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An inconvenient tooth: Evaluating female choice in multiple paternity using an evolutionarily and ecologically important vertebrate clade

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Abstract

Understanding mating systems is a pillar of behavioural ecology, placing the complex interactions between females and males into a reproductive context. The field of multiple paternity, the phenomenon whereby many sires contribute to an individual litter, has traditionally viewed females as passive players in a male–male competitive framework. With the emergence of feminist perspectives in ecological fields, novel alternative mechanisms and evolutionary theories across invertebrate and vertebrate taxa recognize females are active stakeholders in the reproductive process. Despite their evolutionary significance, ecological diversity and myriad reproductive modes, elasmobranch (sharks, skates and rays) research lags behind other fields regarding complex biological processes, such as multiple paternity which is often ascribed to convenience polyandry. Here, we layout hypotheses and resynthesize multiple paternity literature from a female and life history perspective to highlight how alternative mechanisms influence the predominance of multiple paternity across elasmobranchs. We draw upon parallels in other invertebrate and vertebrate taxa to demonstrate how female elasmobranchs can influence multiple paternity outcomes that benefit their reproductive success. Our article challenges dogma that has resulted from years of dismissing the female perspective as important and provides a framework for future advancement using more holistic approaches to studying mating systems.

KEYWORDS
cryptic female choice, ecological feminism, intrasexual competition, lifetime reproductive output, maternal investment, polyandry

1 | INTRODUCTION

Classical theories in evolutionary ecology have often been presented from the male perspective as they were authored or co-opted by men (Trivers, 1972; Williams, 1966). This is particularly true in the field of reproductive biology and the study of the phenomenon of multiple paternity. Multiple paternity—or polyandry, whereby a single litter or brood is sired by multiple fathers—was once thought uncommon (Birkhead & Moller, 1992; Griffith et al., 2002) or only associated with certain modes of external fertilization (DeWoody & Avise, 2001; Johnson & Yund, 2007 e.g., broadcast spawning). Contemporary research highlights that multiple paternity occurs more frequently than previously supposed across multiple vertebrate lineages with varying strategies of parental investment (Cohas & Allainé, 2009; Coleman & Jones, 2011; Isvaran & Clutton-Brock, 2007; Uller & Olsson, 2008). Many theories have been proposed to

explain the widespread occurrence of multiple paternity across taxa and the evolutionary underpinnings driving these patterns (Arnqvist & Nilsson, 2000; Emlen & Oring, 1977; Gowaty, 2012; Jennions & Petrie, 2000). Traditional explanations have centred around convenience polyandry, including the dogma of "promiscuous" males competing for fitness while females are "choosy" (at best), where more often females are portrayed as passive players in a male–male competitive framework. With the relatively recent emergence of feminist perspectives in ecological fields (Gowaty, 2003; Hrdy, 1986, 1999; Orr et al., 2020), alternative mechanisms and evolutionary theories for the widespread occurrence of multiple paternity across vertebrate lineages are gaining traction (Eberhard, 1996; Tregenza & Wedell, 2000; Zeh & Zeh, 1996, 1997, 2001). These alternative hypotheses position females as more active stakeholders in determining sireship within a reproductive event or cycle, especially when resources are exclusively maternally derived.

Across taxa, reproductive studies conducted from the female perspective are uncovering numerous mechanisms by which they can influence sireship of their litters, ranging from anatomical adaptations that control sperm access to eggs (Holt & Fazeli, 2010) to direct influence over which embryos are carried to term (Drickamer et al., 2000). For example, sperm motility and migration can be altered depending on the viscosity of the medium (Kirkman-Brown & Smith, 2011), providing a mechanism by which females may alter sperm access to ova (Holt & Fazeli, 2016). In some insect species, females can cryptically modulate specific seminal fluid molecules to counterbalance their male-driven intended effects (Sirot, 2019). For example, in leaf-cutting ants (*Atta colombica* Guérin-Méneville), females have evolved "antidotes" to counteract the intended effects of seminal fluid molecules to disable sperm from previous males (Dosselli et al., 2019), effectively negating post-copulatory sperm competition. In American mink (*Mustela vison* Schreber), delayed implantation followed by successive ovulations after first mating (superfetation) allows females to solicit other mates, leading to a high frequency of multiple paternity (Yamaguchi et al., 2004). The potential scope for female-based mechanisms to counteract male reproductive prerogatives across disparate lineages necessitates a restructuring of research thinking to consider females as equal players in the reproductive process and the role they play in sexual conflict across taxa.

When parental investment in offspring is maternally skewed, indiscriminate mating could be costly to females. An absence of female choice can produce suboptimal offspring as a result of mating with low-quality males or unviable offspring via mating with genetically incompatible males, either of which potentially lowers her reproductive success and fitness. It is increasingly recognized that parental genomes are not simply additive, and genomic conflict naturally exists between the sexes such that not all female–male pairings will be compatible (Zeh & Zeh, 1996). Over the past couple decades, genetic incompatibility has increasingly been recognized as an important evolutionary factor that may drive females' preference for multiple paternity in order to minimize this risk (Jennions & Petrie, 2000; Tregenza & Wedell, 2000; Zeh & Zeh, 1997). Reproductive

costs to females may be further exacerbated in species with slow life history characteristics such as late onset of maturity and protracted reproductive cycles that limit female lifetime reproductive potential. Elasmobranchs (sharks, skates and rays) are an ancient lineage of vertebrates, characterized by relatively slow life history traits (i.e., late-to-mature, low fecundity) and high degrees of maternal investment in offspring (Wourms & Demski, 1993) that rival or surpass other, more recent and well-studied vertebrate lineages such as birds and mammals. For instance, elasmobranchs provide a wide spectrum of maternal investment to embryos from nutrition derived solely from a yolk-sac (lecithotrophy) to various supplemental forms of maternal provisioning throughout gestation (matrotrophy), such as uterine milk (histotrophy), unfertilized ova (oophagy) or via a maternal–embryo connection (placentatrophy; Conrath & Musick, 2012).

Considering the high investment needed to produce well-developed young combined with relatively low lifetime reproductive potential, the cost to elasmobranch females when producing offspring with low-quality or genetically incompatible males could be substantial, especially without paternal care. In the absence of mate choice, females may lower their fitness risk by increasing the number of sires, which would result in an increase in polyandry. Indeed, the occurrence of multiple paternity across elasmobranch species is widespread (Lamarca et al., 2020), with nearly every species examined exhibiting some degree of multiple paternity (Table 1). Explanations of this phenomenon are most often casually attributed to "convenience polyandry," where females are presumed to mate with multiple males simply because the cost of avoiding rigorous copulatory behaviour is too high (e.gBarker et al., 2019; DiBattista et al., 2008; DiBattista et al., 2008; Feldheim et al., 2004; Griffiths et al., 2011; Lage et al., 2008; Nosal et al., 2013; Pirog et al., 2017; Rossouw et al., 2016). However, empirically demonstrating convenience polyandry as the main driver of multiple paternity is quite difficult (Boulton et al., 2018), and many studies lack the power to make broad conclusions about the mating system in the first place due to low sample sizes or the opportunistic nature of their sampling schemes. Furthermore, the generally low genetic diversity of microsatellite markers, or few numbers of markers used, in elasmobranch studies along with small litter sizes in some species makes demonstrating a lack of multiple paternity even more difficult. Thus, while documenting the presence of multiple paternity is fairly definitive (reaching this benchmark is difficult so detection is likely a true positive), the true absence of multiple paternity is harder to demonstrate considering the above challenges in elasmobranch studies (i.e., higher chance of false negatives). As such, studies that find no evidence of multiple paternity based on single litter or small litter sizes (number of embryos) should be interpreted with caution.

