

A Review of Patterns of Multiple Paternity Across Sea Turtle Rookeries

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Abstract

Why females would mate with multiple partners and have multiple fathers for clutches or litters is a long-standing enigma. There is a broad dichotomy in hypotheses ranging from polyandry having benefits to simply being an unavoidable consequence of a high incidence of male–female encounters. If females simply give in to mating when it is too costly to avoid being harassed by males (convenience polyandry), then there should be a higher rate of mating as density increases. However, if females actively seek males because they benefit from multiple mating, then mating frequency, and consequently the incidence of multiple paternity of clutches, should be high throughout. To explore these competing explanations, here we review the incidence of multiple paternity for sea turtles nesting around the World. Across 30 rookeries, including all 7 species of sea turtle, the incidence of multiple paternity was only weakly linked to rookery size ($r^2=0.14$). However, using high resolution at-sea GPS tracking we show that the specifics of movement patterns play a key role in driving packing density and hence the

likely rate of male–female encounters. When individuals use the same focal areas, packing density could be $100\times$ greater than when assuming individuals move independently. Once the extent of adult movements in the breeding season was considered so that movements and abundance could be combined to produce a measure of density, then across rookeries we found a very tight relationship ($r^2 = 0.96$) between packing density and the incidence of multiple paternity. These findings suggest that multiple paternity in sea turtles may have no benefit, but is simply a consequence of the incidence of male–female encounters.



1. BACKGROUND

While the evolution of male promiscuity holds no mysteries, why females would mate with more than one male to fertilise a clutch of eggs remains an outstanding question despite over a decade of empirical and theoretical study and review (for example, [Byrne and Roberts, 2012](#); [Jennions and Petrie, 2000](#); [Pearse and Avise, 2001](#); [Simmons, 2005](#); [Slatyer et al., 2012b](#); [Taylor et al., 2014](#); [Tregenza and Wedell, 2000](#); [Uller and Olsson, 2008](#)). There are many hypotheses for female multiple mating (polyandry), but it remains equivocal if there are female benefits of multiple mating or if multiple mating is simply a consequence of high male–female encounters. Additionally, male behaviour may influence the mating patterns of females by preventing access to females by other males ([Connor et al., 2001](#); [Olsson et al., 2005](#)) or by aggressive harassment of females ([Griffiths et al., 2012](#)). Whether females benefit from promiscuous behaviour has been frequently reviewed and empirically tested, both experimentally and in natural populations, and in a wide variety of animal models. The suggested benefits include fertilisation assurance ([Caspers et al., 2014](#); [Uller and Olsson, 2005](#)), genetic benefits ([Jennions and Petrie, 2000](#); [Olsson et al., 2011](#); [Slatyer et al., 2012b](#); [Zeh and Zeh, 2001](#)), inbreeding avoidance ([While et al., 2014](#)), postcopulatory sexual selection ([Adams et al., 2005](#); [Caspers et al., 2014](#); [Zeh and Zeh, 2008](#)), “hedge-betting” against infertility, genetic incompatibility or variable environments ([Garcia-Gonzalez et al., 2015](#); [Yasui and Garcia-Gonzalez, 2016](#)) and obtaining protection or resources from additional males ([Arnqvist and Nilsson, 2000](#); [Reichard et al., 2007](#); [Slatyer et al., 2012a](#)). In contrast, while the mate-encounter-rate hypothesis has been explored with theory ([Kokko and Mappes, 2013](#)), suggested as a logistical limit on polygamous mating ([Avise and Liu, 2011](#)), and invoked in cases for which there are no obvious benefits for

females (for example, [Byrne and Roberts, 2004](#); [Griffiths et al., 2012](#); [Uller and Olsson, 2008](#); [Zhao et al., 2016](#)), it has been little explored in natural populations.



2. SEA TURTLES AS A MODEL GROUP FOR EXPLORING PATTERNS OF MULTIPLE PATERNITY

To explore the mate-encounter-rate hypothesis in natural populations, sea turtles are a useful model group since there can be massive differences in rookery (breeding population) sizes (a few 10s to >100,000 nesting females) and, to date, there has been no evidence that females benefit from having multiple mates. For sea turtles, there are no direct benefits for having multiple mates because there is no parental care and no social bonds between the sexes ([Fig. 1](#)). No evidence for genetic (indirect) benefits has so far been detected ([Alfaro-Núñez et al., 2015](#); [Lee and Hays, 2004](#); [Wright et al., 2013](#)) with fitness indicators such as clutch size, hatching success or offspring quality being typically compared between single-fathered clutches and those with multiple fathers. However, it has also been argued that indirect benefits may only be easily detected in genetically impoverished and inbred populations ([Madsen, 2008](#)).



Fig. 1 In sea turtles, males and females congregate to mate close to nesting beaches. They can both mate with multiple partners. After the breeding season males travel to sometimes distant foraging grounds, while females lay multiple clutches of eggs ashore using stored sperm to fertilise clutches. (*Photo courtesy of Kostas Papafitsoros*).

There is an alternative approach to the problem. If females do indeed benefit from multiple mating, then it would be expected that females will actively search for males and so there ought to then be high incidences of multiple paternity across rookeries, so long as density was not a limiting factor. In contrast, if the incidence of multiple paternity was simply a consequence of male–female packing density, we would then expect the incidence of multiple paternity in a rookery to scale with the density of breeding males and females. Indeed [Jensen et al. \(2006\)](#) had shown a correlation between the incidence of multiple paternity and the size of the rookery as indicated by the number of nests or nesting females. However, subsequently some rookeries have been found not to fit with this relationship ([Lasala et al., 2013](#); [Zbinden et al., 2007](#)). We might expect that abundance will only loosely predict male–female encounters, since rookeries with low abundance might occupy very small areas and vice versa and so abundance alone is probably a poor proxy for adult density on the breeding grounds ([Lee, 2008](#)).

