REVIEW ARTICLE

Patterns of multiple paternity and maternity in fishes

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The characterization of patterns of multiple mating is a major facet of molecular ecology and is paramount to understanding the evolution of behaviours associated with parental care and mate choice. Over the last 15 years, fishes have been particularly well studied with respect to multiple maternity and paternity thanks to the widespread application of microsatellite markers. The present review focusses on the impressive literature on genetic parentage in fishes. In studies of natural populations, we find that multiple paternity is extremely common across fish species, whereas rates of multiple maternity are much more variable. In species with nest defence, for example, rates of multiple maternity are strongly bimodal, and the occurrence of multiple dams per brood is either rare or the rule. The sex of the care-giving parent is correlated with the rate of multiple parentage: when males provide uniparental care, rates of multiple paternity are low compared to rates of multiple maternity; when females provide parental care, either alone or assisted by males, rates of multiple paternity are highly variable, whereas rates of multiple maternity are quite low. These patterns may reflect conflicts between the reproductive interests of males and females. We also find that fishes in which females brood the offspring internally display much higher rates of multiple paternity compared to mammals or birds, whereas reptiles are intermediate. Male-nesting fish species, however, show rates of multiple paternity more similar to those found in other vertebrates. © 2011 The Linnean Society of London, Biological Journal of the Linnean Society, 2011, 103, 735–760.

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INTRODUCTION

Multiple mating, which results in multiple dams and sires contributing genetic material to particular nests, clutches, or broods, has a powerful influence on the strength and direction of many evolutionary processes (Andersson, 1994; Birkhead & Møller, 1998). Both the causes and effects of multiple mating have stirred controversy in the evolutionary literature. Why individuals seek multiple mates during a breeding season remains an open question for many taxa, and numerous hypotheses have been proposed (Halliday & Arnold, 1987; Jennions & Petrie, 2000). In addition, multiple mating has myriad effects on important topics ranging from sexual selection and parental care to migration and demography (Ketterson & Nolan, 1994; Sugg & Chesser, 1994; Arnqvist & Nilsson, 2000; Zeh & Zeh, 2001). Our goal is not to review the causes or effects of multiple mating, which have been reviewed elsewhere (Zeh & Zeh, 1996; Jennions & Petrie, 2000). Rather, we review the empirical literature on patterns of multiple mating in fishes in nature, considering insights that have emerged from this literature and providing a resource for future studies of mating patterns.

THE NATURAL HISTORY OF FISH REPRODUCTION: MATING SYSTEMS, PARENTAL CARE, AND SEXUAL SELECTION

Fishes exhibit the full gamut of mating systems, from strict monogamy to rampant polygynandry, polygyny and polyandry (Avise et al., 2002), reflecting ecological opportunities, sexual conflict, sexual selection, and physiological constraints. Most fishes are gonochoristic, having separate sexes. Differentiation of the sexes
sets the stage for conflict, with males and females having different reproductive interests (Emlen & Oring, 1977; Arnqvist & Rowe, 2005). Sexual conflict, sexual selection, and related processes are at the forefront of evolutionary mechanisms driving morphological, behavioural, and physiological evolution in many species (Arnqvist & Rowe, 2005), and patterns of mating play a major role in this evolutionary dance.

In most cases, the reasons that males mate multiply seem obvious. Males usually can increase their Darwinian fitness substantially by fertilizing eggs from multiple females (Bateman, 1948; Arnold & Duvall, 1994; Jones, 2009). In most instances, a male fish will be more limited by access to mates than by his ability to produce gametes, such that males of various species have evolved a number of strategies to maximize mating and fertilization success (Gross, 1996; Taborsky, 2001). One possible scenario can be described as a 'scramble competition', in which males compete to maximize the number of females with whom they mate (Andersson, 1994). Under this scenario, paternal care of eggs or offspring is not expected because males forgo care to seek additional mating opportunities. In other systems, however, males adopt a strategy that involves guarding mates or resources, such as nests or territories (Emlen & Oring, 1977; Birkhead, 1979). In such species, paternal care may be common, and males may advertise their parental quality through elaborate displays and nest construction (Møller & Thornhill, 1998). This strategy is common in many cichlids and sticklebacks, for example, in which males build nests and tend developing broods (Clutton-Brock, 1991). The male often provides parental care alone (Barlow, 2000), and such males might be expected to attempt to attract multiple females to their nests. In some cases, the female provides care along with the male (Goodwin, Balshine-Earn & Reynolds, 1998), and we might predict that a care-giving female would attempt to prevent other females from spawning in the nest. A number of other strategies are possible, such as parasitic reproductive tactics (Taborsky, 1994; Gross, 1996), and, in some extreme cases, males are limited more by their ability to provide parental care than their ability to attract mates (Berglund & Rosenqvist, 1990). Nevertheless, in the majority of cases, we appear to have a reasonable understanding of why males mate with multiple females.

The reasons that females mate with multiple males in many species are much less obvious (Jennions & Petrie, 2000). Often a single mating will be enough to fertilize all eggs, although females mate with multiple males nevertheless, despite substantial costs to mating in some cases (Jennions & Petrie, 1997). Even though female multiple mating appears to be unexpected at first blush, numerous evolutionary explanations for this behaviour have been formulated and substantiated in a wide variety of systems. The factors affecting multiple mating by females are complex and can vary considerably across taxa. In species that provide biparental care, for example, the reproductive interests of males and females may not coincide during the period of parental care. In an effort to maximize her fitness, a female may seek out extra-pair partners of higher genetic quality than her social partner (Petrie & Kempenaers, 1998; Griffith, Owens & Thuman, 2002; Westneat & Stewart, 2003). If the fertilized eggs are laid in the nest of the extra-pair partner, such behaviour might be of little consequence to her social partner. If, on the other hand, the female lays the fertilized eggs in her own nest, then her partner will waste parental effort on eggs and young that provide him no fitness benefit. Such a male is considered 'cuckolded' (Trivers, 1972). Cuckoldry avoidance behaviours have evolved in many species in which the potential for extra-pair copulations exists (Gross, 1996; Taborsky, 2001). In extreme cases, perception of cuckoldry incites some male fish to cannibalize their young rather than provide parental care to potentially unrelated offspring (Gray, Dill & McKinnon, 2007). There may be other explanations for multiple mating by females as well. For example, the maximization of genetic compatibility between mates, fertility assurance, the production of genetically variable offspring, direct benefits, and various social aspects of mating could all play some role in multiple mating by females, depending on the particular species (Halliday & Arnold, 1987; Zeh & Zeh, 1996; Jennions & Petrie, 2000).

These considerations of why males and females seek multiple mates serve as the motivation for delving into the actual patterns of parentage in fish populations. In this review of genetic parentage, we provide a comprehensive summary of studies that have used microsatellite markers to measure multiple mating in natural populations of fishes. Where appropriate, we also consider how mating system, parental care system, and sexual selection may be affected by, and have affected, rates of multiple mating.

A NOTE ON METHODOLOGY

We focus on studies that used microsatellite markers to assess patterns of parentage in natural fish populations. Thus, we ignore a few studies based on allozymes or DNA fingerprinting (Chesser, Smith & Smith, 1984; Greene & Brown, 1991; Rico, Kuhnlein & Fitzgerald, 1991). The justification for excluding such studies is that the vast majority of published analyses of fish parentage are based on microsatellites. In addition, the low levels of polymorphism at allozymes and difficulties associated with the statistical analysis...
of DNA fingerprinting make it difficult to compare studies across marker types. This problem still occurs to some degree in the comparison of species with different levels of microsatellite polymorphism, although most microsatellite-based studies of fish parentage are based on suites of markers with sufficient power to estimate levels of multiple maternity or paternity with very good precision. We also limited our review to studies that provided estimates of individual mating or reproductive success, such that a study comparing, for example, average reproductive success of hatchery-reared fish to average reproductive success of wild fish (McLean, Bentzen & Quinn, 2003; Araki et al., 2007) would not be included unless it also included estimates on a per-individual basis in a natural setting. This restriction was necessary to ensure that results across studies remained directly comparable.

We review 77 studies published from the beginning of the microsatellite revolution in fish parentage in 1995 to the end of 2010. In total, these studies report patterns of genetic parentage in 74 distinct fish species under natural conditions. To evaluate the relationship between sexual dimorphism and parentage, we scored species based on differences between the sexes in terms of size, coloration, and morphological elaboration. These scores were assigned based on discussions with researchers working with particular species, data from the primary literature or descriptions from field guides.

