., 2021). Such conservation programs require a management plan for their captive populations that should consider all the ecological and biological conditions necessary for its success (Prayaga & Reverter, 2007). Furthermore, the genetic management plan must consider and minimize the risks associated with captive breeding, such as inbreeding depression, fixation of deleterious alleles due to genetic drift, and loss of genetic diversity (Frankham, 2008). These management plans should preserve 90% of the original heterozygosity for at least 100 years under the conservation strategy (Ballou et al., 2010; Frankham et al., 2010). To minimize the risks and optimize genetic variability in captivity, genetic management programs must consider the appropriate reproductive groups through the knowledge of kinship relationships among captive individuals (Miller et al., 2018). Consequently, the use of genetic information (e.g., genetic diversity, origin, kinship) in the management plan may well be the key factor for success within *ex-situ* conservation programs (Alacs et al., 2007).

Currently, numerous species belonging to the order Testudines, particularly freshwater turtles, are in danger of extinction, primarily due to human impacts such as pollution, habitat fragmentation, as well as excessive hunting (Kanwal & Kahn, 2018; Stanford et al., 2020). Therefore, many species of turtles and tortoises are being bred in captivity as a conservation strategy (Stanford et al., 2020; He et al., 2010). For example, in Asia captive breeding programs for conservation have been developed with the species *Batagur baska* (Testudines, Geoemydidae, Gray 1830), *Batagur borneoensis* (Testudines, Geoemydidae, Schlegel and Müller, 1844), *Chitra chitra* (Testudines, Trionychidae, Nutphand, 1986) and *Platysternon megacephalum* (Testudines, Platysternidae, Gray) and have reported breeding success in captivity (Van Dijk & Palasuwan, 2000; Love et al., 2013; Spitzweg et al., 2018; Gong et al., 2019). However, these conservation programs have only conducted research related to the genetic diversity of captive individuals (Love et al., 2013; Spitzweg et al., 2018; Gong et al., 2019) and as such have not developed a genetic management plan, an important requisite for breeding selection and maintaining genetic diversity (Alacs et al., 2007; Williams & Osentoski, 2007; Fienieg & Galbusera, 2013).

In Mexico, freshwater turtles have been bred in captivity since the 1970s; but, since 1997, captivity breeding programs have been established at state-sponsored sites such as Management Units for Wildlife Conservation (Pineda-Váquez et al., 2019) (Unidad de Manejo para la Conservación de Vida Silvestre, UMA, by its Spanish acronym; Recino-Reyes et al., 2020). UMAs constitute an important tool for conservation in Mexico-promoting alternative schemes for a rational, orderly, and planned use of wildlife as well as fomenting conservation management (Pineda-Vázquez et al., 2019). By 2017, a total of 11,722 UMAs had been recorded in Mexico, however, only 94 of these are dedicated to the reproduction of freshwater turtles, several of which are in southeastern Mexico (SEMARNAT, 2018; Dirección General de Vida Silvestre & SEMARNAT, 2018). These UMAs have successfully reproduced chelonian species such as *Trachemys spp.* Agassiz, 1857 (Testudines, Emydidae), *Claudius angustatus* Cope 1865 (Testudines, Kinosternidae), *Staurotypus triporcatus* Wiegmann 1828 (Testudines, Kinosternidae), and *Dermatemys mawii* Gray, 1847 (Testudines, Dermatemydidae) (Reynoso et al., 2016; SEMARNAT, 2014).

The Central American river turtle, *D. mawii*, is an important species for conservation; it is the last representative species of the Dermatemydidae family and is endemic to Mesoamerica with a distribution from the southeast of Mexico to Belize and Guatemala (Vogth et al., 2011). Wild populations of *D. mawii* have been hunted and illegally trafficked, and their habitat has become so fragmented that the population of this species has suffered a significant decrease in population over the last few decades (SEMARNAT, 2014; Calderón-Mandunajo et al., 2017; Jennings et al, 2020). Therefore, this turtle species is considered among the 25 most threatened species of turtles in the world (Turtle Conservation Coalition, 2018). It is classified as "critically endangered" by the IUCN Red List, included in Appendix II of CITES, and is classified as "Threatened" in Mexico by the Norma Oficial Mexicana (SEMARNAT, 2010; Macip-Ríos et al., 2015). Furthermore, *D. mawii* is an important freshwater turtle for sustainable use as it is used as a pet and represents an important natural economic resource for captive breeders

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(principally for food, musical instruments, and craftwork). The species has played a historical role in culture and gastronomy since Mayan times (Guevara-Chumacero et al., 2016; Sharpe et al., 2020).

In Mexico, the sustainable use of species listed in CITES is allowed under permit SEMARNAT-08-009 (Government of Mexico, 2023), which is based on articles 53, 54, and 55 of the General Wildlife Law (Diario Oficial de la Federación, 2016) and articles 59, 60, 62, 64, and 65 of the Regulation of the General Wildlife Law (Diario Oficial de la Federación, 2006). Therefore, earnest efforts have been made to develop the appropriate protocol for their reproduction in UMAs, of 94 Mexican UMAs that manage freshwater turtles, 37 are dedicated to reproducing *D. mawii*, of which 17 are in the Tabasco state. These UMAs have been able to successfully reproduce *D. mawii* in captivity.

The principal aims of the UMAs devoted to the captive breeding of *D. mawii* have been to protect this turtle from over-exploitation and reinforce its wild populations (Pineda-Vázquez et al., 2019). UMAs in Mexico are authorized only for native species and, technical assistance and infrastructure are implemented for their development; technicians are trained, the acquisition of a breeding colony is facilitated, and scientific studies on the species are supported (Avila-Foucat & Pérez-Campuzano, 2015). However, these UMAs have experienced several problems, related predominantly to operational and administrative management (García-Garduño et al., 2017). A significant drawback in the majority of UMAs is the lack of a genetic management plan for captive breeding. Furthermore, in most cases, there is no information on the geographical origin of specimens, and therefore UMAs disregard genetic diversity and relationships among their founding breeders. There is only one study of UMAs dedicated to the captive breeding of *D. mawii.* The authors reported an observed difference in heterozygosity between UMAs; they also demonstrated a higher genetic diversity than wild populations (Gallardo-Alvarez et al., 2019). This lack of genetic information in breeding programs could result in inbreeding or outbreeding depression when different UMAs exchange or donate individuals to increase the number of breeding individuals (Williams & Osentoski, 2007; Zarza et al., 2016). These problems can have an important impact on the success of the UMAs; inbreeding depression can affect various life-history traits, such as fertilization, embryo survival, offspring survival, and total lifetime reproductive success (Farquharson et al., 2021). Moreover, although the mechanisms by which outbreeding depression reduces fitness are poorly understood, it is thought that it may increase the susceptibility of hybrid individuals and populations to infectious diseases (Goldberg et al., 2005; Rollison et al., 2014). We can reasonably expect that the lack of genetic studies in UMAs at the time of their establishment is due to the limited and onerous use of molecular tools; the consideration of genetic information in captive management programs is relatively recent and requires technical and financial support that is not always available in Mexico (Torres-Florez et al., 2018).

