Love at First Scent

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We have all heard of love at first sight, but what about love at first smell? It turns out that there are fish in which the females look for someone who smells like dear old dad. Chalk another one up for the astounding diversity of life.

The threespine stickleback (*Gasterosteus aculeatus*) is a small, spiny-finned, scaled fish 2 to 4 inches long (5 to 10 centimeters). The eggs, a clear, milky color, take 10 to 12 days to hatch.
The fish in question are threespine sticklebacks \((Gasterosteus\ aculeatus)\). Two species of these fish share lakes in \textit{British Columbia}, Canada, meaning that they are not geographically isolated, although one species (benthic sticklebacks) stays near the bottom of the lakes while the other species (limnetic sticklebacks) lives in the open water above. Although neighbors, they have remained sexually isolated (they do not interbreed). Genevieve M. Kozak, Megan L. Head and Janette W. Boughman explored this phenomenon in a recent paper published in the \textit{Proceedings of the Royal Society B}. (The research on this paper was done while Kozak and Boughman were at the \textit{University of Wisconsin} in Madison and Head was at the University of Exeter in the U.K.) They found that sexual imprinting — a term that refers to the influence of early experiences on mate selection — plays a large part in keeping the species isolated. More specifically, they discovered that a female stickleback may pick a mate based on how much he smells like her dad.

**Splitting a Species**

In both species, it is the males who mainly take care of the eggs. Male sticklebacks build nests where females then lay eggs. The males fertilize and mind the eggs until they hatch. Because of their role as nurturers, the males are the parent with the possibility of imprinting on the offspring, and so it was their influence that Kozak and her collaborators investigated.

Despite their behavioral similarities, benthic and limnetic sticklebacks have adapted to the different water depths in which they are found. Benthic sticklebacks are substantially larger than limnetic sticklebacks, and the species differ also in coloring, odor and diet. These differences make each species more suited to its environment. Through sexual imprinting, these differences could potentially guide the mate selections of the offspring, leading them to mate with members of their own species.

**Process of Elimination**

You cannot ask a fish a question, or at least it's not a research strategy likely to bear fruit. To determine if sexual imprinting was occurring, and what a female stickleback finds appealing in a mate, the authors instead created an elegant series of different egg-raising situations or treatments, each one involving several families of fish. The five treatments helped the researchers hone in on the factors affecting mate selection.

In the first treatment, the eggs were attended by their biological fathers. In the second treatment, the eggs were swapped after fertilization, so that they were raised by foster fathers of the same species (conspecifically), allowing the researchers to discern how
important being raised by the biological father is to the process of imprinting. In other words, it was designed to show whether being
cared for by a foster father would be enough to interrupt the process of imprinting, or if imprinting would occur as long as the foster
father belonged to the same species as the biological father.

The third treatment also involved an egg swap after fertilization, but this time the eggs were raised by a foster father from the other
stickleback species (heterospecifically). This treatment was designed to reveal whether or not having a foster father from a different
species would make a difference in mate selection. The fourth treatment involved eggs that were fertilized and then left fatherless to
develop independently of nurturing, which would help to determine if imprinting of any kind occurred, or if mate selection preferences
did not depend on upbringing. If offspring from this group preferred mates of their own species to the same extent as fish raised
conspecifically, then genetics, not imprinting, would presumably be the cause of their mate choices. But if they showed less of a
preference for their own species, that would constitute evidence of the importance of imprinting.

Male sticklebacks build nests where females deposit eggs; they then fertilize the
eggs and mind the eggs until they hatch. ABOVE: A male stickleback excavates a
nest site (top left), gathers nest material (top right), glues the nest (bottom left), and
watches over the hatchlings in the nest (bottom right).

The fifth and final treatment involved eggs that were raised conspecifically (either by their biological father or by a foster father of the
same species), but were exposed to the odor of the opposite species during embryonic development. The aim of this treatment was
to investigate if odor played a role in the imprinting process. The exposure to the odor of the opposite species was done by placing a
female of the opposite species (opposite to the egg) about 50 centimeters (roughly a foot and a half) distant from the nest, and out of
visual range of the egg or embryo. A mesh kept the female separated from the nest, and the female was placed at that distance for
two hours a day during the testing period.

