



# Male pregnancy and the formation of seahorse species

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**Seahorses have long been part of the pantheon of imagination-inspiring creatures. The external appearance of this strange fish probably accounts for the widespread appeal of the seahorse. Reproduction in seahorses is even more unusual, as the male rather than the female, becomes pregnant. Recent research on seahorse mating behaviour reveals that male pregnancy in seahorses and their relatives has had profound effects on the evolutionary legacy of these organisms.**

The seahorse is one of the most famous fish, appearing in movies, television shows, greeting cards, and children's toys, just to name a few. The fact that relatively little research has been done on seahorses thus comes as a bit of a surprise. Naturalists have long appreciated that the males of this group carry the young, but it has only been in the last two decades that we have begun to appreciate the evolutionary implications of male pregnancy.

## **The pregnant male and his devoted wife**

Mating in seahorses starts with an elaborate courtship ritual that in some species lasts several hours. Courtship has been described in few seahorse species, but we can grasp the flavour of the event from descriptions of mating interactions in an Australian species known as *Hippocampus whitei* (Vincent and Sadler, 1995). Upon meeting, the male and female brighten in colour and then begin a dance, twisting their tails together and swimming in circles. After the prolonged courtship dance, the female inserts her ovipositor through a small opening into a pouch located on the male's tail (Figures 1 and 2). She transfers unfertilised eggs into the pouch of the male, who releases sperm into

the pouch to fertilise the eggs. The actual transfer of eggs only takes a few seconds.

At this point, the female's investment in the offspring is complete, but the male is left with a pouch full of growing offspring. The male then carries the developing brood for a period of several weeks, and his pouch bulges larger and larger until he finally gives birth. The pouch appears to be a serious burden for pregnant males and they move around very little when pregnant (Kvarnemo *et al*, 2000).

Even though he is solely responsible for care of the developing embryos, the life of a pregnant male seahorse is not entirely lonely. The female, although she provides no parental care, comes by each morning to greet the male (Vincent and Sadler, 1995). These greetings are essentially shortened versions of the courtship ritual, but obviously without a transfer of eggs, since the male is pregnant already. These greetings are not without purpose. Indeed, the female seems to be checking on the progress of the male's pregnancy so she can be ready to re-impregnate him as soon as possible after he gives birth.

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*Title image. Thorny seahorse.*



**Figure 1.** A male (left) and a female of the Western Australian seahorse, *Hippocampus subelongatus*. This species is like most seahorse species in that the two sexes are very similar in overall appearance, with one important exception. The male has a pouch on the underside of his tail in which he carries his developing offspring. The female uses an ovipositor to fill the male's pouch with eggs and the male releases sperm into the pouch. The pouch expands as the offspring grow – the male shown here is pretty far along. Photographs by Glenn I. Moore.

The newly-born offspring are miniature versions of the adults and they are completely on their own, because within a day the male is ready to start his next pregnancy. Here we see another amazing feature of the biology of seahorses. Not only are they monogamous within the course of a single breeding episode, but they maintain pair bonds that persist across mating events within a breeding season (Kvarnemo *et al*, 2000). We do not know whether or not these pair bonds persist for life, because no study spanning breeding seasons has yet been conducted.

### More than a bag full of offspring

The brood pouch on the tail of male seahorses looks much like a big bag of skin, but merely carrying developing offspring in an otherwise functionless bag should not be considered a true pregnancy. In mammalian pregnancy, for example, the embryo implants in the uterus of the mother and the placenta and umbilical cord provide a physiological connection between mother and offspring. An analogous situation occurs during male pregnancy in seahorses. Paternal tissue surrounds the eggs within the male's pouch and blood flow through this tissue provides a placenta-like connection between the male and his offspring. Thus, the male pregnancy in seahorses shows similarities to the intimate parent-offspring relationship we see in mammals, and the brood pouch is a complex structure (Carcupino *et al*, 2002). The male appears to provide nourishment for the developing young. He also controls the concentrations of ions and oxygen within the pouch and provides the obvious protection afforded by the outer pouch wall.