The development of a genetic management plan for the UMAs of *D. mawii* is fundamental to comply with reintroduction protocols established by the IUCN/SSC (IUCN/SSC, 2014), which indicate that reintroduced individuals must provide adequate genetic diversity and that captive individuals should originate from populations with appropriate demographic, genetic, behavioral, welfare and health management. Given that *D. mawii* has small and isolated wild populations (Briggs-Gonzalez et al., 2019), it is vital that when reintroduced into the wild, captive-bred individuals enrich and maintain the genetic diversity of natural populations, therefore increasing their adaptability and resilience to environmental and climatic changes (Refsnider & Janzen, 2016).

Considering the importance of genetic information within management plans in Mexican UMAs of *D. mawii*, we propose for the first time to establish a genetic management plan for the founder population of three UMAs located in the southeast of Mexico. More specifically, our goals were to: (1) To determine the homozygosity level in the founder populations, (2) to determine the kinship relationship among founders for each UMA, and (3) to propose breeding groups for the purposes of conservation, research, and sustainable use. Finally, our results will be discussed within the larger context of conservation and species management throughout the geographic range of this species.

Methods

Wildlife Management Units (UMAs)

Skin samples were collected from founders from three UMAs dedicated to the reproduction of *D. mawii* in the state of Tabasco, Mexico (Figure 1): **1)** "La Encantada" (LE) located in the town of Jalpa de Méndez (18°20'09"N-93°02'53"W; N = 67), the founders individuals for this UMA originated from the wild in Tabasco and some were donated by the Tabasco State Government UMA, **2)** Tabasco State Government UMA (TSG) located in the town of Nacajuca (18°11'23"N-92°59'37"W; N = 28), their founder individuals originated from a river near the border of Chiapas and Guatemala, and **3)** Tabasco State Juarez University UMA (TSJU) located in the city of Villahermosa (17°59'26"N-92°58'16"W; N = 22), their founders originate from TSG and wild individuals but of unknown origin. Samples were obtained using a permit SGPA/DGVS/011,085/16 provided by Mexico´s federal environmental agency (SERMARNAT). Characteristics of UMAs can be found by Gallardo-Alvarez et al. (2019). All founder individuals had a straight-line carapace length of ≥ 38 cm, so were of reproductive age and possibly older than 10 years (Bishop et al., 2021).

We note that UMAs selected for this study have achieved their aims of reproduction, environmental

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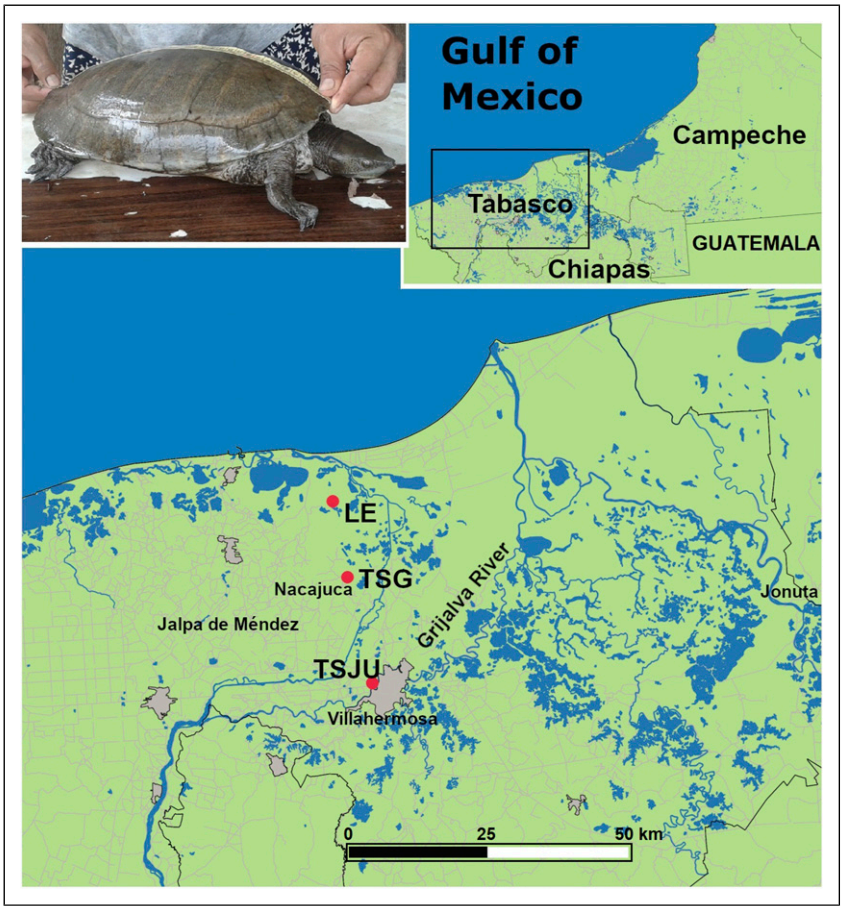

Figure 1. Study area showing UMAs of *Dermatemys mawii* located in the southern Gulf of Mexico. Color points represent the UMA location. Photos credits: Lesher-Gordillo J.M., Zenteno-Ruiz C.E, Gallardo-Alvarez M.I.

education, and research, but to date, no *D. mawii* individuals have been translocated for population restoration. The specific aims of UMAs are included in Article 39 of Mexico´s General Wildlife Law (Diario Oficial de la Federación, 2016).

Sample collection

Skin samples were collected in 2017 by cutting 1 cm of tissue from the interdigital membrane of the legs. Prior to taking samples, the cutting skin area was disinfected with 70% alcohol and methylthioninium chloride as an antiseptic. Founders were identified using the numerical marking assigned in each UMA and captured using a trammel net. After sample collection, all individuals were subject to observation for a period of 2 hours and subsequently, released to their respective ponds. Skin samples were preserved in a salt-saturated solution (250 mM EDTA pH 7.5 and 20% DMSO) and stored at -80°C until DNA extraction (González-Porter et al., 2011). The procedures for capturing individuals, sampling, transporting, and ethical procedures in this study were those recommended by the guide for the management of amphibians and living reptiles of the American Society of Ichthyologists and Herpetologists (American Society of Ichthyologists and Herpetologists, 2004), and by the management plan for *Dermatemys* (SEMARNAT, 2014).

DNA extraction and microsatellite genotyping

DNA was extracted with the Qiagen DNeasy Tissue kit (Qiagen Inc., Valencia, CA). DNA quality and concentration were verified using a UV-Vis spectrophotometer (Thermo ScientificTM NanoDropTM One). We used ten species-specific *D. mawii* microsatellites loci for genotyping all founder individuals; seven of these loci were previously developed (Andree et al., 2010) and used in research on *D. mawii* (González-Porter et al., 2013); three microsatellite primers pairs (Dm4A-11, Dm3A-43, and Dm3A-61) were designs for our previous research (Gallardo-Alvarez et al., 2019), and using the sequences of *D. mawii* reported in GenBank (González-Porter et al., unpublished). Detailed laboratory procedures and microsatellite information are described by Gallardo-Alvarez et al. (2019).