For analysis, we separated species based on the type of parental care provided to developing embryos. We identified five classes of parental care: internal brooding by females (in the body cavity or by maternal mouthbrooding), male pregnancy, male nest defence, biparental nest defence, and no parental care. For species represented by multiple studies or populations, we calculated mean values for each species and used these values in all subsequent analyses. In addition, studies that evaluated multiple parentage from only a single brood or nest were included in the tables (see below) but were excluded from statistical analyses and figures. Most analyses are based on general linear models, and all proportions were arcsine(square root)-transformed prior to analysis. When a model revealed significant effects, Tukey's honestly significant difference test was used to investigate differences among means.

MULTIPLE PARENTAGE IN FISHES WITH DIFFERENT TYPES OF PARENTAL CARE

We summarize the parentage studies for fishes that fall into five different parental care categories in Tables 1, 2, 3, 4, 5. The species represented in these tables are by no means a random sample of fishes, such that patterns must be viewed with some caution. Parentage studies have been especially ardently applied to livebearing fishes, cichlids, syngnathid fishes, and sunfishes. In some cases, the taxonomic bias appears to be a result of convenience because abundant species with easily accessible broods are especially well represented. In other cases, certain species were viewed as providing key opportunities to investigate certain aspects of mating system evolution, leading to numerous studies on a given species or a group of related species. Regardless, some general patterns emerge when we consider multiple parentage as a function of the type of parental care.

FEMALES CARRY ZYGOTES INTERNALLY

Many fishes are characterized by a type of parental care in which females carry the embryos internally (Table 1). In some of these species, females carry offspring in their body cavities. In these species, males transfer sperm directly into the female's reproductive tract and fertilization occurs within the female. Multiple paternity occurs when several males transfer sperm to fertilize a given brood, and many of these species are capable of storing sperm, increasing the likelihood of multiple paternity. In other cases, females brood developing offspring in their mouths. In mouthbrooding species, the female releases the eggs and then scoops them up in her mouth. Depending on the species, fertilization can occur in the external environment before the female picks up the eggs or in her mouth after she picks up the eggs. Thus far, studies have shown that almost all species with internal brooding by females have complete confidence of maternity (i.e. no multiple maternity within broods). The single exception occurs in the maternal mouthbrooding cichlid, Protomelas spilopterus, in which four of the six studied broods included offspring that originated from mothers other than the brooding female (Kellogg et al., 1998).

The evolutionary explanations for multiple mating by females of fishes with internal brooding of offspring are diverse and often difficult to diagnose. In these species, females are responsible for all postzygotic parental investment, such that males provide nothing beyond sperm and associated products. Thus, the most likely direct benefit to females of multiple mating is fertility assurance (Sheldon, 1994). However, female fishes could derive a wide variety of indirect benefits from multiple mating. For example, multiple mating can increase the genetic variance of offspring in the brood, ensure that at least some eggs are fertilized by a father that is genetically compatible with the mother, and provide an arena for sperm or sibling competition (Jennions & Petrie, 2000). Females may also mate multiply to reduce
Table 1. Multiple paternity in species in which females carry embryos internally, either in their body cavities or mouths

| Species                      | Number of marker loci used | Number of progeny assayed | Number of nests or broods assayed | % Broods with multiple paternity | Average number of sires (range) per female | Embryo location | Sexual dimorphism* | Reference                      |
|------------------------------|---------------------------|---------------------------|-----------------------------------|---------------------------------|-------------------------------------------|----------------|-------------------|--------------------------------|
| Carcharhinus altimus        | 8                         | 9                         | 1                                 | NA                              | 2                                         | Body cavity   | 1                 | Daly-Engel et al. (2006)   |
| Carcharhinus galapagensis   | 8                         | 7                         | 1                                 | NA                              | 1                                         | Body cavity   | 1                 | Daly-Engel et al. (2006)   |
| Carcharhinus plumbeus       | 8                         | 7                         | 1                                 | NA                              | 2                                         | Body cavity   | 1                 | Daly-Engel et al. (2006)   |
| Carcharhinus plumbeus       | 6                         | 110                       | 20                                | 40                              | 1.4 (1–2)                                 | Body cavity   | 1                 | Daly-Engel et al. (2007)   |
| Carcharhinus plumbeus       | 5                         | 187                       | 20                                | 85                              | 2.3 (1–4)                                 | Body cavity   | 1                 | Portnoy et al. (2007)      |
| Copadichromis cyclicos      | 2                         | 44                        | 3                                 | 100                             | 3.7 (2–6)                                 | Mouth         | 2                 | Kellogg et al. (1995)      |
| Copadichromis sp.           | 1                         | 16                        | 1                                 | NA                              | 2                                         | Mouth         | ?                 | Kellogg et al. (1995)      |
| Ctenochromis horei          | 4                         | 18                        | 1                                 | NA                              | 1                                         | Mouth         | 2                 | Egger et al. (2006)        |
| Ctenochromis horei          | 4                         | 266                       | 14                                | 57                              | 2.1 (1–5)                                 | Mouth         | 2                 | Sefc et al. (2009)         |
| Embiotoca jacksoni          | 6                         | 305                       | 12                                | 100                             | 3.6 (2–6)                                 | Body cavity   | 0                 | Reisser, Beldade & Bernardi (2009) |
| Embiotoca lateralis         | 4                         | 279                       | 12                                | 100                             | 3.5 (2–9)                                 | Body cavity   | 0                 | Reisser et al. (2009)      |
| Gambusia holbrooki          | 3                         | 823                       | 50                                | 86                              | 2.0 (1–3)                                 | Body cavity   | 2                 | Zane et al. (1999)         |
| Ginglymostoma cirratum      | 1                         | 32                        | 1                                 | NA                              | 4                                         | Body cavity   | 1                 | Saville et al. (2002)      |
| Gnathochromis pfefferi      | 4                         | 23                        | 1                                 | NA                              | 1                                         | Mouth         | 1                 | Egger et al. (2006)        |
| Heterandria formosa         | 3                         | NR                        | 11                                | 15                              | 1.2 (NR)                                  | Body cavity   | 2                 | Soucy & Travis (2003)      |
| (least killifish) ‘Trout Pond’ pop. |               |                           |                                   |                                  |                                           |               |                   |                                |
| Heterandria formosa         | 3                         | NR                        | 13                                | 54                              | 1.6 (NR)                                  | Body cavity   | 2                 | Soucy & Travis (2003)      |
| Species/Mutation                  | n | Weight | Length | % Survival | Mean Age (No. in brackets) | Reproductive Site | Reference                                |
|----------------------------------|---|--------|--------|------------|---------------------------|-------------------|------------------------------------------|
| *Heterandria formosa* (least killifish) 'Wacissa River' | 3 | NR     | 12     | 66         | 1.8 (NR)                  | Body cavity 2     | Soucy & Travis (2003)                   |
| *Melanochromis auratus* (cichlid sp.) | 1 | 22     | 1      | NA         | 1                         | Mouth 3           | Kellogg *et al.* (1995)                 |
| *Negaprion brevirostris* (lemon shark) | 3 | 11     | 1      | NA         | 3                         | Body cavity 1     | Feldheim, Gruber & Ashley (2001)        |
| *Negaprion brevirostris* (lemon shark) | 9 | 119    | 5      | 100        | 2.6 (2–4)                 | Body cavity 1     | Feldheim, Gruber & Ashley (2002)        |
| *Negaprion brevirostris* (lemon shark) | 9 | 707    | 97     | 87         | 2.0 (1–4)                 | Body cavity 1     | Feldheim, Gruber & Ashley (2004)        |
| *Petrochromis fasciolatus* (cichlid sp.) | 4 | 47     | 2      | 50         | 1.5 (1–2)                 | Mouth 2           | Egger *et al.* (2006)                   |
| *Petrochromis polyodon* (cichlid sp.) | 4 | 9      | 1      | NA         | 1                         | Mouth 2           | Egger *et al.* (2006)                   |
| *Petrochromis reticulata* (guppy) low predation | 2 | 774    | 124    | 24.6       | NR                        | Body cavity 3     | Kelly *et al.* (1999)                   |
| *Petrochromis reticulata* (guppy) high predation | 2 | 1038   | 129    | 64.2       | NR                        | Body cavity 3     | Kelly *et al.* (1999)                   |
| *Pseuocilia reticulata* (guppy) | 3 | 264    | 22     | 95         | 3.0 (1–6)                 | Body cavity 3     | Hain & Neff (2007)                      |
| *Pseuocilia reticulata* (guppy) low predation | 3 | 390    | 40     | 97.5       | 3.1 (1–5)                 | Body cavity 3     | Neff *et al.* (2008)                    |
| *Pseuocilia reticulata* (guppy) high predation | 3 | 866    | 61     | 93.4       | 3.7 (1–9)                 | Body cavity 3     | Neff *et al.* (2008)                    |
| *Protomelas sp.* (cichlid sp.) | 2 | 29     | 1      | NA         | 1                         | Mouth ?           | Kellogg *et al.* (1995)                 |
| *Protomelas c.f. spilopterus* (cichlid sp.) | 3 | 200    | 6      | 50         | 1.7 (1–3)                 | Mouth 2           | Kellogg *et al.* (1998)                 |
| *Pseudotropheus c.f. gracilor* | 1 | 36     | 3      | 67         | 1.7 (1–2)                 | Mouth 2           | Kellogg *et al.* (1995)                 |
| *Pseudotropheus c.f. tropheops* | 1 | 18     | 1      | NA         | 2                         | Mouth 2           | Kellogg *et al.* (1995)                 |
| *Pseudotropheus ‘mazinzi blue’* (cichlid sp.) | 2 | 44     | 3      | 100        | 2                         | Mouth 2           | Kellogg *et al.* (1995)                 |
| *Pseudotropheus zebra* (cichlid sp.) | 10 | 100   | 7     | 86         | 3.8 (1–6)                 | Mouth 3           | Parker & Kornfield (1996)               |
| *Sebastes alutus* (Pacific ocean perch) | 5 | 1492   | 66     | 71.2       | 1.9 (1–4)                 | Body cavity 1     | Van Doornik *et al.* (2008)             |
Table 1. Continued