A further factor to consider is sex ratio. The density of animals on the breeding grounds will obviously influence the likelihood of individuals meeting. However, if the operational sex ratio is skewed, the actual mate–encounter–rate will be lower ([Kokko and Rankin, 2006](#)). Operational sex ratios are difficult to assess for sea turtles, but it is possible to estimate the hatchling sex ratio through analyses of nest temperatures ([Mrosovsky, 1994](#)), and these analyses have indicated the hatchling sex ratio of many rookeries are female skewed. However, the operational sex ratio is likely to be more balanced than indicated by hatchling sex ratios since males return to breeding areas more frequently than females ([Hays et al., 2010, 2014](#)). If the operational sex ratio is indeed relatively balanced at most rookeries, then this value cannot explain the variability in the incidence of multiple paternity. Instead, an improved indicator of adult density on the breeding grounds may be what is required.

As an extension to the mate–encounter–rate theory, we suggest that movement, which has not been previously considered, may be a further component in determining animal density on the breeding grounds. Here, we investigate two factors that are likely to influence mate encounter rate, and hence, female promiscuity: abundance (rookery size) and movement. First, we conduct the most extensive review to date for how rookery size is linked to female promiscuity among sea turtles. Second but most crucially, we hypothesise that the area occupied by individuals in the breeding season combined with rookery size may provide a far more realistic estimate of

packing density on the breeding grounds and hence, the incidence of multiple paternity. We test this hypothesis using published tracking data to assess the extent of individual movements in the breeding season. Finally, we objectively develop an index of packing density in the breeding season to compare against the incidence of multiple paternity.



3. THE INCIDENCE OF MULTIPLE PATERNITY VS SPECIES AND ROOKERY SIZE

We begin with a review of studies estimating the incidence of multiple paternity in sea turtle rookeries (breeding sites). Two independent literature searches were conducted (P.L.M.L. with R.I.H. and A.D.M.) using the search engines Web-of-Knowledge (WOK; <http://apps.webofknowledge.com/>), SCOPUS (<http://www.scopus.com/>) and Google Scholar (<http://scholar.google.com/>). Typical keywords used in searches were “polyandry”, “multiple paternity”, “parentage” and “turtle”. We considered conference reports, book chapters and student theses in addition to journal publications, but limited records to studies using molecular markers to estimate the incidence of multiple paternity. Initial searches were started in December 2014, and records continued to be monitored by setting up citation alerts. The references of records were also examined for further reports. The data search was terminated in February 2016.

We considered clutches from the same female in the same breeding season as a single sample. For studies that only reported the incidence of multiple paternity per clutch, we assumed each clutch had been laid by a different female. Studies with sample sizes less than five were excluded, as these were likely to provide the poorest estimates of the incidence of multiple paternity in a rookery. For rookeries with the incidence of multiple paternity estimated in different years, we reduced the data to a single estimate to avoid pseudoreplication. How this was achieved was decided on a case-by-case basis. Older studies were often constrained by low sample size, or used less informative molecular markers (e.g. DNA fingerprints); these were excluded in favour of the more recent study. Alternatively, if the estimates were conducted close in time, sample sizes were similar, and the rookery size did not vary by more than a magnitude, we combined the data as a single estimate.

The two independent literature searches overlapped by 76%, and together yielded reports of the incidence of multiple paternity for 40 sea turtle rookeries (Tables 1 and 2). While there will be studies that were not

Table 1 Incidences of Multiple Paternity (%), Rookery Sizes (Nest Count and the Number of Nesting Females), an Index of Offshore Movement (km) and Their Associated References

Location	Species	Incidence of Multiple Paternity (%)	Sample Size (N)	Year of Study	References	Nest Count (N)	Number of Nesting Females (N)	Variable Counted	Year of Abundance Estimate	References	Offshore Distance (km)	References
Mon Repos, near Bundaberg, Queensland (Australia)	Flatback	67	6	2004/5	Theissing et al. (2009)	90	30	Females	2004	Limpus et al. (2013)	NA	NA
Heron Island, Southern Great Barrier Reef (Australia)	Green	15	13	1991/2, 1993/4	Fitzsimmons (1998)	1641	547	Females	1991/2, 1993/4	Department of Environment and Heritage Protection (2013)	NA	NA
Ascension Island, South Atlantic (British Overseas Territory)	Green	61	18	1999, 2000	Ireland et al. (2003) , Lee and Hays (2004)	11,836	3945	Nests	1999, 2000	Weber et al. (2014)	2.5 ^c	Hays et al. (1999)
Tortuguero (Caribbean coast of Costa Rica)	Green	92	12	2007	Alfaro-Núñez et al. (2015)	177,290	59,097	Nests	2007	Prieto and Harrison (2012)	NA	NA
Alagadi Beach (northern Cyprus)	Green	24	78	2008, 2009, 2010	Wright et al. (2013)	88	30	Both	2008, 2009, 2010	Stokes et al. (2014)	NA	NA
Kosgoda (Sri Lanka)	Green	47	19	2005/6	Ekanayake et al. (2013)	400	133	Nests	2005/6	Ekanayake et al. (2010)	NA	NA
Melbourne Beach, south Florida (USA)	Green	86	28	2011, 2012	Long (2013)	4721	1574	Nests	2011, 2012	US Fish and Wildlife Service (2015)	NA	NA

