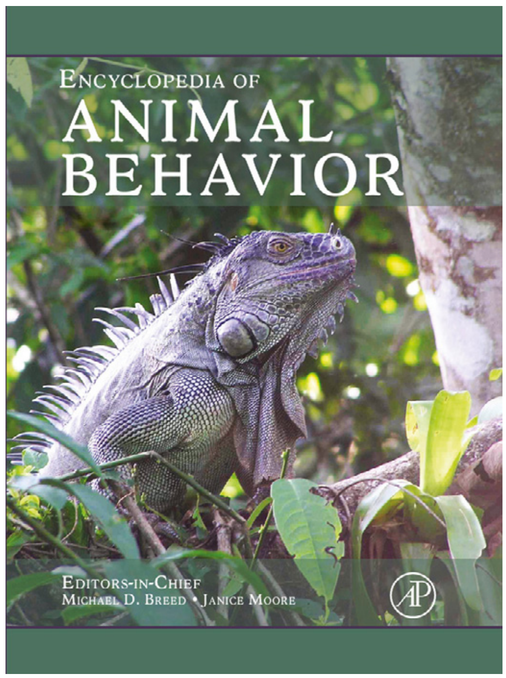

Patricelli G.L. (2010) Robotics in the Study of Animal Behavior. In: Breed M.D. and Moore J., (eds.) Encyclopedia of Animal Behavior, volume 3, pp. 91-99 Oxford: Academic Press.

Robotics in the Study of Animal Behavior

G. L. Patricelli, University of California, Davis, CA, USA

The use of robotics to study animal behavior has been increasing in recent years, as the sophistication of robotic technology increases and costs decrease. There are two main uses of robots in behavioral studies. First, robots have been used in playback experiments in a diversity of invertebrate and vertebrate taxa – to mimic behaviors in a controlled way – in order to study focal animal response. Such experiments allow researchers to study the function and efficacy of different components of the mimicked behavior, in isolation or in combination. Researchers can also examine how response to the mimicked behavior varies in different social and environmental conditions, and assay characteristics of responding animals, for example, measuring their aggressiveness, fearfulness, or responsiveness. The second main use of robots in animal behavior does not involve fooling animals into interacting with robots; rather, robotics is used as a modeling tool to study the mechanisms underlying behaviors. In this type of research, often called biomimetic robotics, researchers program robots with different algorithms and compare the behavior of robots with that of focal animals. By determining which algorithm best approximates natural behavior, researchers can learn about animal behavioral rules and cognitive processes. As technology improves, the division between robots used for playbacks and algorithm testing is beginning to erode, with autonomous robots being tested in interactions with live animals.

What Are Robots?

Robots are machines made to perform actions similar to those of human or non-human animals. They are typically electromechanical systems that convey a sense of agency, by appearance or movements. These movements can be controlled by experimenters, or may be programmed to interact with the environment independently. The degree of similarity between the movements and appearance of the robot and the model organism varies. Some robots are designed to mimic the model animal, as is typically the case in robot playback experiments, whereas others may bear little resemblance, but mimic behavioral mechanisms of interest to the researcher, as is typically the case in biomimetic robotics. As will be seen further in the article, the forms of robots are as varied as the types of research questions they address.

Robotic Playback Experiments

The use of robot technology has allowed researchers to add a new dimension to one of the oldest tools in the behaviorist's kit: the playback experiment. In playback experiments, the signals and cues produced by animal are recorded or reproduced and played back to animals to measure their response. Playbacks are a common tool in the study of animal communication. For example, researchers use recorded or synthesized vocalizations to study acoustic signaling, and painted or taxidermied models or, more recently, recorded or animated video images to study visual signaling. With robots, researchers are able to perform playback experiments with dynamic visual, tactile, and behavioral signals in a way that allows animals to interact with the stimulus in three dimensions. As is described in this article, robots are often used in combination with other types of playback, such as acoustic signals or chemical cues. Like other kinds of playback experiments, the robotic stimulus can be predetermined or interactive – with the experimenter creating a 'response' from the robot, simulating two-way interaction between the robot and the target animal. Interactive playback experiments with robots are still relatively rare, but the use will undoubtedly grow as technology improves.

Moving mechanical models have been used in playback experiments since the time of Nikko Tinbergen. Tinbergen studied the visual signals used by black-backed gulls to stimulate and direct nestling begging, using painted models of a gull's head, which he moved by hand. While simple and effective, models that need to be moved by hand can only be used in limited circumstances. The first successful use of a remotely controlled electromechanical robot in a playback experiment was in 1989, with a robotic dancing honeybee, followed by robotic vertebrates, including a female robotic satin bowerbird and a male dart-poison frog. It is no coincidence that these early examples, which are discussed in the article, used robots to study animal communication, as this is the focus of most playback experiments of any kind. Since these early examples, the use of robotics in animal behavior has grown rapidly, as has the diversity of questions and taxa represented.