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Data analyses

Kinship analysis. The pedigree relationships between founder individuals pooled across UMAs were evaluated using the ML-RELATE program (Kalinowski et al., 2007) which calculates by default the strongest possible relationships (highest likelihood). For each pair of individuals, the following kinship relationships were determined: unrelated (U), half-siblings (HS), full-siblings (FS), and parent-offspring (PO). Each relationship category is assigned based on a test (statistical test and simulations) that determines which relations are consistent with the data (confidence set option: 0.05 level of significance and 1000 simulations) (Kalinowski et al., 2007). Simultaneously, ML-RELATE provides a list of several possible relationships (the putative relationship corresponding to the highest likelihood, and the alternatives) therefore, we used the likelihood ratio test (1000 simulations; specific hypotheses test option) proposed by ML-RELATE to obtain *P* values and evaluate the likelihoods of the possible relationships originally suggested. If *P* was small ($P < 0.05$) the alternative hypothesis was rejected, and the strongest relationship (as indicated by the highest likelihood) was accepted. If the *P* value was large ($P > 0.05$), this indicated that putative and alternative relationships were equally consistent with the data, so the weakest relationship was selected (U < HS < FS < PO) (Kalinowski et al., 2007). Furthermore, we calculated homozygosity by loci (*HL*) using the STORM PROGRAM (Frasier, 2008). The homozygosity index weighs the contribution of each locus depending on their allelic variability with values that range from 0 (all loci are heterozygous) to 1 (all loci are homozygous) (Aparicio et al., 2006).

Formation of breeder groups. Three important considerations have been included while developing the genetic management plan for *D. mawii* in Mexican UMAs: 1) Each UMAs within its facilities have all its founder individuals in the same ponds without considering the pedigree relationships that may exist between them. 2) translocation between UMAs is possible, depending on the level of relationship among individuals, and 3) implementation of the polyandry mating system favors the occurrence of multiple paternity (Fantin et al., 2018). The design of our genetic management plan was based on the level of kinship between males and females; unfortunately, UMAs have no studbook to optimize pair formation for reproduction. The level of homozygosity of the reproducing individuals was considered, because maintaining a high level of heterozygosity between founders is important to ensure sufficient genetic variation. (Williams & Osentoski, 2007). With this information, we propose the formation of three breeder groups to meet several specific purposes. (1) breeder group for conservation; this group aimed to conserve, reintroduce, and share individuals with other UMA. For this group, we selected only males and females with an unrelated kinship relationship (U), and individuals that present a low value of homozygosity (*HL* index ≤ 0.4), (2) breeder group for scientific research; the objective of this group was to maintain genetically valuable individuals with the possibility of transfer to the "conservation breeder group", or translocation to other UMAs to enrich genetic diversity, and to produce individuals for scientific purposes. In this breeder group, we selected males and females with unrelated (U) or half-sibling (HS) kinship relationships and with an *HL* index ≤ 0.6 and finally, (3) breeder group for sustainable uses with an economic purpose, including producing individuals for pets or traditional gastronomy, among others (Pineda-Vázquez et al., 2019). In this group, we included all other individuals. The limit of the *HL* index value proposed for the breeder group for conservation (0.4) is based on reference values reported in wild populations (Agudo et al., 2012; García-Navas et al., 2014).

Genetic diversity retention. Three different methods of evaluating the retention of genetic diversity were explored. **(1)** The following parameters were calculated for each breeding group: the number of alleles (*NA*), the number of effective alleles (*NE*), the observed heterozygosity (H_o), the expected heterozygosity (H_e), and the inbreeding coefficient (*F*) using GENALEX 6.502 (Peakall & Smouse, 2006). **(2)** The offspring genotypes (F1) were simulated for each breeding group with HYBRIDLAB version 1.0 (Nielsen et al., 2006); the program first estimates allele frequencies at each locus in each of the parental populations, and subsequently the multilocus F1 genotypes are created through simulated random mating, as a function of their calculated frequency distributions, taking one allele at each locus from each of the parental populations. Linkage equilibrium, the neutrality of markers, and random mating are assumed (Nielsen et al., 2006). The genetic diversity of each F1 group was estimated with the values of H_o, H_e, and *F* using GENALEX 6.502 (Peakall & Smouse, 2006). **(3)** The offspring genotypes (F1) of each of the breeding groups were determined using Vortex 10.5.5 (Lacy & Pollak, 2021). The program allows population and habitat viability (PHVA) to simulate and project changes in genetic diversity over time (Frankham et al., 2017). We used demographic data from a previous PHVA for *D. mawii* under *ex-situ* management (Zenteno-Ruiz et al., 2016) (Table S1) and the genotypes and allelic frequencies of the ten loci from each proposed breeding group. Each simulation was projected at one year with 1000 iterations, and genetic diversity was calculated through the minimum, maximum, and mean values of the H_e and *F* index for each F1 group.

Genetic diversity projection. We performed two simulations of the long-term genetic diversity of the conservation breeder group using Vortex 10.5.5. For simulations, we used demographic data from Table S1 as well as the genotypes and allele frequencies of the conservation breeder group. The first simulation was established and run through 150 years with 1000 iterations, and the conservation breeder group was considered