Gulisaan, Sabah Turtle Islands (Malaysia)	Hawksbill	20	10	2004	Joseph and Shaw (2011)	514	171	Nests	2006	Marine Research Unit Sabah Parks (2007)	NA	NA
Cousine Island (Seychelles)	Hawksbill	10	77	2007/8–2008/9 ^a	Phillips (2013), Phillips et al. (2013, 2014)	833	278	Females	2007/8, 2008/9	Allen et al. (2010)	NA	NA
Celestún, Yucatan, Yucatan Peninsula (Mexico)	Hawksbill	11	9	2011	González-Garza et al. (2015)	202	67	Nests	2011	González-Garza et al. (2012)	NA	NA
Chenkan, Campeche, Yucatan Peninsula (Mexico)	Hawksbill	0	10	2011	González-Garza et al. (2015)	384	128	Nests	2011	González-Garza et al. (2012)	NA	NA
El Cuyo, Yucatan, Yucatan Peninsula (Mexico)	Hawksbill	10	10	2011	González-Garza et al. (2015)	454	151	Nests	2011	González-Garza et al. (2012)	NA	NA
Holbox, Quintana Roo, Yucatan Peninsula (Mexico)	Hawksbill	17	6	2011	González-Garza et al. (2015)	584	195	Nests	2011	González-Garza et al. (2012)	NA	NA
Rancho Nuevo, Tamaulipas (Mexico)	Kemps Ridley	58	26	Unreported	Kichler et al. (1999)	1562	521	Nests	1994–1998	Turtle Expert Working Group (2000)	NA	NA
South Padre Island, Texas (USA)	Kemps Ridley	52	21	2010	Frankel (2009)	140	47	Nests	2010	National Marine Fisheries Service et al. (2011)	NA	NA

Continued

Table 1 Incidences of Multiple Paternity (%), Rookery Sizes (Nest Count and the Number of Nesting Females), an Index of Offshore Movement (km) and Their Associated References—cont'd

Location	Species	Incidence of Multiple Paternity (%)	Sample Size (N)	Year of Study	References	Nest Count (N)	Number of Nesting Females (N)	Variable Counted	Year of Abundance Estimate	References	Offshore Distance (km)	References
Playa Gandoca, Gandoca-Manzanillo National Wildlife Refuge (Caribbean coast of Costa Rica)	Leatherback	22	18	2008	Figgenger et al. (2016)	3044	1015	Nests	2008	Debade et al. (2009) , Rivas et al. (2015) , Troëng et al. (2004) , and Widecast (2008)^b	20.3 ^d	NA
Playa Grande, Parque Marino Nacional Las Baulas (Pacific coast of Costa Rica)	Leatherback	10	20	1998/99	Crim et al. (2002)	378	126	Females	1998/99	Tomillo et al. (2007)	12 ^e	Shillinger et al. (2010)
Matura Beach (Trinidad)	Leatherback	20	10	2009	Nugent (2012)	5642	3757	Both	2009	Bachan (2009)	19 ^f	Eckert (2006)
Sandy Point National Wildlife Refuge, St. Croix (US Virgin Islands)	Leatherback	27	67	2009, 2010	Stewart and Dutton (2011, 2014)	444	148	Females	2009, 2010	Garner (2012)	30 ^g	Eckert (2002)
Turtle Bay, Dirk Hartog Island, Western Australia (Australia)	Loggerhead	36	14	2013	Tedeschi et al. (2015)	4500	1500	Females	1993/4–1999/2000	Baldwin et al. (2003)	NA	NA

Gnaraloo Bay, Western Australia (Australia)	Loggerhead	86	7	2011	Tedeschi et al. (2015)	397	132	Nests	2011	Hattingh et al. (2014)	NA	NA
Mon Repos, near Bundaberg, Queensland (Australia)	Loggerhead	33	24	1982/3	Harry and Briscoe (1988)	945	315	Females	1982/3	Limpus (2009)	3.5 ^b	Tucker et al. (1996)
Zakynthos Island (Greece)	Loggerhead	93	15	2003, 2004	Zbinden et al. (2007)	1198	399	Nests	2003, 2004	Margaritoulis et al. (2011)	1 ⁱ	Schofield et al. (2013)
Melbourne Beach, south Florida (USA)	Loggerhead	31	70	1996	Moore and Ball (2002)	20,024	6675	Nests	1996	Scarborough (2013)	6.1 ^j	Arendt et al. (2012)
Wassaw National Wildlife Refuge, Wassaw Island, Georgia (USA)	Loggerhead	75	72	2008–2010	Lasala et al. (2013)	123	57	Both	2008–2010	Pfaller et al. (2013)	NA	NA
Quintana Roo, Yucatan Peninsula (Mexico)	Loggerhead	66	41	2006	Nielsen (2010)	1225	408	Nests	2006	Comision Nacional De Areas Naturales Protegidas (2011)	NA	NA
St. George Island, northwestern Florida (USA)	Loggerhead	23	22	2007, 2008	Nielsen (2010)	141	47	Nests	2007	Florida Department of Environmental Protection (2015)	NA	NA

Continued

Table 1 Incidences of Multiple Paternity (%), Rookery Sizes (Nest Count and the Number of Nesting Females), an Index of Offshore Movement (km) and Their Associated References—cont'd

Location	Species	Incidence of Multiple Paternity (%)	Sample Size (N)	Year of Study	References	Nest Count (N)	Number of Nesting Females (N)	Variable Counted	Year of Abundance Estimate	References	Offshore Distance (km)	References
Ostional National Wildlife Refuge (Pacific coast of Costa Rica)	Olive ridley	92	13	2003	Jensen et al. (2006)	375,000	125,000	Females	2003	Conant et al. (2014)	NA	NA
Playa Hermosa National Wildlife Refuge (Pacific coast of Costa Rica)	Olive ridley	31	13	2003	Jensen et al. (2006)	1185	395	Nests	2008	Mast et al. (2014–2015)	NA	NA
Galibi Nature Reserve (East Suriname)	Olive ridley	20	10	1995	Hoekert et al. (2002)	335	112	Nests	1995	Hoekert et al. (2002)	NA	NA
Punta Raton (Honduras)	Olive ridley	75	8	2011–2013	Duran et al. (2015)	NA	NA	NA	NA	NA	NA	NA

^aThese studies were undertaken over 2007/8–2010/11 with a total sample size of 140 (incidence of multiple paternity, 9%) but data for only 2 years were used for analyses since rookery data for the other years were not available.