### Societal implications of male pregnancy

Research on the evolutionary implications of male pregnancy was first spurred by an interest in sex roles and competition for mates. In species with high male investment in offspring, parental investment theory predicted that the females might compete for access to males (Andersson 1994). This argument can be understood from a simple economic perspective. If males provide a large amount of parental care, which is costly, then they will be so busy caring for offspring that they will not be available to mate. In extreme cases, so few males may be available to mate that females will be forced to compete amongst themselves for access to those few available males. In species without male parental care, the male has a much



**Figure 2.** An X-ray of a male seahorse. The pouch is actually an external structure that grows out of the surface of the male. The pouch is not located in the male's body cavity, and it is not protected by the bony plates that cover the rest of the seahorse's body. Brood pouches of this kind occur only in pipefishes and seahorses and are unlike any other structure in the animal world (X-ray obtained courtesy J King, Australian Museum Website, [www.amonline.net.au/fishes/fishfacts/fish/habxray2.htm](http://www.amonline.net.au/fishes/fishfacts/fish/habxray2.htm)).

that sexual selection is weak in a monogamous species is intuitively obvious. If there are equal numbers of males and females in a species with monogamous mating, then every individual will have a mate. If every individual is basically guaranteed a mate and also is incapable of utilising more than one mate, then competition for mates should be very weak. Instead, what we see in seahorses is an interesting mating pattern involving assortative pairing by size (Figure 3). In other words, large males mate with large females and small males mate with small females (Jones *et al*, 2003).

The benefit of such an arrangement stems from the fact that the reproductive potential of both sexes is positively correlated with body size. Larger males have larger brood pouches and larger females produce more eggs than smaller individuals. Consequently, if a large male mates with a small female, she will not be able to completely fill his pouch. If a small male mates with a large female, he will not be able to fit all of her eggs in his pouch. In either case, one of the individuals in the pair is wasting some reproductive potential.

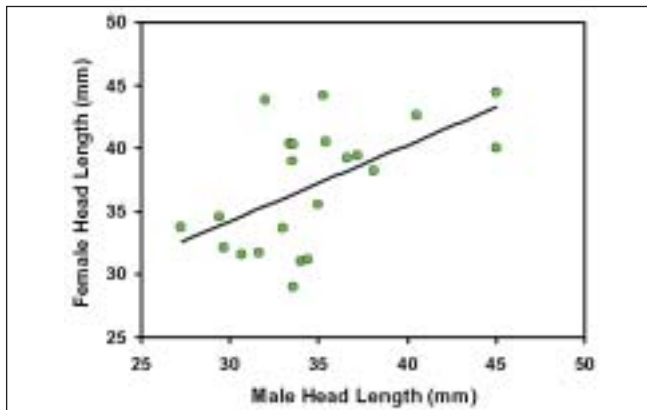
Reproduction has been studied in a fairly small number of seahorse species, but all that have been studied to date exhibit monogamy (Jones *et al*, 2003). Size-assortative pairing has only been studied in two species, both of which engage in such a mating pattern (Vincent and Sadler, 1995; Jones *et al*, 2003). Because size-assortative mating is caused by constraints imposed by monogamy and male pregnancy, this pattern of mating probably occurs in most seahorses, although additional research on this topic is certainly warranted.

higher potential rate of reproduction than the female, so the usual situation is for males to compete for access to females (See Box 1). Consequently, we typically see traits involved in mate acquisition, like antlers on deer or the peacock's tail, evolving in males.

This process, originally proposed by Charles Darwin in the mid-nineteenth century, is known as sexual selection. Species with male pregnancy provide a system in which to test theories related to mating competition and sex roles, because females may be expected to compete for males, resulting in the potential for the evolution of elaborate traits in females. Such a pattern of a reversal of the direction of mating competition has been observed in pipefish, relatives of seahorses that also practise male pregnancy (Jones and Avise, 2001).