The use of robots allows researchers to accomplish tasks that would, in many cases, be impossible without a robot. This article focuses on three such tasks: (1) deconstructing different components of a behavior, such as a visual signal, to measure how individual components affect response and

Encyclopedia of Animal Behavior (2010), vol. 3, pp. 91-99

how they interact; (2) examining the efficacy of the behavior in eliciting a response across a wide range of environmental conditions; and (3) assaying the characteristics of responding animals, for example, so that different responders can be compared by their aggressiveness, fearfulness, or responsiveness to a controlled stimulus. These types of experiments are discussed here, with examples for each.

Measuring the Response to Components of Complex Behaviors

Animal behaviors are often complex, and researchers may want to know which particular features of a complex behavior are necessary and sufficient to elicit a response from other animals. Robots can allow researchers to answer this question by experimentally mimicking a particular feature of the behavior and measuring the response. For example, there was a long-lasting controversy over whether honeybees communicate the location of food sources to other workers with elaborate waggle dances, or whether the dance serves only to focus the attention of other workers, which then use the scent of the pollen to find the food source. Alex Michelson and colleagues were able to separate these two components by creating a robotic honeybee that could dance in an experimentally controlled manner (**Figure 1(a)**). The robot was designed to mimic the waggle movement and sound-producing wing-vibrations of a dancing worker. The robot was scented like the food source, as a dancing worker would be, but it did not look like a bee – in fact, it was made of brass and had a vibrating piece of razor blade for wings. But looks were not important, since the dance occurs in the dark of a hive. By creating an experimental mismatch between the scent and dance signals, researchers were able to direct bees away from the scented target location, to the location indicated by the dance. This showed that the waggle dance independently conveys information about the distance and direction of food sources, though scent cues are clearly important as well.

In addition to being able to decouple and assess the response to different components of behaviors, researchers can examine how these components interact. Peter Narins and his colleagues did just this using a robotic dart-poison frog in a field study in Costa Rica. With the 'Robo-Rana,' Narins could compare the response to the acoustic signal alone, the visual signal of the inflating vocal sac on the throat, and the combination of both signal components (**Figure 1(b)**). They found that only the combination of acoustic and visual displays was effective at eliciting an aggressive response from males. Further, they were able to carefully adjust the timing and spatial position of the acoustic and visual signal sources (the speaker and the robot), to study how separation affected the integration of signal components by receivers (**Figure 2**). In another study examining how multiple signal components interact, Aaron Rundus, Don Owings, Sanjay Joshi, and colleagues built a robotic ground squirrel (**Figure 1(c)**) that could produce both infrared (IR) and tail-flagging (i.e., side-to-side waving) signals used in interspecific communication with rattlesnakes. California ground squirrels heat up their tails while performing a tail-flagging display to rattlers, who have IR-sensing pit organs, but not to gopher snakes, who lack pit organs. Supporting the hypothesis that the IR increases the efficacy of the tail-flagging signal to rattlers, they found that the combination of the flagging and heat was more effective than tail flagging alone in repelling rattlesnakes.

In addition to studies of communication, robots have great promise for studies of social cueing. Social cueing is the use of cues from other individuals to make decisions about group formation, movement, settlement, foraging, and other social behaviors. In a recent study, José Halloy, Grégory Sempo, and colleagues used robots to study group decisions in cockroaches (**Figure 1(f)**). The robots were autonomous, and programmed with a model for how real cockroaches behave, including their response to other cockroaches, creating a closed behavioral loop between the robots and roaches. This allowed Halloy to use the robots as a test for alternative mechanisms of behavior (see section 'Biomimetic Robots') as well as to study how real cockroaches respond to social cues. The robots did not look like roaches, but were scented with roach pheromones. Real cockroaches followed the robots, even when the robots were programmed to lead them from their preferred dark nooks and crannies into unsafe, open areas.

Another form of social cueing is conspecific attraction, where gregarious animals are attracted to areas that have conspecifics present. Conservation biologists have exploited this tendency to positive effect by using model animals to promote settlement of animals into underutilized habitats. In some cases, static decoys may suffice, but robots may increase the effectiveness of this method. One example of this effect – in this case with detrimental effects to the attracted animals – is the use of powered decoys with spinning-wing by hunters to attract ducks. Joshua Ackerman, John Eadie, and colleagues found up to a 50% increase in kills with the use of motorized decoys, suggesting that the visual cue associated with wing movement may be used by ducks in conspecific cueing. The use of robotic models may thus help to determine which cues and signals are used in conspecific attraction, and may have important conservation and management implications.