During the egg raising, the nurturing males' behavior was observed and recorded for 10 minutes each day for eight days. The
researchers were particularly interested in the extent to which the males fanned and rubbed their bodies on the eggs, as well as how
often they deposited spiggin (nest glue), because these behaviors are thought to send olfactory cues to the eggs. After these eggs
hatched, two male and two female offspring from each family were tested to find out their mate selection preferences. In each test,
the fish was given a choice between two potential mates, one benthic and one limnetic. The males were offered two potential mates
at once, and the females were offered one mate at a time. Their preferences were determined based on their behavior.
**Lasting Impression**

Kozak and her collaborators found that while stickleback males' mate choices were unaffected by who had raised the eggs from which they hatched, for stickleback females first impressions really matter. After analyzing the results of all five treatments, they found that there was no difference between the reactions of female offspring hatched from eggs raised by same-species foster fathers and those hatched from eggs raised by their biological fathers. Although replacing the biological father with a foster father of the same species had no impact, replacing him with a heterospecific foster father did; across all treatments, female offspring imprinted on the species of the male who cared for the eggs from which they hatched. Females hatched from eggs that had been raised without a father only showed a mild preference for their own species when choosing a mate, in strong contrast to females whose eggs had been raised conspecifically. Without the opportunity to imprint, females do not consistently select mates of their own species. Imprinting appears to be crucial in ensuring the sexual isolation of these two species.

The fifth treatment, involving females hatched from eggs raised conspecifically but exposed to heterospecific odor during development, had very different results for the two species. The limnetic females were not affected by the exposure (they still showed a strong preference for the species of their caring father), but the benthic females went on to prefer heterospecific mates (males of the opposite species from that of their caring fathers). This treatment shows that odor plays an integral role in the imprinting process for benthic sticklebacks. Additionally, the researchers found that the preference of female offspring for their caring fathers' species was related to how often their father deposited glue on the nest: the more often glue was deposited, the stronger the preference. This implied that odor played a part in mate selection in both species, but the researchers had to verify that.

Doing so was made easier by the researchers' being able to take into account the precise details of how sticklebacks grow. Stickleback eggs develop their olfactory system days before they begin to develop their visual system, so they can receive olfactory cues ahead of visual cues. The researchers refined their analysis by dividing their nest-tending data into developmental stages. They analyzed how often the fathers deposited glue on the nest before the olfactory system developed, how often they did so after the olfactory system had developed but before the visual system had developed, and how often they deposited glue after both systems had developed. They found that the impact of gluing rate on imprinting was related only to the developmental period after the olfactory system had developed but before the visual system had done so. Odor was thus shown to be a major mechanism of sexual imprinting for eggs during development.

Smell is important, but looks matter too. Kozak and her collaborators found that while the body size of the caring father did not affect their daughters' mate choices, body coloring did. Males were given a score to reflect their body coloring — brightness, darkness and hue — and then this data was analyzed statistically for correlations with female offspring mate selection; it was found that coloring did play a role in mate selection, while body size and redness of the throat area — considered separately from the coloration of the rest of the body — did not apparently matter. Therefore, sexual imprinting in sticklebacks seems to include both visual and olfactory cues, and continues through much of egg development.

**Moving Forward**

This study is important because it shows the importance of learning in mate selection and in the process of speciation. Natural selection has resulted in physical differences between the stickleback species that have grown more pronounced over time. Sexual imprinting of stickleback females enables them to take these differences into account when picking a mate. Imprinting on odor and color ensures that mate selection by female sticklebacks will keep stickleback species from interbreeding. But this may not be the end of the story.

More research needs to be done to tease apart the relationship between natural selection and sexual imprinting. In a sort of chicken-and-egg problem, sexual imprinting itself may be selected for in the sticklebacks' environment. The relative influence of visual and olfactory cues on imprinting also needs to be explored, though it is clear that each is important.

It does seem safe to say that females — at least female fish, of the stickleback variety — care about how a guy smells, at least if they've been brought up properly.

**Genevieve M. Kozak: Making Sense of Speciation**

Genevieve M. Kozak is a postdoctoral researcher at the University of Illinois at Urbana-Champaign. In 2004, Kozak graduated summa cum laude from Cornell University with a bachelor's degree in biological sciences. Six years later, she earned her Ph.D. in zoology from the University of Wisconsin-Madison under the supervision of Janette Boughman.

Kozak's research interests include animal behavior, evolutionary biology and speciation. Kozak's current research is focused on "the evolution of postmating incompatibilities between saltwater and freshwater populations of rainwater killfish."

Below are Kozak's February 17, 2011 responses to questions posed to her by Today's Science.
"I study the natural consequences of behavior. That is, how behavior influences interactions between species, how behavior may be a product of an animal's environment, and how behaviors evolve."

Q. When did you realize you wanted to become a scientist?

A. I always was very interested in animals and nature as a child. When I was in high school, my favorite class was biology. I was fascinated by the complexity of living systems: from the intricate biochemical pathways like DNA synthesis to ecological interactions between species. Because of all this, I majored in biology in college and it was during my first two years there that I realized I wanted to be one of the people who made all the discoveries I was reading about. Understanding biological complexity is a challenge I wanted to take up.

Q. How did you choose your field?

A. I knew I wanted to study biology, but I didn't know what aspect. I first began to think about studying animal behavior when I heard Jane Goodall speak about her extraordinary studies of chimpanzees in Africa. Then, when I took classes on animal behavior and evolution, I loved every minute of those classes and I knew what I wanted to do.