| Species                          | Number of marker loci used | Number of progeny assayed | Number of nests or broods assayed | % Broods with multiple paternity | Average number of sires (range) per female | Embryo location | Sexual dimorphism* | Reference                          |
|----------------------------------|----------------------------|----------------------------|-----------------------------------|----------------------------------|---------------------------------------------|-----------------|-------------------|------------------------------------|
| *Sebastes atrovirens* (kelp rockfish) | 7                          | 671                        | 7                                 | 100                              | 2.1 (2–3)                                   | Body cavity     | 1                  | Sogard et al. (2008)            |
| *Sebastes inermis* (black rockfish) | 4                          | 250                        | 5                                 | 20                               | 1.2 (1–2)                                   | Body cavity     | 0                  | Blanco Gonzalez et al. (2009)    |
| Simochromis babaulti (cichlid sp.)  | 4                          | 13                         | 1                                 | NA                               | 1                                           | Mouth           | 0                  | Egger et al. (2006)             |
| Simochromis diaphramma (cichlid sp.)  | 4                          | 13                         | 1                                 | NA                               | 1                                           | Mouth           | 0                  | Egger et al. (2006)             |
| Simochromis pleurospilus (cichlid sp.)  | 4                          | 17                         | 1                                 | NA                               | 1                                           | Mouth           | 0                  | Egger et al. (2006)             |
| Sphyrna tiburo (bonnethead shark) | 4                          | 188                        | 22                                | 18.8                             | 1.23 (1–3)                                  | Body cavity     | 2                  | Chapman et al. (2004)          |
| Squalus acanthias (spiny dogfish) | 7                          | 50                         | 10                                | 30.0                             | 1.3 (1–2)                                   | Body cavity     | 1                  | Lage et al. (2008)             |
| Squalus mitsukurii (shortspine spurdog) | 8                          | 178                        | 27                                | 11.1                             | 1.11 (1–2)                                  | Body cavity     | 1                  | Daly-Engel et al. (2010)       |
| Tropheus moorii (cichlid sp.)      | 4                          | 165                        | 19                                | 0                                | 1                                           | Mouth           | 1                  | Egger et al. (2006)             |
| Xiphophorus helleri (green swordtail) | 5                          | 241                        | 14                                | 57                               | 1.57 (1–2)                                  | Body cavity     | 3                  | Simmons, Beveridge & Evans (2008) |
| Xiphophorus helleri (green swordtail) | 9                          | 1476                       | 69                                | 64                               | 1.8 (1–4)                                   | Body cavity     | 3                  | Tatarenkov et al. (2008)       |
| Xiphophorus multilineatus (swordtail sp.) | 7                          | 244                        | 18                                | 28                               | 1.39 (1–3)                                  | Body cavity     | 3                  | Luo et al. (2005)              |

NA, not applicable; NR, not reported.

*0 = sexually monomorphic; 1 = dimorphic in size only; 2 = dimorphic in elaborate coloration or morphology – such as elongate fins; 3 = sexually dimorphic in elaborate coloration and morphology.
harassment from suitors (DiBattista et al., 2008) or as a consequence of a correlated response to selection for high rates of mating in males (Halliday & Arnold, 1987). Regardless, an important part of diagnosing the causes of multiple mating by females with internal brooding is to document its occurrence in nature, and this step has been accomplished for a diverse array of fishes.

Parentage studies have found a wide range of rates of multiple paternity in species in which females carry zygotes internally (Table 1). Patterns of paternity are unexpectedly similar for mouthbrooders compared to species that brood inside the body cavity. Maternal mouthbrooders exhibited multiple paternity in an average (among species) of 63.8% of broods, whereas this figure was 60.1% for females carrying broods internally, and the difference is nonsignificant (t-test, d.f. = 12, P = 0.93). The average number of sires was almost identical between the two groups, with means of 2.2 and 2.0 sires per brood for mouthbrooders and body cavity brooders, respectively. The percentage of broods with multiple paternity was in the range 0–100% (Fig. 1A), and the average minimum numbers of sires per brood was in the range 1–3.8 (Fig. 1B).

An interesting point regarding fishes with internal gestation of offspring is that most cartilaginous fishes fall into this category. Eight different species of sharks are listed in Table 1, and they are either viviparous or ovoviviparous. The one ray (Raja clavata) that has been studied from a parentage perspective is oviparous, such that it falls into the category of ‘no parental care’ (see below). The species of shark that have been studied are similar in patterns of multiple paternity to the bony fishes. If we restrict attention to the studies with reasonably large sample sizes, the percentage of broods with multiple paternity ranges from 11.1% in the shortspine spurdog to 87% in the lemon shark (Table 1). The average number of sires per litter are in the range 1.1–2.6 in

Figure 1. Histograms showing the distribution of rates of multiple paternity (A) and number of sires (B) among species in which females carry embryos internally. These data are from the studies listed in Table 1 and include species in which at least two broods were assayed (N = 23). For species with multiple populations represented, we used the mean among populations.

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the sharks that have been studied in detail. Thus, the maximum number of sires per clutch tends to be higher in multiply mating bony fishes compared to their cartilaginous counterparts, and this difference probably stems from the often high fecundities of the bony fishes relative to elasmobranchs.

Overall, multiple paternity is extremely common in species in which females carry offspring internally. Species in which all (or almost all) females mate with multiple males per brood are much more common than those in which most females mate with one male per brood (Fig. 1A). Many studies found evidence that some females mated with three or more males, with the most extreme cases finding females with up to nine mates per brood (Table 1). Actual rates of multiple mating could be even higher because these high figures are approaching the limits of detection for most suites of microsatellite markers. These patterns lead to two unanswered questions. First, why have such high rates of multiple mating evolved in so many taxa? Second, why are a few species, or populations within a species, characterized by mating systems in which most females mate with only one male per brood? Further work, integrating ecological, behavioural, and comparative approaches, could profitably be applied to these questions.

MALES CARRY EMBRYOS ON OR IN THEIR BODIES

Some species of fish are characterized by uniparental care in which the male carries the developing offspring on or in his body. The most well-known examples of this type of parental care include male mouthbrooding and male pregnancy. In male mouthbrooders, which occur in a number of widely divergent groups, the males take the embryos into their mouths shortly after fertilization. No male mouthbrooders have yet been subjected to microsatellite-based parentage analysis, despite a number of interesting questions relating to patterns of multiple mating and paternity assurance. The term ‘male pregnancy’ is usually applied to fishes of the family Syngnathidae, which includes pipefishes, seahorses, and sea dragons. In these species, females transfer eggs to the male’s ventral surface and fertilization occurs during or after egg transfer. Some species, including seahorses and many pipefish, have a fully or partially enclosed pouch into which the female deposits eggs. In other syngnathid species, such as sea dragons, females attach the eggs to the male’s ventral surface with no outer covering. Mouthbrooding and male pregnancy, although comprising the best-known examples, are not the only ways in which males carry offspring. For example, nurseryfish (Kurtus gulliveri) carry the embryos on a hook attached to the male’s forehead (Berra & Humphrey, 2002). Thus far, however, of the species in which males carry the embryos, only fishes of the family Syngnathidae have been subjected to microsatellite-based parentage analysis.