^bData for Gandoca, Tortuguero and Pacuare were combined ([Debade et al., 2009](#); [Rivas et al., 2015](#); [Widecast, 2008](#)) and doubled following [Troëng et al. \(2004\)](#) as the three beaches are considered to be part of the same nesting rookery ([Troëng et al., 2004](#)).

^cBased both on the mean distances moved offshore of tracked individuals as well as diving data indicating individuals typically rested at depths of <20m, a bathymetric contour readily seen on nautical charts.

^dBased on the mean value recorded for other leatherback tracking studies reported in this Table (see footnotes e, f, g).

^eBased on the reported 50% Kernel Utilisation Density of tracked individuals.

^fBased on the reported 50% Kernel Utilisation Density of tracked individuals.

^gBased on the mean daily distances moved offshore of tracked individuals.

^hBased on the reported radio telemetry locations, of which 38% of locations were concentrated within the “turtle protection special management area”.

ⁱBased on the reported 50% Kernel Utilisation Density of tracked individuals.

^jBased on the reported minimum convex polygon core area use of tracked individuals during the breeding period.

NA indicates missing data.

Table 2 Details of Studies Reporting Multiple Paternity in Sea Turtles That Were Excluded From Analyses

Location	Species	Incidence of Multiple Paternity (%)	Sample Size (N)	Year of Study	References	Reason for Exclusion
Peak Island, Queensland (Australia)	Flatback	67	3	2004/5	Theissinger et al. (2009)	Small sample size <5
Tortuguero (Caribbean coast of Costa Rica)	Green	63	8	Unreported	Peare et al. (1998)	Replaced by a more recent study by Alfaro-Núñez et al. (2015)
Tortuguero (Caribbean coast of Costa Rica)	Green	33	3	Unreported	Parker et al. (1996)	Small sample size <5; replaced by a more recent study by Alfaro-Núñez et al. (2015)
Pangumbahan (Java)	Green	50	10	Unreported	Purnama et al. (2013)	Interannual variability of nest numbers was too great to accept an average value from multiple years given lack of information about the year that MP samples was taken
Colola (Mexico)	Green	100	2	Unreported	Lara-De La Cruz et al. (2010)	Small sample size <5; also, interannual variability of nest numbers was too great to accept an average value from multiple years
Khram Island (Thailand)	Green	100	3	2001	Mudsuk et al. (2004)	Small sample size <5
Las Coloradas, Yucatan Peninsula (Mexico)	Hawksbill	0	4	2011	González-Garza et al. (2015)	Small sample size <5

Continued

Table 2 Details of Studies Reporting Multiple Paternity in Sea Turtles That Were Excluded From Analyses—cont'd

Location	Species	Incidence of Multiple Paternity (%)	Sample Size (N)	Year of Study	References	Reason for Exclusion
Xicalango-Victoria, Yucatan Peninsula (Mexico)	Hawksbill	0	2	2011	González-Garza et al. (2015)	Small sample size <5
Bungalup Beach, Western Australia (Australia)	Loggerhead	25	4	2013	Tedeschi et al. (2015)	Small sample size <5
Melbourne Beach, south Florida (USA)	Loggerhead	33	3	1994	Bollmer et al. (1999)	Small sample size <5; replaced by a more recent study by Moore and Ball (2002)
Pacuare (Caribbean coast of Costa Rica)	Leatherback	9	11	1996	Curtis et al. (2000)	Replaced by a more recent study by Figgenger et al. (2016)
Playa Grande, Parque Marino Nacional Las Baulas (Pacific coast of Costa Rica)	Leatherback	0	4	Unreported	Rieder et al. (1998)	Small sample size <5; replaced by a more recent study by Crim et al. (2002)
Sandy Point National Wildlife Refuge, St. Croix (US Virgin Islands)	Leatherback	0	4	Unreported	Dutton et al. (2000)	Small sample size <5; replaced by more recent study by Stewart and Dutton (2011)

Escobilla (Mexico)	Olive ridley	50	16	Unreported	Zurita et al. (2008)	This conference abstract did not include any detail on methodology, so it was not possible to assess the reliability of the study—in addition, there was conflicting data from a previous study (100% MP of 4 nests), which also lacked information about methodology
Timor Island (Indonesia)	Olive ridley	Unreported	Unreported	2013/14	Dima et al. (2015)	Multiple paternity was detected, but neither the degree of multiple paternity in the rookery nor the sample size was reported

found (e.g. student theses and unreported projects), this presents the most comprehensive set of sea turtle multiple paternity data to date, including all data up to February 2016 in ISI-listed journal publications for all seven species of sea turtle: green turtle *Chelonia mydas* (Linnaeus, 1758), loggerhead *Caretta caretta* (Linnaeus, 1758), Kemp's ridley *Lepidochelys kempii* (Garman, 1880), olive ridley *Lepidochelys olivacea* (Eschscholtz, 1829), hawksbill *Eretmochelys imbricata* (Linnaeus, 1766), flatback *Natator depressus* (Garman, 1880) and leatherback *Dermochelys coriacea* (Vandelli, 1761).

The incidence of multiple paternity varied hugely across rookeries (Fig. 2A and B), being found, for example, in 92.3% and 91.7% of clutches for olive ridley turtles nesting in Ostional (Costa Rica) and green turtles nesting in Tortuguero (Costa Rica), respectively; but only 10.0% and 20.0% of clutches for leatherback turtles nesting in Playa Grande (Costa Rica) and Matura (Trinidad), respectively. There were marked and significant (ANOVA, $F_{5,24} = 3.7$, $P = 0.013$) differences in the incidence of multiple paternity across species. For example, leatherback turtles had a significantly lower incidence of multiple paternity (mean 19.8%, $n = 4$ rookeries) than either loggerhead turtles (mean 55.4%, $n = 8$ rookeries, $T_8 = 3.42$, $P < 0.01$) or green turtles (mean 54.3, $n = 6$ rookeries, $T_5 = 2.60$, $P = 0.04$). While the incidence of multiple paternity was uniformly low at leatherback turtle rookeries, it was more variable in other species. For example, for loggerhead turtles the incidence of multiple paternity in clutches ranged from 22.7% (St. George Island, Florida) to 93.3% (Zakynthos Island, Greece).