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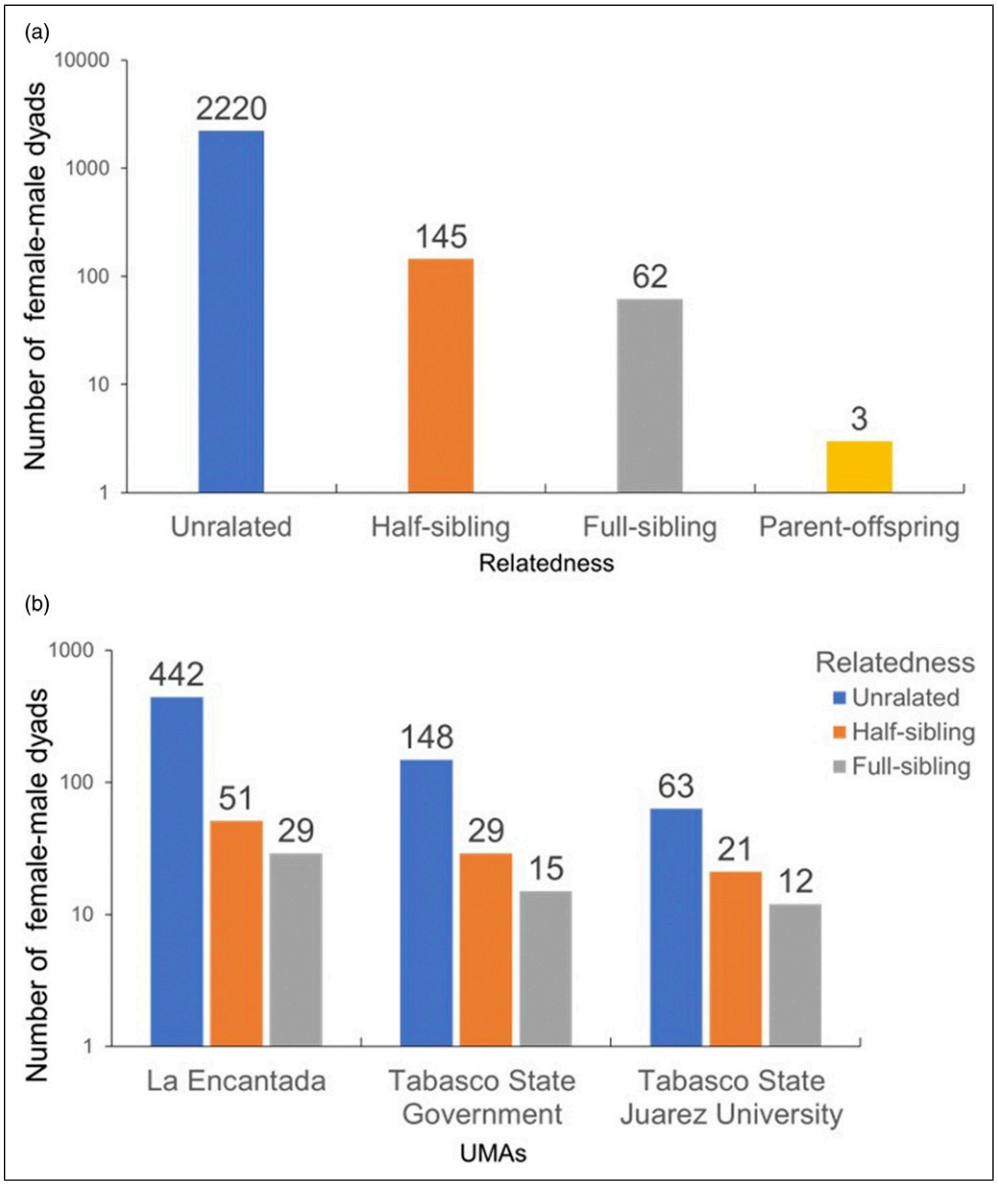

Figure 2. Total number of female-male dyads for different levels of relatedness for *Dermatemys mawii* from three UMAs in southeast Mexico.

without supplementation where the only demographic rates are birth and death (closed population). In the second simulation, the conservation breeder group was considered with supplementation, between which movement of individuals is demographically significant (open population) (Hixon et al., 2002). Therefore, we include a theoretical wildlife population with an initial size of 100 individuals and indicated that this population would be supplemented by the conservation breeder group with 20 individuals aged between 5 and 6 years (10 females and 10 males) every three years. Additionally, we simulated the supplementation of individuals from the conservation breeder group to the theoretical wildlife population with 10 individuals aged 5 to 6 years (5 females and 5 males) every three years. This simulation was set to 150 years with 1000 iterations.

Results

A total of 117 founder individuals' genotypes were analyzed from the three UMAs (90 females and 27 males, sex ratio 1: 0.3). UMA LE has a total of 58 females and 9 males (sex ratio = 1:0.15), UMA TSG has a total of 16 females and 12 males (sex ratio =1: 0.75) and UMA TSJU has a total of 16 female and 6 males (sex ratio =1:0.375).

Kinship analysis

A total of 2,430 female-male dyads were obtained from all genotypes analyzed, and the mean *HL* index value was 0.46 (min: 0 and max: 1). Kinship analysis indicated that 2,220

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Table 1. Selection of *Dermatemys Mawii* Individuals to Constitute Breeding Groups for UMAs in Southeast Mexico.