Measuring Environmental Effects on Response

Not only are behaviors often complex, but they also occur in a complex world that varies in space and time; to be successful, animals need to produce behaviors that are effective and advantageous in the social and environmental context in which they are used. Robots allow researchers to examine how the efficacy of signals and other

Figure 1 Examples of robots used for playbacks experiments. (a) The robot honeybee used by Michelsen and colleagues to study communication; the robot can imitate the waggle dance and direct workers toward an experimental food source. Photo courtesy of A. Michelsen. Reproduced from Michelsen A, Andersen BB, Stom J, Kirchner WH, and Lindauer M. (1992) How honeybees perceive communication dances, studied by means of a mechanical model. *Behavioral Ecology and Sociobiology* 30: 143–150. (b) The 'Robo-Rana' dart-poison frog used by Peter Narins and colleagues to study male territorial signaling; to the left is a speaker for acoustic playbacks, centers is the model male with inflatable vocal sacs, right is a real male attacking the robot. Illustration courtesy of P. Narins. Reproduced from Narins PM, Grabul DS, Soma KK, Gaucher P, and Hodl W (2005) From the cover: Cross-modal integration in a dart-poison frog. *Proceedings of the National Academy of Sciences of the United States of America* 102: 2425–2429. (c) The robot squirrel used in playbacks of tail-flagging to rattlesnakes; the tail can be heated to mimic the infra-red signals produced by ground squirrels. Photo reprinted with permission from the National Academies of Science. Reproduced from Rundus AS, Owings DH, Joshi SS, Chinn E, and Giannini N (2007) Ground squirrels use an infrared signal to deter rattlesnake predation. *Proceedings of the National Academy of Sciences of the United States of America* 104: 14372–14376. (d) A robotic female sating bowerbird used by Gail Patricelli and colleagues to study male how male response to female signaling affected male success in courtship; the robots can look side to side – to appear more realistic – and perform female signals of interest in the courting male – crouching downward and spreading their wings. Photo courtesy of G. Patricelli. Reproduced from Patricelli GL, Uy JAC, Walsh G, and Borgia G (2002) Sexual selection: Male displays adjusted to female's response. *Nature* 415: 279–280. (e) The robotic female greater sage-grouse used by Gail Patricelli and Alan Krakauer to study how males adjust their displays in response to female proximity; the robot can look back and forth, move toward target males on model train tracks and rotate to face them; she is outfitted with an on-board microphone and video camera to measure male display from a female perspective. Photo courtesy of G. Patricelli. Reproduced from Patricelli GL and Krakauer AH (2010) Tactical allocation of effort among multiple signals in sage grouse: An experiment with a robotic female. *Behavioral Ecology* 21: 97–106. (f) The robotic cockroach used to study collective decision making and movements in cockroaches. The autonomous robot is programmed to interact with real cockroaches, and can elicit novel behaviors from them. Photo courtesy of J. Halloy.

behaviors varies in these different contexts. For example, Terry Ord and Judy Stamps tested how the presence or absence of an alert component (a push-up display) in an *Anolis* lizard affected the response of territorial males to the main part of the signal (the 'headbob') in varying light conditions. They used a robotic male anole, which could be programmed to produce different patterns and combinations of push-ups and headbobs, and deployed in the

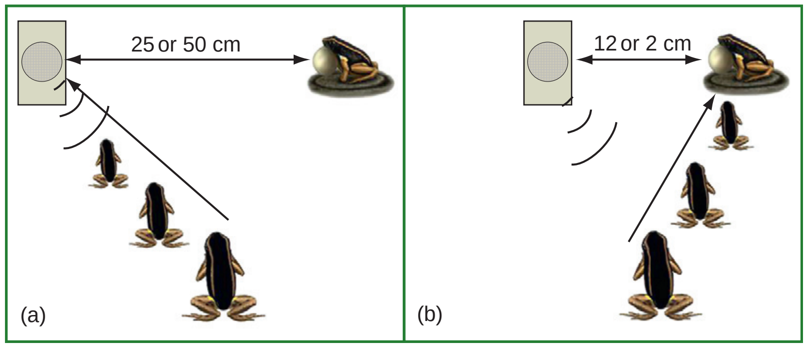

Figure 2 Results from Narins and colleagues, who used a robotic male dart-poison frog to study investigating cross-modal integration in dart-poison frogs. Trials in which the speaker and visual stimulus (the robot with moving vocal sac) were separated by 12 cm elicited significantly less aggressive behavior than with separation of 25 or 50 cm. Figure reprinted Narins PM, Grabul DS, Soma KK, Gaucher P, and Hodl W (2005) From the cover: Cross-modal integration in a dart-poison frog. *Proceedings of the National Academy of Sciences of the United States of America* 102: 2425–2429, with permission from the National Academies of Science.