We then conducted literature searches for data on rookery sizes. Since rookery size may fluctuate from year to year, we attempted to collect rookery size data for the year when the incidence of multiple paternity had been estimated. For cases where this was not possible (e.g. the year of study was not reported), we examined the rookery size data for 5 years prior to the date of publication of the report and took an average value if the size did not vary by more than an order of magnitude during this period. Rookery size was usually reported as the number of nests counted in a breeding season, but sometimes the number of nesting females was reported. Where only one type of data was available, we converted between the data by assuming that female sea turtles laid an average of three clutches in a breeding season (Hirth, 1980). We applied an average value for consistency across the data because specific clutch frequency information was not available for all rookeries in our database.

Rookery size and the incidence of multiple paternity were obtained for 30 rookeries spanning the 7 species (Fig. 2 and Table 1). We found that the

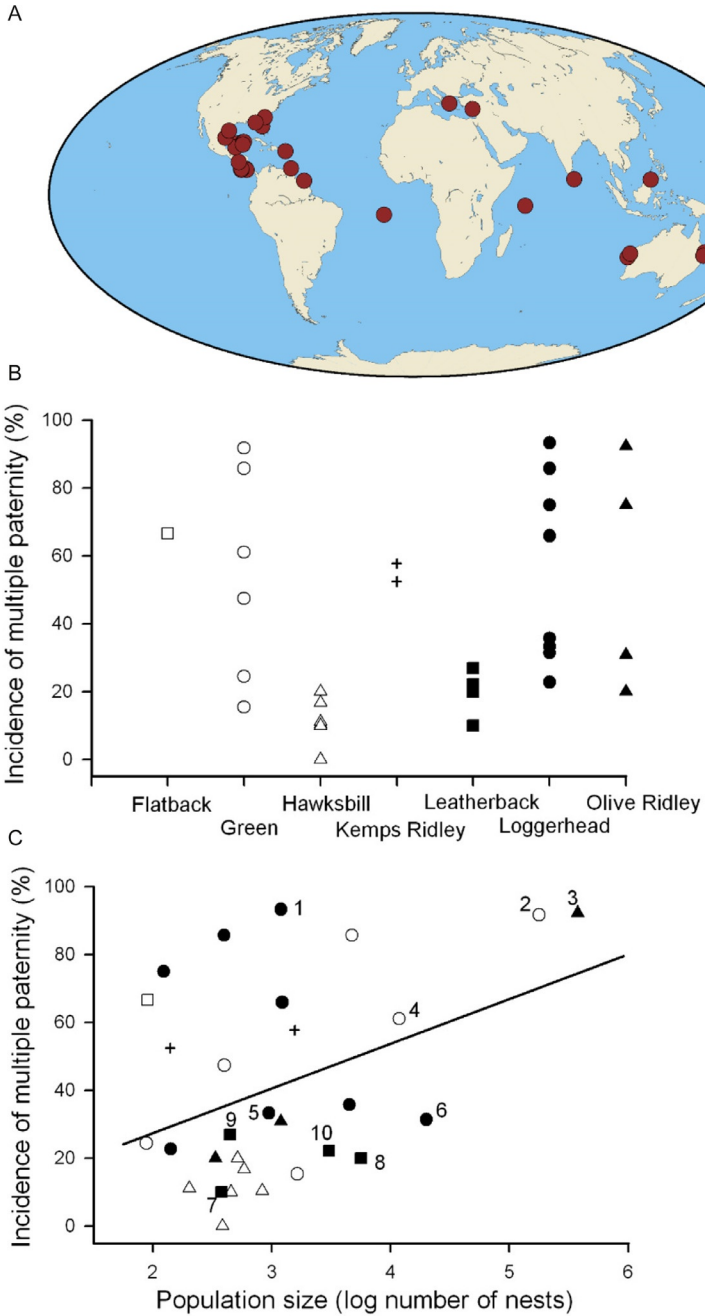


Fig. 2 The incidence of multiple paternity in sea turtle rookeries around the world. (A) Locations around the World where the incidence of multiple paternity has been (Continued)

incidence of multiple paternity was only weakly linked to rookery size ($F_{1,28} = 5.25$, $R^2 = 0.158$, $P = 0.03$, $n = 30$) (Fig. 2C). For example, while the incidence of multiple paternity was high at rookeries where nesting numbers were massive (e.g. 125,000 and 59,000 nests per year, respectively, at Ostional and Tortuguero), at smaller rookeries the incidences of multiple paternity were highly variable and poorly predicted by population size. For example, for loggerhead turtles at Chenkan (Mexico) where the rookery size was 945 nests, the incidence of multiple paternity was 33.3%, while for loggerhead turtles at Zakynthos (Greece) which had a similar rookery size (1198 nests) the incidence was 93.3% (Fig. 2C).



