

Robots in the service of animal behavior

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As reading fiction can challenge us to better understand fact, using fake animals can sometimes serve as our best solution to understanding the behavior of real animals. The use of dummies, doppelgangers, fakes, and physical models have served to elicit behaviors in animal experiments since the early history of behavior studies, and, more recently, robotic animals have been employed by researchers to further coax behaviors from their study subjects. Here, we review the use of robots in the service of animal behavior, and describe in detail the production and use of one type of robot – “faux” frogs – to test female responses to multisensory courtship signals. The túngara frog (*Physalaemus pustulosus*) has been a study subject for investigating multimodal signaling, and we discuss the benefits and drawbacks of using the faux frogs we have designed, with the larger aim of inspiring other scientists to consider the appropriate application of physical models and robots in their research.

To better understand an animal’s behavior, biologists can experimentally manipulate the animal or its environment. One time-honored manipulation is to present live animals with artificial renderings (physical models) to examine behaviors in the real animals, either in the field or in the laboratory. The history of introducing physical models into animal behavior studies has progressed into a recent surge of animatronics, or the use of kinetic models. We produced robotic “faux” frogs to better understand the signaling and mate selection behavior of a tropical frog in a multimodal (acoustic + visual signals) context. Here, we present our experiences using faux frogs in the broader context of robots as experimental tools to tackle challenges such as those posed by studying multimodality. By sharing our approach’s effectiveness and limitations, we wish to trigger greater production of and discussion about the use of physical models in studies of animal behavior.

The Challenges of Multimodality

Considering how difficult it can be to experimentally test hypotheses that result in definitive answers about an animal’s behavior based on its vision, hearing, touch, taste, or smell, it becomes far more difficult to design experiments that give clear answers involving a combination of these perceptual modalities. In humans, for example, the acoustic perception of speech phonemes changes when the listener is also able to see the movement of the speaker’s lips – the well-known McGurk effect.¹ Receiver responses can be modulated by interactions among signal components in nonhuman animals as well, sometimes in unexpected ways.² Adding to the confusion is that traits conspicuous to humans are sometimes surprisingly unimportant as signal components in nonhuman animals.^{3,4} Controlling aspects of one perceptual modality and

not another would be useful when investigating animal behavior, but is often impossible when working exclusively with living organisms. This challenge has led researchers to seek means other than relying exclusively on living animals to answer biological questions.

Use of Physical Models in the Study of Animal Behavior

Why would a biologist choose to conduct research with physical models rather than with living animals? Artifice, when introduced wisely, can broaden the scientist’s toolbox and hypothesis-testing potential. Physical models can be easier to handle than real animals, and can allow for a precise manipulation of traits. Physical models can imitate complicated phenomena,⁵ or be simple^{6,7} and inexpensive.⁸ Researchers are not only able to control the way physical models look, but can control where they are placed in the environment, contributing to a more standardized, repeatable experimental design and for causal analysis of behavior. Physical models, especially robots, make it feasible to test the influence of individual signal components on receivers, as well as examine interactions among signal components. Robots can also be effective in determining the salience of putative signal components. A researcher using fake animals can fabricate and even exaggerate these components to render a super stimulus. One can also distort a signal in unnatural but useful ways, as with testing the consequences of asynchrony between acoustic and visual courtship components when a living animal is incapable of such behavior.²

Use of physical models has successfully contributed to our understanding of a wide range of biological topics, with the study of animal behavior benefitting from physical models since at least

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the field's earliest publications.⁹ Bizarre, impossible taxidermy of predatory birds,¹⁰ fake chameleon heads on sticks,¹¹ horse mannequins,¹² zebra costumes,¹³ glass beads as termite eggs,¹⁴ two-dimensional gull puppets,⁶ a cotton-filled fabric Indian cobra,¹⁵ and ewes of fake fur over wire and wood¹⁶ are among the hordes of physical, non-robotic models that have been effectively placed among live animals in the service of animal behavior.