			Male																											
	ID UMA		[b]No ID	[c]205	[c]207	[c]149	[b]No ID	[b]No ID	[c]158	[b]No ID	[c]204	[c]28	[b]111	[b]115	[b]116	[b]118	[b]119	[b]124	133	[b]134	[b]137	[b]139	[b]7001	[b]141	[a]101	[b]PROFEPA	23	108	10
	UMA		LE	LE	LE	LE	LE	LE	LE	LE	LE	TSG	TSG	TSG	TSG	TSG	TSG	TSG	TSG	TSG	TSG	TSG	TSG	TSJ	TSJ	TSJ	TSJ	TSJ	TSJ
	ID UMA	UMA	*HL*	0,58	0,42	**0,31**	0,47	**0,20**	**0,20**	0,52	**0,30**	**0,28**	0,57	0,55	0,49	0,49	**0,38**	0,56	0,58	0,68	0,48	0,50	0,57	0,43	0,44	**0,20**	0,48	1,00	0,73	0,78
	[b]145	LE	0,41	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]170	LE	0,42	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]164	LE	0,42	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]269	LE	**0,24**	U	FS	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]193	LE	**0,32**	U	HS	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]6	LE	**0,37**	HS	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]254	LE	0,44	HS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]5	LE	0,55	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]154	LE	0,42	HS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]4	LE	**0,38**	HS	HS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[c]185	LE	**0,28**	FS	U	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[c]171	LE	**0,34**	HS	FS	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]152	LE	**0,24**	HS	HS	FS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]181	LE	0,42	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]No ID	LE	0,49	U	U	U	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]No ID	LE	**0,36**	U	U	U	HS	HS	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]No ID	LE	**0,38**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U
	[a]201	LE	**0,38**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U
	[a]No ID	LE	**0,38**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]176	LE	0,42	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]244	LE	0,41	U	U	U	U	U	HS	U	HS	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]172	LE	0,41	U	U	U	U	FS	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U
	[b]179	LE	0,76	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]3	LE	**0,13**	U	U	U	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]219	LE	0,52	U	U	U	U	HS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]197	LE	**0,39**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]266	LE	**0,32**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]No ID	LE	**0,31**	U	U	HS	FS	HS	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]No ID	LE	**0,23**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]203	LE	**0,31**	U	U	U	U	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]189	LE	0,46	U	U	U	U	U	FS	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]153	LE	0,41	U	U	U	U	U	U	U	HS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]253	LE	**0,39**	U	U	U	U	HS	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]No ID	LE	0,41	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U
	[b]237	LE	0,42	U	U	U	U	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	HS	U	U	U	U
	[b]208	LE	0,48	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]264	LE	**0,36**	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]183	LE	0,41	U	U	U	U	U	U	U	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]160	LE	**0,38**	U	U	U	U	U	FS	HS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]232	LE	0,58	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U
	[b]222	LE	**0,33**	U	U	U	U	U	FS	HS	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[a]No ID	LE	**0,34**	U	U	U	U	U	HS	U	HS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]241	LE	**0,37**	U	U	U	U	U	U	HS	FS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]191	LE	**0,28**	U	U	U	U	U	FS	U	FS	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]174	LE	**0,35**	U	U	U	U	U	FS	HS	HS	HS	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U
	[b]203	LE	**0,25**	U	U	U	U	U	FS	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U
	[b]212	LE	0,42	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U
	[a]262	LE	**0,22**	U	U	U	U	U	U	U	FS	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U
	[a]156	LE	**0,37**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	FS	U	U	U	U	U	U	HS
	[a]No ID	LE	**0,37**	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U
	[c]170	LE	**0,11**	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U
	[a]No ID	LE	**0,26**	U	U	U	U	U	U	U	FS	U	U	U	U	U	U	U	U	HS	U	PO	U	U	U	U	U	U	U	U
	[a]No ID	LE	0,55	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	HS	U	HS	U	U	U	U	U	U	U	U
	[c]206	LE	**0,00**	U	HS	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	PO	U	U	U	U	U	U	U	U
	[b]157	LE	**0,28**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]164	LE	**0,18**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	FS	U	U	U	PO	U	U	U	U
	[b]175	LE	**0,22**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	HS	U	U	U
	[a]221	LE	**0,38**	U	U	U	U	U	U	HS	U	U	U	U	HS	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[c]24	TSG	0,57	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[c]42	TSG	0,41	U	U	U	U	U	U	U	U	U	HS	HS	U	HS	FS	FS	U	U	HS	U	U	U	U	U	U	U	U	U
	[a]100	TSG	**0,34**	U	U	U	U	U	U	U	U	U	HS	U	HS	HS	U	U	U	U	U	U	HS	HS	U	U	U	U	U	U
	[c]105	TSG	0,55	U	U	U	U	U	U	U	U	U	U	FS	U	U	U	U	FS	U	U	U	U	U	U	U	U	U	U	U
	[c]112	TSG	0,59	U	U	U	U	U	U	U	U	U	U	FS	U	HS	U	HS	FS	U	U	U	U	U	U	U	U	U	U	U
	[c]120	TSG	0,42	U	U	U	U	U	U	HS	U	U	U	FS	U	HS	HS	FS	FS	U	U	U	U	U	U	U	U	U	U	U
	[c]122	TSG	0,85	U	U	U	U	U	U	U	U	U	HS	FS	FS	HS	HS	U	HS	U	U	U	U	U	U	U	U	U	U	U
	[c]123	TSG	0,51	U	U	U	U	U	U	U	U	U	U	FS	U	HS	U	HS	HS	U	HS	U	U	U	U	U	HS	U	U	U
	[c]125	TSG	0,56	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	FS	U	U	U	U	U	U	HS	U	HS	U	U
	[c]129	TSG	0,73	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	HS	U	U	U	U	U	U	U	U	U	U	U	U
	[c]130	TSG	0,67	FS	U	U	U	U	U	U	U	U	HS	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U
	[c]131	TSG	1,00	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U
	[a]132	TSG	**0,37**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U
	136	TSG	0,46	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	FS	FS	U	U	U	U	U	U	U	U	U	U
	[b]138	TSG	0,52	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
	[b]140	TSG	0,51	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	HS	U	U	HS	U	HS	U	HS
	[c]15	TSJ	0,54	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	FS	HS	U	U	U	U	U	U
	[b]7	TSJ	**0,32**	U	U	U	HS	FS	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	HS	U	U	U	U	U
	[b]103	TSJ	**0,32**	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	HS	HS	U	U	U	U	HS	U	U	U	U	U
	[b]52	TSJ	0,48	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	HS	HS	U	U	U	U
	[a]4	TSJ	**0,36**	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	FS	HS	FS	U	U	U
	[b]PROFEPA	TSJ	0,62	U	U	U	U	U	U	U	U	U	FS	U	U	HS	HS	U	U	HS	U	U	HS	U	U	U	U	U	U	U
	[c]100	TSJ	0,76	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	U	U	U	U	U	U	U	FS	HS	
	[c]1	TSJ	0,87	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	HS	U	U	U	U	HS	FS	U	FS		
	[b]13	TSJ	0,51	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	FS	HS	HS		
	[c]31	TSJ	1,00	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	FS	HS	HS		
	[b]107	TSJ	0,85	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U		
	[c]110	TSJ	0,86	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	FS	U		
	[c]114	TSJ	0,63	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	FS	HS		
	[c]128	TSJ	0,76	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	FS	FS	U		
	[c]131	TSJ	0,85	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	U	U	U	U	U	U	FS	HS	U		
	[c]143	TSJ	0,71	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	HS	HS	HS		

female-male pairs were unrelated (Figure 2). Three female-male pairs have a PO relationship when all UMAs were considered. All pedigree relationships between female-male pairs and *HL* index values are presented in Table 1.

A detailed analysis per UMA shows that the UMA LE has a total of 522 female-male pairs (58 females and nine males). Their pedigree relationships are the following: 442 U (85% of dyads), 51 HS (10% of dyads), and 29 FS (5% of dyads). The *HL* index values range from 0.00 to 0.76 with a mean value of 0.365. The UMA TSG has a total of 192 female-male pairs (16 females and 12 males). Their pedigree relationships are the following, 148 U (77% of dyads), 29 HS (15% of dyads), and 15 FS (8% of dyads). The *HL* index values range from 0.34 to 1 with a mean value of 0.547. Finally, the UMA TSJU has a total of 96 female-male pairs (16 females and six males). Their pedigree relationships are the following, 63 U (66% of dyads), 21 HS (22% of dyads), and 12 FS (12% of dyads). The *HL* index values range from 0.44 to 1 with a mean value of 0.639.

Selection of candidate breeders

Selection of candidate breeders for conservation. To ensure the high genetic diversity of the offspring and to limit the negative effects of captive breeding, we selected males with an *HL* index < 0.4 and females that were unrelated (*U*) to these males and with an *HL* index < 0.4. A total of seven males were considered (five from LE, one from TSG, and one from TSJU) and 16 females (14 from LE and two from TSG) (individuals highlighted with the superscript "a" in Table 1).

Selection of candidate breeders for research. We selected all males with *HL* index values from 0.43 to 0.6, resulting in a total of 16 males (four from LE, 10 from TSG, and two from TSJU). Subsequently, we considered all females with an *HL* index < 0.6 and with a *U* or *HS* relationship with those males. We selected a total of 45 females (36 from LE, three from TSG, and six from TSJU) (individuals highlighted with the superscript "b" in Table 1).

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Table 2. Genetic Diversity of Three Selected Breeder Groups and F1 Genotype Simulated Groups of *Dermatemys Mawii* from Three UMAs of Tabasco, Mexico.