Puerto Rican forest habitat of the anoles. They found that signals with an alert were detected more quickly in environments with poor lighting than those without an alert. In good lighting, however, the advantage of the alert disappeared. This supported the hypothesis that alerts are important for calling attention to the main part of the signal and that their effectiveness varies with environmental conditions. Using only observations of natural behaviors, such comparisons of the efficacy of the same behavior in different conditions would be impossible, since animals often change their behavior to match the background.

Assaying Responder Traits

Animal behaviorists often need to assay the traits of known individuals to determine how different aspects of behavior relate to each other or to life history traits, like fitness. For example, researchers may want to know how males differ in their courtship behavior, and how these differences relate to male success at convincing females to mate. These kinds of relationships can be difficult to measure in observational studies, since successful males are more likely to be found courting receptive females, and female receptivity behaviors may encourage males to court more enthusiastically. One of the most important uses of playback experiments is to assay the responses of different individuals to a controlled stimulus, allowing researchers to compare individuals on a level playing field.

For example, in collaboration with Gerald Borgia and colleagues, I used a robotic female satin bowerbird to ask whether male satin bowerbirds that display more intensely are more successful in courtship, or whether differences in display intensity are due to differences in the receptivity behaviors of courted females. The robot was able to mimic female signals of receptivity to courtship and could be deployed in the field where courtship would normally occur (Figure 1(d)). We found that successful males indeed displayed more intensely, even when female behaviors

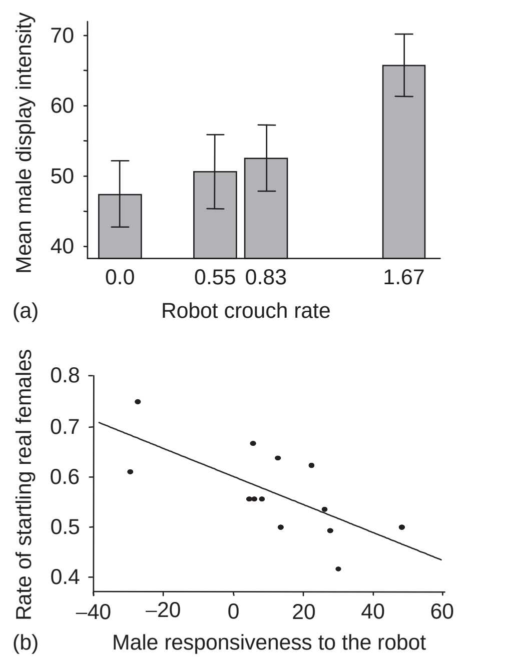

Figure 3 Results from Patricelli and colleagues, who used a robotic female satin bowerbird to assay male courtship behaviors. (a) Males increased their display intensity in response to increasing signals of interest (crouching) from the robot. (b) Males who adjusted their intensity more strongly (i.e., more responsive males) startled real females less often during courtship, and were thus more successful in courtship. Reprinted with permission from Nature Publishing Group.

were held constant using a robot. Moreover, we examined how males adjusted their display intensity in response to female crouching signals. We found that males increase the intensity of their displays in response to increased crouching (Figure 3(a)) and that males that adjust their display intensity more strongly (i.e., are more responsive) threaten real females less often (Figure 3(b)) and are thus more successful in courtship.

More recently, I worked with Alan Krakauer to examine how male greater sage-grouse adjust their display rate with proximity to females, and how this affects the quality of their displays. Using a robotic female sage-grouse that can be moved toward males on model train tracks (Figure 1(e)), we were able to control for the fact that real females tend to approach successful males more closely, which elicits faster strutting from the males. We found that successful males strut at a higher rate toward the robot and they adjust their displays more strongly with proximity to the robot, which allows them to produce higher-quality signals. The sage-grouse robot was also outfitted with an onboard audio and video recorder, so that it could be used as a data-collection tool as well as a playback stimulus; this allowed us to record male signals from the receiver's perspective – literally getting inside the head of a female during courtship. In both the sage-grouse and bowerbird studies, the use of a robot allowed us measure male responsiveness to controlled female behaviors, and to examine how this responsiveness varies with other male display traits and components of male fitness.

Practical Considerations for Robotic Playbacks

When is it appropriate to use robots in playback experiments? As discussed earlier, robotics is a powerful tool in playback experiments, but simpler tools may suffice in many cases. For example, if an animal will respond to video playbacks of the behavior of interest, then this may allow far more flexibility in manipulating the experimental stimulus (Figure 4). Using available video and animation