Rise of the Robots

Advances in technology, and accessibility and affordability of equipment have led to a new era of physical models used in biology, with the number of robots on the rise. Humans frequently exploit nature to design better robots,¹⁷ and we occasionally design robots to increase our understanding of nature.¹⁸ By simulating biological entities, robots can shed light on natural selection,^{19,20} animal physiology,^{21,22} biomechanics,²³⁻²⁶ and behavior^{18,27-30} without ever having to interact with living organisms.

Introducing robots to living organisms offers the biologist new opportunities to answer otherwise strategically problematic questions about natural social interactions. Robotic animals have been introduced to living mammals,^{31,32} birds,³³⁻³⁶ reptiles,^{37,38} fish³⁹⁻⁴¹ and invertebrates.⁴²⁻⁴⁶ For a cursory review of robots used in animal behavior studies see refs. 47-48.

Robotic amphibians have also graced the ethological stage, with the introduction of electromechanical dart-poison frog models by Narins et al. to study aggression⁴⁹ and cross-modal integration.⁵⁰ Roland Rupp created these dart-poison frogs using silicone rubber with pneumatically-inflated vocal sacs, which when painted and presented on a turntable in a naturalistic setting, effectively elicited behaviors in naturally-occurring frogs. Likewise, Bryant Buchanan painted plaster models of squirrel treefrogs (*Hyla squirella*), which were employed by RCT. These simple treefrog robots had manually inflatable vocal sacs made of condoms, and were used to test the role of visual vs. acoustic signals in mate choice.⁵¹ Later, Taylor et al. introduced automated robotic túngara frogs (*P. pustulosus*) to continue testing aspects of multimodal signaling,⁵² the subject of this article. A comparative study of signaling by squirrel treefrogs and túngara frogs again relied on responses of real frogs to robots.⁴ Finally, Caldwell et al.⁵³ staged contests between real red-eyed treefrogs (*Agalychnis callidryas*), then tested whether a male's tremulations triggered contests by using models for visual and vibrational playback. Loosely connected limbs allowed the frog model (fabricated by David McCornack) to tremulate when coupled with an electronic shaker. In each of these studies: dart-poison frogs, squirrel treefrogs, túngara frogs, and red-eyed treefrogs, behaviors of real frogs were elicited in a repeatable, standardized fashion by robots. Another shared aspect of these faux frog studies was the aim to understand the relative importance of signals catering to different perceptual modalities.

Robots and Realism

How realistic does a robot need to be? When producing models, erring on the side of realism has its advantages as well as its

disadvantages. The time, energy, and expense invested producing realistic models may be wasted if the information it provides is beyond the perceptual capacity of the animal recipient. A realistic model can add unwanted or excessive information, obfuscating the actual components responsible for eliciting responses in real animals. For instance, a realistic model made of materials that produce odors undetected by the human researcher could conceivably confound results when exposed to a test subject. Parsimony is often the goal for a researcher because with a simple design one can strive to reach a simple answer. What, then, can be gained by having a realistic model over a simplified model? Realistic models offer the opportunity to match natural inputs as completely as possible so that something meaningful can be said of naturally occurring phenomena. An overly simple model, while it could help us to focus on the salient feature or features of potential interest, can also miss out on revealing behaviors that are more biologically relevant. If the sight of a moving sphere is attractive to a female, it says little about how alluring that moving sphere is in the context of acoustic, tactile, and additional visual elements accompanying the moving sphere in a natural setting. An important first step is to observe how animals behave under natural conditions in order to recognize natural reactions by animals when introduced to robots. One could experimentally test for the minimum threshold of desired realism that is practical, but such testing can be time-consuming, and may never satisfy our desire to know what is actually happening in nature.