Regardless, the frequent use of convenience polyandry as the first and "go to" explanation for many multiple paternity studies disregards the complex biological processes occurring after mating that lead to the development of a fully formed embryo, which may involve intricate and often intimate connections between mothers and embryos. Rather, the overrepresentation of androcentric

TABLE 1 Elasmobranch polyandry studies meeting the search criteria are presented with the number of loci markers and program method utilized to determine the presence of multiple paternity as well as a summary of litter characteristics

| Study	Species	Common name	Number of markers	Number of litters	Litter size range	Range of sires	Method
Janse et al. (2013)	*Aetobatus narinari*	Spotted eagle ray	8	20	1–2	1–2	Allele counting
Barker et al. (2019)	*Carcharhinus acronotus*	Blacknose shark	23	27	3–6	1–4	COLONY
Daly-Engel et al. (2006)	*Carcharhinus altimus*	Bignose shark	8	1	9	2	Allele counting
Green et al. (2017)	*Carcharhinus amblyrhynchos*	Grey reef shark	14	6	2–5	1–2 (1–3)	GERUD (COLONY)
Daly-Engel et al. (2006)	*Carcharhinus galapagensis*	Galapagos shark	8	1	7	1	Allele counting
Pirog et al. (2017)	*Carcharhinus leucas*	Bull shark	21	4	5–11	1–2	COLONY
Bester-van der Merwe et al. (2019)	*Carcharhinus limbatus*	Blacktip shark	5	14	4–10	1–3 (1–6)	GERUD (COLONY)
Rossouw et al. (2016)	*Carcharhinus obscurus*	Dusky shark	5	14	3–14	1–2 (2–7)	GERUD (COLONY)
Daly-Engel et al. (2006)	*Carcharhinus plumbeus*	Sandbar shark	8	1	7	2	Allele counting
Daly-Engel et al. (2007)	*Carcharhinus plumbeus*	Sandbar shark	6	20	3–8	1–2	GERUD
Portnoy et al. (2007)	*Carcharhinus plumbeus*	Sandbar shark	5	20	4–13	2–4(2–5)	GERUD (COLONY)
Chapman et al. (2013)	*Carcharias taurus*	Sand tiger	10	15	2	1–2	GERUD
Townsend et al. (2015)	*Carcharias taurus*	Sand tiger	7	6	1–2	1–2	Cervus
Gubili (2008)	*Carcharodon carcharias*	White shark	7	1	8	2	GERUD
Holmes et al. (2018)	*Galeocerdo cuvier*	Tiger shark	9	4	26–36	1	COLONY
Hernandez et al. (2014)	*Galeorhinus galeus*	Tope	6	5	23–34	1–4	GERUD
Heist et al. (2011)	*Ginglymostoma cirratum*	Nurse shark	12	3	29–39	5–7	COLONY
Saville et al. (2002)	*Ginglymostoma cirratum*	Nurse shark	3	1	32	4	Restriction fragment length polymorphism
Larson et al. (2011)	*Hexanchus griseus*	Bluntnose sixgill shark	10	1	71	6(9)	GERUD (COLONY)
Corrigan et al. (2015)	*Isurus oxyrinchus*	Shortfin mako	5	1	8	3	GERUD
Gubili (2008)	*Isurus oxyrinchus*	Shortfin mako	4	4	10–16	2–3	GERUD
Boomer et al. (2013)	*Mustelus antarcticus*	Gummy shark	8	29	3–37	1–3(1–4)	GERUD (COLONY)
Farrell et al. (2014)	*Mustelus asterias*	Starry smoothhound	4	12	5–18	1–2(1–3)	GERUD (COLONY)
Byrne and Avise (2012)	*Mustelus henlei*	Brown smoothhound	4	14	4–17	1–3	GERUD
Chabot and Haggin (2014)	*Mustelus henlei*	Brown smoothhound	4	18	3–10	1–2	GERUD
Boomer et al. (2013)	*Mustelus lenticulatus*	Spotted estuary smoothhound	8	19	2–6	1–2(1–3)	GERUD (COLONY)
Maduna et al. (2018)	*Mustelus mustelus*	Common smoothhound	11	1	22	1	GERUD
Marino et al. (2015)	*Mustelus mustelus*	Common smoothhound	9	19	NA	1–3	GERUD
Rossouw et al. (2016)	*Mustelus mustelus*	Common smoothhound	6	6	5–18	1–2(3–6)	GERUD (COLONY)

TABLE 1 (Continued)

Study	Species	Common name	Number of markers	Number of litters	Litter size range	Range of sires	Method
Marino et al. (2015)	Mustelus punctulatus	Blackspotted smoothhound	9	13	NA	1–2	GERUD
DiBattista, Feldheim, Thibert-Plante, et al. (2008); DiBattista, Feldheim, Gruber, et al. (2008))	Negaprion brevirostris	Lemon shark	11	NA	NA	1–4	Genetic reconstruction
Feldheim et al. (2001)	Negaprion brevirostris	Lemon shark	3	1	13	3	Allele counting
Feldheim et al. (2004)	Negaprion brevirostris	Lemon shark	NA	NA	NA	1–4	Genetic reconstruction
Chevolot et al. (2007)	Raja clavata	Thornback ray	5	4	38–52	4–6	GERUD
Schmidt et al. (2010)	Rhincodon typus	Whale shark	9	1	29	1	COLONY
Griffiths et al. (2011)	Scyliorhinus canicular	Small-spotted catshark	12	13	4–28	1–3(1–4)	GERUD (COLONY)
Rossouw et al. (2016)	Sphyrna lewini	Scalloped hammerhead	5	13	3–16	1–5(1–8)	GERUD (COLONY)
Green et al. (2017)	Sphyrna lewini	Scalloped hammerhead	10	5	13–25	2–4(2–8)	GERUD (COLONY)
Chapman et al. (2004)	Sphyrna tiburo	Bonnethead	4	22	3–18	1–3	GERUD
Craven et al. (2018)	Squalus acanthias	Spiny dogfish	5	3	5–7	1	Allele counting
Lage et al. (2008)	Squalus acanthias	Spiny dogfish	8	10	3–7	1–2	GERUD
Veríssimo et al. (2011)	Squalus acanthias	Spiny dogfish	7	29	4–11	1–2	GERUD
Daly-Engel et al. (2010)	Squalus mitsukurii	Shortspine spurdog	8	27	3–10	1–2	Allele counting
Nosal et al. (2013)	Triakis semifasciata	Leopard shark	4	17	11–33	1–2	GERUD
Lyons et al. (2017)	Urobatis halleri	Round stingray	5	20	3–6	1–3(1–5)	GERUD (COLONY)

explanations may be due to other, unrecognized factors in the pursuit of knowledge. For example, the fact that elasmobranch research has traditionally been dominated by men may have inadvertently contributed to this bias, and should not be dismissed offhand (Figure 1; Supporting Information and Table S1). While scientists aim to be objective, numerous research demonstrates that we, as human beings, bring our own implicit biases into scientific interpretation of data (Greenwald & Krieger, 2006; MacCoun, 1998; Sprague, 2016) and how we evaluate the work of others (Foschi, 2000; Handley et al., 2015; Steinpreis et al., 1999). While convenience polyandry as the most commonly cited explanation may result from simple past-precedence, social context may also have unconsciously favoured an explanation that also happens to be androcentric. This is not to say that no past study has considered female-based mechanisms to explain multiple paternity, as several have (Chapman et al., 2004; DiBattista, Feldheim, Thibert-Plante, et al., 2008; Feldheim et al., 2004); however, explaining the manifestation of a particular multiple paternity outcome is exceedingly difficult, with convenience polyandry having become the default explanation. While potentially true in some instances, the convenience polyandry dogma ignores a whole suite of mechanisms that could also result in multiple paternity.

The breadth of elasmobranch diversity—from degrees and modes of maternal investment, range of reproductive strategies, modes of trophic ecology and unique physiology—provide a broad platform for testing hypotheses related to mating systems across vertebrates. Furthermore, elasmobranch mating systems are not confounded
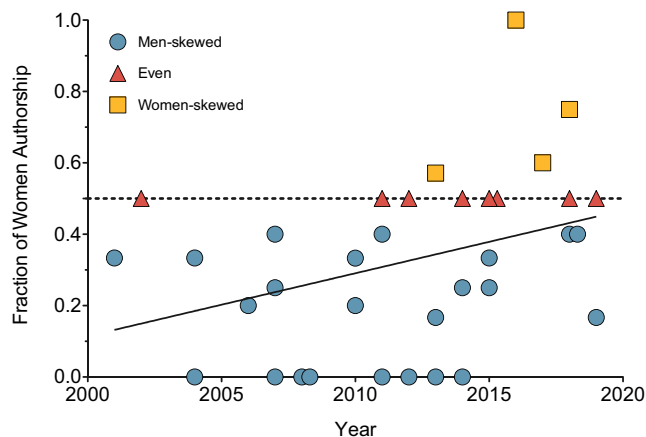
FIGURE 1 Comparison of gender composition of authored papers included in the present study across time. Dashed line represents studies where gender ratio is equal (red triangles), below the horizontal, dashed line is skewed towards men (blue circles) and below the line skewed towards women (yellow triangles). The solid line indicates a significant increase in the fraction of women authorship over time (p = .032, $F_{1,33}$ = 4.99, r^2 = .14). We recognize gender is not governed by biological sex and is not a binary variable. We used the best information available online to evaluate gender on a binary scale, which we acknowledge is an over-simplification. This preliminary analysis is presented merely to demonstrate a point and could benefit from further examination (see Supporting Information and Table S1)

with premating (e.g., harems, mate guarding or lekking behaviour) or post-birth (e.g., parental care) drivers found in other vertebrate taxa, providing useful models with fewer confounding variables relative to other taxa. Despite their advantages as a study system, elasmobranchs are an underutilized group for testing broader evolutionary theories (Mull et al., 2020). Fortunately, there has been a surge of multiple paternity investigations recently as molecular tools have advanced and costs have reduced; however, little investigation into possible mating dynamics has been made besides simply stating that multiple paternity is present.

