The Eurasia Proceedings of Science, Technology, Engineering & Mathematics (EPSTEM)
ISSN: 2602-3199

The Eurasia Proceedings of Science, Technology, Engineering & Mathematics (EPSTEM), 2019

Volume 8, Pages 12-19

ICVALS 2019: International Conference on Veterinary, Agriculture and Life Science

Do the Female Sea Turtles Benefit from Multiple Paternity? A Review of the Frequencies of Multiple Paternity Across Sea Turtle Rookeries

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Abstract: Sea turtles are promiscuous breeders. Since it is very difficult to observe individuals of a marine species while mating and usually impossible to determine the successful mating, molecular studies provide a tool to make an inference about mating system of this species. Recent molecular studies on sea turtle mating systems have demonstrated that polyandry is much more common than polygyny in sea turtles. It is well known that multiple paternity (MP) is evident in all sea turtle populations with polyandrous mating system. Determination of frequency of MP is of great importance for understanding of mating system and population structure of endangered populations and contributes to the conservation efforts. The frequency of MP shows great inter- and intra-specific variability. But why does this frequency vary greatly within and among species? Why does a female sea turtle mate multiple times within a season? Do the females benefit from MP? To elucidate these questions, here I review the frequency of MP for sea turtles nesting around the world. Based on data for several rookeries throughout the world, there were significant differences in the frequency of MP among species ($p < 0.01$). The frequency of MP was statistically correlated to neither clutch size (eggs) nor female size (curved carapace length [CCL]) ($p > 0.05$). However, there was a moderate positive correlation between the frequency of MP and hatching success (defined as the rate of hatchlings emerging successfully from the eggs) ($r^2 = 0.45$, $p < 0.05$). These findings suggest that MP, contrary to common belief, does not work in favour of larger females and does not result in increased clutch size, but hatching success increases with the increasing frequency of MP. It can be concluded from these evaluations that MP in sea turtle may have at least some benefits: increased genetic diversity and heightened offspring viability and variability.

Keywords: Sea turtle, Multiple paternity, Female size, Clutch size, Hatching success

Introduction

Mating System of a Species

Determination of a species' mating system is a crucial component of understanding natural history of that species (Bjorndal et al., 1983). Mating system is particularly substantial within small populations, since it may influence genetically effective size of population and evolution of the species (Arden & Kapuscinski, 2002; Charlesworth, 2009). Accurately estimating population size, population structure, and reproductive behaviour is of great importance to improve current conservation priorities and make effective management decisions on endangered species. In populations whose mating system is polyandrous, multiple paternity influences the effective population size (Sugg & Chesser, 1994) and the genetic variability within the population (Baer & Schmid-Hempel, 1999). Small population size and a skewed ratio of males to females available for mating at a nesting season may decrease genetic variation and adaptation ability to new environmental changes (Montgomery et al., 2000).

Sea Turtles

There are seven species of sea turtles living in the oceans: green turtle, *Chelonia mydas* (Linnaeus, 1758); loggerhead, *Caretta caretta* (Linnaeus, 1758); leatherback, *Dermochelys coriacea* (Vandelli, 1761); Kemp's ridley, *Lepidochelys kempii* (Garman, 1880); olive ridley, *Lepidochelys olivacea* (Eschscholtz, 1829); hawksbill, *Eretmochelys imbricata* (Linnaeus, 1766); and flatback, *Natator depressus* (Garman, 1880). They have been living for more than 100 million years (Hirayama, 1998), but they are under protection all around the world (Hamann et al., 2010). Today, sea turtles face numerous threats in each of their life stages (Spotila et al., 2000), which are caused by both natural and anthropogenic factors. Some of the natural factors influencing sea turtles are climate change, predation by domestic animals, erosive waves, and flooding (Wetterer & Lombard, 2010; Witt et al., 2010). Since sea turtles possess temperature-dependent sex determination (Bull, 1980; Wibbels et al., 2000), climate change is a unique threat to them; increases in temperature can result in extreme sex ratio biases (i.e., Mitchell & Janzen 2010). On the other hand, egg harvesting and turtle hunting (Kamezaki & Matsui, 1997), marine captures in fishery regions (Peckham et al. 2007), habitat degradation by coastal buildings (Kamezaki et al., 2003), and various types of pollution (Lewison & Crowder, 2007) are included to anthropogenic factors. Interactions of these and this kind of threats have caused a dramatic decline in sea turtle populations worldwide (Wyneken et al., 1988; Scherer-Lorenzen & Coomes, 2014), and that is why sea turtles are under protection. However, long-term monitoring and conservation projects have recently started to give the results in terms of population sizes (see Casale, 2015; Casale & Tucker, 2015).

