Robotic Squirrel Models

Study of Squirrel–Rattlesnake Interaction in Laboratory and Natural Settings

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In this article, we employ robotic/mechatronic squirrel models for the study of ground squirrel/rattlesnake interaction, both in the laboratory and rugged natural environments. These robotic models are unique because they must interact with live, potentially hostile animals. Our robots are now being used for long-term studies on rattlesnake behavior after squirrel encounters. Many of these studies would be difficult, if not impossible, to perform without the robotics technology.

Collaboration between scientists from robotics and biology has created a number of important new directions in research for both the fields. Specific biological constructs are being used to develop many novel robotic designs and control architectures (commonly referred to as biorobotics [1], [2]). In another application of biorobotics, robotic and mechatronic tools and models are being used to understand the basic science of animal behavior [1], [3]. These robotic/mechatronic animal models are not necessarily designed to look and move like a real animal in all aspects; rather they are carefully engineered to explore a particular biological hypothesis about animal behavior [1], [3]–[6]. The robotic tools are not meant to replace other

Digital Object Identifier 10.1109/MRA.2011.942121
Date of publication: 8 December 2011

1070-9932/11/$26.00©2011 IEEE

forms of biological and animal behavior study techniques (e.g., observation, dissection, and computer modeling) but are meant to contribute one more tool that biologists can use to understand their subjects. However, the robotic tools offer animal behaviorists with new possibilities for empirical research. These new tools become especially powerful when live animals can be induced to interact with robots. For example, individual components of signaling behavior can be isolated and tested, thus providing definitive empirical tests of how a specific signal component elicits a specific response. Robotic/mechatronic animal models have been interactively used with live animals primarily to study three different areas of animal behavior: animal communication (e.g., [7]–[9]), mate selection (e.g., [10]–[12]), and predator–prey interactions (current study). In our research program, we have formed a joint team—composed of roboticists and animal behavior researchers—that has designed, fabricated, and performed experiments in which robotic/mechatronic squirrels interact with live rattlesnakes, both in the laboratory and natural settings (Figure 1).

Here, we present not only engineering details from our research but also biological results to illustrate how the biological context of our experiments has framed our engineering efforts. In our studies, the biologists contribute to robot design and building, and engineers contribute to behavioral data collection in the field and laboratory. In this way, both specialties gain a deeper understanding of the possibilities and constraints of each other's discipline, which ultimately leads to new research results.

Rattlesnake–Squirrel Interaction and Effect of Tail Heating

The predator–prey relationship between ground squirrels and snakes is ancient [13], extending to the ancestors of the modern species approximately 10 million years ago [14], [15]. Rattlesnakes (*Crotalus* spp.) can consume up to 34% of all California ground squirrel (*Spermophilus beecheyi*) newborn pups [16], [17], which can comprise up to 69% of rattlesnake diet. However, adult California ground squirrels have evolved the ability to neutralize rattlesnake venom [18], [19]. Consequently, a rattlesnake bite can injure but not kill adult squirrels. Because they are resistant to rattlesnake venom, adult ground squirrels have the option of behaving assertively while dealing with rattlesnakes [20]–[23]. This is an option squirrels are especially likely to exercise if they are maternal females defending vulnerable pups [24]. During such confrontations, adult ground squirrels exercise impressive skills, such as tail flagging (wagging the tail from side to side) and blasting loose dirt, while effectively evading the snakes' defensive strikes [25] and vocalizing to their pups [24], [26]. Adult ground squirrels do at times attack and even kill snakes, occasionally including rattlesnakes [16], [21], [27], [28]. Such behavior by adult squirrels protects pups by redirecting rattlesnake behavior from hunting to self-defense [29] and preempting pup confrontation of the snake [30]. On the other hand, rattlesnakes have evolved a specialized infrared-sensitive pit organ that can exquisitely sense heat, which has significantly enhanced their effectiveness as predators on small mammals [31]–[33]. Also, snakes rely extensively on their specialized chemosensory abilities to locate and identify prey [34], [35] but are less sensitive to airborne sounds and fine visual details [36], [37].