While convenience polyandry or low mate encounter rates remain viable explanations for (or the lack of) multiple paternity, they are limited in their focus and ignore other equally parsimonious drivers that could be at play in elasmobranchs. Given the high degree of maternal investment into offspring, the presumption that female elasmobranchs play no role in the reproductive process besides being passive vessels to receive sperm seems unlikely. High levels of maternal investment with potential risks to their fitness predicts that females should exert some influence over sireship through any combination of pre-/post-copulatory or post-fertilization mechanisms (Zeh & Zeh, 2001); however, little research has been conducted to examine drivers of multiple paternity from the female perspective in elasmobranchs. Therefore, the primary objective of this paper is to demonstrate the possibility of alternative mechanisms that explain multiple paternity across elasmobranch species through an analysis of available data from peer-reviewed literature viewed through the female lens. We start by laying out a series of predictions across species for how rates of multiple paternity, rates of sireship, sireship skew and relative sireship in relation to lifetime reproductive output may be altered if male or female pre- or post-copulatory mechanisms are at play. We holistically examine how the current literature on elasmobranch multiple paternity conforms to these predictions. Finally, we lay the ground for future studies to explore these other mechanisms through hypothesis-driven science.

2 | METHODS

2.1 | Theoretical predictions

Given the stakes elasmobranch females have in the reproductive process, we made a point of including the female perspective in the development of our predictions. Drawing on knowledge from across various vertebrate and invertebrate systems, we assumed at the outset that both female and male drivers could play a role in determining the prevalence of multiple paternity in any given scenario. Drivers were attributed to the sex with the most presumed influence and classified as pre- or post-copulatory. We then hypothesized how these factors may push or pull a system in a particular direction (for details on Figure 2, see Box 1). Our objective was not to determine the relative influence any of these have in relation to one another, but rather to compare these competing drivers against empirical

(a) % Multiple Paternity

(b) Sireship

(c) Skew in polyandrous litters

(d) Cost to Females
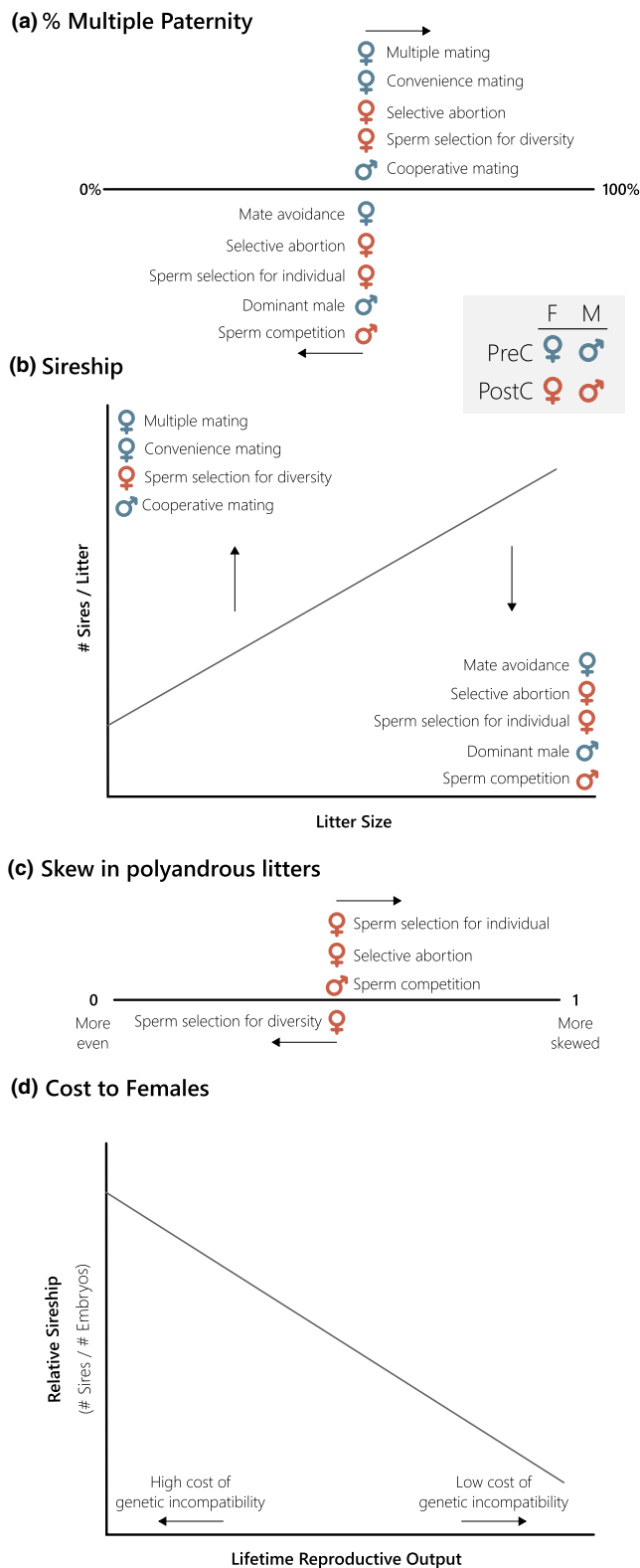
FIGURE 2 Theoretical predications for female and male drivers of incidences of (a) multiple paternity, (b) sireship (number of sires per litter) against increasing litter size, and (c) skew in polyandrous litters. See Box 1 for descriptions of the rationale. (d) The predictive relationship between relative sireship and lifetime reproductive potential

data to give insights into the forces that may influence particular multiple paternity patterns in a given system.

Our first model examines the potential influence that each of these drivers have on a population's incidence of multiple paternity (Figure 2a). When multiple paternity occurs, our second model predicts an increasing number of sires with increasing litter size across populations and species (Figure 2b). As litter size increases, and females mate with multiple males, there are more physical opportunities (ova) for males to fertilize; thus, we predict an overall positive relationship across species between litter size and number of sires/litter. However, each driver may increase or decrease the theoretical number of sires per litter relative to the trend inferred by litter size alone. Our third model addresses drivers that may affect sire skew in polyandrous litters (Figure 2c). Here, skew is defined as a lack of evenness in sireship (i.e., a single or small subset of sires account for a disproportionate number of fertilizations in a given litter).

Finally, our fourth model considers a novel perspective by which to consider patterns of multiple paternity: through the lens of species' life history and the theory of genetic incompatibility (Jennions & Petrie, 2000; Tregenza & Wedell, 2000; Zeh & Zeh, 1996). Females vary in terms of their potential lifetime reproductive output (LRO), or the maximum potential number of offspring (embryos) produced per lifetime, as a function of female age at maturity, species' longevity, breeding period and litter size. Here, our usage of LRO does not consider natural or other factors of mortality of offspring after birth, but rather represents the sum of all potential embryos a female of a given species could produce across her lifetime. However, we recognize use of LRO in this manner is liberal as species with high fecundity are predicted to have lower rates of offspring survival during the juvenile stage (Branstetter, 1990; Jaquish et al., 1991). This creates interspecific variation for the relative importance of each individual offspring to their mother's overall reproductive fitness. Stated another way, offspring of species with low LRO contribute more per individual to their mother's reproductive success than those of species with higher reproductive outputs. Thus, copulations and subsequent fertilizations with incompatible males that result in unviable offspring are costlier to females with lower LRO, leading to a predicted negative relationship between number of sires per litter and species' estimated LRO (Figure 2d). Because of this, evolutionary drivers may select for diverse sireship to reduce the probability of fertilizing eggs with genetically incompatible males, which inevitably leads to variation in multiple paternity across species.

Empirical data from the literature were compared against our theoretical models. Deviations from predicted trends may provide insights into types of drivers that may be particularly influential for specific species.

2.2 | Literature search

A comprehensive literature search was conducted to identify every available study that addressed multiple paternity in elasmobranchs

BOX 1 (a,b) % Multiple paternity and Sireship

Towards increased rates of multiple paternity rates and/or sireship:

Female precopulatory – multiple mating: females soliciting multiple copulations would be expected to increase prevalence of multiple paternity as well as the number of sires per litter.

Female precopulatory – convenience mating: females submitting to multiple copulations would be expected to increase prevalence of multiple paternity as well as the number of sires per litter.

Female postcopulatory – selective abortion: females selectively aborting embryos from certain sires would be expected to increase multiple paternity if females are selecting for litters with a diverse sireship.

Female postcopulatory – sperm selection for diversity: females enacting mechanisms to enable sperm from multiple sires to fertilize eggs would be expected to increase multiple paternity as well as the number of sires per litter.

Male precopulatory – cooperative mating: males utilizing behaviours that enable multiple males to copulate with females in a group setting would be expected to increase rates of multiple paternity as well as the number of sires per litter.

Towards decreased rates of multiple paternity and/or sireship:

Female precopulatory – mate avoidance: females enacting behaviours to avoid males would be expected to decrease rates of multiple paternity because they are creating situations where mating with multiple males is reduced. Number of sires per litter is also expected to be lower.

Female postcopulatory – selective abortion: females selectively abort embryos from particular males, which could have the effect of reducing number of sires per litter as well as lower rates of multiple paternity.