Species in which males carry the offspring may mate multiply for many of the same reasons that internally brooding females mate multiply. For example, males might mate multiply because they are capable of carrying more eggs than a single female can provide. Alternatively, males that carry the offspring could mate multiply for reasons including genetic compatibility, offspring variability, and so forth. Precisely why multiple mating by males occurs in any given species in which males carry offspring on their bodies remains an open question.

Studies of parentage in species in which the males carry offspring have focused on seven species in three genera, including two seahorses in the genus Hippocampus, one pipefish in the genus Nerophis, and five pipefish in the genus Syngnathus (Table 2). The rate of multiple mating by males is highly variable in these taxa. For example, the Western Australian seahorse is characterized by genetic monogamy and long-term pair-bonding, whereas the males in some of the pipefish species mate with an average of three or more females per pregnancy. In addition, two of the species, Syngnathus scovelli and Nerophis ophidian, are characterized by males that typically mate only once per pregnancy and females that mate multiply, representing rare examples of classical polyandry. Future studies involving more syngnathid taxa and other species outside of Syngnathidae in which males carry the young would be interesting and welcome additions to the literature.

SPECIES WITH OFFSPRING DEFENCE

Many species of fish care for developing offspring within nests or territories. In such species, the male is usually the sex that provides care, although some species are characterized by biparental care or uniparental tending of nests by the female. Thus far, studies have addressed parentage in species with uniparental male nest defence (Table 3) and biparental nest defence (Table 4), although none have addressed parentage in species in which females tend offspring in nests or territories without the help of the male. The lack of studies of species characterized by uniparental female nest tending probably stems from the fact that this mode of parental care is extremely rare among fishes (Blumer, 1982). One example of a species with exclusive female defence of nests is the sockeye salmon (Oncorhynchus nerka), in which females defend their nesting site from rival females for several days after spawning (McPhee & Quinn, 1998). In this species, as in many other salmonid
### Table 2. Multiple maternity in species with male pregnancy

| Species                        | Number of marker loci used | Number of progeny assayed | Number of broods assayed | % Broods with multiple maternity | Average number of dams (range) per brood | Sexual dimorphism* | Reference                          |
|--------------------------------|---------------------------|---------------------------|--------------------------|----------------------------------|------------------------------------------|-------------------|------------------------------------|
| *Hippocampus abdominalis* (pot-bellied seahorse) | 4                         | 335                       | 8                        | 0                                | 1                                        | 1                 | Wilson & Martin-Smith (2007)        |
| *Hippocampus subelongatus* (W. Australian seahorse) | 4                         | 440                       | 15                       | 0                                | 1                                        | 0                 | Jones et al. (1998a)               |
| *Hippocampus subelongatus* (W. Australian seahorse) | 3                         | 396                       | 30                       | 0                                | 1                                        | 0                 | Kvarnemo et al. (2000)             |
| *Nerophis ophidion* (straight-nosed pipefish)        | 3                         | 248                       | 11                       | 0                                | 1                                        | 3                 | McCoy, Jones & Avise (2001)        |
| *Syngnathus auliscus* (barred pipefish)              | 4                         | 280                       | 7                        | 86                               | 2.14 (1–3)                               | 2                 | Wilson (2006)                      |
| *Syngnathus floridus* (dusky pipefish, St. Joe, FL pop. 1994) | 4                         | 924                       | 22                       | 73                               | 1.86 (1–3)                               | 2                 | Jones & Avise (1997b)             |
| *Syngnathus floridus* (dusky pipefish, Virginia pop.) | 4                         | 1260                      | 30                       | 93                               | 2.60 (1–4)                               | 2                 | Mobley & Jones (2007)              |
| *Syngnathus floridus* (dusky pipefish, St. Joe, FL pop. 2003) | 4                         | 924                       | 22                       | 73                               | 2.00 (1–4)                               | 2                 | Mobley & Jones (2007)              |
| *Syngnathus floridus* (dusky pipefish, North Carolina pop.) | 4                         | 1008                      | 24                       | 63                               | 1.75 (1–3)                               | 2                 | Mobley & Jones (2009)              |
| *Syngnathus floridus* (dusky pipefish, Tampa Bay, FL pop.) | 4                         | 1260                      | 30                       | 50                               | 1.50 (1–2)                               | 2                 | Mobley & Jones (2009)              |
| *Syngnathus floridus* (dusky pipefish, Texas pop.)    | 4                         | 546                       | 13                       | 31                               | 1.31 (1–2)                               | 2                 | Mobley & Jones (2009)              |
| *Syngnathus leptorhynchos* (bay pipefish, California pop.) | 4                         | 217                       | 7                        | 86                               | 2.14 (1–3)                               | 2                 | Wilson (2006)                      |
| *Syngnathus leptorhynchos* (bay pipefish, Oregon pop.) | 4                         | 317                       | 8                        | NR                               | 3.62 (NR)                                | 2                 | Wilson (2009)                      |
| Species | Number of marker loci used | Number of progeny assayed | Number of broods assayed | % Broods with multiple maternity | Average number of dams (range) per brood | Sexual dimorphism* | Reference |
|---------|---------------------------|---------------------------|-------------------------|---------------------------------|------------------------------------------|-------------------|-----------|
| *Syngnathus leptorhynchus* (bay pipefish, Washington pop.) | 4 | 440 | 11 | NR | 3.72 (NR) | 2 | Wilson (2009) |
| *Syngnathus leptorhynchus* (bay pipefish, Alaska pop.) | 4 | 317 | 8 | NR | 3.25 (NR) | 2 | Wilson (2009) |
| *Syngnathus scovelli* (Gulf pipefish, Gulf of Mexico pop.) | 4 | 838 | 40 | 3 | 1.03 (1–2) | 3 | Jones & Avise (1997a) |
| *Syngnathus scovelli* (Gulf pipefish, Atlantic pop.) | 4 | 294 | 21 | 0 | 1 | 3 | Jones et al. (2001a) |
| *Syngnathus typhle* (broad-nosed pipefish, Sweden pop. 1996) | 4 | 1344 | 30 | 90 | 3.1 (1–6) | 2 | Jones et al. (1999) |
| *Syngnathus typhle* (broad-nosed pipefish, Sweden pop. 2006) | 3 | NR | 10 | 100 | 3.7 (3–4) | 2 | Rispoli & Wilson (2007) |
| *Syngnathus typhle* (broad-nosed pipefish, Italy pop.) | 3 | NR | 8 | 13 | 1.25 (1–3) | 2 | Rispoli & Wilson (2007) |
| *Syngnathus typhle* (broad-nosed pipefish, France pop.) | 3 | NR | 10 | 80 | 2.7 (1–4) | 2 | Rispoli & Wilson (2007) |
| *Syngnathus typhle* (broad-nosed pipefish, Portugal pop.) | 3 | NR | 10 | 100 | 2.9 (2–5) | 2 | Rispoli & Wilson (2007) |

NR, not reported.

*0 = sexually monomorphic; 1 = dimorphic in size only; 2 = dimorphic in elaborate coloration or morphology – such as elongate fins; 3 = sexually dimorphic in elaborate coloration and morphology.*
Table 3. Multiple parentage in species with male nest defence