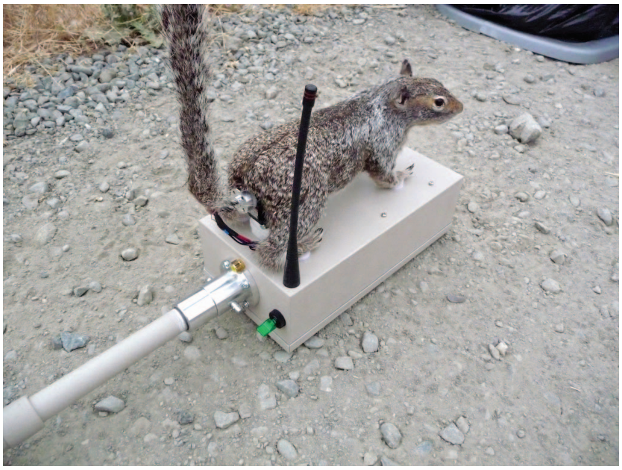

Figure 1. Field-ready squirrel robot waits at Camp Ohlone in the Sunol Regional Park, Sunol, California. (Photo courtesy of R. Johnson.)

In an intriguing laboratory observation, California ground squirrels were observed to increase their tail temperature when confronting rattlesnakes with tail flagging, but tail flagging without added tail heat when confronting gopher snakes (*Pituophis melanoleucus*), a species that hunts California ground squirrels but has no infrared sensory system [29]. This suggested that tail heating was important in discouraging rattlesnake engagement, but controlled trials were needed to compare the effects of tail flagging with and without tail heating. Unfortunately, these kinds of controlled studies would be impossible with live squirrels as there was no easy way to prevent them from heating their tail in the presence of rattlesnakes (to compare the effects of presence/absence of this modality). Therefore, we set out to create a believable squirrel model (to the rattlesnake) that could be used for controlled testing of tail flagging and heating, both separately and simultaneously. The robot squirrel model needed to 1) flag its tail from side to side at various rates (in open loop and/or in closed loop contingent upon the distance between the snake and squirrel), 2) heat and tightly maintain its core body temperature to mimic conditions seen in the field, 3) heat and tightly maintain its tail temperature to precise levels (independent of core body temperature), and 4) generally look and smell like a believable squirrel. The general experimental setup is shown in Figure 2. The robot squirrel model displays various signals to a live rattlesnake. Behavior and relative position of the two animals (one real and one robot) is observed either by a human or by an external video camera. The external observer then dictates the movement of the robot, either in automatic closed loop for the laboratory experiments or via teleoperation from remote control in the field. The field versions of the robot contain built-in video cameras to monitor the snake from the robot and data logging of internal robot control signals via a secure digital (SD) card.

Laboratory Robosquirrel Test Bed and Results

Robot Design and Features

The laboratory robot was created using a taxidermically mounted adult female California ground squirrel (*Spermophilus beecheyi*) [29]. The interior of the squirrel's body was filled with coiled Nichrome 80 resistance wire, and its tail contained a cartridge heater. Both the Nichrome wire and the cartridge heater were connected to thermostats wired with thermocouples placed inside the body and tail allowing for precise and independent control of both tail and body temperature (Figure 3). The thermostats used a proportional-integral differential (PID) control loop to regulate the duty cycle of the relays that provided power to the two heaters. The tail was mounted on a servo, allowing the robot to tail flag at commanded intervals. Control of the tail-flagging behavior was accomplished using MATLAB software via a mini synchronous serial channel microcontroller.

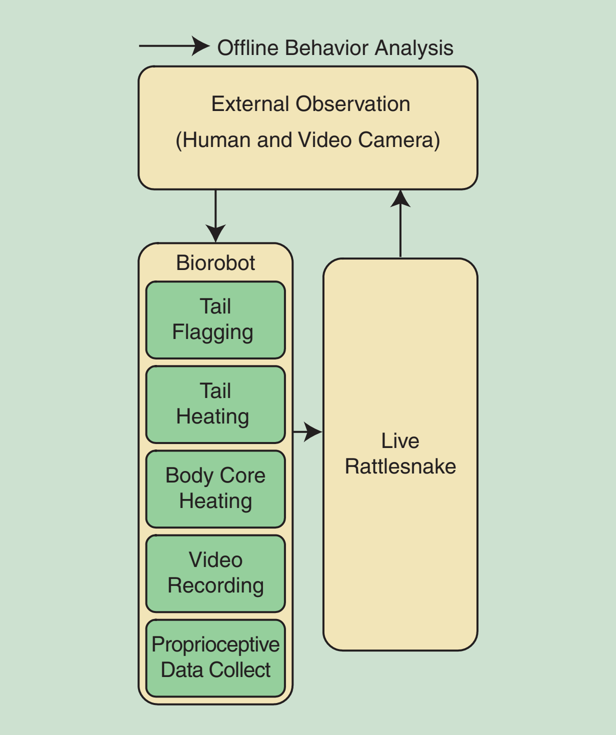

Figure 2. Experimental interaction between the robot, live rattlesnake, and external observer. The robot conducts playback displays to the snake. The external observer then records the snake behavior and initiates further robot behavior (either through closed-loop automatic control or human teleoperation). The figure shows the five main functions of the robot, including onboard video recording and internal control signal data logging in the field version of the robot.