Type groups	Use	# Individuals	N	Na	Ne	Ho	He	F
Selected breeder groups	Conservation breeder group	23	19.500	6.8	4.996	0.596	0.768	0.252
	Research breeder group	61	49.500	8.0	5.229	0.491	0.782	0.383
	Sustainable breeder group	33	24.500	6.6	3.790	0.312	0.696	0.563
HYBRIDLAB F1 groups	Conservation offspring group	100	100.000	6.8	4.860	0.838	0.769	−0.089
	Research offspring group	100	100.000	7.8	4.822	0.798	0.772	−0.033
	Sustainable offspring group	100	100.000	6.6	3.120	0.730	0.639	−0.153
Vortex simulation F1 groups	Conservation offspring group	99.19	—	6.3187	—	—	0.738	0.232
	Research offspring group	99.87	—	7.5847	—	—	0.768	0.218
	Sustainable offspring group	99.75	—	6.0316	—	—	0.667	0.304

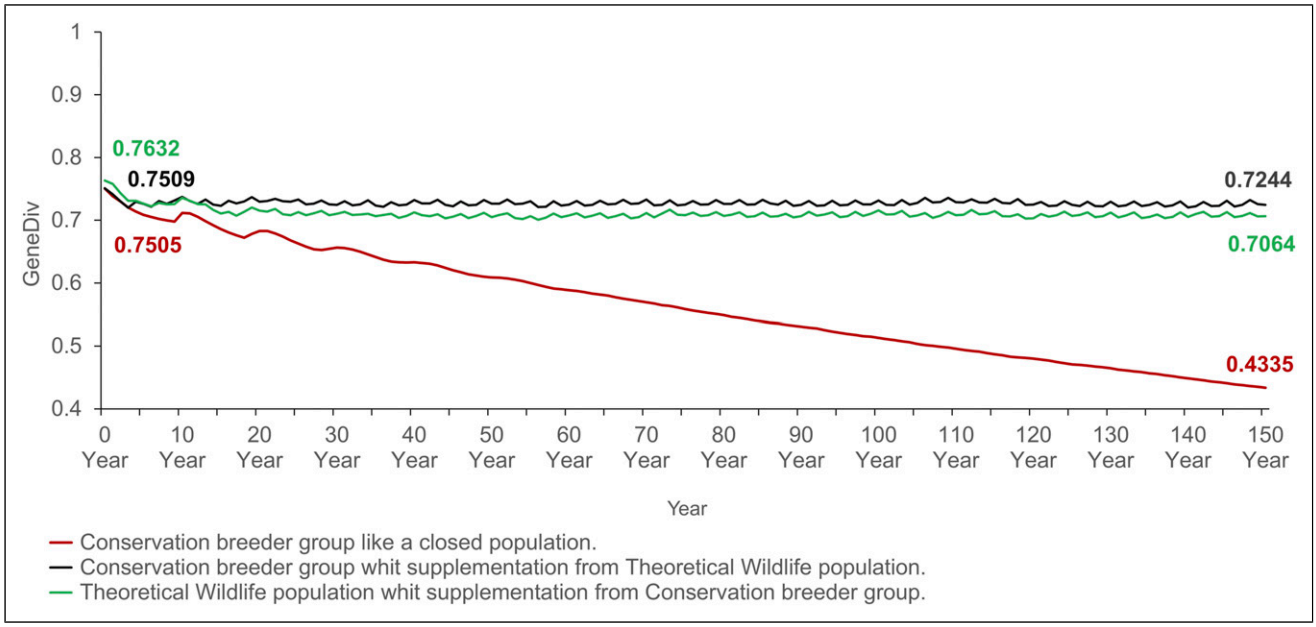

Figure 3. Projected long-term genetic diversity of the conservation breeder group of *Dermatemys mawii.*

Selection of candidate breeders for sustainable uses. This group mainly consists of individuals from the TSG and TSJU UMAs which comprised of individuals with the highest degree of homozygosity. In this group, we proposed four males (one from TSG and three from TSJU) and 29 females (eight from LE, 11 from TSG, and 10 from TSJU) (individuals highlighted with the superscript "c" in Table 1).

Genetic diversity retention. In general, genetic diversity values (H_o, H_e) were highest for the conservation breeder group and research breeder group (Table 2). Results indicated that the conservation breeder group presented the highest H_o value (0.596) and lowest F value (0.252), while the sustainable breeder group had the lowest H_o value (0.312) and highest F value (0.523). The highest H_e value (0.782) was observed in the research breeder group. For F1 simulated genotypes, the conservation breeder group projected F1s had the highest H_o value (0.828) and lowest F value (-0.089), while the projected F1s of the research breeder group presented the highest H_e value (0.772). Finally, genetic diversity from Vortex simulations at one year indicated that the F1 research breeder group had the highest H_e value (0.738) and the lowest F value (0.218).

Genetic diversity projection. The projected long-term genetic diversity in the conservation breeder group decreased to 42% when simulated as a closed population. However, when the conservation breeder group was simulated as an open population, results indicated that genetic diversity was largely stable, decreasing by only 3.5% (Figure 3).

Discussion

Captive breeding programs that are informed by population genetic analyses are recommended for endangered species as they permit the determination of kinship relationships and

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establishment of sound genetic management for the maintenance of genetic diversity (IUCN/SSC, 2014; Mahood et al., 2021) to obtain demographically self-sufficient and genetically healthy populations (Ivy & Lacy, 2012). An important aspect of captivity is the use of unrelated breeding pairs to minimize the risk of inbreeding (Ivy & Lacy, 2010; Miller et al., 2010). In Mexico, this conservation strategy is followed at Wildlife Management Units (Zenteno-Ruiz et al., 2021). Our research determines the kinship relationships in *D. mawii* which is required for the genetic management of captive populations, a new approach for UMA conservation in Mexico. Different captive breeding programs for endangered species of reptiles have used this strategy, including the loggerhead sea turtle (*Caretta caretta*, Linnaeus, 1758; Sakaoka et al., 2012), the Siamese and saltwater crocodiles (*Crocodylus siamensis*, Schneider, 1801 and *C. porosus*, Schneider, 1801; Lapbenjakul et al., 2017), and the Galapagos giant tortoise (*Chelonoidis spp.*; Miller et al., 2018).

The captive reproduction of freshwater turtles has been implemented for commercial purposes (pet or human consumption) and to recover populations of endangered species as demonstrated in the following examples: (1) the red-eared slider (*Trachemys scripta elegans*, Wied-Neuwied, 1839) is reproduced exclusively for commercial purposes (Mali et al., 2015), (2) the Asian giant softshell turtle (*Pelochelys cantorii*, Gray, 1864) is managed in captivity, then released into the wild where populations are monitored (Xiaoyou et al., 2019), and (3) the critically endangered turtle *B. baska* was managed to recover wild populations in Bangladesh´s Bhawal National Park (Weissenbacher et al., 2015). However, few captive reproduction programs for freshwater turtles have contemplated genetic management which is critical for their success and the reintroduction of endangered species. The captive reproduction of *D. mawii* in UMAs of southeast Mexico has been successful (Vogt et al., 2011); however, genetic analysis to identify the kinship relationships of reproductive individuals has not been implemented and therefore the offspring have only been used for commercial purposes (Dirección General de Vida Silvestre & SEMARNAT, 2018). Here, we present the first study that considers genetic relationships to form breeding groups in UMAs.