Faux Túngara Frogs

Male túngara frogs (*P. pustulosus*) produce courtship vocalizations, and these vocalizations are accompanied by a conspicuous inflation of a large vocal sac in the male's throat. We created replicas of male túngara frogs to decipher which signaling components, or combination of signaling components (acoustic + visual), are important for a female when selecting a mate. BAK fabricated mixed-media models with expandable latex vocal sacs (Fig. 1), and JS designed and built a pneumatic system to remotely control the timing of the faux frog's vocal sac inflations and the timing of digitized calls (Fig. 2A and B). These calls were broadcast by speakers in an arena constructed by RCT in which real female frogs were presented with faux male frogs or only a speaker playing synthesized male courtship calls (Fig. 2C). In this system, a servo motor drives a pump into a standard 20 mL syringe with Luer-Lok air fitting (Becton, Dickinson and Co.) which pushes air to expand the vocal sac. This system controls volume of air and speed of inflation/deflation. The audio input circuit board allows the researcher to manually adjust the synchrony of the vocal sac inflation as it relates to the audio output of the experiment. In this paper, we present a more visually explicit, step-wise description of the production of our models than in previous publications, but for further details about methods and materials, see reference 52 and www.pupating.org.

How realistic does a male túngara frog robot need to be? Females apparently respond to the inflating artificial vocal sac as the call is being played no differently than they do when



Figure 1. For figure legend, see page 4.

the model of the frog's body accompanies these stimuli.⁵² Is the inflating artificial vocal sac sufficiently alluring and did we needlessly surpass this threshold of visual stimulation when creating realistic models to accompany the vocal sacs (Fig. 1L, M and N)? When túngara male frogs court, the vocalization is the dominant signal component, but females respond significantly more when the call is accompanied by an inflating artificial vocal sac,^{52,54} and when both the call and the vocal sac inflation

are in synchrony.² Frogs are visually responsive to motion and nocturnally active frogs may process relatively low-resolution images,^{55,56} so the moving latex vocal sac may be sufficient for the female under certain testing conditions. If greater realism stimulates more natural reactions in the female, other testing conditions may benefit from having the model of the male frog's body along with the inflating artificial vocal sac and call. The value of such realism when light levels vary, or additional

Figure 1. Production of faux frog models. To create a proportionally and structurally accurate male túngara frog, molds were made of a preserved frog specimen. **(A)** The specimen was partially embedded in a non-sulfur based clay (so as not to react with silicone) and surrounded by a cardboard dam. Depressions were made in the clay to serve as “keys” to lock the resulting two-part mold. Feet from the deceased specimen were severed and adhered to the bottom of a cardboard box using cyanoacrylate glue, and a one-part mold was made. Once the silicone molds cured and the frog specimens were removed, **(B)** urethane casts were made of the emaciated, preserved frog body, and a body was sculpted to appear inflated using sculpting epoxy over the urethane cast and over wire armature legs. Details, including body texture and eyes, were added using Elmer’s glue. The completed prototype was molded by **(C)** embedding it in clay, **(D)** pouring the first part with silicone, and, once cured, **(E)** peeling the clay off, spraying the silicone with a mold release (or brushing with Vaseline), then pouring the second part. The keys to lock this two-part mold took the form of a square ridge **(E)** and canal. Urethane casts were poured, and touched up by removing flashing, and by sanding seams. The feet were produced by **(F)** injecting hotmelt glue into the silicone mold, **(G)** cutting out the feet with surgical or sewing scissors, then **(H)** attaching to the body by heating each foot base with a soldering gun and pressing to the distal end of each urethane leg. Drilling holes in leg and foot, and inserting wire in both ends prior to heating the foot base strengthened the connection. A drill (Dremel Inc., New York) was used to hollow out the body from mouth to anal region, and tiny screws were glued into drilled holes in venter using two-ton epoxy. **(I)** The frogs were painted by mixing acrylics to match colors found on live frogs, **(J)** spraying with an airbrush as basecoats, then **(K)** applying acrylic paints with a fine brush. To match the glistening surface of a live male, the models were sprayed and sealed, then left to dry. Several inexpensive materials can function as vocal sac surrogates, including latex balloons or condoms **(L)**, but urinary catheters appeared to last longest. **(M)** The catheter balloons were partially inflated, then painted by spraying with flexible automotive paint and brushing white stripes with a fabric paint. **(N)** Finally, the catheter was threaded through the model body and connected to the controller unit. Image N is a composite of two photographs. Scale bars **(B, H, N)** = 1 cm. Product details can be found in ref. 52.