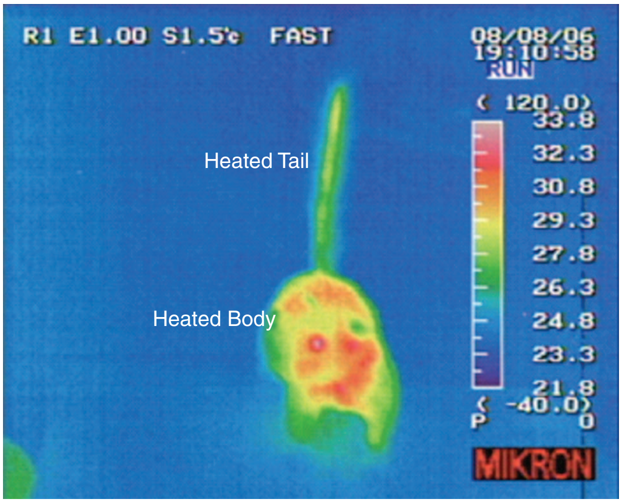

Figure 3. Infrared image of a robotic ground squirrel model (front facing) with body and tail both heated. The infrared signature of the model closely approximates that of a rattlesnake-engaged California ground squirrel. (Photo courtesy of A. Rundus.)

Closed-Loop Experimental Test Bed

An overhead camera monitored the arena in which the robot was mounted. A small removable red light-emitting diode (LED), powered by a 3-V coin cell battery, was placed on each rattlesnake subject prior to its experimental trial. As snakes entered the arena, snake and arena images were analyzed via MATLAB to determine the distance between the squirrel and the LED and the subsequent rate

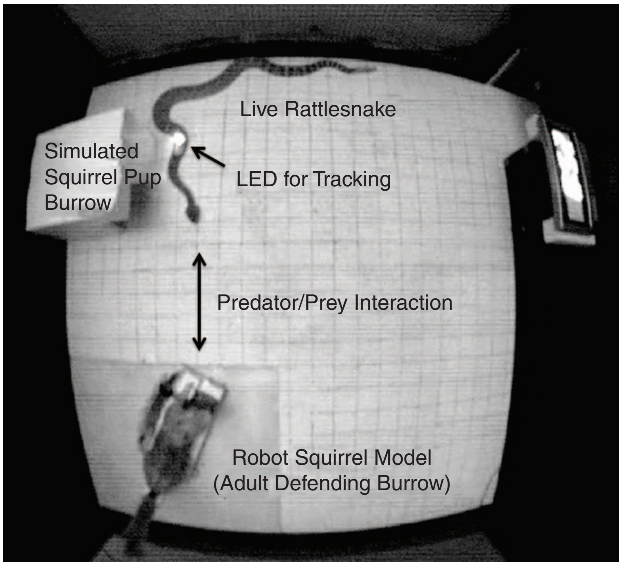

Figure 4. Image of a rattlesnake next to the simulated squirrel burrow oriented toward the ground squirrel model during a test trial. Note the LED on the rattlesnake, enabling automated tracking and subsequent closed-loop adjustment of the rate of tail flagging by the model. (Photo courtesy of A. Rundus.)

of tail flagging (Figure 4). Our code first identified the LED pixels within the image and then converted the pixel coordinates to physical coordinates using an arena preregistration. As the distance between the squirrel and rattlesnake decreased, the squirrel increased the number of cycles of tail flagging per bout (the number of times the tail completes 180° of side-to-side motion). Regardless of the number of cycles per bout, the squirrel models tail flagged at random intervals with an average of 5 bouts/min. Rates of tail flagging were based on previous field observations of ground squirrel and rattlesnake encounters [38]. The entire robot was mounted on a wooden stage beneath which the heater relays and thermostats were mounted. All electronics for the original robotic model were designed to run off 60-Hz, 110-V power. Squirrel models were stored in sealed plastic containers with used squirrel bedding before and between experimental trials to impregnate them with ground squirrel odor. The robotic model was controlled entirely by a computer during testing.