| Species                  | Number of marker loci used | Number of progeny assayed | Number of nests or broods assayed | % Nests with cuckoldsry | % Nests with takeovers or egg thievery | % Nests with multiple maternity | Average number of dams (range) per nest | Sexual dimorphism | Reference                                    |
|--------------------------|----------------------------|---------------------------|-----------------------------------|-------------------------|-----------------------------------------|---------------------------------|------------------------------------------|------------------|--------------------------------------------|
| Cottus bairdi (mottled sculpin) | 5                          | 1259                      | 23                                | 0                       | 4                                       | 65                              | 2.2 (1–4)                                               | 2                | Fiumera et al. (2002)                      |
| Ethoestoma olmstedii (tessellated darter) | 6                          | 610                       | 16                                | 6                       | 13                                      | 92                              | 3.20 (1–4)                                              | 2                | DeWoody et al. (2000b)                     |
| Ethoestoma virgatum (striped darter) | 3                          | 987                       | 19                                | 0                       | 21                                      | 100                             | 4.74 (3–7)                                              | 2                | Porter et al. (2002)                       |
| Gasterosteus aculeatus (three-spined stickleback) | 3                          | 1393                      | 14                                | 21                      | 36                                      | NR                              | NR                                                      | 2                | Largiadér, Fries & Bakker (2001)           |
| Gasterosteus aculeatus (three-spined stickleback) | 5                          | 1197                      | 44                                | 20                      | 9                                       | 27                              | 2.46 (1–5)                                              | 2                | Blais, Rico & Bernatchez (2004)            |
| Gobiusculus flavescens (two-spotted goby) | 4                          | 902                       | 21                                | 5                       | 0                                       | 100                             | 4.29 (2–6)                                              | 3                | Mobley et al. (2009)                      |
| Hexagrammos otakii (fat greenling) | 2                          | 120                       | 2                                 | 100                     | 0                                       | NR                              | NR                                                      | 1                | Munehara & Takenaka (2000)                |
| Ictalurus punctatus (channel catfish) | 7                          | 175                       | 5                                 | 0                       | 1                                       | 0                               | 1                                                       | 1                | Tatarenkov et al. (2006)                  |
| Lepomis auritus (redbreast sunfish) | 2                          | 996                       | 25                                | 12                      | 8                                       | 100                             | 3.70 (2–6)                                              | 2                | DeWoody et al. (1998)                     |
| Lepomis macrochirus (bluegill sunfish) | 11                         | 1677                      | 38                                | 92                      | 0                                       | NR                              | NR                                                      | 2                | Neff (2001)                                |
| Lepomis marginatus (dollar sunfish) | 3                          | 1015                      | 23                                | 4                       | 4                                       | 83                              | 2.50 (1–7)                                              | 2                | Mackiewicz et al. (2002)                  |
| Lepomis gibbosus (pumpkinseed sunfish) | 5                          | 1715                      | 35                                | NR                      | NR                                      | NR                              | 3.60 (NR)                                               | 1                | Rios-Cardenas (2005)                      |
| Lepomis gibbosus (pumpkinseed sunfish) | 5                          | 2695                      | 55                                | NR                      | NR                                      | NR                              | NR                                                      | 1                | Rios-Cardenas & Webster (2005)            |
| Lepomis gibbosus (pumpkinseed sunfish) | 5                          | 2695                      | 55                                | 43                      | 0                                       | NR                              | NR                                                      | 1                | Rios-Cardenas & Webster (2008)            |
| Species | Number of marker loci used | Number of progeny assayed | Number of nests or broods assayed | % Nests with cuckoldry | % Nests with takeovers or egg thievery | % Nests with multiple maternity | Average number of dams (range) per nest | Sexual dimorphism* | Reference |
|---------|--------------------------|---------------------------|---------------------------------|-----------------------|----------------------------------------|-------------------------------|-----------------------------------------|-------------------|-----------|
| *Lepomis punctatus* (spotted sunfish) | 2 | 1440 | 30 | 40 | 3 | 93 | 4.37 (1–6) | 2 | DeWoody et al. (2000a) |
| *Ophiodon elongatus* (lingcod) | 5 | 1434 | 13 | 62 | 17 | 0 | 1 | 1 | Withler et al. (2004) |
| *Pimephales promelas* (fathead minnow), substrate limited | 5 | ~669 | 21 | 10 | 29 | 100 | 3.63 (3–5) | 3 | Bessert et al. (2007) |
| *Pimephales promelas* (fathead minnow), not substrate limited | 5 | ~669 | 21 | 24 | 5 | 100 | 2.86 (2–4) | 3 | Bessert et al. (2007) |
| *Pomatoschistus minutus* (sand goby), Baltic | 3 | 912 | 17 | 35 | 6 | 91 | 3.00 (1–5) | 1 | Jones et al. (2001c) |
| *Pomatoschistus minutus* (sand goby), North Sea | 3 | 981 | 24 | 50 | 5 | 100 | 3.40 (2–6) | 1 | Jones et al. (2001b) |
| *Scartella cristata* (Molly Miller) | 3 | 1536 | 23 | 83 | 0 | 100 | 4.90 (3–8) | 1 | Mackiewicz et al. (2005) |
| *Spinachia spinachia* (fifteen-spined stickleback) | 6 | 1307 | 28 | 18 | 17 | 71 | 2.56 (1–7) | 2 | Jones et al. (1998b) |
| *Symphodus ocellatus* (ocellated wrasse) | 6 | 954 | 10 | 100 | 0 | NR | NR | 3 | Alonzo & Heckman (2010) |

NR, not reported.

*0 = sexually monomorphic; 1 = dimorphic in size only; 2 = dimorphic in elaborate coloration or morphology – such as elongate fins; 3 = sexually dimorphic in elaborate coloration and morphology.*
Table 4. Multiple parentage in species with biparental care

| Species                              | Number of marker loci | Number of progeny assayed | Number of broods assayed | % Nests with multiple paternity | Average number of sires per nest (range) | % Nests with multiple maternity | Average number of dams per nest (range) | Type of parental care | Sexual dimorphism* | Reference                        |
|--------------------------------------|----------------------|---------------------------|--------------------------|---------------------------------|-----------------------------------------|---------------------------------|----------------------------------------|----------------------|------------------|----------------------------------|
| Eretmodus cyanostictus (cichlid sp.)† | 3                    | 203                       | 14                       | 0                               | 1.04 (1–2)                              | 20                              | 1.24 (1–3)                             | Nest                 | 0                | Taylor et al. (2003)              |
| Julidochromis ornatus (cichlid sp.)   | 4                    | 290                       | 62                       | 23                              | NR                                     | 8                               | NR                                     | Nest                 | 0                | Awata, Munehara & Kohda (2005)     |
| Micropterus salmoides (largemouth bass) | 5                    | 1088                      | 26                       | 4                               | 1.42 (1–2)                              | 0                               | 1                                       | Nest                 | 1                | DeWoody et al. (2000c)             |
| Neolamprologus meili (cichlid sp.)    | 3                    | 22                        | 7                        | NR                              | NR                                     | NR                              | NR                                     | Nest                 | 1                | Sunobe & Munehara (2003)           |
| Neolamprologus pulcher (cichlid sp.)  | 5                    | 43                        | 12                       | 42                              | 1.29 (1–2)                              | 14                              | 1.14 (1–2)                             | Nest                 | 1                | Dierkes, Taborsky & Achmann (2008) |
| Neolamprologus pulcher (cichlid sp.)  | 3–12                 | 42                        | 4                        | 75                              | 2.00 (1–3)                              | 50                              | 1.5 (1–2)                              | Nest                 | 1                | Stiver et al. (2009)               |
| Telmatichromis temporalis (cichlid sp.) | 2                    | 100                       | 21                       | 29                              | 1.29 (1–2)                              | 14                              | 1.14 (1–2)                             | Nest                 | 1                | Katoh, Munehara & Kohda (2005)      |
| Variablichromis moorii (cichlid sp.)  | 6                    | 556                       | 10                       | 100                             | 4.70 (2–9)                              | 0                               | 1                                       | Nest                 | 0                | Sefc et al. (2008)                 |

NR, not reported.

*0 = sexually monomorphic; 1 = dimorphic in size only; 2 = dimorphic in elaborate coloration or morphology – such as elongate fins; 3 = sexually dimorphic in elaborate coloration and morphology.

†Eretmodus cyanostictus is interesting in that the female initially broods the fertilized eggs and early fry in her mouth, before passing them to the male, who carries the larger fry in his mouth.
species, parentage analysis has been applied to address a number of interesting questions, although only a handful of salmonid studies provide data that permit the evaluation of patterns of multiple mating in nature on a per-spawning basis.

Species in which males participate in the defence of nests or territories containing offspring raise additional interesting issues with respect to patterns of parentage and, by examining these species, we may gain some insight into conflict between the sexes. In most of these species, the male expends significant energy tending developing embryos until hatching (and sometimes significantly beyond). Thus, evolutionary theory predicts that parents in such species should behave in ways that minimize the number of unrelated offspring ‘accidentally’ raised (Trivers, 1972; Gray et al., 2007). At the same time, however, selection favours males who can inflict this situation on others, resulting in cuckolded males raising unrelated offspring and thereby increasing the relative fitness of the cuckold. In internally fertilizing species, this sort of cuckoldry could arise, in principle, if a female uses stored sperm from a previous mating to fertilize some eggs. However, almost all fish species with uniparental male care fertilize eggs externally (Gross & Sargent, 1985). In these species, cuckoldry involves sneaker males intruding on the spawning activities of a spawning pair and releasing sperm, thereby fertilizing some of the eggs.