However, because seahorses are monogamous, sexual selection is weak. Their mating patterns are nevertheless interesting and evolutionary significant for an entirely different reason. The reason





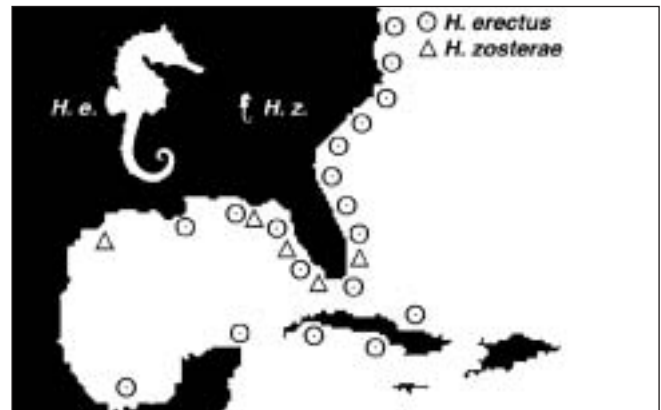
**Figure 3.** Assortative mating in seahorses. A genetic study of parentage in the Western Australian seahorse shows that males and females pair by size in natural populations (Jones et al., 2003). This graph plots the male's head length versus the length of his mate's head. Head length is used as the measure of body size because it is easier than total length to measure on live specimens and it is correlated with total body size. This graph shows that large males mate with large females and small males mate with small females. This so-called size-assortative mating has important implications for speciation in seahorses.

### Male pregnancy and sympatric speciation

Why make such a big deal of male pregnancy? As noted above, the implications of male pregnancy with respect to mating competition were anticipated decades ago by evolutionary thinkers. And the promise of species with male pregnancy has been fulfilled with respect to the study of sexual selection over the last two decades, as these species have had a major impact on our understanding of mating competition and sex roles (Jones and Avise, 2001). However, an unanticipated consequence of male pregnancy is that it also appears to have affected the formation of new species in the seahorse genus (Jones et al., 2003).

The idea that male pregnancy could affect rates of speciation was prompted by the observation of size-assortative mating. In fact, the most widely used functional concept of what constitutes a species is based upon the idea of assortative mating. According to Ernst Mayr (1942), one of the most influential figures in the history of speciation theory, 'Species are groups of actually or potentially interbreeding populations, which are reproductively isolated from other such groups.' Hence, members of Species A, say, only mate with other members of Species A, and members of Species B only mate with other members of Species B. Speciation thus involves assortative mating with respect to geographic location or some other phenotypic trait that distinguishes species.

One of the most active areas of research in speciation theory is the question of whether or not new species can originate in the absence of barriers to migration. Essentially all evolutionary biologists accept that geographic isolation can lead to speciation, as separate populations build up genetic differences as a consequence of random changes in their gene pools or natural selection in response to distinct environments (so-called allopatric speciation). However, recent theoretical investigations indicate that a single population can give rise to two species even in the absence of physical barriers to gene flow, a phenomenon known as 'sympatric speciation' (Via, 2001). Interestingly, all models of sympatric speciation require some sort of assortative mating to prevent differences among genetically differentiated forms from being broken down by sexual reproduction. The challenge for sympatric speciation theory is to come up with conditions under which phenotypic divergence and assortative mating can evolve simultaneously in



**Figure 4.** Geographic distributions of two North American species of seahorses, the lined seahorse (*H. erectus*) and the dwarf seahorse (*H. zosterae*), that may have diverged through sympatric speciation (Jones et al., 2003). These species appear from genetic data to be close relatives, and the range of the dwarf seahorse is completely encompassed by the range of the lined seahorse. The silhouettes indicate the relative adult sizes of these two species, which clearly differ dramatically in size. This pattern is exactly what would be expected of the sympatric speciation scenario.

a single population. It is this situation that can produce sympatric speciation.