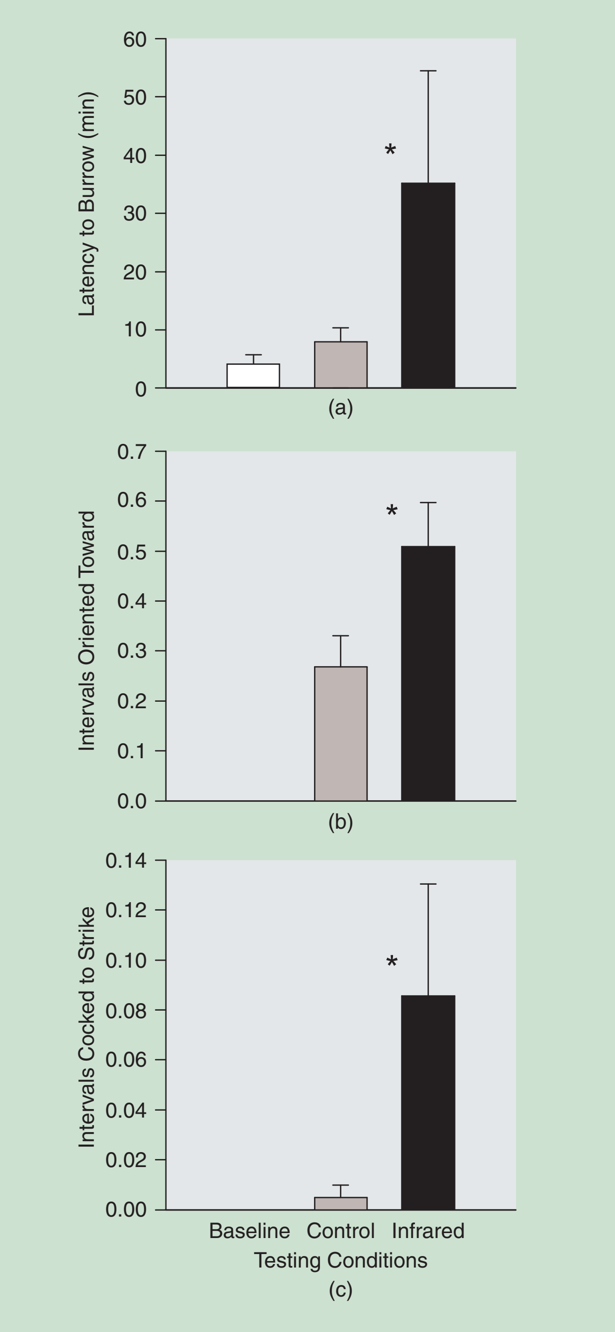

Figure 5. Behavioral responses of rattlesnakes to the squirrel models. (a) Latency in minutes for the snake to enter the simulated burrow. Proportion of time intervals spent by the snakes (b) oriented toward the squirrel model and (c) in a cocked-to-strike posture. Bars show means ± standard error of the mean and * indicates $P < 0.05$. Baseline condition represents no squirrel model in arena. Control condition represents squirrel model present with tail flagging but no tail heating. Infrared condition represents squirrel model present with both tail flagging and tail heating. Redrawn from [29]. (Photo courtesy of A. Rundus.)

Experimental Protocols, Testing, and Results

Fourteen adult northern Pacific rattlesnakes (*Crotalus oreganus*) were collected in 2004 from several locations on the western edge of the central valley of California. All experimental trials were conducted in an enclosed two-chamber apparatus consisting of a 0.51 m × 0.63 m × 0.79 m starting chamber connected by a runway to a 1.17 m × 1.22 m × 0.79 m testing chamber containing a simulated squirrel burrow (Figure 4). All snake subjects were conditioned to feed on euthanized rat pups placed inside the squirrel burrow for a period of 14 weeks prior to experimental trials. The testing chamber was maintained at an illumination of 70 lx and a temperature of 22 °C. These reflect the summertime conditions in Winters, California, at dusk, one of our snake-collection sites.