Multiple Paternity in Sea Turtles

Sea turtles are promiscuous breeders, and both males and females may mate with multiple mates (FitzSimmons, 1998; Hamann et al., 2003). However, male sea turtles do not emerge on the beach and are difficult to observe at sea, the number of males contributing to a population is difficult to characterize. In addition, it is very difficult to observe individuals of sea turtles during the mating and generally impossible to determine the successful mating. Therefore, molecular studies provide an informative tool to make an inference about mating strategies of sea turtles. Recent molecular studies on sea turtle mating systems have demonstrated that in sea turtles, polyandry, which is described as mating of females with multiple males, is much more common than polygyny, which is described as mating of males with multiple females.

In sea turtle species, multiple paternity studies have been carried out over last several decades (i.e., Jensen et al., 2006; Theissinger et al., 2009; Figgener et al., 2016). These studies provide precious information regarding mating patterns and enable the researchers to understand population structure. The frequency of multiple mating is critical for understanding of the evolution of the mating systems and for the conservation of endangered populations (Kichler et al., 1999; Moore & Ball, 2002). It is well known that multiple paternity is evident in all polyandrous sea turtle populations (Sari et al., 2017).

Variations in the Frequency of Multiple Paternity Among Sea Turtle Species and Rookeries

It is believed that the frequency of multiple paternity shows great inter- and intra-specific variability. But why does this frequency vary greatly among and within species? To be able to answer this question, I conducted a literature search and reviewed the studies estimating the frequency of multiple paternity in sea turtle rookeries (described as breeding sites). Following this search, summary of the obtained data belonging to several multiple paternity studies on sea turtle species and rookeries were obtained (Table 1).

Table 1. Summary data of several multiple paternity studies on sea turtle species

Locality	Clutches analysed	Nesting females	Frequency of multiple paternity (%)	Marker	Study year	Reference
Green turtle, *Chelonia mydas*						
Ascension Island	18	18	61.0	Micro	1999-2000	Lee & Hays, 2004
Ascension Island	3	3	100.0	Micro	1999	Ireland et al., 2003
Tortuguero, Costa Rica	12	-	92.0	Micro	2007	Alfaro-Núñez et al., 2015
Kosgoda, Sri Lanka	24	19	47.0	Micro	2005-2006	Ekanayake et al., 2013
Melbourne Beach, Florida, U.S.A.	28	28	85.7	Micro	2011-2012	Long, 2013
Southern Great Barrier Reef, Australia	22	13	9.1	Micro	1991-1993	Fitzsimmons, 1998
Michoacán, Mexico	16	10	75.0	Micro	1998-2000	Chassin-Noria et al., 2017
Alagadi Beach, Cyprus	94	78	24.4	Micro	2008-2010	Wright et al., 2012
Cousine Island, Seychelles	9	3	0.0	Micro	2007-2008	Phillips et al., 2017
Alagadi Beach, Cyprus	94	78	24.4	Micro	2008-2010	Wright et al., 2013
Akyatan Beach, Turkey	22	22	59.0	Micro	2009	Turkozan et al., 2019
Loggerhead, *Caretta caretta*						
Zakynthos, Greece	20	15	93.3	Micro	2003-2004	Zbinden et al., 2007
Dalyan Beach, Turkey	25	10	70.0	Micro	2014	Sari et al., 2017
Wassaw Island, Georgia, U.S.A.	72	72	75.0	Micro	2008-2010	Lasala, 2011; Lasala et al., 2013
Mon Repos Beach, Queensland, Australia	29	29	65.5	Micro	2011-2012	Howe et al., 2017