In species with biparental or paternal nest defence, multiple paternity within broods indicates that the nest-defending male has been a victim of cuckoldry. In other words, a male defending a nest fathered by multiple sires must be raising some offspring that are not his own. From the female’s perspective, in species with biparental nest defence (Table 4), it may sometimes be beneficial to actively solicit fertilizations from nonsocial mates to increase the genetic quality or diversity of offspring (Petrie & Kempenaers, 1998; Westneat & Stewart, 2003). In these same species, multiple maternity within broods suggests that ‘sneaker’ females sometimes deposit eggs in a caregiving female’s nest. Whether care-giving males solicit the deposition of eggs from females other than their social partners, and whether females actively solicit fertilizations from nonsocial partners, as is well documented in birds (Petrie & Kempenaers, 1998; Westneat & Stewart, 2003), is a question that calls for further investigation.

In our review of the literature, we found that in species with male nest defence (Table 3), the rate of multiple paternity was skewed, with most species having low rates of multiple paternity (Fig. 2A). In other words, nest-defending males are usually the true sires of most of the offspring in their nests. However, most of the species do show evidence of a low level of cuckoldry. Across all species, approximately 35.8 ± 8.6% (mean ± SE) of nests showed signs of cuckoldry, with the complete range of 0–100% represented across taxa. However, the number of eggs fertilized by cuckolders during a sneaking event is typically much smaller than the number of eggs fertilized by the guardian male. In the species studied thus far, for instance, the observed proportions of eggs fertilized by sneakers at a population level were less than 20% for all species (Mackiewicz et al., 2005), except the bluegill sunfish and ocellated wrasse, in which 21.8% and 28% of offspring were fertilized by sneakers, respectively (Neff, 2001; Alonzo & Heckman, 2010).

The literature on nest-guarding males also shows evidence for nest takeovers or egg thievery (Table 3). Such events are normally documented as clutches in which all offspring are genetically incompatible with the guardian male, such that, from a genetic perspective, these two causes of alloparental care are indistinguishable. Nest takeovers or egg thievery events occur in approximately 8.9% of nests across species, with a range of 0–22.5%, making them much less common than sneaking (Table 3). This pattern is perhaps not especially unexpected because the fitness advantages to a sneaking male are entirely obvious. Why males steal fertilized eggs or nests containing them is a much more difficult question to answer. In many cases, thievery of nests or eggs can be explained by a female preference for males whose nests already contain eggs (Ridley & Rechten, 1981; Porter, Fiumera & Avise, 2002). However, egg or nest thievery may also be a strategy that allows a male to obtain a nest when suitable nesting sites are a limited resource (DeWoody et al., 2000b; Bessert, Brozek & Ortí, 2007) or to facilitate cannibalism of unrelated offspring (Sargent, 1989).

The rate of multiple maternity in these species with uniparental male nest or territory defence showed a very different pattern compared to multiple paternity. Most of these species exhibit very high rates of multiple maternity (Fig. 2B). This pattern is not unexpected because, in most of these species, the male has the capacity to guard a very large number of eggs. Thus, males can maximize their fitness by attracting many females to their nests and spawning with several. Of the 14 species with male nest defence in which multiple maternity was assessed, all but two showed evidence of multiple maternity, and the mean percentage of nests with multiple mothers, averaged across these 14 species, was 73.3% (Table 3). Importantly, the mode is almost 100%. In addition, the mean number of females contributing to each nest across species was 3.1, with within-species means in the range 1.0–4.9 mothers per nest. This pattern contributes additional evidence that multiple mating
by both sexes is extremely common in fishes, and cases of monogamy within a brood are exceptional.

In most studies of male-nesting species in open populations, multiple mating by females has been difficult to document directly. This problem arises because multiply mating females deposit eggs in multiple nests, although, usually, the proportion of nests sampled in a given study is small, meaning that these multiple mating events often go undetected. Nevertheless, two studies of male-nesting fishes have successfully inferred some aspects of female mating patterns. In the fifteen-spine stickleback, at least some females deposit eggs in multiple nests, sometimes over large distances (Jones, Östlund-Nilsson & Avise, 1998b), and each mottled sculpin female appears to deposit her entire complement of eggs in the nest of a single male (Fiumera et al., 2002).

However, the investigation of multiple mating by females in most of the species listed in Table 3 awaits future study. Two exceptional species, channel catfish and lingcod, show single maternity within a clutch but, even in these cases, the fathers may have substantially higher potential reproductive rates than the females. In both species, the females apparently spawn only once per breeding season, and some males defend multiple clutches per breeding season, either simultaneously or sequentially (Withler et al., 2004; Tatarenkov et al., 2006).

The story is somewhat different in species with biparental offspring defence (Table 4). Fewer species with biparental nest defence have been subjected to parentage analysis, making statistical comparisons

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**Figure 2.** Histograms showing the distributions of rates of multiple paternity (i.e. cuckoldry) (A), rates of multiple maternity (B), and the average minimum number of mothers per brood (C) in species with uniparental male nest defence. The data are from the studies listed in Table 3. We include only studies with at least two assayed nests (N = 18). For studies with multiple populations, we use the mean across populations.
difficult. However, multiple paternity, indicative of cuckoldry, was relatively common in species with biparental nest defence. Across species, the mean percentage of nests with multiple paternity was 35.8%, with a range of 0–100%. The mean minimum number of sires per brood was 1.9, with a range of 1–4.7. These patterns of paternity are similar to those for species with uniparental male defence (Fig. 3). Among species with biparental nest defence, the cichlid Variabilichromis moorii, a species characterized by social monogamy, distinguishes itself by showing a frequency of cuckoldry that is unusually high for any species with male parental care (Table 4). The major difference between species with biparental care and those with uniparental male care is that the species with biparental care have much lower rates of multiple maternity per nest (Fig. 3). The mean number of females contributing to each nest in species with biparental care was only 1.1, with a range in species means of 1.0–1.25 (Table 4). This pattern is understandable if the care-giving females actively prevent other females from spawning in the nest or territory.

**Species with no parental care**

Parentage is much more difficult to study in species without parental care, such that we found only eight studies in such taxa that measured rates of multiple paternity or maternity at the level of individuals in a natural context. Many species without parental care fertilize eggs externally, possibly in the water column, and there may not be discrete egg masses to subject to analysis. The few species without parental care that have proven amenable to study either spawn in well-defined locations that are subsequently abandoned or have internal fertilization followed by egg laying. For the six species without parental care studied thus far (Table 5), the results are perhaps not unexpected. Multiple paternity appears to be more common than multiple maternity in the majority of the species. The average minimum number of sires per nest was in the range 1.2–8.0 across these species, whereas the average minimum number of dams tended to approach 1. The pirate perch appears to be a bit of an exception because the scant data indicate that many males and females may spawn in a given oviposition site. Regardless, the study of parentage in species without parental care remains a substantial challenge for future studies.

**Comparison of parentage patterns among care types**

As can be inferred from our discussion above, we found significant differences in rates of multiple paternity and multiple maternity depending on the type of parental care. Parental care class significantly affects the rate of multiple paternity (with male pregnancy included: $F_{4,34} = 7.40, P < 0.001$; without male pregnancy included: $F_{4,48} = 2.91, P = 0.04$). Post-hoc comparisons showed only that male pregnancy differs significantly from other classes of parental care, although the significant result from the model with male pregnancy removed appears to stem from the difference between male nesters and species with internal female care (Fig. 4, top). This result is understandable, given that multiple paternity in species with male nesting represents cuckoldry, an occurrence that care-giving males should be selected to prevent. Rates of multiple paternity are zero in species with male pregnancy (Fig. 4, top). This result is not unexpected either because fertilization in syngnathid fishes occurs within a pouch or on the body of the male and the evolution of such a complex mechanism of paternal care may be likely only in species with high confidence of paternity (Trivers, 1972). Species with no parental care or with biparental care show reasonably high rates of multiple paternity, although too few species from each of these groups have been subjected to parentage analysis to cleanly rank them relative to the other care categories (Fig. 4, top).