4. CASE STUDIES: THE EXTENT OF INDIVIDUAL MOVEMENTS ACROSS ROOKERIES

We suggest that the extent to which adults move within the breeding area could determine the packing density within rookeries. For breeding sites of two different species, loggerhead and leatherback turtles, we have previously tracked individuals in the breeding season. For loggerhead turtles at Zakynthos Island (Greece 37°43'N 20°53'E), we used GPS loggers (Navsys Ltd. TrackTag TM GPS loggers; Colorado Springs, CO, USA; <http://www.navsys.com>) to track breeding females in 2006 (three females), 2007 (four females) and 2008 (six females). For details on permits, turtle capture, attachment and retrieval techniques see Schofield et al. (2007, 2013). Here, we filtered the GPS fixes (average of 51 fixes per turtle per day) by selecting the central location for each hour for each turtle (Tremblay et al., 2006). For leatherback turtles nesting in Grenada (Caribbean), we

Fig. 2—Cont'd measured, excluding rookeries where the samples size was <5 clutches. (B) Variation in the degree of multiple paternity across different species of sea turtle. Variation within species was particularly evident across rookeries of loggerhead turtles, olive ridley turtles and green turtles, whereas leatherbacks and hawksbills had uniformly low incidence of multiple paternity. (C) The relationship between the incidence of multiple paternity and the size of different rookeries as indicated by the number of nests. *Plot symbols* indicate different species as identified in (B). Selected sites are identified as they appear in Fig. 4. 1 = loggerhead turtles Zakynthos (Greece); 2 = green turtles Tortuguero (Costa Rica); 3 = olive ridley turtles Ostional (Costa Rica); 4 = green turtles (Ascension Island); 5 = loggerhead turtles Mon Repos (Australia); 6 = loggerhead turtles, Melbourne Beach, Florida (USA); 7 = leatherback turtles Playa Grande (Costa Rica); 8 = leatherback turtles Matura (Trinidad); 9 = leatherback turtles St. Croix (US Virgin Islands); 10 = leatherback turtles Gandoca (Costa Rica).

recorded the extent of their movements in the breeding season using Argos satellite tags (see Georges et al., 2007 for details of attachments and data processing).

We found that between breeding loggerhead turtles at Zakynthos (Greece) and leatherback turtles in Grenada (Caribbean) there were massive differences in the extent of individual movements. Loggerhead turtles at Zakynthos tended to have very restricted movements, generally staying within 1 km of their breeding beaches. By contrast, leatherback turtles breeding in Grenada travelled many 10s of km from their breeding beaches ranging over an area of around 25,000 km² (250 km by 100 km; Fig. 3). These contrasting movement behaviours from the two case studies justified the logic of incorporating movement data into estimates of density.



5. PACKING DENSITY AND INCIDENCE OF MULTIPLE PATERNITY

While tracking is often lacking during the breeding season, we used the available data to estimate the packing density across rookeries. We calculated a packing density metric as: \log_{10} (number of nesting individuals)/distance travelled offshore during the breeding season. To maximise the power of this analysis, we assembled the “distance travelled offshore” metric across rookeries in several ways. First where available, we used maps of the 50% Kernel Utilisation Density or maps that showed the core area used. Where kernel density maps were not available, we used the reported mean location of individuals during the breeding season or visually inspected the published tracks to estimate the typical distances travelled offshore. Where available data indicated a strong consistency across rookeries of the same species for the extent of their movements in the breeding season, we applied mean species values for movements offshore to rookeries where individuals have not been tracked. Finally, for rookeries where nesting numbers were exceptionally high (orders of magnitude higher than other rookeries) and so rookery size alone likely resulted in high packing densities, we assumed the maximal packing densities calculated from other sites with tracking data.

For rookeries across the World where we were able to estimate packing density, this density scaled very tightly with the incidence of multiple paternity ($F_{1,8} = 241$, $R^2 = 0.97$, $P < 0.001$; Fig. 4). The high degree of multiple paternity in the Zakynthos rookery corresponded with the high packing density of loggerhead turtles at this location, with this density driven by

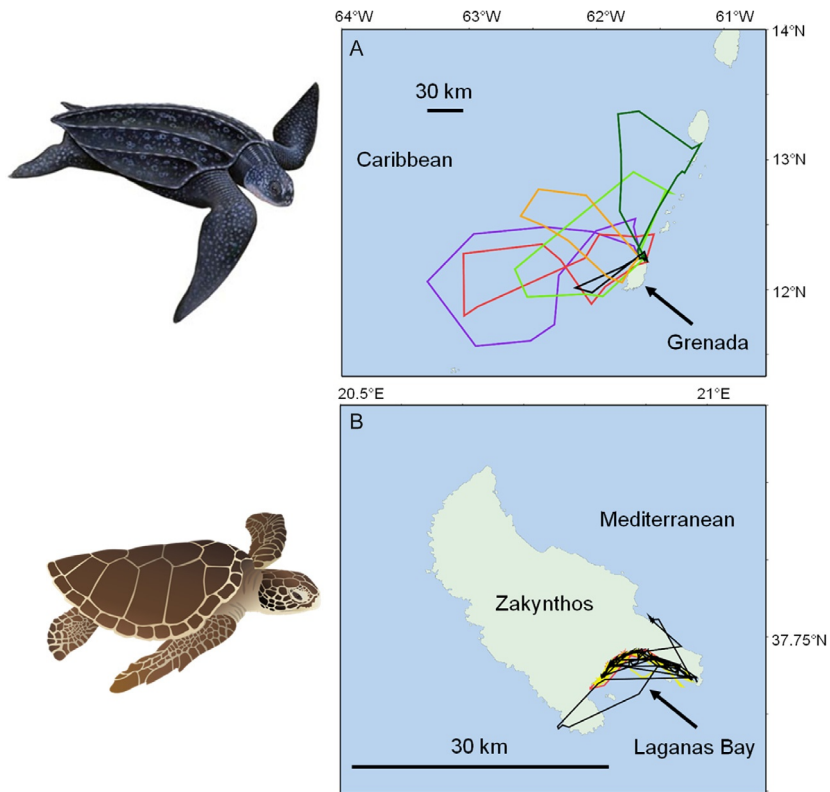


Fig. 3 The variable extent of movements during the breeding season across rookeries. (A) Leatherback turtles breeding in Grenada (Caribbean) and (B) loggerhead turtles breeding in Zakynthos (Greece). Panel (B) shows the tracks of three individuals tracked in 2006 with similar movements recorded in 2007 and 2008. Individuals made occasional excursions but >90% of locations were within Laganas Bay (Zakynthos, Greece) and individuals spent the vast majority of their time very close to the nesting beaches. In contrast, leatherback turtles at Grenada (Panel A) travelled far more extensively in the breeding season, often more than 100 km from their nesting beaches. Tracks recorded during six separate interesting intervals are shown.