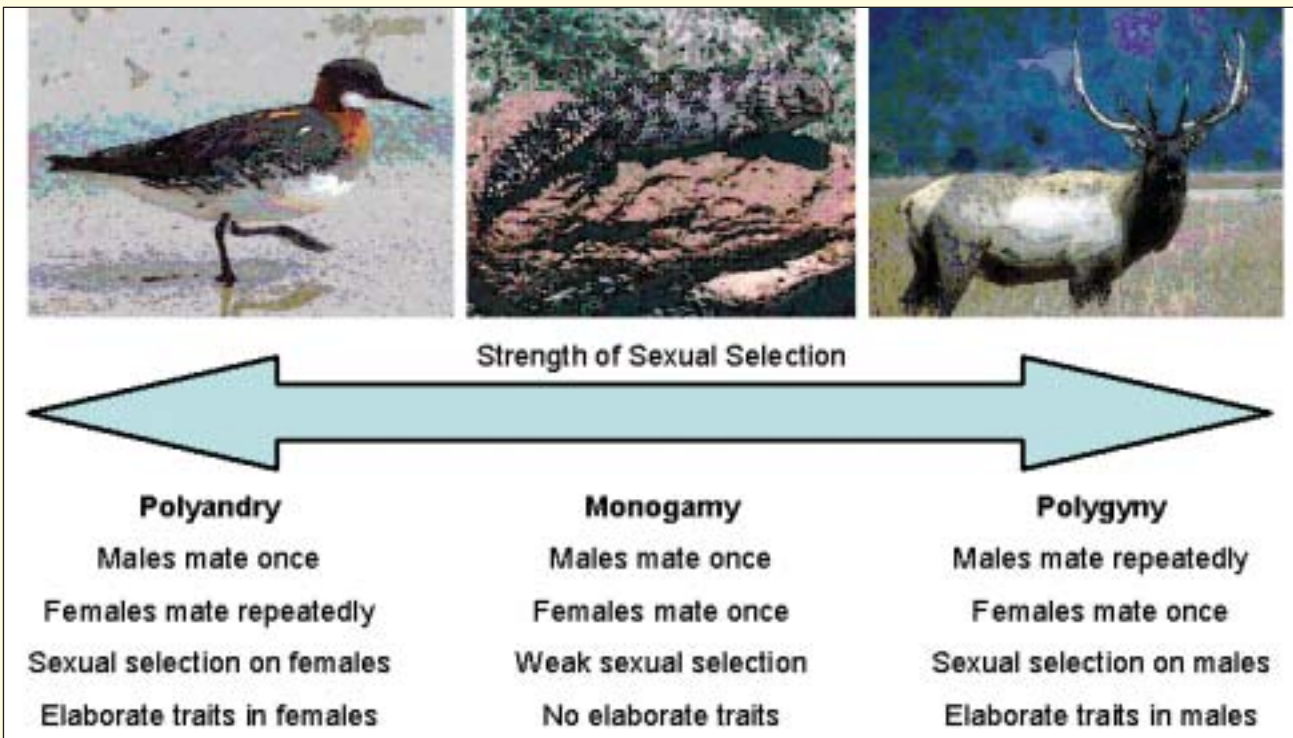
And this fact brings us back to the seahorse example. If assortative mating evolved for reasons unrelated to the speciation process, for example as a consequence of male pregnancy, then the assortatively mating population would be predisposed to form new species whenever the appropriate regime of natural selection arose. The type of natural selection that can produce sympatric speciation is known as disruptive selection, which refers to a situation in which the extreme phenotypes are most likely to survive and reproduce, whereas the intermediate phenotypes are less likely to leave descendants. Given disruptive selection and assortative mating, the progression toward sympatric speciation is obvious.