Rates of multiple maternity also vary depending on the type of parental care ($F_{4,20} = 14.0, P < 0.001$). This
Table 5. Multiple parentage in species with no parental care

| Species                  | Number of marker loci | Number of progeny assayed | Number of broods assayed | % Broods with multiple paternity | Average number of sires per brood (range) | % Broods with multiple maternity | Average number of dams per brood (range) | Sexual dimorphism* | Reference                    |
|--------------------------|-----------------------|---------------------------|--------------------------|----------------------------------|------------------------------------------|-----------------------------------|------------------------------------------|-------------------|------------------------------|
| *Aphredoderus sayanus* (pirate perch) | 3                     | 351                       | 3                        | 100                              | NR                                       | 100                               | NR (range)                              | 1                 | [@Fletcher et al. (2004)] |
| *Leuresthes tenuis* (California grunion) | 4                     | 682                       | 17                       | 88                               | 3.18 (1–5)                               | 0                                 | 1                                        | 1                 | [@Byrne & Avise (2009)] |
| *Raja clavata* (thornback ray) | 5                     | 173                       | 4                        | 100                              | 4.5 (4–6)                                | 0                                 | 1                                        | 1                 | [@Chevolot et al. (2007)] |
| *Salmo salar* (Atlantic salmon) | 10                    | 1075                      | 85                       | 12                               | NR (1–3)                                 | 17                                | NR (1–3)                                | 3                 | [@Taggart et al. (2001)] |
| *Salmo salar* (Atlantic salmon) | 7                     | 563                       | 12                       | 100                              | 7.3 (3–16)                               | 0                                 | 1                                        | 3                 | [@Grimardias et al. (2010)] |
| *Salmo salar* (Atlantic salmon) | 6                     | 920                       | 18                       | 94                               | 8 (1–16)                                 | 6                                 | 1.06 (1–2)                              | 3                 | [@Weir et al. (2010)] |
| *Salmo trutta* (brown trout)† | 15                    | 1856                      | NA                       | NR                               | 1.5 (1–7)                                | NA                                | NA                                       | 3                 | [@Serbezov et al. (2010)] |
| *Salvelinus fontinalis* (brook trout) | 7                     | 600                       | 20                       | 20                               | 1.2 (1–2)                                | 0                                 | 1                                        | 3                 | [@Blanchfield, Ridgway & Wilson (2003)] |

NA, not applicable; NR, not reported.

*0 = sexually monomorphic; 1 = dimorphic in size only; 2 = dimorphic in elaborate coloration or morphology – such as elongate fins; 3 = sexually dimorphic in elaborate coloration and morphology.

†Estimates are from complete breeding seasons rather than specific broods of offspring, so the values shown here are per female as opposed to per brood.
pattern is mainly driven by species with uniparental male nesting, in which extremely high rates of multiple maternity have been observed (Fig. 4, bottom). As discussed above, this result stems from the fact that males of most nest-tending species can care for clutches from many females, comprising a behaviour that is clearly beneficial in terms of reproductive success. Among the fishes that fall into the other categories of parental care, rates of multiple maternity tend to be low but vary considerably among species (Fig. 4, bottom).

RATES OF MULTIPLE PARENTAGE IN MARINE AND FRESHWATER FISHES

Perhaps the most obvious habitat distinction for fish involves freshwater versus marine environments. Freshwater fishes, for example, tend to occupy more fragmented environments, in which they maintain less within-population molecular genetic variation (DeWoody & Avise, 2000) and experience higher rates of local extinction (Mank & Avise, 2006) compared to marine fishes. In addition, parental care is more common in freshwater fishes than in marine fishes (Baylis, 1981; Blumer, 1982; Gross & Sargent, 1985; Gebhardt, 1987). Given the multitude of differences between freshwater and marine environments, we might expect patterns of parentage to differ.

Despite the expectation that marine environments might produce different rates of multiple paternity or maternity, we found no such pattern. With respect to species in which females carry offspring internally (Table 1), the rate of multiple paternity did not differ significantly between species from marine and freshwater environments (t-test, d.f. = 19, P = 0.43). We did find that freshwater fish with internal female brooding were more sexually dimorphic than marine fish with the same form of parental care (t-test, d.f. = 21, P < 0.001). However, the freshwater fish in this comparison were entirely cichlids and livebearers, which are renowned as paragons of intense sexual selection. Among species with uniparental male nest defence, we detected no differences between marine and freshwater fishes in terms of rates of multiple maternity (t-test, d.f. = 7, P = 0.99) or sexual dimorphism (t-test, d.f. = 8, P = 0.63). Rates of cuckoldry are significantly higher, although only barely so, in marine fish compared to freshwater species (t-test, d.f. = 10, P = 0.04). Given the haphazard nature of sampling with respect to phylogeny and mode of parental care in the two environments, these results should be viewed as preliminary. However, the balance of evidence so far suggests that the type of parental care is a much more direct determinant of patterns of parentage compared to the habitat type in terms of marine versus freshwater.

POPULATION-LEVEL VARIATION IN MULTIPLE PARENTAGE WITHIN SPECIES

A handful of studies have investigated patterns of paternity or maternity in multiple geographically distinct populations within a species with the goal of determining ecological factors that may be responsible for determining the patterns of parentage. The study of geographic variation in fish mating systems is in its infancy, such that no clear patterns have yet been revealed. Some studies have found almost no variation in patterns of paternity or maternity between populations. For example, sand gobies from the Baltic and North Sea exhibit almost identical patterns of parentage, even though the two environ-
ments differ substantially with respect to abundance of nesting substrate (Table 3) (Jones et al., 2001b, c). Similarly, Gulf pipefish from the Atlantic and Gulf coasts of North America have almost identical genetic mating systems (Table 2) (Jones & Avise, 1997a; Jones, Walker & Avise, 2001a). However, a handful of studies have identified populations that differ with respect to multiple paternity or maternity (Daly-Engel et al., 2007; Portnoy et al., 2007), and some preliminary correlations suggest that certain environmental variables may be important. We discuss some of these correlations below, although it is important to recognize that each correlation is based on a small number of populations, such that caution in interpretation or extrapolation is warranted.

**Population density**

Population density is one variable that has been implicated as a possible source of variation in mating systems. Soucy & Travis (2003) investigated variation in multiple paternity among three populations of the livebearing least killifish, *Heterandria formosa*. They found that the percentage of broods with multiple paternity was correlated with population density: in low density populations, the frequency of females showing concurrent multiple paternity was low, whereas, in high density populations, broods with concurrent multiple paternity were relatively common. These results are consistent with the hypothesis that encounter rate is an important factor affecting whether females mate with multiple males per brood (Kokko & Rankin, 2006). In a low density population with correspondingly low encounter rates between males and females, it may benefit a female to allow a single male to fertilize her entire brood. By contrast, in high density populations, where females will encounter relatively higher numbers of suitable mates, a female may benefit by manipulating male fertilization success such that each male fertilizes only a fraction of her brood. In this way, a female may increase the genetic diversity of her offspring, a primary hypothesized benefit of multiple mating (Jennions & Petrie, 2000). However, Soucy & Travis (2003) examined only three populations, such that the correlation is based on a very limited analysis.

**Female body size and multiple mating**

Especially in species with internal gestation by the female, body size may be causally related to the rate of multiple paternity. Even though we avoided studies based on markers other than microsatellites in this review, one study based on allozyme markers deserves mention. Trexler, Travis & Dinep (1997) examined variation in multiple paternity among four populations of the livebearing sailfin molly, *Poecilia latipinna*. This species is characterized by female preferences for males with large dorsal fins and by intense intrasexual competition for females. Trexler et al. (1997) found that the frequency of females carrying broods with concurrent multiple paternity was higher in populations with greater variation in female fertility than in populations with low variance in female fertility. Among populations, no relationship was found between rates of multiple paternity and female body size. Overall, these results suggest that female body size alone does not explain rates of multiple paternity but, instead, the key factor is variation in the fertility of females within the populations: when large (i.e. fertile) females are rare, males compete intensely for matings with these females, resulting in higher rates of multiple paternity than in populations where females are all of similar size. Even though their study did not show a simple relationship between female body size and rates of multiple paternity in the sailfin molly, other studies have shown a tendency for broods of larger females to have more sires. For example, the rate of multiple paternity is positively correlated with female body size in bonnethead sharks (Chapman et al., 2004), least killifish (Soucy & Travis, 2003), and Pacific ocean perch (Van Doornik et al., 2008). Nevertheless, this pattern is not ubiquitous because other studies have failed to find a significant relationship (Zane et al., 1999; Portnoy et al., 2007; Neff, Pitcher & Ramnarine, 2008; Daly-Engel et al., 2010), indicating that many factors, which probably differ in relative importance among species, conspire to shape female mating patterns.

**Predation and multiple mating**

Guppies (*Poecilia reticulata*) inhabit a wide range of environments, and one key environmental variable is the predation intensity. Kelly, Godin & Wright (1999) examined rates of multiple paternity in guppy populations from high and low predation sites and found that the frequency of multiple mating was considerably higher in high predation sites. This pattern was interpreted as being consistent with male displays being limited by predation in high predation sites, resulting in a higher incidence of sneaked copulations in the presence of strong predation. However, subsequent work, taking advantage of a more informative suite of molecular markers, challenged these data by showing that rates of multiple paternity in guppies are above 90%, regardless of predation regime (Neff et al., 2008). Hence, the influence of predation on patterns of multiple mating in guppies, as well as in fishes in general, remains an open question.