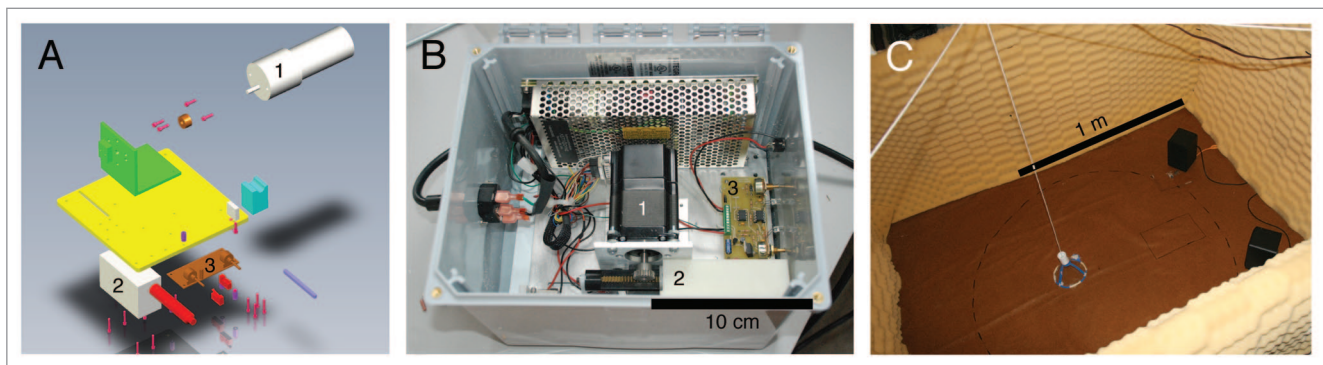


Figure 2. Robotic frog controller, shown as **(A)** an exploded view of digitally-rendered components and **(B)** in box with opened lid. Components include (1) Servo Motor with built-in programmable controller, (2) 20 ml syringe embedded in a block of milled Delrin, and (3) audio input and controller circuit. **(C)** Arena (1.8 x 1.8 m) within which female was released from under a centrally-placed funnel to select one of two potential call sources (black speakers) with or without a robotic male. Product details, including additional controller components, can be found in ref. 52.

perceptual modalities (touch, smell, and taste) are investigated in terms of how they affect a female’s decision-making is a subject for future studies.

Challenges and Areas For Improvement

Using robotic models comes with assumptions. Although our frog models appear realistic, they are imperfect, and we assume the deviations from nature are unimportant (the behavior suggests this is true). Replicating nature has its challenges, and the most influential challenge we encountered when creating faux túngara frogs relates to their small size (ca. 1.5 g). As a result, our controller and mechanical parts were externalized. The pneumatic system allowed us to deliver air to a tiny location, controlling speed and volume of vocal sac inflations. Settling on standard pneumatic components allowed us to focus on vocal sac (balloon) strength, durability, and realism. After testing an array of balloons and condoms, we chose medical urinary catheters for their strength and regularity in terms of their duration of operation. While the system has survived years of successful operation, several aspects of our system could be improved.

1. The pneumatic system with servo creates considerable mechanical noise when operating. In the field, this has resulted in the unit being placed in a fabricated sound-isolation box to minimize noise.

2. The artificial vocal sac itself produces mechanical noise when it is inflated and deflated. Depending on the perceptual capacities of living subjects exposed to the calling robot and the questions posed by researchers, the experimental design may require controlling for this noise.

3. The pump mechanism uses a standard 20 mL syringe, which has a limited duration of only 1–2 mo, after which this part malfunctions or fails entirely. While this is not an expensive component, it requires time to replace because much of the controller must be taken apart to access it.

4. Each catheter inflates approximately 250 times (30/min for 8–9 min) before failing. The catheters are both expensive as disposable units and labor-intensive in terms of their preparation.