Let us take body size as an example. If large individuals usually mate with large individuals, small individuals usually mate with small individuals, and the few intermediate individuals produced each generation leave very few descendants, then it is only a matter of time before the intermediate individuals disappear altogether, leaving two distinct classes of individuals (small and large) that are reproductively isolated from one another.

Size-assortative mating in seahorses thus predisposes them to form new species whenever strong enough disruptive natural selection on body size occurs. Hence, one remaining question is whether or not disruptive selection of the appropriate strength has occurred in the evolutionary history of seahorses. We may never be able to directly obtain the answer to this question, but several indirect lines of evidence suggest that sufficiently strong directional selection on body size may have occurred. First, in many places, several different species of pipefishes or seahorses, which differ from one another in size, co-occur within the same habitat. We can thus imagine that there are multiple different optimal sizes in a given habitat. If the environment changed and a species colonised a new locale or a new competitor moved in, then a species could find that its average size no longer is no longer optimal. Then natural selection would favour those individuals that were larger or smaller (or both) than average. Such a scenario could lead to disruptive selection if the average size of the species was somewhere between two different optimal sizes for a given habitat. Theoretical

**Box 1. The relationship between mating patterns and the strength of sexual selection**

We are used to thinking about species like the North American elk (right), in which males defend harems and most females just mate with the dominant male. In such a system, males compete for access to females and consequently traits (like antlers) evolve to aid the males in these contests for mates. Thus, the antlers of elk only occur on the males. In genetically monogamous species, like seahorses or the gidgee skink (middle), sexual selection is usually weak, because if there are equal numbers of males and females, then every individual in the population will have a mate, making competition for mates unnecessary. Finally, a few exceptional species are sex-role reversed, with females competing for access to mates. Such a situation arises when males become a limiting resource for reproduction. If each successful female mates with multiple males but each male mates with only one female, as has been observed in the red-necked phalarope (a female is shown here at left) and some species of pipefish, then the males available to mate in the population will be used up before every female gets a mate. This situation results in females competing for access to males, and traits that aid in mating competition consequently evolve in the females of these species. In the red-necked phalarope, for example, the females are colourful but the males are drab. Similar patterns are seen in some pipefish species, in which the ultimate cause of sex-role reversal is the reduction of reproductive rate in the male associated with his pregnancy. Photos were provided by the Wyoming Section of the Society for Range Management (elk), the Honolulu Zoo (gidgee skink; [www.honolulu.zoo.org](http://www.honolulu.zoo.org)), and Silvio Sommazzi and Giuliano Gerra (red-necked phalarope; <http://gianfvil.gamersrevolt.it/home.htm>).



models show that brief periods of disruptive selection would be sufficient to produce sympatric speciation in seahorses, so disruptive selection need not be common to have a significant effect on speciation in seahorses (Jones *et al*, 2003).

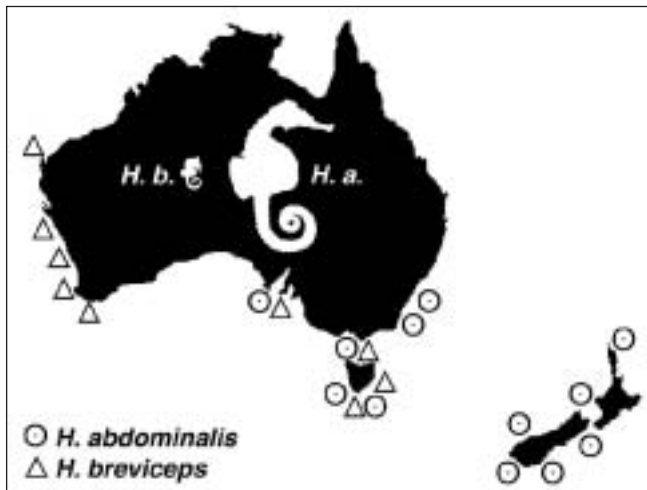
A second line of evidence that sympatric speciation may have been important in seahorses comes from the distribution of species. If sympatric speciation occurred as a consequence of size-assortative mating and disruptive selection on body size, then the speciation events should be reflected in present-day geographical ranges of seahorse species. In particular, we would expect closely related species of different sizes that are sympatric over all or parts of their ranges.

