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Prevalence of polygyny in a critically endangered marine turtle population

Alexander R. Gaos[a,b,c,*], Rebecca L. Lewison[d], Michael J. Liles[c,e,f], Ana Henriquez[c,f], Sofía Chavarría[c,f], Ingrid L. Yañez[c], Kelly Stewart[g], Amy Frey[h], T. Todd Jones[i], Peter H. Dutton[h]

[a] Joint Institute for Marine and Atmospheric Research, Pacific Islands Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Marine Turtle Biology and Assessment Program, Honolulu, HI 96818, USA
[b] Ocean Associates Inc, under contract to the Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Marine Mammal and Turtle Division, La Jolla, CA 92037, USA
[c] Eastern Pacific Hawksbill Initiative, San Diego, CA 92117, USA
[d] San Diego State University – USA, Biology, San Diego, CA 92182, USA
[e] University of Texas at El Paso, Biology, El Paso, TX 79968, USA
[f] ProCosta, San Salvador, San Salvador, El Salvador
[g] The Ocean Foundation, Washington, DC 20036, USA
[h] Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration – USA, Marine Mammal and Turtle Division, La Jolla, CA 92037, USA
[i] Pacific Islands Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration - USA, Marine Turtle Biology and Assessment Program, Honolulu, HI 96818, USA

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ABSTRACT

Genetic analyses of nuclear DNA (e.g., microsatellites) are a primary tool for investigating mating systems in reptiles, particularly marine turtles. Whereas studies over the past two decades have demonstrated that polyandry (i.e., females mating with multiple males) is common in marine turtles, polygyny (i.e., males mating with multiple females) has rarely been reported. In this study we investigated the mating structure of Critically Endangered hawksbill turtles (*Eretmochelys imbricata*) at Bahía de Jiquilisco in El Salvador, one of the largest rookeries in the eastern Pacific Ocean. We collected genetic samples from 34 nesting females and hatchlings from 41 clutches during the 2015 nesting season, including one nest from each of 27 females and two nests from seven additional females. Using six highly polymorphic microsatellite loci, we reconstructed the paternal genotypes for 22 known male turtles and discovered that seven (31.8%) sired nests from multiple females, which represents the highest polygyny level reported to date for marine turtles and suggests that this is a common mating structure for this population. We also detected multiple paternity in four (11.8%) clutches from the 34 females analyzed, confirming polyandrous mating strategies are also employed. The high level of polygyny we documented suggests there may be a limited number of sexually mature males at Bahía de Jiquilisco; a scenario supported by multiple lines of empirical evidence. Our findings highlight key management uncertainties, including whether polygynous mating strategies can compensate for potential ongoing feminization and the low number of adult males found for this and possibly other marine turtle populations.

1. Introduction

Mating strategies are life history features under selective pressure to maximize reproductive success (Uller and Olsson, 2008). These strategies vary within and among species according to numerous biotic and abiotic influences (Bollmer et al., 1999; Pearse and Avise, 2001). Marine turtles are reptiles that present particular challenges for mating system research as they are wide-ranging and spend the majority of their lives at sea. Although direct observations of mating can lend insights into mating behavior, direct approaches provide limited information on fertilization levels (versus strictly mating) and paternity.

During the past two decades, nuclear (n) DNA markers (e.g., microsatellites) have emerged as a primary tool to understand mating systems in marine turtles (Fitzsimmons, 1996; Hoekert et al., 2002; Zbinden et al., 2007; Jensen et al., 2013; Phillips et al., 2013). These studies have demonstrated that polyandry, or females mating with

* Corresponding author.
E-mail addresses: alexander.gaos@noaa.gov (A.R. Gaos), rlewison@mail.sdsu.edu (R.L. Lewison), mliles@gmail.com (M.J. Liles), hepoc5@yahoo.com (A. Henriquez), schavarria@hawksbill.org (S. Chavarría), ingrid@hawksbill.org (I.L. Yañez), Kelly.Stewart@noaa.gov (K. Stewart), Amy.Frey@noaa.gov (A. Frey), todd.jones@noaa.gov (T.T. Jones), Peter.Dutton@noaa.gov (P.H. Dutton).

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Table 1
Available genetic studies of hawksbill mating structure. MP = Multiple Paternity.