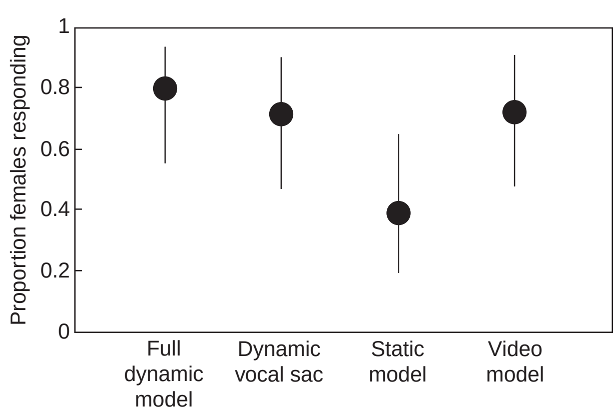

Figure 4 Comparison of different robotic túngara frog robots with video playback. Taylor and colleagues compared the proportion of females responding to a robotic model with a moving vocal sac, a moving vocal sac alone, a static model and a video playback of a displaying male. Females were given a choice between these stimuli and a speaker broadcasting the same call but lacking the visual stimulus of a model frog or video. Reprinted Taylor RC, Klein BA, Stein J, and Ryan MJ (2008) Faux frogs: Multimodal signalling and the value of robotics in animal behaviour. *Animal Behaviour* 76: 1089–1097, with permission from Animal Behaviour, Elsevier.

software, video stimuli can be manipulated to change the form, color, size, behaviors, background, etc. Comparable manipulations with a robot would typically be more expensive and require more specialized training to construct, and in cases where behavior patterns are very rapid and complex, may simply be impossible with present technologies. But videos are not better in all cases – among other issues, they are two-dimensional and fail to elicit responses from some animals. Both robotic and video playbacks have pros and cons; researchers must choose which option will be cheaper, simpler, more reliable, and more flexible, considering the natural history of the study organism, the logistics of the study, and the questions being addressed.

In deciding whether to use a robot, researcher must also consider whether the focal species will respond to a robot. If the mimicked behavior is extremely complex, then it may be prohibitively expensive (or impossible) to build a robot that is sufficiently realistic to elicit a natural response. Thus far, robotic playbacks have been used primarily when behaviors are relatively simple, and/or the sensory systems or selectivity of the focal animal is sufficiently permissive. For example, researchers have elicited natural responses from male and female frogs, using robots that mimic male territorial and sexual signals. These robots look and move in a strikingly realistic way, with painted rubber or plastic models representing the body of the frog and inflatable vocal sacs (Figures 1(b) and 5). In contrast, the sexual signals of male birds are often extremely complex, involving rapid movement and flight, such that even the best plastic or rubber bird models look far from real. Studies with robotic birds have therefore mimicked the simpler behavioral patterns of females, and have used jointed taxidermied mounts of the target species (Figure 1(d) and 1(e)). Further, these studies have thus far been conducted on polygynous species, in which males are not very choosy about which females they court. No successful studies have yet focused on monogamous species, in which males and females are both choosy during courtship and in which the bar for a realistic model would likely be higher. Unfortunately, there is no way to predict whether a species will respond to a robot and how realistic the robot must be to elicit a natural response; trial and error is thus required in the early stages of the research.

Biomimetic Robots

Mathematical and computational models have provided scientists with powerful tools for testing hypotheses for the mechanisms underlying behaviors. For example, scientists can test hypotheses about the neural and muscular mechanisms underlying locomotion by constructing models of these mechanisms and their interaction with the environment. They can then test whether their

Figure 5 Photographs comparing real (left) and robotic (right) túngara frogs used by Taylor and colleagues to study female mate choice. The body of the robot is urethane, cast from a real túngara frog, and painted to match. The inflatable vocal sac is made from a latex catheter. Reprinted Taylor RC, Klein BA, Stein J, and Ryan MJ (2008) Faux frogs: Multimodal signalling and the value of robotics in animal behavior. *Animal Behavior* 76: 1089–1097, with permission from Animal Behavior, Elsevier.

models approach the behaviors observed in real animals. Robotics has provided another tool in this modeling toolkit and is often used in concert with mathematical and computational models. Here scientists test hypotheses about mechanisms by building physical models – robots – that use these proposed mechanisms and interact with stimuli in the outside world. This field is often called 'biomimetic robotics' or 'biorobotics' to distinguish it from other fields of robotics. Since the real world is typically more complex than even the most complex mathematical and computation models – even in the laboratory, where many factors are controlled – robotics provides a robust test of hypotheses and a powerful tool for generating new predictions and refining models. These studies may also help researchers design more effective robots – thus animal behavior may contribute in turn to the development of robot technology.

Barbara Webb describes the process of robotic modeling as involving the following steps: 'identifying a target issue to be explained; offering an explanation; demonstrating that it accounts for observations; deriving further predictions and testing them.' Webb argues that the power of this approach is that it forces researchers to confront how the environment and body design affect behavioral capabilities, often causing researchers to reevaluate their assumptions. In some cases, robotic modeling approaches have demonstrated that the previous models were too simple to account for the complexity of observed behaviors in animals. In other cases, the opposite has been found – the simpler models can accomplish a task without the sensory or cognitive complexity that was assumed necessary. Researchers typically begin with the simplest possible mechanisms and add complexity as needed until the robot approaches natural behaviors.