Q. Are there particular scientists, whether you know them in person or not, that you find inspiring?

A. As a woman in science, I have always been inspired by some of the women scientists who pioneered the way for the rest of us, such as Marie Curie and Jane Goodall.

Q. When you tell people that you are a behavioral ecologist, what is their reaction? What do you think is the biggest misconception about your profession?

A. When I was a graduate student and told people I studied animal behavior, they often thought I wanted to be a vet or work in a zoo. But I study the natural consequences of behavior. That is, how behavior influences interactions between species, how behavior may be a product of an animal's environment, and how behaviors evolve.

Q. If benthic sticklebacks mate with limnetic sticklebacks, do they produce viable offspring, and are those offspring as capable of reproducing as pure benthic or limnetic sticklebacks? Are there evolutionary disadvantages, that is, to interbreeding?
A. Benthics and limnetics do produce hybrid offspring that survive well in the lab, but these offspring rarely reach adulthood in the wild. Previous work had shown that limnetics and benthics eat very different types of food and hybrids are less skilled at feeding on the type of food favored by either parent. Therefore, when in competition with benthics and limnetics, hybrids fare poorly.

Q. In general in animal species, is mating with animals of similar but different species an issue or a problem? Is imprinting of the kind you find with sticklebacks a common way of avoiding this?

A. Mating with a closely related species is often a problem, since between-species hybrids usually don't survive as well and have trouble finding mates. A common way to avoid this is if females refuse to mate with males of another species. Imprinting is one way females can tell what males to avoid (that is, males that are different from their father). Imprinting had been thought to be a typical way of avoiding hybridization in birds, but only recently have we begun to see that mammals and fish might imprint on parents too.

Q. Did you observe any evidence of visual imprinting in embryos that had already developed visual abilities?

A. Further research has to be done on visual imprinting in sticklebacks. While we found strong effects of father odor, daughters did seem to pay attention to their father's body color as well. We do not yet understand if this may give rise to a preference for males of their own species.

Q. Is it common in fish for different species to evolve at different depths of a body of water?

A. It is fairly common in fish (especially in large lakes or lakes without many other fish) to evolve different species at different depths. Some other examples are whitefish in the Great Lakes and Arctic char in Icelandic lakes.

Q. What made you decide to study these particular fish?

A. Benthic and limnetic sticklebacks only occur together in six lakes in British Columbia even though other stickleback species can be found all over the northern hemisphere. Stickleback behavior has been studied for over 50 years, so they represent a unique opportunity to study how new species form and how behavior may affect that.
research. Then I work with animal care staff and undergraduates when performing my experiments.

Q. What do you find most rewarding about your job? What do you find most challenging about your job?

A. Discovering something new, piecing together the scientific truth from the results of experiments is very exciting. Especially when you get a result you didn’t expect. What is most challenging for me is the statistical analysis of data, since it requires a detailed knowledge of both mathematics and computing. Luckily, my colleagues in the statistics department are often willing to help out.

Q. What has been the most exciting development in your field in the last 20 years? What do you think will be the most exciting development in your field in the next 20 years?

A. I think the most exciting development in the field has been the development of genetic tools for many organisms in which we know much about their behavior and ecology. For instance, sticklebacks have had their genome sequenced. Because of this, we can now ask questions about the genes underlying adaptation and behavior. I think this will continue to lead to advances in the future.

Q. How does the research in your field affect our daily lives?

A. I think research on animal behavior and evolution helps us understand how animals will respond to changes in their environment. Environments are constantly changing, often because of what humans do (if we cut down a forest, release a non-native species into a new habitat, or release chemicals into a stream). We have to understand how animals will respond in order to make sure we do not harm species that are very important to us (for example, honeybees) or very important ecologically. It will also help us prevent species extinctions.

Q. For young people interested in pursuing a career in science, what are some helpful things to do in school? What are some helpful things to do outside of school?

A. If you are interested in science, I suggest taking extra science and math classes in school. I also recommend programs during the summer which allow high schoolers to help out in science laboratories. Also, there are many good books written about science for a general audience which are a great way to learn about all the exciting discoveries being made.

Discussion Questions

Can you think of other species in which imprinting is significant to subsequent behavior? Can you think of why there might be an evolutionary advantage to having preferences determined by imprinting, as opposed to genetically?

Journal Abstracts and Articles

(Researchers' own descriptions of their work, summary or full-text, on scientific journal websites.)

"Sexual imprinting on ecologically divergent traits leads to sexual isolation in sticklebacks" rspb.royalsocietypublishing.org/ content/ early/ 2011/ 01/ 20/ rspb.2010.2466.abstract.

Bibliography


Keywords

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