Female postcopulatory – sperm selection for individual: females selecting for sperm from particular males would be expected to reduce rates of multiple paternity as one male would be preferentially selected while reducing success of sperm from other males. Lower number of sires per litter is also expected.

Male precopulatory – dominant male: male behaviour limiting other male access to females, thereby lowering/preventing other males from copulating, would be expected to lower rates of multiple paternity and lower rates of number of sires per litter.

Male postcopulatory – sperm competition: sperm from particular males that outcompetes sperm from other males will lead to lower rates of multiple paternity if he is successful at siring a majority (if not all) of a litter. Lower number of sires per litter is also expected.
(c) Skew in polyandrous litters.

Towards more skewed litters

Female postcopulatory – sperm selection for individual: preference given for particular sperm could lead to more of a litter being sired by one or a few particular males. This would create litters where sireship diversity is reduced.

Female postcopulatory – selective abortion: removal of embryos that are sired by particular males would have the effect of reducing litter sireship diversity, and therefore skew litter sireship composition towards one particular sire.

Male postcopulatory – sperm competition: the most competitive sperm would be expected to sire a more available ova than less competitive males, which would skew litter sireship towards particular individuals.

Towards more even litters

Female postcopulatory – sperm selection for diversity: females employ mechanisms to counteract sperm competition or utilize mechanisms to enable sperm equal chances at fertilizing ova. This would be expected to result in litters with more evenly distributed sireship.
(d) See main text.

up to October 2019. To accomplish this a combination of taxonomic category ("elasmobranch," "chondrichthyes," "shark," "ray," "skate") and polyandry synonym ("polyandry," "multiple paternity," "sireship") was searched in both the Google Scholar database and Web of Science. To be included in this study, papers had to report either results of their genetic analysis of females and their litters or provide a robust parental reconstruction based on genetic data.

From each suitable study, we extracted species information, location of sample collection, number of litters evaluated, number embryos per litter, type and number of genetic markers used,

method used to identify multiple paternity (GERUD, COLONY or simple allele counting) and number of sires per litter. Several studies reported separate multiple paternity estimates for distinct populations or stocks of the same species (e.g., Boomer et al., 2013; *Mustelus antarcticus* from four distinct stocks). Because we lacked detailed information regarding populations for each location, we chose to retain each multiple paternity estimate as a distinct observation. Additionally, we retained parentage estimates based on method as distinct observations due to different calculations of multiple paternity. GERUD calculates the minimum number of sires per litter and is considered more conservative (Jones, 2005), while COLONY estimates the most likely number of sires per litter (Jones & Wang, 2010). When available, data on maternal length were noted as well as whether the authors attributed multiple paternity to at least convenience polyandry. For each of the species included in this study, an additional literature search was conducted to determine if that species is known to exhibit any form of sperm storage. Additionally, reproductive mode and life history parameters to estimate LRO for each species were mined from the Sharkipedia life history database (www.sharkipedia.org).

2.3 | Calculations

The incidence (percentage) of multiple paternity within each population was determined by dividing the number of litters exhibiting multiple paternity by the total number of litters analysed multiplied by 100. Multiple paternity incidences were calculated separately if multiple parentage reconstruction methods were used. It should be noted that metrics measured in wild-caught females of egg-laying species are likely to be underestimated, as studies using oviparous females were collected from the wild and subsequently kept in isolation in captivity over the course of a laying season without opportunity to solicit further copulations.

Following Neff et al. (2008), a skew metric was determined by first calculating the effective number of sires per litter ($Sires_{Effective}$):

$$Sires_{Effective} = 1/\Sigma \left(rs_i/brood\ size \right)^2,$$

where rs_i represents the number of offspring assigned to sire i summed across all the sires in a litter. Skew for each litter was then calculated as:

$$Skew = 1 - \left(Sires_{Effective}/Sires_{Actual} \right),$$

where $Sires_{Actual}$ represents the actual number of sires in that litter. Thus, values closer to 0 represent litters that have more even sireship and values closer to 1 represent litters where sireship is more skewed. Mean (± SD) skew was calculated for each population per study; however, only litters where at least two sires were identified were included in the analysis (i.e., singly sired litters were excluded).

Finally, the mean number of sires per offspring (herein referred to as relative sireship) was determined by dividing the number of sires per litter by the number of embryos in that litter and taking the mean and standard deviation (SD) across all the litters analysed for that study. Sireship was calculated separately for multiple species, populations, or methods were reported. LRO was calculated as the mean number of potential offspring a female can produce in her lifetime:

$$LRO = \left(A_{max} - A_{mat} \right) /R_{interval} * F.$$

where A_{max} represents maximum age, A_{mat} represents the age at maturity, $R_{interval}$ represents the reproductive interval or the number of years between litters (e.g., 1 for annual breeders, 2 for biennial breeders, etc.) and F represents fecundity. Species were excluded from our analysis of the relationship between LRO and relative sireship if litter paternity information was incomplete (whale shark *Rhincodon typus* Smith; Schmidt et al., 2010), basic life history data were not available (bluntnose sixgill shark *Hexanchus griseus* Bonnaterre; Larson et al., 2011) or mating along with pup birth occurred in an aquarium setting not reflecting natural conditions (spotted eagle ray *Aetobatus narinari* Euphrasén; Janse et al., 2013).

All calculations and analyses were performed in R (version 3.6.1; R Core Team). We chose to not use phylogenetic correction given the relatively small samples size (<50 species) and because many families were only represented by a single species.

2.4 | Incidence of infertility

If females are able to detect when fertilizations with incompatible males have occurred, then we would predict females to have mechanisms by which to selectively terminate development to avoid the energetic toll of bringing on an unviable embryo to term (Heideman, 1988; Kozlowski & Stearns, 1989). Therefore, a second literature search was performed for studies that mentioned occurrence of seemingly unfertilized (i.e., resorbing or nondeveloping) eggs or embryo deformities in the uterus of pregnant females, referred to here as "infertility" or "deformities," respectively, to distinguish between instances where an egg did not develop or where a visible embryo was clearly not going to be carried to term (i.e., missing tail, necrotic, arrested development not associated with diapause, etc.). While we cannot know the root cause of why some ovulated eggs failed to develop, in nearly every instance where this was observed, it occurred alongside normally developing littermates, suggesting that sperm limitation was not a factor. Thus, for the purpose of demonstrating a point about the widespread nature of these events that often are considered "unremarkable," we refer to them by their most-referenced name (i.e., "infertile eggs"), while recognizing that there may be deliberate mechanisms that account for why these eggs failed to develop (e.g., genetic incompatibility) but we are unable to test for. Deformities mentioned ranged from embryos with missing/malformed tails to those undergoing necrosis, and were assumed to be unviable and, therefore, represented a failed reproductive event for that individual embryo. For each study, we either calculated the occurrence of either of these events in a litter out of
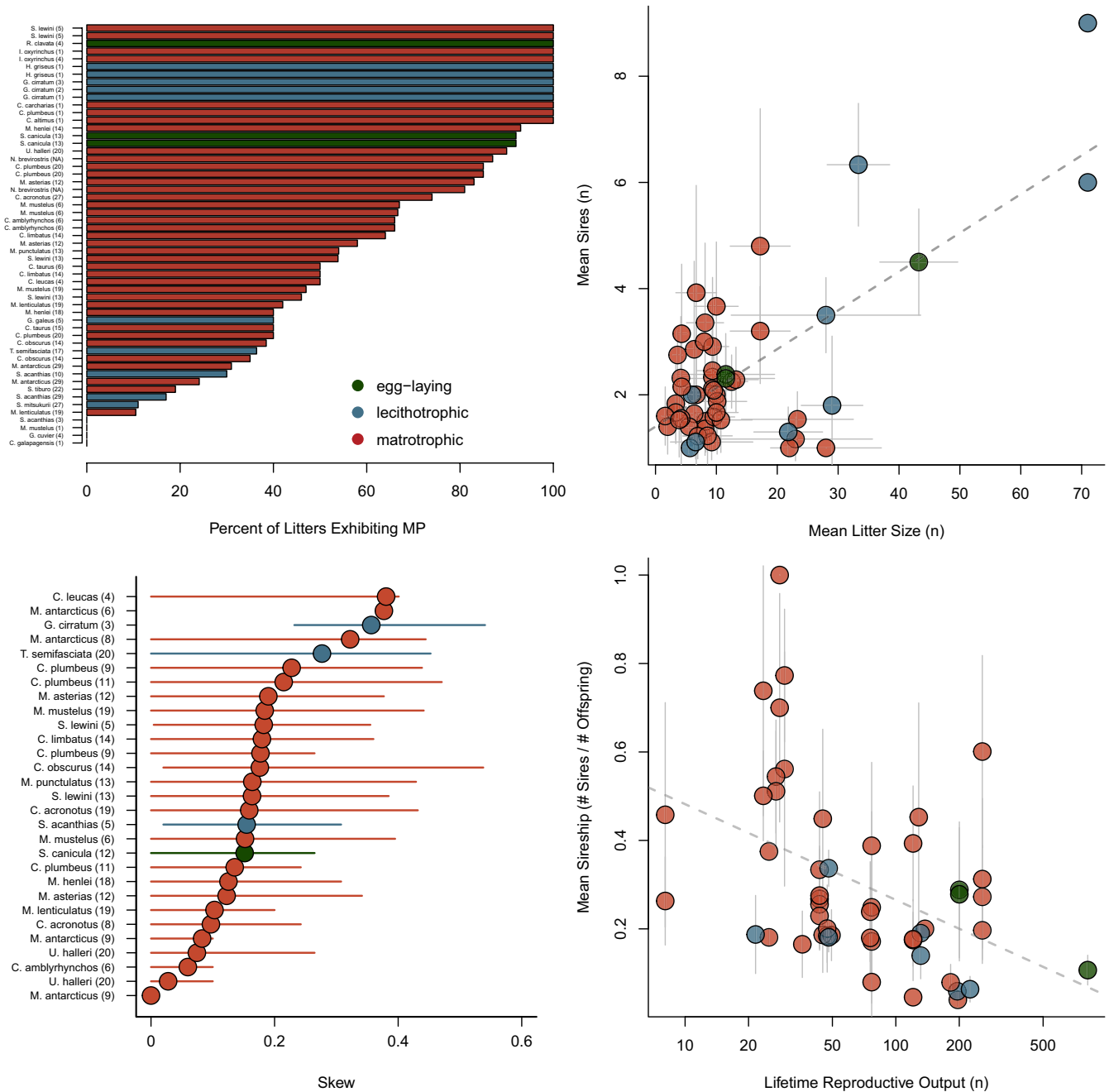
FIGURE 3 (a) Occurrences of polyandrous litters in a study were compared across populations by matrotrophic mode. Note that some studies report multiple populations of the same species and we include each population as a separate observation. Where both COLONY and GERUD results were reported, both are represented. Litter size for each species by study is given in parentheses. (b) Mean number of sires per litter positively increased with mean litter size across elasmobranch species. Species variation in sire number and litter number across studies is represented by the grey crosses. (c) For polyandrous litters, a skew metric based on Neff et al. (2008) was calculated for species with individual sire data per litter. Litters with higher skew (i.e., uneven sireship) are closer to 1. Note that some studies report multiple populations of the same species and we include each population as a separate observation. Where both COLONY and GERUD results were reported, both are represented. Mean skew is denoted with the circle and the standard deviation is noted with the lines for each species. (d) For each species where multiple paternity data and sufficient biological information existed, estimated lifetime reproductive output was determined and compared against mean relative sireship (number of sires/number of embryos). Litter size for each species by study is given in parentheses. Maternal investment strategy is indicated as lecithotrophic (i.e., yolk-sac live-bearing) in blue, matrotrophy (i.e., providing supplemental nutrition) in red, and egg laying in green