The biomimetic robotics approach has thus far focused on simple behaviors, or simple aspects of complex behaviors, since there are more developed models of the underlying mechanisms for testing in these cases. The list of modeled behaviors includes escape behavior, locomotion, learning, recognition, social aggregation, collective behavior, and movement toward a stimulus source (taxis). A few examples of biomimetic research on taxis behavior are given in the following section.

Modeling Taxes

One of the most common behaviors addressed with biomimetic robots is taxis – directed movement toward a stimulus source, such as light (phototaxis), sound (phonotaxis), contact (thigmotaxis), and chemical cues (chemotaxis). For example, Frank Grasso, Jelle Atema, and colleagues have used robotic lobsters ('robolobsters') to examine the mechanisms that allow lobsters to efficiently locate the source of a chemical plume in turbulent water (Figure 6(a)). The robolobsters are designed to mimic the scale of a lobster in size, speed, maneuverability, and olfactory sampling, but not the biomechanics of movement (they roll on wheels). The robolobsters are programmed with several hypothesized mechanisms for localization, and the resulting behavior of the robolobster is compared with the behaviors of real lobsters facing the same task in the same conditions. Using this method, the researchers were able to reject hypothesized mechanisms for failing to reproduce lobster behavior, and direct future biological research toward more likely mechanisms.

Phonotaxis has been studied by Barbara Webb and colleagues in another invertebrate, the cricket. The robots created by Webb and her group model the sensory, cognitive, and biomechanical systems involved in phonotaxis (Figure 6(b)). Their robotic model of directional hearing suggested that female preference for a particular frequency (i.e., pitch) of male song may be a consequence of the physiology of the cricket ear, since only preferred frequencies can be localized by the robot. In addition to directional hearing, mate searching requires female crickets to recognize calls with the appropriate timing, and then orient and move toward the sound source. Webb and colleagues have modeled each step of this process. Currently, robots are being developed that integrate more

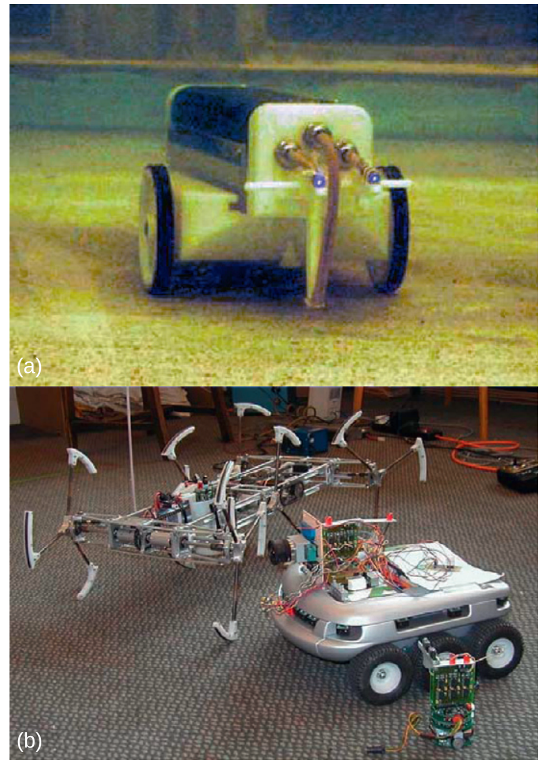
(a)
(b)

Figure 6 Examples of biomimetic robots. (a) A robotic lobster ('robo-lobster') used by Grasso and colleagues to test alternative mechanisms of chemotaxis, the localization and tracking of chemical signals, in this case in a current of water. Real lobsters were tested with an identical task for comparison. Reprinted Grasso FW and Atema J (2002) Integration of flow and chemical sensing for guidance of autonomous marine robots in turbulent flows. *Environmental Fluid Mechanics* 2: 95–114, with permission from Environmental Fluid Dynamics. (b) Three biomimetic crickets produced by Webb and colleagues to test hypothesized mechanisms of cricket behavior. Front, a robot that performs phonotaxis; middle, a robot that combines auditory and visual behaviors; rear, a robot that mimics insect-walking behaviors. Reprinted Webb B (2008) Using robots to understand animal behavior. In: Brockmann HJ, Roper TJ, Naguib M, Wynne-Edwards KE, Barnard E, and John CM (eds.) *Advances in the Study of Behavior*, pp. 1–58. New York: Academic Press, with permission from Advances in the Study of Behavior, Elsevier.

explicitly our increasing knowledge of the neurophysiology of the sensory and locomotor systems involved with phonotaxis. Ultimately, the goal is to develop a complete cricket model, which integrates all of the sensory modalities, as real animals do, to examine the interactions between sensory modalities and behaviors.