Mon Repos Beach, Queensland, Australia	24	45	33.0	Allo	1982-1983	Harry & Briscoe, 1988
Melbourne Beach, Florida, U.S.A.	3	3	33.0	Micro	1994	Bollmer et al., 1999
Melbourne Beach, Florida, U.S.A.	70	70	31.4	Micro	1996	Moore & Ball, 2002
Dirk Hartog, Australia	14	NA	35.7	Micro	2013	Tedeschi et al., 2015
Bungelup, Australia	4	NA	25.0	Micro	2013	Tedeschi et al., 2015
Gnaraloo, Australia	7	NA	85.7	Micro	2011	Tedeschi et al., 2015
Gulf of Mexico, Florida, U.S.A.	51	51	70.0	Micro	2013-2015	Lasala et al., 2018
The Port of Nagoya Public Aquarium, Japan*	7	4	42.9	Micro	2000-2002	Sakaoka et al., 2011
The Port of Nagoya Public Aquarium, Japan*	11	4	27.3	Micro	2001-2003	Sakaoka et al., 2013
Hawksbill, *Eretmochelys imbricata*						
Bahía de Jiquilisco, El Salvador	41	34	11.8	Micro	2015	Gaos et al., 2018
Gulisaan, Malaysia	12	10	20.0	Micro	2004	Joseph & Shaw, 2011
Cousine Island, Seychelles	85	43	9.3	Micro	2007-2008	Phillips et al., 2013
Xicalango-Victoria, Campeche, Mexico	2	2	0.0	Micro	2011	González-Garza et al., 2015
Chenkan, Campeche, Mexico	16	10	0.0	Micro	2011	González-Garza et al., 2015
Celestun, Yucatan, Mexico	9	9	11.1	Micro	2011	González-Garza et al., 2015
El Cuyo, Yucatan, Mexico	4	4	0.0	Micro	2011	González-Garza et al., 2015
Las Coloradas, Yucatan, Mexico	12	10	8.3	Micro	2011	González-Garza et al., 2015
Holbox, Quintana Roo, Mexico	7	6	14.3	Micro	2011	González-Garza et al., 2015
Leatherback, *Dermochelys coriacea*						
Playa Grande, Costa Rica	50	20	10.0	Micro	1998-1999	Crim et al., 2002
Playa Gandoca, Costa Rica	35	18	22.2	Micro	2008	Figgener et al., 2016
St. Croix, U.S. Virgin Islands	38	12	41.7	Micro	2009	Stewart & Dutton, 2011
St. Croix, U.S. Virgin Islands	55	55	23.6	Micro	2010	Stewart & Dutton, 2014
Olive ridley, *Lepidochelys olivacea*						
Suriname	10	10	20.0	Micro	1995	Hoekert et al., 2002
Playa Hermosa, Costa Rica	13	13	30.8	Micro	2003	Jensen et al., 2006
Ostional, Costa Rica	13	13	92.3	Micro	2003	Jensen et al., 2006
Honduras	8	8	75.0	Micro	2012-2013	Duran et al., 2015
Kemp's ridley, *Lepidochelys kempii*						
Tamaulipas, Mexico	35	26	57.7	Micro	NA	Kichler et al., 1999
Flatback, *Natator depressus*						
Mon Repos Beach, Queensland, Australia	16	9	68.8	Micro	2004-2005	Theissinger et al., 2009

Micro refers to microsatellites and allo refers to allozymes.
* indicates that the study was carried out on captive sea turtles.
NA indicates missing data.

The frequency of multiple paternity varied greatly from 0% up to 100% among rookeries (Figure 1). After analysing these data, it was found that there were marked and significant differences in the frequency of multiple paternity among species (ANOVA, $F_{6,\ 36} = 4.06$, $p < 0.01$). For instance, hawksbill turtles had a significantly lower frequency of multiple paternity (8.3%) than both loggerhead turtles (52.9%) (t-test, $T = 6.27$, $df = 14$, $p > 0.001$) and green turtles (52.5%) (t-test, $T = 4.16$, $df = 11$, $p > 0.01$). Similarly, leatherback turtles had a significantly lower frequency of multiple paternity (24.4%) than both loggerhead turtles (t-test, $T = 3.04$, $df = 9$, $p > 0.05$) and green turtles (t-test, $T = 2.30$, $df = 12$, $p > 0.05$). Whereas the frequency of multiple paternity was uniform at hawksbill and leatherback turtle rookeries, it was more variable in other species. The great inter- and intra-specific variation in the frequency of multiple paternity detected in this study may be resulted from the differences in incidence of male-female encounters, population sizes, ratios of males to females available for mating at a nesting season, or breeding grounds or be considered as a consequence of the combination of these factors.