the total number of pregnancies examined by species for each study or obtained the rate of infertility if it was directly reported by the study's authors. We were able to obtain information on infertility

and embryo deformities from a range of species by mining a long-term data set spanning 1978–2018 collected from the US northwest Atlantic (US National Marine Fisheries Service, unpublished data).

For these species, we calculated the occurrence of either infertile eggs or deformed embryos in a litter per total number of pregnant females of that species examined over the 40-year period. Since most species identified were live-bearing, incidences of reported infertility and/or embryo deformities were also compared by their matrotrophic mode (lecithotrophy, histotrophy, oophagy or placentatrophy), although there was too little information across modes to conduct a formal analysis.

Since studies of multiple paternity are inherently more difficult in egg-layers, most studies of these species occurred by capturing reproductive females in the field and holding them in the laboratory, where sireship was determined for eggs subsequently laid in isolation. While the lack of access to new males probably influences multiple paternity outcomes, we were able to extract information on egg "infertility" for the small-spotted catshark (*Scyliorhinus canicula* Linnaeus; Griffiths et al., 2011). In their supporting information, we found instances where eggs were laid but never developed, and thus no DNA was extractable for multiple paternity analysis. Although the author attributes these events to lack of fertilization, for many females they laid successful eggs subsequent to nonsuccessful eggs, suggesting they were not sperm-limited. Thus, to demonstrate that development failure can occur in oviparous species as well, we compared infertility variability across mothers examined by Griffiths et al. (2011).

3 | RESULTS

3.1 | Frequency of multiple paternity

Multiple paternity was observed in most studies conducted on elasmobranchs (87%, 34 out of 39 studies). There was considerable variation in the incidence of multiple paternity among the 39 studies analysed, ranging from 0% to 100% across species (Figure 3a). While there was no clear connection between the program used to determine sireship and rate of polyandry, variation across and within species was potentially attributed to sample size differences. In 13 studies—covering predominantly large to moderately sized live-bearing sharks and a single species of skate—every litter analysed exhibited multiple paternity. Of these 13, seven studies were only conducted on a single litter, probably overestimating the occurrence of multiple paternity for these species. Studies that found no evidence of multiple paternity were similarly confounded by smaller sample sizes. Two of four studies with no multiple paternity observed were only conducted on a single litter (common smoothhound *Mustelus mustelus* Linnaeus and Galapagos shark *Carcharhinus galapagensis* Snodgrass & Heller), and both common smoothhound and spiny dogfish (*Squalus acanthias* Linnaeus) exhibited multiple paternity in other studies. Tiger shark (*Galeocerdo cuvier* Péron & Lesueur) was the only species to exhibit no multiple paternity, though only four litters were examined (mean number of litters examined across studies: 10.4 ± 8.9), making evidence against multiple paternity weak.

3.2 | Sireship

The mean number of sires per litter increased with fecundity (sires = 0.7 * litter size + 1.4, $F = 48.73$, $df = 51$, $r^2 = .48$; Figure 3b). Out of 54 studies, sire number per litter ranged from one (no multiple paternity) to nine, though most litters were sired by fewer than four males (mean ± SD, 2.35 ± 1.5 sires). There were no clear differences in sireship between reproductive modes.

3.3 | Sireship skew

Of the 55 instances where multiple paternity was examined for a species (includes both methods and separation by subpopulation if examined), only about half ($n = 29$, 52%) had information available to calculate sireship skew (see Table S2). Of these, a majority exhibited some degree of sireship skew (28/29), although values varied both within and among species (Figure 3c). Most instances contained at least one litter with no sireship skew (25/29), indicating sire contributions to the litter were even among fathers. Highlighting variability within species, in nine litters of gummy shark (*Mustelus antarcticus* Günther) from South Australia no sireship skew was observed; however, the same study identified sireship skew in the same species from nearby areas in New South Wales (0.08 ± 0.015), Victoria (0.38) and Western Australia (0.322 ± 0.14; Boomer et al., 2013). The highest degree of sireship skew was observed in litters with three or more sires, where an apparent single male sired a majority of offspring. In particular, only two litters from different species exhibited sireship skew over 0.5. In a litter of dusky shark (*Carcharhinus obscurus* Lesueur) from the east coast of South Africa, four putative fathers sired offspring in a ratio of 10:2:1:1 for a calculated sireship skew of 0.54. Similarly, a litter of nurse shark (*Ginglymostoma cirratum* Bonnaterre) also had a sireship skew of 0.54, where sireship was distributed among seven sires 17:12:6:1:1:1:1.

3.4 | Lifetime reproductive output

Potential lifetime reproductive output varied from 8.05 potential offspring in blacktip shark (*Carcharhinus limbatus* Müller & Henle) to over 800 in thornback ray (*Raja clavata* Linnaeus; see Table S3). Across species, a negative relationship was found between mean relative sireship (number of sires/number of offspring) and lifetime reproductive output, such that as female reproductive potential increased the number of sires contributing to litter paternity decreased (relative sireship = −0.21 * lifetime reproductive output + 0.7, $F = 11.53$, $df = 49$, $r^2 = .17$; Figure 3d).