At least two such examples occur in seahorses (Figures 4 and 5). In North America, the range of the dwarf seahorse, *Hippocampus zosterae*, is completely encompassed by the range of its close relative, the lined seahorse *H. erectus* (Figure 4). The dwarf seahorse is one of the smallest seahorse species, with a typical adult length of just over two centimetres. The lined seahorse, on the other hand, is a medium-sized species with an adult length of about 12 cm. Another example comes from two sister species from Australia, *H. abdominalis* and *H. breviceps*. These species overlap in Southeastern Australia and Tasmania (Figure 5),

but also have areas in Western Australia and New Zealand where they do not overlap. These species also differ in adult size, as *H. breviceps* is one of the smaller species of seahorses at around 6 cm, whereas *H. abdominalis* is one of the largest at about 20 cm.

Considerable excitement was generated recently with the discovery of the world's smallest seahorse (Lourie and Randall, 2003). Adults of this newly described species, known as *H. denise* (Figure 6), are just over one centimetre in length. Interestingly, they are sympatric with a slightly larger species, *H. bargibanti*, whose typical adult length is just below 2 cm. Based on morphological criteria, these two species appear to be very close relatives. Their geographic distributions are not yet well defined, but they appear to co-occur over large parts of their ranges. In fact, individuals of *H. denise* originally were believed to be young specimens of *H. bargibanti*. Thus, this species pair represents another possible example of sympatric speciation.

If sympatric speciation has been common in seahorses, we should expect additional cases of this type, in which two species are very similar in appearance but differ markedly in size. Under such circumstances, it should not be surprising if the smaller species is mistakenly believed to be the young of the larger. We are in dire need of additional research on



**Figure 5.** Another possible pair of seahorses that may have diverged through sympatric speciation (Jones et al., 2003). The pot-bellied seahorse (*H. abdominalis*) and the short-snouted seahorse (*H. breviceps*) are sister species, and they overlap in Southeastern Australia and Tasmania. The pot-bellied seahorse is one of the largest seahorse species and the short-snouted seahorse is among the smaller species.

the evolutionary relationships and taxonomy of seahorses, and such research should reveal additional cases of putative sympatric speciation if they exist.

### Geographic barriers to gene flow

Even though sympatric speciation may have occurred in some lineages of seahorses, most speciation in these fishes has probably been due to geographic barriers to gene flow (i.e. allopatric speciation). Seahorses occur in tropical and temperate oceans and seas throughout the world. All continents except Antarctica are home to at least a few seahorse species. It seems likely that many of these species arose as a consequence of a single population being divided into two or more populations by a change in ocean currents, movements of land masses, or some other obstacle that seahorses were unable to swim across.

Male pregnancy not only facilitates sympatric speciation (as noted above) but also should be expected to increase the likelihood of allopatric speciation. Imagine that two populations are split by a geographic barrier and evolve a body size that is advantageous in the local environment. There will be two populations that differ in body size. If the geographic barrier to dispersal breaks down and the two populations again come into contact, size-assortative mating as a consequence of male pregnancy will prevent them from interbreeding and their genetic distinctiveness will be maintained. Thus, assortative mating in seahorses not only increases the likelihood of sympatric speciation, but it also increases the ease with which species can form in general.

### Species richness in seahorses and their relatives

If speciation in seahorses is facilitated by their mating patterns, then we may expect seahorses to be a group with a particularly large number of species. This prediction is supported by seahorse taxonomy. All seahorses are grouped into the single genus *Hippocampus*, and a recent revision of the genus recognizes 33 species (Lourie et al., 1999). Some authors believe there may be as many as 50 or more species of seahorses, but they have not been studied in sufficient detail in many parts of the world for us to be certain. The relevance of the number of species of seahorses is best considered in light of their close relatives.