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OTHER STUDIES OF GEOGRAPHIC VARIATION IN MATING PATTERNS

Several additional studies have addressed geographic variation in mating patterns, and these studies offer some data that bear on hypothesized causes of differences among populations. For example, Rispoli & Wilson (2007) found that rates of multiple maternity in pregnant male broad-nosed pipefish, _Syngnathus typhle_, were negatively correlated with the degree of sexual dimorphism across four populations subjected to parentage analysis. Similarly, Wilson (2009) found that body size and the number of mothers per brood both increased with increasing latitude in the bay pipefish, _Syngnathus leptorhynchus_. In another study of geographic variation in pipefish mating systems, Mobley & Jones (2009) found that the rates of multiple maternity in pregnant males of the dusky pipefish, _Syngnathus floridus_, varied substantially among five populations from the Atlantic and Gulf coasts of North America. With only five populations in the analysis, causal relationships were difficult to ascertain, although the data suggested that a number of demographic and habitat characteristics could be responsible for variation in the genetic mating system.

By contrast to the studies on sand gobies (Jones et al., 2001b, c), which found no differences between two population with differences in nest substrate abundance, Bessert et al. (2007) found that nest substrate availability did affect patterns of multiple mating and nest usurpation in the fathead minnow, _Pimephales promelas_. The comparison involved only two populations, but in the population characterized by limited nesting substrate, males mated with a larger number of females per nest and showed a higher rate of nest-takeovers.

TEMPORAL VARIATION IN MATING PATTERNS

In addition to geographic variation in mating systems, temporal variation almost certainly occurs as well. In one study, Sefc, Hermann & Koblmüller (2009) used microsatellite markers to examine patterns of parentage in _Clenochromis horai_, a maternally mouthbrooding cichlid from Lake Tanganyika, during the rainy and dry seasons. Their results showed that all broods were multiply sired during the rainy season, whereas only 14% of broods had multiple sires during the dry season. The authors noted that turbidity was much higher during the rainy season than during the dry season, leading to the hypothesis that water clarity affects the mating system of this species. Clear water may facilitate mate guarding by males, whereas more turbid water may make it easier for nonpair males to surreptitiously fertilize eggs or for females to escape a guarding male. Even though more work will be required to resolve these hypotheses, temporal variation in mating patterns provides a potentially valuable, underutilized resource for the study of the evolution of mating systems.

A FEW CONCLUSIONS REGARDING GEOGRAPHIC AND TEMPORAL VARIATION IN MATING PATTERNS

The parentage analyses conducted so far show that many species exhibit substantial variation in rates of multiple paternity and multiple maternity among populations. We predict that future work will also confirm that temporal variation in patterns of parentage is common in fishes. However, essentially none of the published studies of temporal or geographic variation in parentage have been sufficiently large to conclusively document the ecological factors responsible for variation in mating patterns in natural populations of fishes. The continued study of geographic and temporal variation in parental care, ecology, and reproductive behaviour has tremendous potential to illuminate key aspects of mating system evolution, so that such studies, although difficult, would be a worthy target of future work.

MULTIPLE PARENTAGE AND SEXUAL DIMORPHISM

Given that the mating system is expected to play a major role in the operation of sexual selection, we might expect patterns of multiple mating to be correlated with the evolution of sexual dimorphism. Among species in which females carry zygotes internally (Table 1), we found no relationship between the mean multiple paternity rate and the degree of sexual dimorphism (linear regression, \( N = 22, P = 0.73 \)). In species with male pregnancy (Table 2), visual inspection of the data suggests that species with intermediate degrees of sexual dimorphism have higher rates of multiple maternity than species with low or higher degrees of sexual dimorphism. This pattern is consistent with sexual selection theory. The species with no (or very little) multiple mating by males are either strictly monogamous (_Hippocampus species_) or classically polyandrous (_S. scovelli_ and _N. ophidion_), mating systems that are expected to produce very little sexual selection or strong sexual selection, respectively. The species with high rates of multiple mating by males, however, are polygynandrous (i.e. characterized by frequent multiple mating by both sexes), a mating system that is expected to produce an intermediate intensity of sexual selection.

In species with nest defence (Table 3), sexual dimorphism was more pronounced in species with uniparental care than in species with biparental care.
This result could be explained by two possible hypotheses. One possibility is that the social interactions between males and females in species with biparental care act in such a way as to constrain the operation of sexual selection, reducing the total intensity of sexual selection in these taxa. The other possibility is that sexual selection may act on both sexes in biparental species, with mutual mate choice driving relatively equal rates of evolutionary elaboration of the same secondary sexual traits in males and females. This result must also be interpreted with some caution, however, because all but one of the species with biparental nest defence represented in Table 4 are cichlids, resulting in a distinct lack of phylogenetic independence.

COMPARISONS OF MULTIPLE PATERNITY AMONG VERTEBRATE CLASSES

Recent reviews of multiple paternity in birds (Griffith et al., 2002), reptiles (Uller & Olsson, 2008), and mammals (Soulsbury, 2010) allowed us to compare rates of multiple paternity between these taxa and fishes. For this comparison, we included only fishes with male nest defence and internal brooding by females, and we kept these categories of parental care separate for statistical analysis. We found significant effects of taxonomic group on rates of multiple paternity (\(F_{4,264} = 21.4, P < 0.001\); Fig. 5). The most striking result is that fishes with internal brooding by females have substantially higher rates of multiple paternity compared to mammals and birds (Fig. 5). Reptiles have significantly higher rates of multiple paternity than birds, although they are not significantly different from mammals or either parental care class in fishes (Fig. 5).

The lower rate of multiple paternity in birds is not unexpected for at least two reasons. First, birds tend to have small clutch sizes compared to fishes with internal brooding by females and most reptiles. Multiple paternity is more difficult to detect in smaller clutches, and the clutch size also places an upper bound on the maximum number of mates per brood. Second, the widespread occurrence of social monogamy in birds likely limits mating opportunities in avian species compared to their fish, mammalian, and reptilian counterparts. Fishes, reptiles, and mammals exhibit a wide variety of social interactions, often with a lack of prolonged attachments between pairs of individuals. The extensive paternal care typical of many bird species results in strong selection on males to avoid cuckoldry, consequently reducing rates of multiple paternity in females. The same sort of selective pressure explains why males in fish species with paternal nest defence show lower rates of multiple paternity compared to fish species with internal brooding by the female (Fig. 5).

CONCLUSIONS AND FUTURE DIRECTIONS

The most striking result from the first 15 years of microsatellite-based studies of parentage in fishes is the amazing diversity of mating systems. Fishes display a wide range of social systems, and patterns of multiple paternity and maternity mirror this variation. A couple of surprises have emerged as well. For example, multiple paternity and maternity are perhaps even more pervasive than would have been predicted a decade ago. An unexpectedly large number of species have rates of multiple parentage approaching 100%. It is also unexpected that even closely-related species sometimes have very different mating systems and that these differences can have substantial evolutionary implications.

The main purpose of this review is to provide a summary of studies in hopes of catalyzing future investigations, and the literature so far suggests that much remains to be accomplished. For example, the taxonomic representation in parentage studies is so narrow that many major fish lineages remain untouched. Although more work on the well-characterized systems is certainly warranted, additional breadth in taxonomic coverage also would be
desirable. Another major challenge in fishes stems from the diversity of parental care and fertilization modes. In the comparison of fishes with internal fertilization in females to species with male nest defence, for example, even the identification of a common currency for comparison is a major challenge. Multiple paternity in male nesters, for example, has entirely different evolutionary implications than multiple paternity in pregnant females. These types of differences effectively dilute the fish parentage literature because only small subsets of studies are directly comparable with one another. Thus, even though natural mating systems have been characterized for dozens of distinct species of fishes, many categories of parental care are represented in only a handful of studies, making generalities difficult, if not impossible, to discern.

These considerations indicate a substantial need for additional work in a number of different areas. First, more studies targeting a greater diversity of fish species would be welcome. In particular, under-represented forms of parental care, such as biparental and male mouthbrooding, would be appealing targets for future work. Second, we need more studies addressing why patterns of parentage differ among populations and species of fish. Such studies could take advantage of temporal or geographic variation to examine correlations between environmental variables and mating system variation, possibly with follow-up studies in experimental populations. Another appealing approach might be to conduct comparative mating system analyses in a phylogenetic framework. Finally, our reading of the literature makes clear that we do not fully understand the consequences of variation in mating patterns among species or populations. Thus, future theory and empirical work could profitably explore the ecological and evolutionary ramifications of variation in patterns of parentage.

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