While lecithotrophic live-bearing species tended to have lower relative sireship over the range of lifetime reproductive output, there was no significant difference observed between other reproductive modes (all pairwise slope and intercept comparisons, $p > .05$). For instance, species with the highest relative sireship
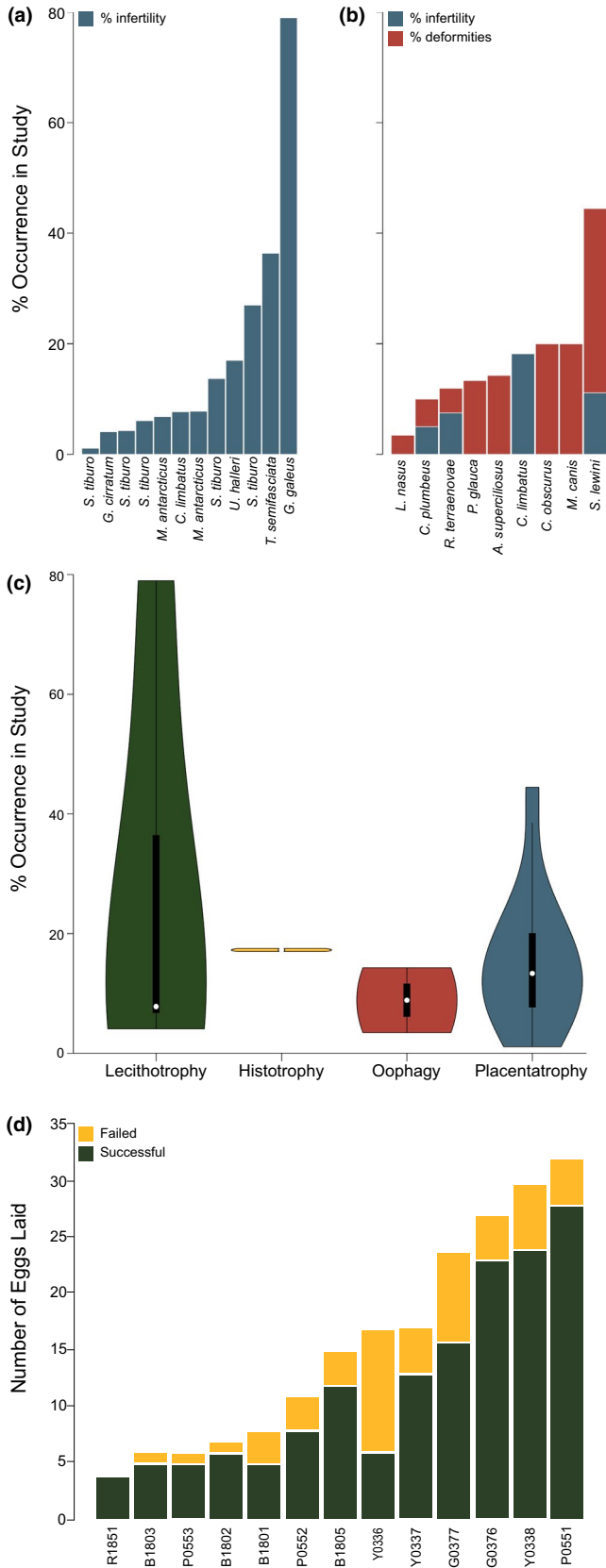
FIGURE 4 (a) Infertility rate (blue bars) was noted in elasmobranchs where studies explicitly stated the rate of occurrence of ovulated eggs that failed to develop. Note that infertility for bonnethead *Sphyrna tiburo* is listed multiple times to distinguish infertility rates noted at disparate locations. (b) Likewise, both rates of infertility (defined as eggs that failed to develop, blue bars) and embryo deformities (red bars) were noted across a 40-year period for data collected by the US National Marine Fisheries Service. (c) Rate of infertility and/or embryo deformities were compared against species' matrotrophic strategy. (d) Infertility was also noted in the supporting information provided by Griffiths et al. (2011) and has been visually re-created here

COLONY: 0.74 ± 0.28) with similar LRO on the lower end of the spectrum (23–30). By contrast, blacktip sharks exhibited the lowest potential lifetime reproductive output, but only a moderate degree of relative sireship (0.26 ± 0.1, GERUD; 0.46 ± 0.25, COLONY), which was probably constrained due to their low fecundity (mean 4.6 pups per litter), biennial reproductive cycle and short longevity (estimated 10 years maximum age) compared to other elasmobranchs in this data set.

3.5 | Incidence of infertility

Among live-bearing elasmobranchs, 12 studies across eight species explicitly reported the presence of nondeveloping eggs or deformed embryos alongside normal developing embryos (Figure 4a). The occurrence of these events ranged both within and across species and matrotrophic modes. In one study of tope shark (*Galeorhinus galeus* Linnaeus), 79% of females (*n* = 203) had at least one or two nondeveloping uterine eggs with a mean litter size of 29 (Peres, 1991). Bonnethead (*Sphyrna tiburo* Linnaeus) had one of the lowest rates of infertility recorded; however, this varied by location along the west coast of Florida (1%–27%; Manire, 2002; Parsons, 1993). Similarly, in a longer term data set, out of 23 available species where at least one pregnant female was sampled, nine species had documented cases ranging from undeveloped eggs to a variety of embryo deformities (Figure 4b). The occurrence of infertility ranged from ~3% in porbeagle shark (*Lamna nasus* Bonnaterre) to 44% in scalloped hammerhead (*Sphyrna lewini* Griffith & Smith). For reproductive modes with the largest sample sizes (placentotrophy and lecithotrophy), there was a high degree of variation among species for occurrences of infertility and/or embryo deformities (Figure 4c).

The incidence of infertility can also vary within an egg-laying species as well. Out of 13 small-spotted catshark females, 12 demonstrated some degree of egg development failure, with occurrences variable across females ranging from 12% to 65% (Griffiths et al., 2011; Figure 4d). The probability that nonviable eggs were a result of sperm limitation was low considering that most females (10/12, 83%) laid eggs subsequently after nonviable ones where these embryos developed as a result of sexual reproduction (i.e., not as a result of parthenogenesis).

exhibited a range of matrotrophic strategies from placental (blacknose shark *Carcharhinus acronotus* Poey, COLONY: 0.77 ± 0.15) to adelphophagy (sand tiger *Carcharias taurus* Rafinesque, GERUD 0.7 ± 0.26) to histotrophy (round stingray *Urobatis halleri* Cooper,

4 | DISCUSSION

Our study provides a comprehensive analysis and novel approach for considering the drivers of multiple paternity in elasmobranchs. While it is becoming clear that polyandry is more the rule than the exception (Lamarca et al., 2020), the exact mechanisms behind this phenomenon have received little attention beyond the notion of convenience polyandry, which is difficult to empirically demonstrate (Boulton et al., 2018) and has not been formally tested in elasmobranchs. While we do not discount male-based drivers as playing an important role in the reproductive process, we caution against these being used as the only explanations for the high occurrence of polyandry across elasmobranch mating systems in the absence of empirical testing. Instead, we advocate multiple paternity be considered in a more holistic view of the entire reproductive process and the context in which it occurs (Kokko & Rankin, 2006; Parker et al., 2013), as drivers may vary in importance and intensity both across and within species. Our findings support the role of additional mechanisms, particularly cryptic female choice. The strength of any one mechanism for increasing parental fitness will depend on the individual mating system of any given species as well as impact on a single reproductive cycle or over an entire reproductive lifespan. We discuss three scenarios influencing multiple paternity outcomes below in more detail: (i) male–male competition, (ii) female choice and (iii) the effect of lifetime reproductive output.

4.1 | Male–male competition

Male-driven factors are the most commonly credited explanations for polyandry in elasmobranchs. This is in part due to often physically rigorous copulation characterized by single male or multiple males harassing and biting females and subsequent presumed female acquiescence (Marshall & Bennett, 2010; Pratt & Carrier, 2001; Whitney et al., 2004), making it an easy explanation for why litters comprise multiple sires. Male–male competition is probably a strong determinant for multiple paternity outcomes for particular mating systems. For instance, in species where conspecific density and female fecundity are high, male–male competition may be the strongest factor influencing occurrences of polyandry. Mating behaviour has been extensively studied in nurse sharks (Carrier et al. 1994; Pratt & Carrier, 2001), where the presence of more males increases cooperative copulation success, suggesting that behaviour may play a role in male access to females. In other high-density species, such as the whitetip reef shark (*Triaenodon obesus* Müller & Henle), the few recorded instances of group mating behaviour were attributed more to male–male competition for access to the female than male cooperation (Whitney et al., 2004). Thus, precopulatory behaviour between males may also be important for determining multiple paternity outcomes within the ecological context of the species.

The evolution of internal fertilization probably increased sexual conflict in elasmobranchs. As the physical process of sperm–egg fusion from the male perspective moved to "behind closed doors,"

copulation becomes an unreliable measure of fertilization. Thus, males must rely on other external cues to gauge conspecific mating activity. Males' perception of their degree of intraspecific competition is often inferred through reproductive morphometrics in a population, specifically comparing relative testes mass as a proxy for sperm production capability (Kenagy & Trombulak, 1986; Moller & Briskie, 1995; Stockley et al., 1997). In round stingrays, high variation in testes mass suggests that males perceive their degree of intrasexual competition to be high, which is likely considering the high density of stingrays in sampling locations (Lyons et al., 2017). In small-spotted catsharks, other male reproductive tract morphometrics (epididymis and seminal vesicle diameter, clasper length, testes mass) are significantly larger in one population, which authors attribute to possible differences in sperm competition (Finotto et al., 2015). Variation in reproductive morphometrics suggests male–male competition cannot be excluded as an important driver of multiple paternity when population densities and male/female ratios are high. In particular, further work documenting male/female ratios in the context of reproductive receptivity (i.e., mature, reproductivity active males and mature, nongravid females) rather than as the total number of males and females that may be present in a system could provide deeper insights. However, this requires dedicated sampling efforts to understand the study population's biology beyond what is usually done, where assumptions about the population are made retroactively. Furthermore, for males to accurately assess mating competition depends on their ability to detect or perceive their competition. Unless mating is occurring at regular locations at predictable times in clear water, this may be more difficult for males than is typically assumed because males are not omniscient. Future studies characterizing male reproductive behaviour and conspecific interaction can help fill these gaps. Along these lines, male–female social dynamics and/or drivers of aggregation or sexual segregation may also be important factors to consider as well (Jacoby et al., 2012). An individual's presence (or absence) may influence the behaviour of conspecifics, which could have downstream effects on mating behaviour that ultimately underpins multiple paternity. As technology advances, incorporation of multidisciplinary tools may allow these behavioural aspects to be considered in our understanding of elasmobranch mating systems (Sims, 2005; Sims et al., 2001).