5. The combination of pneumatic parts and catheters was originally intended to be a flexible system that could be adapted to other frog experiments with vocal sacs of different sizes. In fact, the system has run into physical limits due to the limited

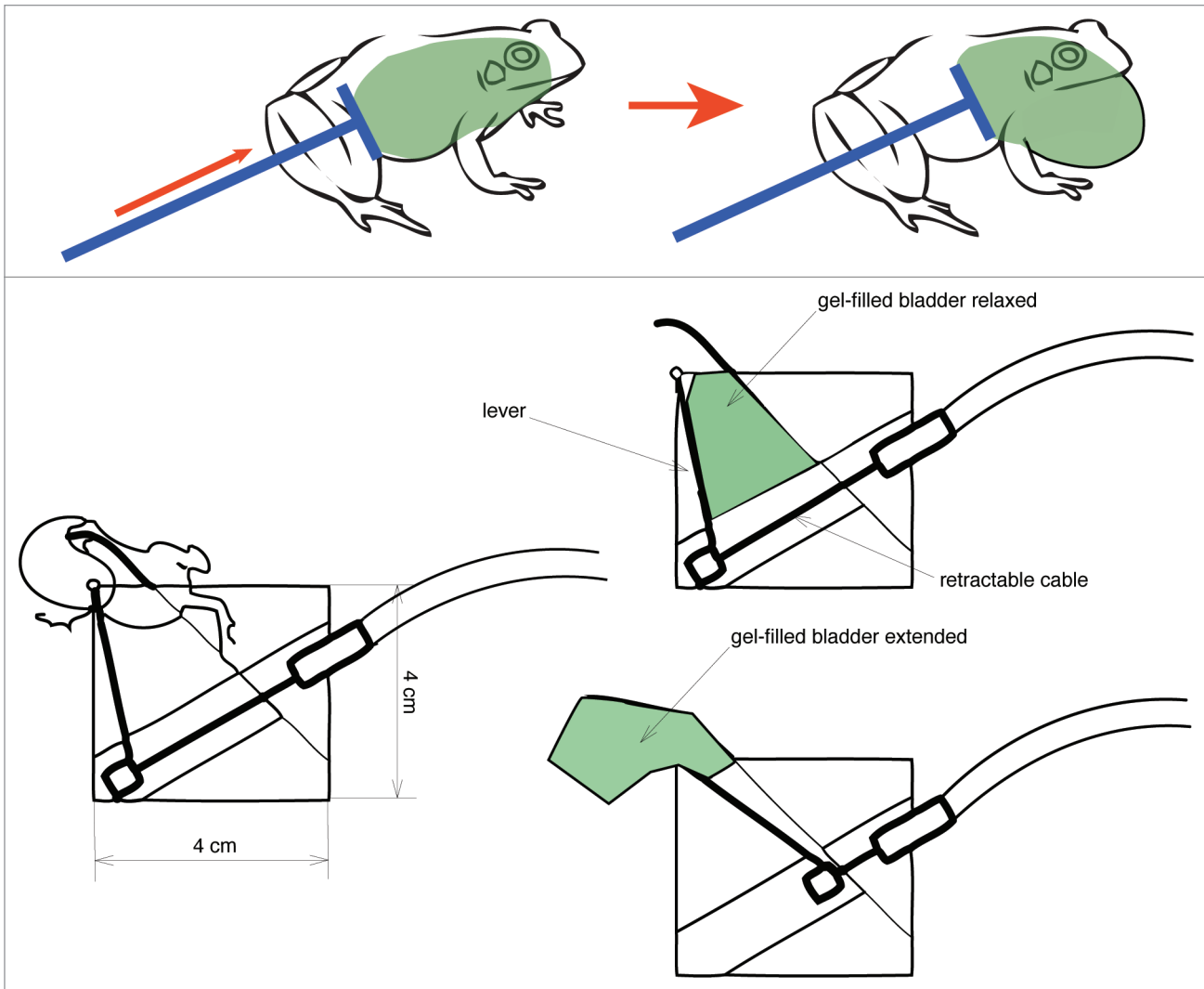


Figure 3. Premise for possible alternative designs of model frog with extendable vocal sac made of gel-filled balloon.

expansion capacity of the catheters in combination with the loss of transmitted volume due to air compression. The longer the tube leading to the catheter balloon means less air reaching the balloon itself, and the slower the inflation and deflation rate of the balloon. These physical limitations demand careful calibration that does not presently allow for great flexibility in terms of replacing with different catheter models.