Author	Ocean region	Location	Nesting females	Clutches analyzed	Hatchlings per clutch	Males Identified	# loci used	MP levels	Polygyny levels
Joseph and Shaw, 2011	South China Sea	Gulisaan, Malaysia	10	12	14–40	12	5	20.0%	0%
Phillips et al., 2013	West Indian Ocean	Cousin Island, Seychelles	43	85	20	47	32	9.3%	0%
Phillips et al., 2014a, 2014b	West Indian Ocean	Cousin Island, Seychelles	128	249	3–20	91	32	9.3%	0%
González-Garza et al., 2015	Caribbean Sea	Yucatan Peninsula, Mexico (various rookeries)	41	50 (2–16)	25	45	12	6.0%	0%
Natoli et al., 2017	Arabian/Persian Gulf	United Arab Emirates (Various rookeries)	53[a]	68 (5–40)	1–5	74–80	33	0–67%	0–15%
Gaos et al. this study	East Pacific Ocean	Bahia de Jiquilisco, El Salvador	34	41	15–20	22	6	14.7%	31.8%

[a] Maternal genotypes were not used in study.

multiple males (i.e., as evidenced via multiple paternity of clutches), is a common mating strategy employed by the taxon (Theissinger et al., 2009; Stewart and Dutton, 2011; Wright et al., 2012; Lasala et al., 2018). This strategy may confer selective advantages, such as fertility assurance, heightened offspring viability, and increased genetic diversity (Chapman et al., 2009; Phillips et al., 2017). In contrast, polygyny, or males mating with multiple females, has rarely been reported for marine turtles (but see Crim et al., 2002; Stewart and Dutton, 2014; Natoli et al., 2017), despite the existence of > 30 studies that have assayed > 1000 maternal families (see Tedeschi et al., 2015; Lee et al., 2018).

Hawksbill turtles (*Eretmochelys imbricata*) are a highly threatened marine turtle species that inhabit tropical and subtropical regions of the world's oceans. Previous genetic research of hawksbill mating systems in different ocean regions (Table 1) has found varying levels of polyandry and differences in mating strategies, highlighting variation among hawksbill populations. Hawksbills within the regional management unit (RMU, sensu Wallace et al., 2011) of the eastern Pacific Ocean are considered some of the world's most endangered and least resilient populations (Fuentes et al., 2013), with < 700 reproductively active females estimated to remain in the region (Gaos et al., 2017a). One of the two primary rookeries in this RMU is located at Bahía de Jiquilisco, El Salvador, where a research and nest conservation program has operated since 2008 (Liles et al., 2011, 2015). Recent genetic research has indicated that hawksbills nesting at this site represent a distinct management unit (MU sensu Moritz, 1994) that is strongly differentiated from other rookeries in the region, including a nearby rookery located only 115 km to the south (F_{ST} = 0.3706, P < .001; Gaos et al., 2016, 2018). Nesting beach monitoring efforts at Bahía de Jiquilisco have identified < 200 individual females to date (Gaos et al., 2017a), highlighting the need for acute conservation attention.

Despite the depleted status of hawksbills at Bahía de Jiquilisco and across the eastern Pacific, genetic research on hawksbill mating strategies and male population status in the region is lacking. Understanding male marine turtle populations and their mating strategies in particular, is likely to be increasingly important with the projected rise in global temperatures and the potential for feminization of many marine turtle populations (Hawkes et al., 2009; Eckert et al., 2012; Pike, 2014; Jensen et al., 2018). In an effort to fill current data gaps, we used nDNA microsatellite markers to evaluate mating systems in hawksbills nesting at Bahía de Jiquilisco. More specifically, we sought to assess levels of polygamy for both males and females, gain insights into the number of breeding males during the 2015 nesting season, and estimate a single-season breeding sex ratio (i.e., proportion of males and females that successfully mate; Stewart and Dutton, 2014) for the population.

2. Materials and methods

2.1. Study site and sample collection

This study used tissue samples collected in 2015 from nesting female hawksbills and their offspring (i.e., hatchlings) within the Bahía de Jiquilisco Biosphere Reserve (6°33′ N, 80°02′ E), a large mangrove-lined estuary in eastern El Salvador (Fig. 1). Bahía de Jiquilisco represents one of the two largest hawksbill rookeries in the eastern Pacific Ocean, hosting an average of 168.5 (± 46.7) nests per season and accounting for 24.4% of annual nesting by the species in the region (Gaos et al., 2017a). Because nest poaching is virtually 100% without protection efforts (Liles et al., 2014), the ongoing conservation activities include relocating most nests to a protective hatchery (Liles et al., 2015).

We applied Inconel flipper tags (National Band & Tag, Newport, KY, USA) and Passive Integrated Transponder (PIT; Avid, Norco, CA, USA) tags to all female turtles encountered to confirm and track identity throughout the nesting season. Using sterile techniques, we took a skin