In concert with precopulatory forms of male competition, post-copulatory mechanisms, specifically sperm competition, may factor into male reproductive success as well. In systems with a high degree of intraspecific male competition, reproductive success may become more skewed such that more fertilizations within a litter are attributed to an individual sire. In systems where sperm competition is the main driver of multiple paternity, which may increase with female's ability to store sperm, we would predict high skew within litters. Likewise, systems with a lower-than-expected mean number of sires based on litter size may also indicate sperm competition, if most fertilizations can be attributed to an individual male at the exclusion of others. Interestingly, a handful of studies on smoothhounds (family Triakidae) have lower than predicted sires (~1.3 per litter; Boomer et al., 2013; Farrell et al., 2014; Hernandez

et al., 2014; Marino et al., 2015; Nosal et al. 2013), given their moderate litter sizes (~25 embryos), relatively high population densities and their highly migratory nature (Figure 2b). In these instances, paternity was often dominated by a single sire, and may indicate that sperm competition is an important factor influencing multiple paternity outcomes in these species.

4.2 | Cryptic female choice

The disparity in reproductive investment between female and male elasmobranchs follows classical sexual conflict theory, where an increasing number of copulations has different consequences for fitness between the sexes (Emlen & Oring, 1977; Trivers, 1972). Since males do not contribute energetic resources to offspring creation or postpartum care, his reproductive fitness is predicted to be solely related to the number of successful copulations (Avise & Liu, 2010). In contrast, females are limited in the number of offspring they can produce, and their fitness is more likely to be closely linked to annual and lifetime fecundity and the survival of offspring than to the number of copulations. Thus, female reproductive fitness is probably more dependent on "quality" of mates than "quantity" to create viable offspring. The sex-related differences between these reproductive fitness strategies, and the high cost incurred by females to physically create offspring, makes it unlikely that female elasmobranchs have no mechanisms by which to exert choice over the paternity process.

While the ecological context of mating systems varies across elasmobranchs (density-dependence, mate encounter rates, copulatory behaviours, etc.), multiple paternity is prevalent in most species. Regardless of mating dynamics, we demonstrate that female choice may play a role in how multiple paternity manifests itself in litters. While a positive relationship between the number of sires and litter size is predicted based on increased fertilization opportunities, the high variance in sires per litter, especially in species with low litter size (<10), suggests other mechanisms are at play besides those that are male-mediated. Theoretically, male-mediated mechanisms of multiple paternity should result in lower numbers of sires per litter with high rates of skew as certain males monopolize fertilizations. The outcomes of female-mediated mechanisms are less clear and the expectation depends on the specific costs and the ability of females to gauge males. When females can ascertain male fitness or compatibility, we might expect them to select for fewer sires and allow compatible males more access to fertilization, resulting in fewer sires and high skew, similar to the outcomes of male–male competition. Alternatively, if females cannot gauge male quality or compatibility before mating, and the potential fitness costs are high, we might predict the opposite where she opts for more fertilization opportunities to more sires with lower rate of skew. Interestingly, for those species with smaller litter sizes (<10), we observed a substantial number of them having increased sire numbers per litter compared to species with larger litters (>10). Considering that there is less opportunity for multiple paternity to occur and be detected with small litters,

instances with higher-than-expected sire numbers may indicate situations where female choice is preferentially selecting for a higher diversity of sires. The selection for a higher number of sires could represent a bet-hedging strategy by females to buffer against the probability of mating with poor quality or incompatible males, which we discuss in more detail below.

4.3 | Lifetime reproductive output

While the dynamics and costs of multiple paternity are often examined in the context of a single reproductive event, the opportunity cost of future reproductive success is potentially a strong driver influencing female choice. Considering that potential female fecundity is limited and that only a certain number of ova are produced during the course of vitellogenesis, females should theoretically work to maximize the probability of offspring survival without reducing their chances for future reproductive success. While female elasmobranchs will always incur a physical cost due to rigorous copulation, whether with single or multiple males, the hidden opportunity costs of mating with suboptimal or incompatible males vary depending on her potential lifetime reproductive output. Genetic incompatibility (Jennions & Petrie, 2000; Tregenza & Wedell, 2000; Zeh & Zeh, 1996), and the cost that may impose on female reproductive success (Stockley, 2003), may provide insights into why multiple paternity appears to be a key feature of elasmobranch mating systems. For females, mating with a genetically incompatible male and producing unviable offspring has direct, negative impacts to her reproductive success as those fertilizations cannot be regained through additional copulations, unlike males. This cost increases for females with lower lifetime reproductive potential such that mating with incompatible or suboptimal males becomes riskier. Males, conversely, incur lower costs when mating with a genetically incompatible female because he can still mate with other females in the same reproductive season. Thus, the cost of genetic incompatibility is expected to disproportionately affect females.

The cost of mating with a genetically incompatible male is also predicted to not be equitable across species (Zeh & Zeh, 2001). Females that have low lifetime reproductive potential face a higher cost by mating with genetically incompatible males because they have fewer chances to pass their genes onto the next generation than females that are more fecund, have a longer reproductive lifespan or have a shorter interbreeding interval. Therefore, it may be risky for females to mate with a single male or allow a single male to sire a full litter when lifetime reproductive output is low. Supporting this we found a significant negative association between the number of sires per litter and estimated lifetime productivity, suggesting that multiple paternity may be more important for females producing fewer offspring over their lifetime. For females with lower reproductive outputs, the opportunity costs of genetic incompatibility may outweigh the physical cost of multiple mating. Thus, females with low lifetime reproductive output may be averse to "putting all her eggs in one reproductive event basket" by having only one sire. On

the other hand, females with high lifetime reproductive potentially incur a lower cost due to genetic incompatibility, such that the physical costs of avoiding mating may not outweigh any benefits gained from multiple copulations.

Another factor that has received limited consideration with regard to multiple paternity is female investment into embryo production, specifically as it relates to relative embryo mass as a proxy for degree of investment. How heavily females invest resources into each offspring is expected to impact mating systems in several ways. First, females that invest substantial resources into individual embryos may inversely limit litter size, particularly in viviparous females where total offspring production is constrained by maternal body size. Likewise, heavy investment may leave females energetically unprepared to enter a subsequent reproductive cycle, and could be a reason why reproductive rest periods are part of some species natural life history cycle (Castro, 2009). Together, both of these would be expected to result in lower lifetime reproductive output, which could underpin multiple paternity patterns seen in particular elasmobranch species. Second, the degree of investment may be an important factor for identifying candidate species where female sperm selection could be playing a role in that species' mating system. Females that invest heavily into each individual offspring would be expected to be more selective over which sperm fertilizes her eggs compared to females that invest less resources into each offspring. Thus, life history characteristics may prove to be a valuable (and necessary) factor when considering all possible explanations for observed multiple paternity patterns for the species at hand.

Little is known about elasmobranch females' ability to distinguish between sperm of individual males and to discern genetic incompatibilities prior to fertilization. For the purposes of the present argument, we assume genetic incompatibilities between mates are probably undetectable prior to mating and fertilization. As a result, genetic incompatibilities may manifest themselves as failed ovulated eggs, where normal embryo development does not occur. Ovulated eggs that failed to develop have been widely observed in elasmobranchs across matrotrophic modes (Castro, 2000; Griffiths et al., 2011; Hanchet, 1988; Manire, 2002; Nosal et al., 2013; Parsons, 1993; Walker, 2007). Often, these incidents are attributed as "infertility" with little further thought. Considering that these instances occur alongside other successfully developing embryos, androcentric (e.g., sperm limitation) or environmental possibilities are less likely, with genetic incompatibility representing an alternative explanation. Furthermore, "infertility" via sperm limitation as an explanation is weakened with the increased recognition that elasmobranch females can reproduce parthenogenically (i.e., in the absence of male inputs) (Dudgeon et al., 2017; Fields et al., 2015), highlighting the variety of physiological adaptations females have at their disposal. Nevertheless, we observed variation in the frequency of failed ovulated eggs both intra- and inter-specifically, suggesting this might be a more common occurrence among elasmobranchs than previously credited. Because these failed eggs represent a potentially significant energetic cost and missed opportunities to reproduce, thereby

having consequences for female reproductive success, further explorations into the link between these observations and genetic incompatibility are warranted. The data currently available are from opportunistic observations, preventing examination of the exact causes underpinning incidents of infertility, though we outline opportunities below.