6. The frog body was sculpted to appear inflated so that a female would perceive either an inflated vocal sac or an inflated body when approaching a model. A more accurate model would alternate inflations of these two body regions.

Alternative Robots and Alternatives To Robots

Although expense of technical components is generally decreasing, designing and fabricating systems from scratch can be prohibitively expensive for many researchers. Alternatives to our design are many, and less expensive approaches include creating frogs with vocal sacs made of different materials (Fig. 1L), or

vocal sacs that inflate by hand.⁵¹ The controller unit can also change significantly, and we are presently in the process of testing a controller unit that is powered by compressed air rather than by a motor. A mechanical alternative to our robotic frog's pneumatics would be to use gel-filled balloons which, when squeezed, produce the desired vocal sac volume and shape, while withstanding repeated use and rubbing against the vocal sac opening in the model (Fig. 3).

Research questions should be the motivating force behind designing alternative methods. A túngara frog researcher, for example, may wish to investigate the importance of a frog's body cavity inflations during courting, or of a male frog's response to external inputs, such as the physical collision by a female frog, which elicits a change in the male's call composition.⁵⁷ For questions relating to body cavity inflations, a robot with alternating vocal sac and body inflations would be desirable. For questions relating to a male frog's response to collisions with females, a "smart" frog model that changes its call composition in response to female proximity or female contact would be the design

objective. An alternative to the smart, automatically responsive robot could be a remotely-controlled robot, as used by Patricelli et al.³⁵

Alternatives to using robots exist, of course, and the choice of using still images, mirrors, static models, video or audio playbacks, or manipulated playbacks should be made with careful consideration of questions posed, with availability of technical expertise and financial resources also taken into consideration. Modifying living animals can be effective, as with painting wings of moths in studies of mimicry,⁵⁸ or implanting interfaces to remotely control flight in cyborg beetles.^{59,60} Cybernetics has the potential to revolutionize animal behavior research by offering a novel means of controlling behavior in a standardized, repeatable way, although one drawback is that not all of the cyborg's actions may be predictably standardized or controlled for. Controlling a cyborg's flight direction, for example, could hypothetically result in an undesirable emission of chemicals by the cyborg, with untold behavioral consequences on sender or receiver. A well-tested, powerful, and flexible alternative to physical model production is the use of computer-animated stimuli⁶¹ to stage animal interactions. Like robots, computer animations can provide dynamic visual stimuli, but unlike robots, computer animations offer the benefit of total control over movement properties and capture complex behavioral nuances that may not be feasible or possible with robots. Limitless programming aside, however, computer animations presently suffer from human sensory-biased limitations⁶¹ in the same ways as do videos.^{52,62} Whether or not technological innovations overcome limitations such as matching visual sensitivity of nonhuman animal subjects, or include 3D virtual realities that respond to an untethered

subject's motions, they will help to define the future of artifice in the study of animal behavior.

Conclusion

The relatively recent panoply of robotic animals in animal behavior studies is an effect of technological progress and is driven by questions that would otherwise demand unreasonable control over or manipulation of a living animal's behavior. Biologists can address complicated questions related to multimodal signaling by testing real animals' responses to robots. Robots, when appropriately constructed and used, can open avenues of experimental study, and this paper is, in part, a methodological behind-the-scenes exposé of one type of robot, with a discussion of its assets and drawbacks. More elaborate robots have been used in the service of animal behavior and far more intricate, versatile robots are doubtlessly on the way. Future discussions of the value and applicability of robotics in animal behavior should and will become more frequent as technological progress continues, and hypotheses probe what have been historically untenable realms.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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