Studies of taxis behaviors can also lead to a more complete understanding of social aggregation and cueing. Christopher May, Jeffrey Schank, Sanjay Joshi, and colleagues developed robotic rat pups to study the apparently self-organizing and intentional behaviors of real rat pups in an arena. They programmed robots with either a random or a 'wall-following' response to contact with the edge of the arena (thigmotaxis), and they compared

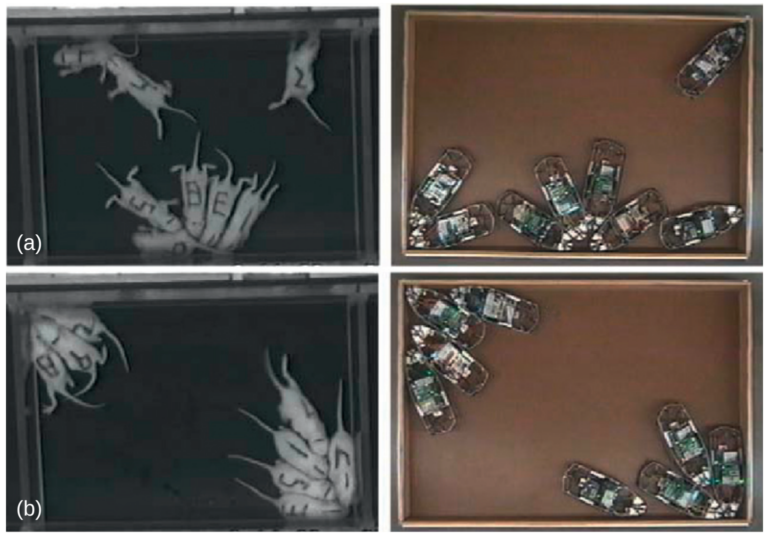

Figure 7 Biomimetic robots using a random-movement algorithm reproduce the aggregation behaviors of real rat pups. Examples of aggregation patterns of seven (a) and ten (b) day-old rat pups (on the left) and robots (on the right) in experimental arenas. Reprinted May CJ, Schank JC, Joshi S, Tran J, Taylor RJS, and Esha I (2006) Rat pups and random robots generate similar self-organized and intentional behavior. *Complexity* 12: 53–66, with permission from Complexity.

the resulting behavior with the behavior of real rat pups in the same arena. They found that the simpler, random mechanism yielded behaviors strikingly similar to those of real rat pups (Figure 7). This does not suffice to prove that rat pups move randomly as well, but it clearly demonstrates that seemingly directed and complex behaviors can emerge from mechanisms far simpler than those previously assumed.

Biomimetic Playbacks: A Fusion of Approaches

Biomimetic robotics is distinguished from robotic playbacks, in that biomimetic robots are built to model the internal mechanisms of focal animals, rather than to mimic the outward behaviors in order to fool real animals. Since conspecifics are part of the environment experienced by animals, there are many cases where a combination of approaches – using biomimetic robots in interactions with real animals – is ideal. This approach can be used to test alternative hypotheses about mechanisms of response to social cues (biomimetic modeling), and may also be used to learn more about the signals and cues used by responding animals in mediating social interactions (playback experiments). The case discussed previously in which robotic cockroaches were used to study the cues used to coordinate group movements, is an example of this hybrid approach which yielded information about both the mechanisms and functional consequences of social cues. As technology improves and collaboration between animal behaviorists and engineers increases, this approach will undoubtedly become more common.

Limitations and Challenges

The use of robotics holds a great deal of promise for animal behavior research, but it is important to recognize the limitations and challenges to this approach as the field moves forward.

An important challenge for any behavioral study with robotics is how to validate the assay, demonstrating that the robot elicits or reproduces naturalistic behaviors. In playback experiments, this is often accomplished by testing whether an animal's response to the robot is correlated with its response to natural stimuli or by comparing the mean response of animals to the robotic and natural stimuli. In biomimetic robotics, the behavior of the robots is often compared with the behaviors of real animals. In both cases, researchers must decide what variable(s) to measure to assess validity. In addition, the strength of the relationships between robotic and natural cases will depend on many factors, and researchers must decide on a threshold to accept the assay as valid. In some cases, statistical significance may be used as a threshold, but in other cases, especially in biomimetic robotics, a closer relationship between the robot and real animal may be expected. Since it is difficult to imagine a single standard that would apply to all cases, devising methods and thresholds for validation will remain a challenge in future studies.

Even if a strong relationship between real and robotic behaviors emerges during validation, researchers must recognize that a similarity of outcome does not prove similarity of causation. While this concern is important in playbacks, it is a particular concern in biomimetic robotics, where explaining the mechanism is the primary goal. As discussed in the examples above, robotic modeling has the most power when it is used to eliminate untenable hypotheses and focus attention on more likely – and new – hypotheses for further study.