the very restricted movements of turtles at that site during the breeding season. We can also explain the high instances of multiple paternity at the massive rookeries (olive ridleys at Ostional and green turtles at Tortuguero), where the abundance of individuals will help ensure a high rate of male-female encounters. In contrast, the leatherback turtles of St. Croix, Matura and Playa Grande demonstrate relatively low instances of multiple paternity, in line with their low packing density and hence individuals will be more diffusely distributed.

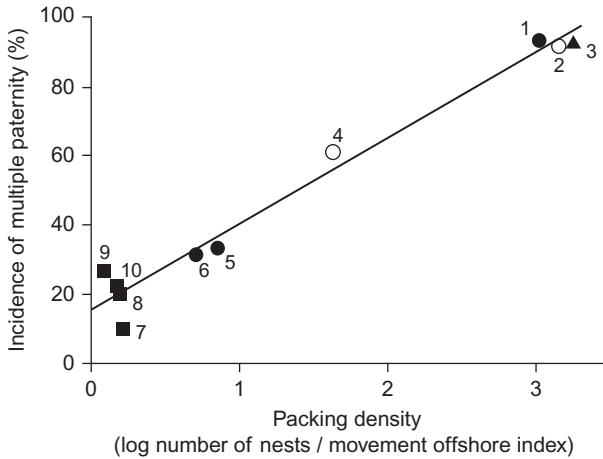


Fig. 4 The incidence of multiple paternity scales tightly with the packing density, where packing density was determined as the log of the number of nests divided by the offshore movement index (see Table 1). Plot symbols indicate different species as identified in Fig. 2A. The three points at the highest packing density are jittered so that they do not lie on top of each other. 1 = loggerhead turtles Zakynthos (Greece); 2 = green turtles Tortuguero (Costa Rica); 3 = olive ridley turtles Ostional (Costa Rica); 4 = green turtles (Ascension Island); 5 = loggerhead turtles Mon Repos (Australia); 6 = loggerhead turtles, Melbourne Beach, Florida (USA); 7 = leatherback turtles Playa Grande (Costa Rica); 8 = leatherback turtles Matura (Trinidad); 9 = leatherback turtles St. Croix (US Virgin Islands); 10 = leatherback turtles Gandoca (Costa Rica).



6. MOVEMENT APPEARS CRITICAL TO ESTIMATING DENSITY AND MATE ENCOUNTER RATE

Theoretical considerations have predicted that population density and sex ratios will often drive male–female encounter rate, although the implications for the resulting incidence of multiple paternity are not simple to predict and may depend on the relative costs vs benefits to females of multiple matings (Kokko and Mappes, 2013; Kokko and Rankin, 2006). Set against this backdrop, we might expect that where the extent of individual movements varies across populations, then population size alone may not provide a good approximation of density. Yet surprisingly this impact of animal movement does not appear to have been widely considered. Our findings provide strong evidence that the extent of individual movements in the breeding season varies widely across sea turtle rookeries and species, and has a profound impact on density and thereby male–female encounter rates and the incidence of multiple paternity. As such, we provide some

of the strongest empirical evidence to date for the hypothesis that female sea turtles simply “give in” to unwanted mating attempts, termed “convenience polyandry” (Thornhill and Alcock, 1983).

Both the weak links between rookery size and the incidence of multiple paternity in sea turtles, as well as the broad differences in this incidence across species point to the profound role of their movement behaviour in driving male–female encounter rates. As a general rule, the instances of multiple paternity were high where nesting numbers were massive, such as for olive ridley turtles nesting at Ostional National Wildlife Refuge (Costa Rica) and green turtles nesting at Tortuguero (Costa Rica), where there are many tens of thousands of breeding individuals. At these sites, the high numbers of individuals alone likely ensure high rates of male female encounters. However, in contrast, the incidence of multiple paternity was very variable where nesting numbers were smaller, consistent with variable extents of individual movement at these rookeries. This variable extent of movement certainly seems to apply both across and within species. For example, generally leatherback turtles range broadly during the breeding season, with typical distances moved offshore of several 10s of km (Eckert, 2002, 2006; Shillinger et al., 2010), most likely because this species often forages in deep water far from land. The broad dispersion of breeding leatherback turtles appears linked to the generally very low incidence of multiple paternity in this species, since even when nesting numbers are high the likely density, and hence male–female encounter rates, will be low. In contrast, green turtles tend to both feed and rest in shallow water, and hence their movements in the breeding season will generally be far less than in leatherbacks. For example, at Ascension Island (South Atlantic), satellite tracking has shown that individuals typically move only a few km offshore from their nesting beaches (Hays et al., 1999), a finding that is corroborated by records of depth utilisation that show individuals rest on the seabed in shallow water which is only found close to land at this site (Hays et al., 2004). In addition to the broad difference between species in the extent of their movements in the breeding season, even across rookeries of the same species, the extent of movement may vary. For loggerhead turtles in Greece, we showed very localised movements as have been reported previously at this site (Schofield et al., 2010), yet elsewhere, for example, in Florida, this species ranges more widely during the breeding season (Arendt et al., 2012).