**Figure 6.** Last year, a new seahorse species, *H. denise*, was described. This species is the smallest seahorse yet documented, and specimens of *H. denise* were originally thought to be the young of a related species, *H. bargibanti*. This type of pattern would be expected if sympatric speciation in seahorses had occurred with reasonable frequency during their diversification. Photo courtesy of Larry and Denise Tackett (tackettproductions.com).

The seahorses are in the family Syngnathidae, which includes seahorses as well as about 180 species of pipefishes in approximately 50 genera and two species of sea dragons. All species in this family are characterised by male pregnancy, but the seahorse is noteworthy for having the most complex brood pouch. Some species of pipefishes have a superficially similar brood pouch configuration to seahorses, but with a zipper-like ventral seam instead of a small opening at the top of the pouch. Some species of pipefishes just have the eggs glued to the male's body without an external covering of any kind.

The large number of species in the family Syngnathidae is particularly striking in comparison to other families of fishes that are believed to be closely related to seahorses. Ghost pipefishes (family Solenostomidae), sea moths (Pegasidae), trumpetfishes (Aulostomidae), flutemouths (Fistulariidae), shrimpfishes (Centriscidae), snipefishes (Macrorhamphosidae), and sticklebacks (Gasterosteidae) are all considered to be fairly closely related to Syngnathidae, yet none of these families contains more than about 12 recognised species. Thus, it looks like there was a fairly marked burst of speciation during the evolution of pipefishes, seahorses and sea dragons (Wilson et al., 2001).

Is there something about male pregnancy that increased the rate of speciation throughout the family Syngnathidae? We do not yet have a clear answer, but this question is stimulating additional research. Of course, widespread size-assortative mating in pipefishes could account for increased speciation rates. However, patterns of assortative mating have not yet been studied in detail in nature for any pipefish. In addition, most pipefishes studied to date are not monogamous, so the reason for size-assortative mating would have to be different from that in seahorses, which mate size-assortatively in an attempt to exactly match their reproductive rates with those of their mates. However, in some species of pipefishes, males and females both prefer larger mates, providing for the possibility that mutual mate choice could produce size-assortative mating. If larger mates are preferred, then only the most attractive, largest individuals may actually be able to choose their mates and they would, of course, choose the largest individuals for mates. The small individuals would then have to mate with the leftovers, which would also be small. Hence, it is conceivable that size-assortative mating is a widespread feature of the family Syngnathidae and has provided



a boost in the rates at which new species arise (either in sympatry or in allopatry). We do not know for sure, though, and we need more research on this topic.

Another possibility is that the evolution of male pregnancy increased speciation rates by decreasing juvenile dispersal ability. In many species, pipefishes and seahorses are born as miniature versions of the adults with essentially no remaining egg yolk. They are believed to settle relatively quickly within their natal sea grass meadow to begin their life of mimicking sea grass and eating small zooplankton. Consequently, most scientists believe that their opportunities to move across wide expanses of ocean to other sea grass beds are extremely limited. Only two studies have examined patterns of genetic variation between populations of pipefishes or seahorses. These studies detected high levels of genetic differentiation among populations, a pattern consistent with the idea that male pregnancy decreases rates of migration over large distances. If this situation is common in the family Syngnathidae, then fairly minor barriers to dispersal could reduce gene flow among pipefish populations sufficiently to result in the formation of new species.

In summary, male pregnancy is an unusual phenomenon, but we are very fortunate that it evolved because it provides some unparalleled opportunities to study interesting biological topics from a unique perspective. The evolutionary consequences of male pregnancy have been quite impressive, affecting a wide array of phenomena from sexual selection to the very nature of speciation. We have only begun to scratch the surface of the interesting biology of seahorses, pipefishes, and sea dragons, so the coming years should be very exciting as additional work further clarifies the natural history of male pregnancy and its role in evolution.

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