Researchers using robots in playback experiments must also consider the possibility of pseudoreplication – the use of the same stimulus in multiple experimental trials, which can artificially inflate the degrees of freedom. Pseudoreplication is problematic in any kind of playback experiment, when researchers use one or a few playback stimuli but generalize their results to all possible stimuli. Pseudoreplication can be minimized by the use of multiple playback stimuli or a stimulus that represents the average among multiple possible stimuli. These approaches may be feasible in some robot studies. But unfortunately, building multiple robots is far more difficult and expensive than recording or synthesizing multiple acoustic playback stimuli, and may not be possible or ethical when taxidermied mounts are used in building the robots. Many robotic playback studies to date have used only one or a few robots, and thus we do not have sufficient data to address whether different robots are likely to elicit different responses. Nonetheless, this issue must be addressed, and if not resolved, then at least acknowledged as a limitation of the study.

Despite the challenges and limitations discussed throughout this article, it is clear that robots will allow animal behaviorists to pursue questions that would be difficult or impossible to address otherwise. Used in combination with other approaches, robotics will allow us to generate new hypotheses and test existing ones to explain both the mechanisms and functions of animal behaviors.

See also: Acoustic Signals; Agonistic Signals; Alarm Calls in Birds and Mammals; Bowerbirds; Cockroaches; Collective Intelligence; Communication and Hormones; Communication: An Overview; Dance Language; Experiment, Observation, and Modeling in the Lab and Field; Group Movement; Herring Gulls; Honeybees; Insect Social Learning; Mate Choice in Males and Females; Mating Signals; Multimodal Signaling; Niko Tinbergen; Norway Rats; Playbacks in Behavioral Experiments; Robot Behavior; Sound Localization: Neuroethology; Túngara Frog: A Model for Sexual Selection and Communication; Visual Signals.

Further Reading

Göth A and Evans CS (2004) Social responses without early experience: Australian brush-turkey chicks use specific visual cues to aggregate with conspecifics. *Journal of Experimental Biology* 207: 2199–2208.

Grasso FW (2001) Invertebrate-inspired sensory-motor systems and autonomous, olfactory-guided exploration. *The Biological Bulletin* 200: 160–168.

Halloy J, Sempo G, Caprari G, et al. (2007) Social integration of robots into groups of cockroaches to control self-organized choices. *Science* 318: 1155–1158.

Martins EP, Ord TJ, and Davenport SW (2005) Combining motions into complex displays: Playbacks with a robotic lizard. *Behavioral Ecology and Sociobiology* 58: 351.

May CJ, Schank JC, Joshi S, Tran J, Taylor RJS, and Esha I (2006) Rat pups and random robots generate similar self-organized and intentional behavior. *Complexity* 12: 53–66.

Michelsen A, Andersen BB, Storm J, Kirchner WH, and Lindauer M (1992) How honeybees perceive communication dances, studied by means of a mechanical model. *Behavioral Ecology and Sociobiology* 30: 143–150.

Narins PM, Grabul DS, Soma KK, Gaucher P, and Hodl W (2005) From the cover: Cross-modal integration in a dart-poison frog. *Proceedings of the National Academy of Sciences of the United States of America* 102: 2425–2429.

Ord TJ and Stamps JA (2008) Alert signals enhance animal communication in noisy environments. *Proceedings of the National Academy of Sciences of the United States of America* 105: 18830–18835.

Partan SR, Larco CP, and Owens MJ (2009) Wild tree squirrels respond with multisensory enhancement to conspecific robot alarm behaviour. *Animal Behaviour* 77: 1127–1135.

Patricelli GL, Uy JAC, Walsh G, and Borgia G (2002) Sexual selection: Male displays adjusted to female's response. *Nature* 415: 279–280.

Patricelli GL and Krakauer AH (2010) Tactical allocation of effort among multiple signals in sage grouse: An experiment with a robotic female. *Behavioral Ecology* 21: 97–106.

Rundus AS, Owings DH, Joshi SS, Chinn E, and Giannini N (2007) Ground squirrels use an infrared signal to deter rattlesnake predation. *Proceedings of the National Academy of Sciences of the United States of America* 104: 14372–14376.

Taylor RC, Klein BA, Stein J, and Ryan MJ (2008) Faux frogs: Multimodal signalling and the value of robotics in animal behaviour. *Animal Behaviour* 76: 1089–1097.

Webb B (2000) What does robotics offer animal behaviour? *Animal Behaviour* 60: 545–558.

Webb B (2008) Using robots to understand animal behavior. In: Brockmann HJ, Roper TJ, Naguib M, Wynne-Edwards KE, Barnard E, and John CM (eds.) *Advances in the Study of Behavior*, pp. 1–58. New York: Academic Press.