Our key conclusion, that the incidence of multiple paternity scales with the density of turtles, could clearly be improved by further tracking studies

both across other rookeries but also by having comparable raw tracking data sets collected with the same accuracy so that the same movement metrics could be applied easily across studies (Urbano et al., 2010). So we acknowledge that it is not ideal to develop a movement metric from disparate studies, and we encourage initiatives for data-sharing and archiving of data that are now becoming widespread both in the animal tracking community (e.g. Dwyer et al., 2015; Hunter et al., 2013; Kranstauber et al., 2011) and more broadly (Soranno et al., 2015). Furthermore, given the strong links we identified between packing density and the incidence of multiple paternity, for sites where there is no tracking data for breeding individuals we predict that for relatively large rookeries with a low incidence of multiple paternity, the breeding individuals likely range relatively more (e.g. green turtles at Heron Island, Australia) and vice versa. Given the wide availability of techniques for tracking marine species including sea turtles (Hays et al., 2016), testing these predictions for the extent of movement, should be a rewarding avenue to pursue.

Our findings suggest that females are not actively seeking to mate with multiple males, which would be expected if there were fitness benefits for females from promiscuous behaviour, but rather they simply give in to unwanted male mating. According to this hypothesis, females will generally resist mating more than once, unless the cost of resistance exceeds that of mating. Thus, females simply make the “best of a bad job” by opting for the less costly choice (Watson et al., 1998). Convenience polyandry has been demonstrated for some species of invertebrates (e.g. Cordero and Andrés, 2002; Rowe, 1992; Thiel and Hinojosa, 2003; Watson et al., 1998; Weigensberg and Fairbairn, 1994) and is the obvious hypothesis where there are little evident benefits of multiple mating to females, such as been found for some species of amphibians (Byrne and Roberts, 2004; Zhao et al., 2016), sharks (Griffiths et al., 2012; Nosal et al., 2013) and reptiles (Garner et al., 2002). Both multiple mating and resistance to mating are costly for females. However, if the costs of mating were high relative to costs of resistance, then there would be little or no multiple paternity occurring. Alternatively, should the costs of mating to females be sufficiently small, as appears to be the case in sea turtles, then where male encounter rates are high, submission to male coercion and hence higher levels of multiple paternity, are likely to occur. Certainly, there appear to be costs of resistance to mating in female turtles. For example, cameras attached to females have shown that they may need to swim fast and dive deeply to avoid mating which may incur high energetic costs (Reina et al., 2005). So when density

is high, there may be little point in resisting male mating attempts, as another male will then soon arrive even if the current one is successfully rejected (Arnqvist, 1992; Rowe et al., 1994). Our evidence provides some of the strongest evidence to date that this scenario of not resisting male mating attempts occurs widely for sea turtles.

Our results extend on recent studies of other animals such as mammals and birds that are also starting to show that higher density can lead to increased female promiscuity (Ishibashi and Saitoh, 2008; Mayer and Pasinelli, 2013), with experimental work on insects further demonstrating that this can occur without females benefiting from multiple mating (Sandrin et al., 2015). Our findings also point to the value of being able to estimate encounter rates, for example, by directly tracking individuals. Certainly for a broad range of animals high-resolution tracking is possible, opening up the possibilities for these types of movement study across a broad spectrum of species (Hays et al., 2016), ideally improving on our approach here by tracking both males and female simultaneously. Furthermore, as well as improved tracking data sets, our approach of estimating packing density could be improved by estimating operational sex ratios, i.e., the relative number of breeding males and females. Generally, the number of breeding male turtles tends to be poorly known across sea turtle rookeries (Hays et al., 2010), but can potentially be assessed with targeted studies (e.g. Casale et al., 2014; Chaloupka and Limpus, 2001).

In summary, our work helps resolve a long-standing conundrum by supporting the suggestion (Alfaro-Núñez et al., 2015; Jensen et al., 2006; Lee and Hays, 2004; Wright et al., 2013) that multiple paternity generally offers no fitness benefits to female sea turtles and simply scales with the density of turtles on the breeding grounds. The use of movement data to estimate male–female encounter rates may allow the broader applicability of this conclusion to be assessed for other taxa.



7. CONCLUSION

We confirmed that the incidence of multiple paternity in sea turtles was only weakly linked to adult abundance at rookeries. For some species, such as the leatherback turtle, the incidence of multiple paternity was relatively low regardless of the size of the population, while for other species, such as the loggerhead turtle, the incidence of multiple paternity was highly variable, even for rookeries of similar size.

1. If females benefit from mating many times, then we suggest that females ought to actively seek out mates and consequently, the incidence of multiple paternity should be generally high regardless of rookery size. Instead, our review found that the incidence of multiple paternity in sea turtles varied greatly among species and rookeries, and could be relatively low even for rookeries of moderate size. Therefore, for sea turtles, we suggest there is no indication that females are benefiting from promiscuous behaviour. Instead, it is more likely that females are acquiescing to extraneous matings to avoid the high costs incurred by attempting to reject the unwanted mates.
2. Our detailed tracking information on individuals supported our hypothesis that individual movement could determine the local packing density and potentially, the rate of encounter among breeding individuals within that particular locality.
3. Having incorporated movement data with rookery size data to obtain an estimate of packing density, we found a tight relationship between packing density and the incidence of multiple paternity. We predict that for relatively large rookeries with a low incidence of multiple paternity, breeding individuals are possibly ranging relatively more and vice versa. Testing these predictions should be a rewarding aim for future studies.
4. Advances in techniques in high-resolution tracking and remote monitoring of individuals should open up the possibilities for movement study in the context of understanding mating strategies across a broad spectrum of species, and improve on our approach here by tracking both males and female simultaneously, and estimating mate encounter rate more directly.

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AUTHORS' CONTRIBUTIONS

P.L.M.L. and G.C.H. conceived the study, analysed the data, prepared the figures and led the writing with contributions from all authors. P.L.M.L., G.S., R.I.H. and A.D.M. assembled the data.

COMPETING INTERESTS

The authors declare no competing interests.

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