Our results indicate that most individuals in the TSG and TSJU UMAs have *HL* values between 0.5 and 1, a moderate to low level of heterozygosity (Aparicio et al., 2006). The geographical origin of these individuals may explain these results. The owners of the TSG UMA mention that their founding colony probably originates from a single wild population close to Guatemala (Gallardo-Alvarez et al., 2019) increasing the risk of related individuals in founders, a hypothesis supported by our HS and FS relationship results that attain a value of 23%. This value is superior to the HS and FS relationship in the UMA LE (15%) which has a *HL* value of 0.365, suggesting a higher level of heterozygosity (Aparicio et al., 2006). These results suggest that the wild founding population was probably small which is to be expected considering that *D. mawii* is almost extirpated in Mexico and is exceedingly rare and difficult to capture (Vogt & Flores-Villela, 1992). For example, in the Rio Escondido catchment basin, southern Quintana Roo, Calderón-Mandujano et al. (2017) captured 52 *D. mawii* individuals (a mean of 1.74 turtles caught per net) from February 2009 to August 2010 and recorded a low recapture rate during their field samplings (three individuals). In the northeastern part of the Pantanos de Centla Biosphere Reserve (RBPC, Tabasco), (eight nets and 384 hours of catches per net) very few turtles were captured; a mean of 0.312 and 0.041 turtles caught per net for the Tabasquillo and the Grijalva Rivers respectively during the dry season, and a mean of 0.500, 0.083, and 0.041 turtles caught per net in the Tabasquillo, the Grijalva, and the Usumacinta Rivers respectively during the rainy season (Zenteno-Ruiz et al., 2010). In addition, the kinship relationships observed for the founder individuals in the TSG UMA could reflect the social behavior generally present in freshwater turtles. *Dermatemys mawii* shows nest-site fidelity and, over a period of several years juvenile individuals move over a smaller area than adults (Rowe et al., 2005; Sheridan et al., 2010). For example, it has been reported that the European pond turtle (*Emys orbicularis*, Linnaeus, 1758) can remain in the same distribution area for an extended period (31 years) (Escoriza et al., 2020). Similarly, in a population of Eastern Box Turtles (*Terrapene carolina carolina,* Linnaeus, 1758), several captured individuals demonstrated a high level of relationship (Moore et al., 2020). Therefore, our results in the TSG UMA suggest that founder individuals came from a small population of highly related individuals and therefore, the founding colony in this UMA presents a high proportion of HS and FS relationships.

The translocation of individuals between UMAs could have a significant impact on our results. The TSG UMA was the first in Mexico to breed *D. mawii*, and its offspring have served as the foundation batch for other UMAs such as TSJU and LE. Almost all the founder individuals from TSJU originate from TSG which presents a high proportion of FS or HS relationships due to individuals sharing the same parents. Our results show that the HS and FS relationships in the TSJU UMA were both 34%, higher than in the TSG and LE UMAs. Furthermore, the owners of the LE UMA comment that their founding colony not only originates from TSG UMA individuals but also from wild individuals which could explain the lower level of related individuals in this UMA and the fact that most individuals have a small *HL* value signifying a higher level of heterozygosity (Aparicio et al., 2006). The identification of these valuable individuals is crucial for genetic management because they could constitute the breeder group for conservation and maximize reproductive success in captivity. It has been shown that individuals with higher heterozygosity, in relation to those of the same sex, have greater fitness (Brown, 1997; Garcia-Navas et al., 2009) and that females use diverse strategies when selecting males (good genes, genetic compatibility, and lower relatedness)

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which could increase offspring genetic diversity and reduce deleterious recessive allele expression (Zajitschek et al., 2009; Cutrera et al., 2012; Pilakouta & Smiseth, 2017; Fan et al., 2021), important aspects for successful captive breeding conditions. In this context, our simulation suggested that the genetic diversity of F1 populations is increased. A previous study to maximize the genetic diversity of a captive breeding population on the Galapagos tortoise (*Chelonoidis becki*) showed through simulations that genetic diversity will be maximized when tortoises are organized into relatively small breeding groups (Quinzin et al., 2019).

The number of founder individuals is a key factor for the success of any breeding program (Miller et al., 2010; Willoughby et al., 2017), and it has been proposed that an initial number of more than 20 founder individuals would normally ensure that captivity programs preserve 90% of the original genetic diversity for 200 years (Soulé et al., 1986). In addition, the genetic diversity of the founding individuals should be high to avoid negative genetic consequences on captive breeding (e.g., genetic diversity loss, inbreeding, among others) that may result in lower survival success, higher risk of extinction, decrease in population growth, diminished fitness, and reduced potential for evolution and response to environmental change (Willoughby et al., 2014; Thorstensen et al., 2019). Increasing the wild-type genetic contributions to captive breeding programs is one solution to these problems, as it may improve the survival in the wild of captive-bred offspring (Sahashi & Morita, 2022).

Some successful turtle captive breeding programs started with few individuals as is the case of the Hood Island giant tortoise (*Chelonoidis hoodensis,* Van Denburgh, 1907), which started with 15 individuals (in Miller et al., 2018), or *Batagur baska* (Gray, 1830) which began with 20 individuals (Weissenbacher et al., 2015). These studies, among others, have shown that a conservation captive breeding program for threatened freshwater turtles can be initiated with a small colony and can be successful in hatchling production and reintroduction into the wild. This consideration supports the size of our captive breeding group of *D. mawii*, composed of 23 individuals. Although the conservation breeder group is small, it presents high genetic diversity, and the simulated F1 population indicated that genetic diversity can be retained. We propose the genetic management of the species, based on the kinship relationship between the founding individuals to maximize the genetic variability of the population, as other authors have previously suggested (Lacy, 1994).

There are several other examples of captive conservation initiatives for *D. mawii*. For example, the Hicatee Conservation and Research Center (HCRC; http://hicatee.org/hcrc/), in Belize, embarked on a project to recover populations of *D. mawii*, commencing with 22 individuals in 2014. One year later, their first offspring was born, and currently, their founding colony is made up of 45 individuals (Briggs-Gonzalez et al., 2019). Although the HCRC project did not follow a genetic approach, founder individuals were collected from a range of locations that represented a broad genetic diversity (González-Porter et al., 2013) (Marlin A. Jacob, executive director of Belize Foundation for Research and Environmental Education, *personal communications*). In Guatemala, there is no documented information on *D. mawii*, however, it is estimated that over 4,000 turtles exist in the lowland Maya Biosphere Reserve in Guatemala (García-Anleu et al., 2007). Finally, in Mexico, the conservation of *D. mawii* is conducted in UMAs that promote the sustainable use of this freshwater turtle (Zenteno-Ruíz et al., 2019). However, *D. mawii* UMAs have been created without genetic considerations, hence our study contributes to conservation actions for *D. mawii* and demonstrates the utility of a molecular approach in the captive program of freshwater turtles. This approach could be followed to enrich the captive management program already established in UMAs.