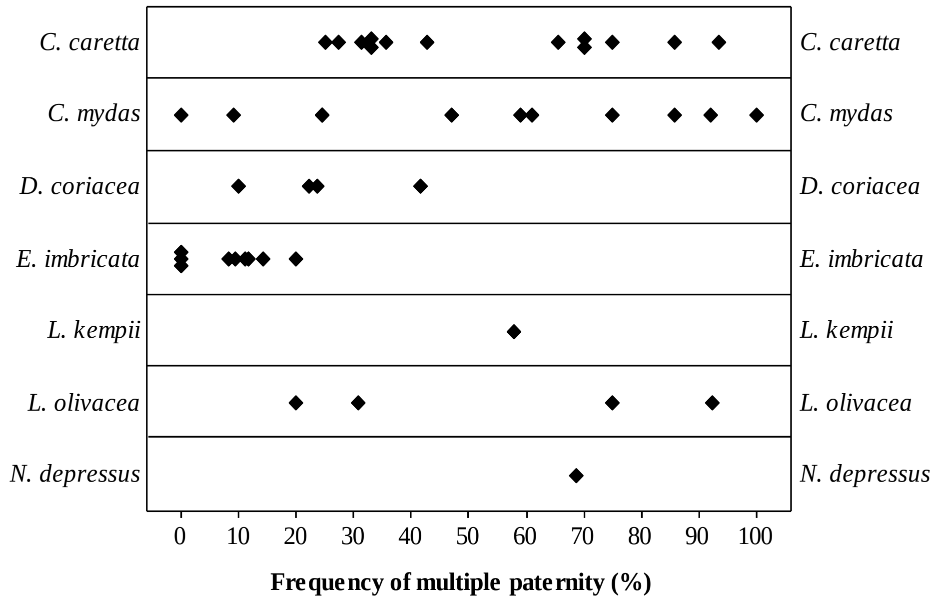

Figure 1. Variation in the frequency of multiple paternity in sea turtles.

Female Size vs Frequency of Multiple Paternity in Sea Turtles

Does the size of female sea turtles affect the frequency of multiple paternity? Is there a relationship between them? To explore this relationship (if there is), the results of the studies on multiple paternity involving female size data (curved carapace length [CCL]) (Table 2) were statistically analysed. It was found that the frequency of multiple paternity was not correlated to female size (Pearson correlation, $p > 0.05$). This finding implies that male sea turtles do not prefer the larger and hence older females, and larger female sea turtles do not prefer to mate with multiple males and are not acceptive for more than one male.

Table 2. Mean values of assessed parameters for sea turtle species from reviewed multiple paternity studies

Species	**Frequency of multiple paternity (%)**	**Female size (cm)**	**Clutch size (eggs)**	**Hatching success (%)**	**Reference**
Chelonia mydas	61.0	114.6	117.8	82.0	Lee & Hays, 2004
	92.0	108.7	117.6	85.8	Alfaro-Núñez et al., 2015
	47.0	106.5	NA	NA	Ekanayake et al., 2013
	85.7	107.2	130.0	66.7	Long, 2013
	24.4	NA	109.8	NA	Wright et al., 2012
	0.0	109.7	90.8	62.9	Phillips et al., 2017
	24.0	NA	111.4	NA	Wright et al., 2013
Caretta caretta	93.3	84.6	121.2	79.1	Zbinden et al., 2007
	70.0	76.9	82.6	87.0	Sari et al., 2017
	75.0	98.6*	114.7	78.3	Lasala, 2011; Lasala et al., 2013
	65.5	95.9	126.4	NA	Howe et al., 2017
Lepidochelys olivacea	30.8	NA	100.8	52.1	Jensen et al., 2006
	92.3	NA	99.5	74.6	Jensen et al., 2006
	20.0	NA	117.9	62.6	Hoekert et al., 2002
Eretmochelys imbricata	11.8	NA	173.4	NA	Gaos et al., 2018
Natator depressus	68.8	NA	55.0	83.0	Theissinger et al., 2009

* indicates that the female size value is straight carapace length (SCL), while the remaining are curved carapace length (CCL).
NA indicates missing data.