4.4 | Mechanisms

Despite few studies having considered multiple paternity from the female elasmobranch perspective, aspects of their anatomy provide a platform that could enable females to place their fin print on the reproductive process (Birkhead et al., 1993; Zeh & Zeh, 1997). Many anatomical studies have noted the wide variation in oviducal gland morphology (Finotto et al., 2015; Hamlett et al., 1998; Henderson et al., 2014; Maia et al., 2015; Pratt, 1993), or "shell gland," located between the ovary and the uterus, where fertilization is thought to take place (Hamlett et al., ,2002, 2005; Pratt, 1993). The terminal zone at the posterior of the gland is also the site where sperm storage occurs in species that are purported to utilize that strategy (Soto-López et al., 2020). The high variation in the microstructure of this zone provides females an opportunity to interface with sperm to varying degrees, which may provide an arena for female-mediated sperm selection to take place (Dutilloy & Dunn, 2020). This may be especially true for species with low mate encounter rates that undergo potentially long periods of sperm storage (Pratt, 1993). Ironically, previous discussions of sperm storage in elasmobranchs focused solely on the potential for sperm competition, despite the fact that sperm in these situations are completely reliant on female biology to maintain their health and viability until ovulation (Hamlett et al., 2005). This provides ample time and proximity for females to alter or influence sperm access to ovulated eggs (Zeh & Zeh, 1997). Furthermore, the oviducal gland is largely composed of glandular cells, the secretions of which could also influence sperm motility, and thus fertilization success, as has been documented in other fish species (Rosengrave et al., 2008). This arena provides substantial opportunities for cryptic female choice to occur.

Selective ovulation (Petrie & Williams, 1993) represents another possible mechanism by which females may influence multiple paternity outcomes by regulating when sperm are allowed to interact with eggs. In this scenario sperm from individual males only gain access during specific ovulation windows, leaving subsequent ovulations open to other males. This has been hypothesized to occur in round stingrays where examination of sireship placement of embryos in the right and left uteri indicated that females may cryptically alter ovulation patterns to produce more evenly skewed litters (Lyons et al., 2017). Other species, such as nurse sharks, have protracted ovulation windows where females release eggs over the course of several weeks (Castro, 2000). While sireship with respect to fertilization order has not been examined in this species, it may be a mechanism that females can use to solicit

copulations from different males or provide time for sperm selection or competition to occur to prevent all offspring from being sired by a single male. Further study of ovulation patterns across species with differing degrees of multiple paternity may reveal this as an important mechanism females have at their disposal to regulate sireship.

Finally, the evolution of matrotrophy, specifically placentotrophy, affords females further opportunities to exert choice such that mothers may control the fate of individual embryos through selective abortion (Gosling, 1986; Hertig & Rock, 1949; Zeh & Zeh, 1996) or diversion of resources (Cunningham & Russell, 2000) through the intimate connection they share with their offspring (Zeh & Zeh, 1997). A female's ability to manipulate litter number or composition has been particularly studied in systems where a mother's reproductive success is not equal amongst offspring, such that bearing sons or daughters has different outcomes depending on the context of the present environment or attractiveness of sires (Sato & Karino, 2010; Trivers & Willard, 1973). While litter sex ratios remain fairly even across elasmobranchs, the takeaway point from these studies, as it applies to the present work, is the agency that vertebrate females have to directly alter litter number and/or characteristics. We present preliminary data revealing the possibility that elasmobranch females employ selective abortion tactics comparable to those found in other vertebrates. If true, this could alter multiple paternity outcomes, and we advocate for studies to examine this hypothesis empirically. Across a variety matrotrophic modes, we found multiple occurrences of "deformed/resorbing" embryos, where one or more embryos within a litter were not undergoing proper development. These common observations may be evidence for female-directed selective abortion and strongly warrants further investigation framed in the context of female choice instead of disregarded as unimportant. If females are choosing to give up opportunities to produce offspring, it suggests there are important underlying reasons. For instance, Fischer's pygmy fruit bat (*Haplonycteris fischeri* Lawrence) utilize a method of delayed implantation that enables mothers the opportunity to selectively abort embryos that may present abnormalities (Heideman, 1988). As this species has one of the longest gestation periods among bats, the ability to detect nonviable offspring may be important to conserve resources and maximize survival of offspring that will be viable. Given that elasmobranchs also have close, intimate connections with their offspring with gestational periods up to 2 years or more, the potential exists that females also employ similar mechanisms to manipulate litter sizes, altering multiple paternity outcomes outside of male influence.

4.5 | Future directions

The prevalence and continued discovery of multiple paternity across elasmobranch species indicates this is an important feature of mating systems in this taxon. However, simply reporting that multiple paternity was detected (or not) in a species falls short of providing sufficient information to truly understand the evolutionary underpinnings driving these patterns and progress the field forward. Reporting the incidence of multiple paternity tends to be a particular focus of many studies, yet without directed and robust sampling these data are not informative and make it difficult to extrapolate these findings to the larger population. Future studies should aim and take care to collect and report other information (skew, embryo placement in uteri, embryo morphometrics, etc.) that will enable deeper exploration of polyandry and the evolutionary strategies involved. Furthermore, finding ways to clearly quantify the costs incurred by mating compared to the cost of genetic incompatibility (i.e., lost reproductive opportunities) may be a fruitful line of inquiry. While fresh mating wounds are no doubt substantial, caution should be used so as to not inadvertently over value this cost just because it looks bad from a human perspective. Recent comparative genomic analyses indicate that genes involved in wound healing may be under positive selection in elasmobranchs (Marra et al., 2019), resulting in their remarkable wound healing capabilities. The evolution of these adaptations may lead to wounds incurred via multiple mating to not be as costly as originally expected. However, further work quantifying these costs would be important for understanding if females do in fact mate "conveniently" to reduce these costs as is so often cited.

We have demonstrated the potential for female choice and the role that females could play in influencing multiple paternity outcomes among elasmobranchs based on evolutionary factors such as lifetime reproductive output and genetic incompatibility. Considering that various organisms across disparate invertebrate and vertebrate clades have evolved a myriad of sophisticated mechanisms enabling female agency in reproduction, it seems unlikely that female elasmobranchs would not have evolved similar mechanisms to counteract male reproductive prerogatives. To not consider the female role in multiple paternity outcomes is naïve at best. We strongly encourage future studies to explore the various adaptations females may utilize to provide themselves agency in the reproductive process such as mechanisms of female choice, the role of matrotrophy, quantification of the cost of genetic incompatibility, and determining the processes by which females may utilize selective abortion to further their reproductive success. Beginning with a comparison of sireship of viable and unviable embryos would be a start to examine possible indications of female-directed choice.

Finally, future studies should take care to consider multiple paternity from both the female and male perspective. Historically, sexual conflict has only been considered through the male lens, possibly because a majority of past literature in this taxon and others has been written by men. For instance, in the elasmobranch polyandry review by Fitzpatrick et al. (2012), only variation in male genitalia was examined with no consideration for the coevolution of complementary female reproductive anatomy. The context in which many multiple paternity studies take place and the implicit biases that influence our interpretations of data may also important to consider, especially in patriarchal Western culture (Baum &

Martin, 2018; Harding, 1991, 2015). While some studies do point out female-related drivers of multiple paternity, these are often casually mentioned.

Simply, elasmobranch multiple paternity research needs to move away from convenience polyandry as the default explanation. In addition, more care should be taken to design and implement studies so that substantive progress can be made, while not squandering the platform provided by elasmobranch mating systems that is ripe for future exploration. Most multiple paternity studies appear to occur opportunistically and typically from late-term embryos, which represent the end result of a culmination of complex processes, many of which physically occur within the female body from sperm storage (if used) to ovulation, fertilization and gestation. To focus on the single snapshot of "is multiple paternity present or not?," without consideration of other lines of evidence, such as details on embryo uterine arrangement and morphometrics to reproductive characteristics of both adult males and females in the study population, leaves the field vulnerable to stagnation and waning interest. Intersexual conflict can only take place if males and females participate. If elasmobranch females also play a role in intersexual conflict as we hypothesize, we would predict comparative morphology studies of female reproductive tracts to reveal high variance across species as is seen in males (Fitzpatrick et al., 2012). Pairing reproductive information from both males and females provides a more holistic approach to understanding the evolutionary pressures driving underlying mating systems across species. Considering the central role female elasmobranchs play in producing offspring, continuing to rely solely on androcentric explanations of multiple paternity will miss critical pieces of this puzzle.

AUTHOR CONTRIBUTIONS

K.L. wrote initial draft of the manuscript and contributed to figure generation, D.K. contributed to data analysis, and C.G.M. performed analyses and figure generation. All authors were involved in concept development and contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

Data collated from previously cited works in this study can be found on Dryad (https://doi.org/10.5061/dryad.cjsxksn5c). Note that a majority of the data utilized in this study can be found in the Supporting Information.

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SUPPORTING INFORMATION

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