In the UMAs, where the present research was carried out, we recommend the creation of three new breeding groups, each with different goals: 1) species conservation, 2) species research, and 3) sustainable use of species. This proposal is based on the following arguments: (a) This strategy can decrease the expression of recessive deleterious alleles and the possibility of inbreeding due to the presence of less related individuals for reproduction, principally in conservation and research groups; (b) a genetic rescue (GR) is promoted, which is defined as an increase in population fitness (growth) due to the immigration of new alleles (Ingvarsson, 2001). For management and conservation, GR is especially useful because it restores genetic diversity and increases fitness in small populations that generally suffer from the inbreeding effect (Whiteley et al., 2015). Different programs have demonstrated the importance of GR in captivity or for reintroduction projects (Hasselgren et al., 2021; Hedrick & Fredrickson, 2010) supporting the need to promote GR in UMAs. Our F1 populations, simulated for each of the three proposed, showed that genetic diversity increased; therefore, this result could support our recommendation; (c) support the UMA administration to define their specific goals. In Mexico, the UMA management plan proposes combining conservation and sustainable use goals at the same time. In Tabasco, turtle UMAs have different degrees of development and different levels of operational and productive consolidation (Zenteno-Ruiz et al., 2021), thus, our proposal could help define more specific goals according to interests (commercial, conservation, or both); (d) due to limitations at UMA facilities, only one breeding group could be hosted at each site. (e) In addition, we believe that cooperation between the three UMAs could be advantageous. Therefore, it is essential UMAs organize themselves to promote the exchange of reproducers.

In Mexico, genetic management plans for endangered species are crucial. *Dermatemys mawii* has been bred in captivity for conservation and sustainable purposes, however, some breeding sites are owned by communities or private companies that prioritize breeding for commercial purposes. These sites frequently obtain a high number of individuals without considering their genetic relationship or the

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geographical origin of the founding colony. In contrast, sites that breed the species for conservation purposes have obtained their founding colony through the capture of wild individuals or donations from other Wildlife Management Units, without paying sufficient attention to the genetic integrity or phylogeography of these individuals. The lack of concern for these aspects may be due to a lack of awareness of the importance of genetics in the conservation of endangered species. Additionally, in Mexico and Mesoamerica, it is difficult to obtain funding to apply molecular techniques in the development of genetic management plans for endangered species, as these techniques are expensive and represent a challenge for institutions responsible for the conservation of captive wildlife. Ongoing research on the genetic structure and diversity of *D. mawii* populations throughout their natural distribution range is essential. It has been determined that *D. mawii* has at least three lineages made up of 16 haplotypes; the first lineage is located between Belize and Guatemala, the second is in the Papaloapan River, and the third includes a larger distribution encompassing the Grijalva-Usumacinta basin, between Mexico, Belize, and Guatemala (González-Porter et al., 2011). According to the available information, the founder individuals in our study come from wild populations of the states of Chiapas and Tabasco (Gallardo-Alvarez et al., 2019), thus, belonging to the third lineage. Expanding genetic information for *D. mawii* will help make more informed decisions when capturing wild individuals to enrich the genetic pool of UMAs dedicated to turtle conservation. Additionally, suitable sites for releasing individuals could be identified, reducing the risk of potential outbreed issues.

The LE UMA's primary goal is production to obtain economic benefits, and therefore we suggest establishing links with the corresponding market to promote the commercialization of products obtained from the turtles while complying with legal requirements. As the legal sale under government supervision of *D. mawii* individuals bred in UMAs has been proposed (CCA, 2017; article 39, LGSV), the important issue of laundering wild individuals as captive-bred needs to be urgently addressed. The registry of the legal commercialization of individuals born in the UMAs could be used to help prevent such problems (Zenteno-Ruiz et al. 2021). However, because this proposal could indirectly promote the laundering of wild individuals as captive-bred, we suggest that the following be considered:

1) Compliance with Articles 40 and 78bis of the General Wildlife Law and Article 103 of the Wildlife Regulation of Mexico and reporting requirements (Articles 42 and 43 of the LGVS), including a description of the marking system (specimens, parts, and derivatives), periodic reporting on activities, and random inspections to detect inconsistencies in inventories or reports.
2) Promote environmental education by experts to raise awareness of environmental ethics against the illegal trafficking and trade of species (Almanza, 2008).
3) Encourage more effective and ethical communication between UMAs and inspectors from the Federal Attorney for Environmental Protection of Mexico (Procuraduría Federal de Protección al Ambiente, PROFEPA).
4) Increase the training and the number of PROFEPA inspectors to ensure effective enforcement of laws and regulations (Salazar & Domínguez, 2023).

Finally, considering our results, we suggest the following actions: (1) exchange or donation of females with a high level of genetic diversity from LE UMA to the TSG and TSJU UMAs, and that the 37 females identified for sustainable purposes are located in the LE UMA; (2) the TSG UMA should receive the 32 individuals to form a research group and should exchange males with the TSJU UMA to balance the sex ratio; (3) since the main aim of the TSJU UMA is conservation, it is the best equipped to manage the conservation breeding group as it has the facilities and scientists that specialize in freshwater chelonians. This UMA must work collaboratively with TSG UMA to obtain other allelic combinations from the research breeding group; (4) According to our long-term simulation, new individuals must be periodically integrated into breeding groups (at least every 3 years) to ensure that genetic diversity remains stable.

Implications for Conservation

Our study proposes, for the first time, a genetic management plan for the captive breeding of *D. mawii* in Mexico. This pioneering plan for UMAs establishes three reproductive groups with specific objectives: a conservation group, a research group, and a sustainable farming group. This genetic management strategy will improve the reproduction of the species, avoiding inbreeding problems and the fixation of deleterious alleles in the captive colonies. Our proposal to create three breeding groups with defined objectives will enrich conservation actions and the sustainable use of *D. mawii* at national and international levels. Furthermore, for optimum protection and management of *D. mawii*, the creation of a conservation program for this species in Mexico is required comprehensive *in-situ/ex-situ* management under the IUCN guidelines (IUCN/SSC, 2014). There are numerous natural sites in Mexico where *D. mawii* can still be found, many of them close to UMAs; thus, our proposed genetic management strategy will serve as a guideline for future research involving the genetic analysis of wild populations of *D. mawii*. This research will improve decision-making processes regarding reintroduction and enrichment programs between UMAs and wild sites still inhabited by *D. mawii*. In addition, subsequent genetic monitoring of individuals would provide a measure of the success of the reintroduction project. Other countries, such as Guatemala and Belize, may show interest in combining efforts to undertake regional conservation actions. Therefore, our work may also serve to strengthen the conservation efforts of the species within the

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Mesoamerican biological corridor (CONABIO, 2009; Zenteno-Ruiz et al., 2016).

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Data Availability Statement

Knowledge Network for Biocomplexity site, with identifier doi:10.5063/F1X065HW, (Gallardo, 2021) contains the R-values data file. The datasets analyzed for this study are available from the corresponding author upon reasonable request.

Supplemental Material

Supplemental material for this article is available online.

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