Clutch Size vs Frequency of Multiple Paternity in Sea Turtles

It is believed that larger female sea turtles have larger pelvic opening structures compared with those of smaller ones, and this structure constrains egg size and hence offspring size. Since larger females can accumulate more resources and/or bigger eggs, because of their larger pelvic opening, they can therefore produce more eggs (Wilbur & Morin, 1988). Therefore, the relationship between clutch size and frequency of multiple paternity reported by the reviewed studies (Table 2) was statistically analysed. Accordingly, no statistical correlation was found between them (Pearson correlation, $p > 0.05$).

Frequency of Multiple Paternity vs Hatching Success in Sea Turtles

Why does a female sea turtle mate multiple times within a season? Do the females benefit from multiple paternity? Increased offspring viability, offspring genetic diversity, fertilisation assurance, and procurement of compatible gametes are believed to be some of the benefits of multiple paternity (FitzSimmons, 1998; Uller & Olsson, 2008). It has been assumed by Sari et al. (2017) that one of the simplest ways to investigate viability of the offspring is to investigate hatching success (defined as the rate of hatchlings emerging successfully from the eggs). To see the relationship between frequency of multiple paternity and hatching success (if there is), data reported by the studies for these two parameters (Table 2) were statistically analysed. Accordingly, a moderate positive correlation between the frequency of multiple paternity and hatching success was detected (Pearson correlation, $r^2 = 0.45$, $p < 0.05$) (Figure 2). This finding suggests that multiple paternity results in increased hatching success and multiple paternity contributes to the persistence of the populations, since the hatchlings which are able to emerge from the eggs and then from the nests are strong enough to crawl on the sand and to swim in the ocean.

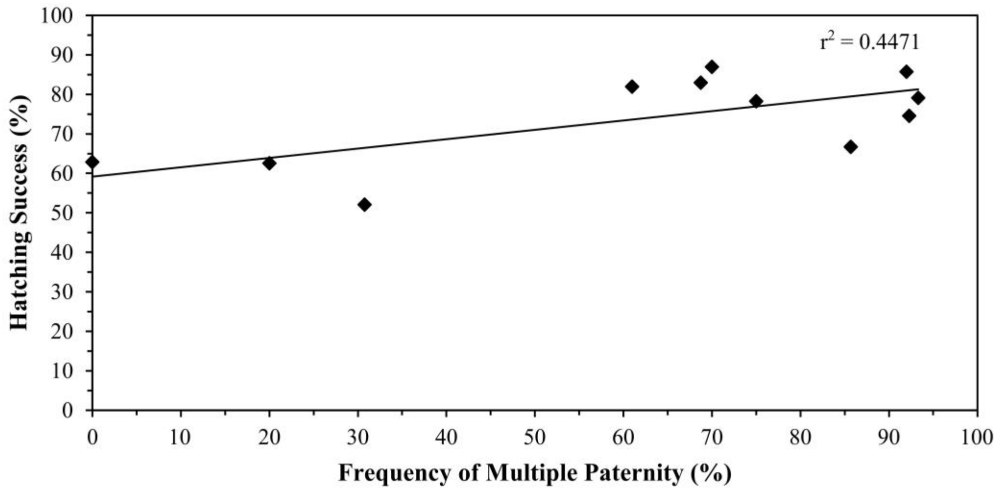

Figure 2. Relationship between frequency of multiple paternity and hatching success in sea turtles.

Conclusion

The frequency of multiple paternity varies greatly from 0% up to 100% among rookeries, and it shows marked and significant differences among species. It can be suggested that multiple paternity, contrary to common belief, does not work in favour of larger females and does not result in increased clutch size, but hatching success increases with the increasing frequency of multiple paternity. It can be concluded from these evaluations that multiple paternity in sea turtle may have at least some benefits: increased genetic diversity and heightened offspring viability and variability.

Recommendations

Multiple paternity studies have great importance, since they provide valuable and crucial information about reproductive behaviour of sea turtles. Multiple paternity levels of sea turtle populations should be taken into account for management and conservation strategies, since they influence effective population size and diversity. Genetic diversity plays a key role in the ability of the sea turtle species to adapt themselves to environmental alterations and their survival in the future.

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