Rattlesnakes responded to the robot in the same way as they would to a natural squirrel encounter [20], [24],[31], [38], suggesting that the robot was an appropriate surrogate to a live squirrel. Rattlesnakes engaged with the squirrel models behaved more cautiously, spending less time moving and less time in an elongated posture compared with baseline trials (no squirrel model present). Furthermore, trials with the robotic squirrels evoked rattling by the snakes and defensive postures such as coiling and cocking-to-strike that were not seen in the baseline trials [29]. However,this shift from predatory to defensive behavior was much more pronounced in the trials in which the squirrel's tail was heated with tail flagging (infrared test condition). Latencies to enter the simulated squirrel burrow were greatest for rattlesnakes in the infrared test condition compared with baseline trials, and the snakes tended to enter with larger latencies compared with control trials [tail flagging but no tail heating, Figure 5(a)]. During infrared trials, rattlesnakes spent more time oriented toward the model [Figure 5(b)] and more time in a cocked-to-strike posture [Figure 5(c)]. Additionally, rattlesnakes adopted defensive coiled postures and exhibited rattling behavior only in the trials in which the squirrel model's tail was heated [29].

Field Robosquirrel Test Bed and Results

Our success with the laboratory squirrel model encouraged us to use a similar model to study squirrel–rattlesnake interaction in natural settings. Several open questions remain in this interaction that could be answered using a field-ready model. Initial analyses of natural squirrel displays toward free-ranging rattlesnakes indicate that there is a strong correlation between the number of tail flag displays given to a snake and the probability that the snake abandons its attempt to ambush squirrels from a particular site (unpublished data). However, it is difficult to establish a causative link between these behaviors without being able to conduct empirical trials. Although such trials would be impossible with live squirrels, we can use a squirrel robot to conduct experimental playbacks with variable numbers of tail-flag displays and then track the rattlesnakes for long periods in the wild.

Prototype Robot Design and Features

Our strategy to transition from the laboratory to the field was first to quickly modify our laboratory robot to perform initial field tests and then use the experience gained in the field tests to inform a complete outdoor robot redesign. The previous laboratory heating control system, consisting of the thermostats and relays, was repackaged to be housed in a toolbox to provide a secure mounting location, safely enclose the 110-V electronics, and provide convenient transportation (see red toolbox in Figure 6). The 110-V power for the heaters and thermostats was provided by a Duracell Powerpack inverter (see orange power pack in Figure 6).

To remove the requirement for a desktop computer to process data and cue the tail flagging, an 8-b radio controller was built from encoder/decoder ICs. This allowed a remote control to be used from a distance (successfully tested at >50 m) to trigger tail flagging. Four buttons were available on the remote controller that triggered one–four tail flags in quick succession. The receiver circuit was located in a metal enclosure and fed the states of the tail flag switches on a remote control to a BASIC Stamp mounted on an evaluation board. The receiver circuit included LEDs to aid in debugging any possible radio communication issues that might arise. The BASIC Stamp drove the tail servo depending on the states of the switches on the remote control. Power for both the microcontroller and the receiver circuit came from a 9-V battery tied into the evaluation board.

Prototype Field Testing and Lessons Learned

Fielding a robot in a natural rattlesnake setting is a complicated undertaking, both in terms of the terrain itself and the staging requirements of each trial (Figures 6–8). Initial field testing was done at the Santa Margarita Ecological Reserve (SMER) outside the town of Fallbrook, California, operated by San Diego State University. SMER contains avocado orchards and orange orchards, as well as large quantities of rough terrain covered in dense brush (Figure 7). At SMER, six red diamond rattlesnakes (*Crotalus ruber*) were previously radio tagged for extended study. The tagging involved surgically implanting a sealed radio transmitter and antenna into the body cavity of the snake. Each transmitter broadcast at a specific frequency that allowed each individual to be located and tracked by radio antenna over an area of several square kilometers (see Figure 7).

Testing was started in early September 2008 and continued intermittently through late October 2008. Red diamond rattlesnakes have been observed to be actively foraging and preying on California ground squirrels during those months. The snakes were located via radio telemetry prior to testing. If the snakes were located above ground in an accessible position, they were presented with one of two treatments: the enclosure and squirrel with body and tail heating or just the metal enclosure without the robot (control). During the trials, one observer would position the robot from behind the blind and control the

Figure 6. Prototype field-ready robotic squirrel sits on hillside in SMER outside the town of Fallbrook, California. Red toolbox contains thermal controllers and orange box contains power inverter. (Photo courtesy of S. Joshi.)

Figure 7. Researcher uses radio antenna to search for previously radio-tagged red diamond rattlesnakes. Finding the snakes sometimes involves hiking from a few meters to several hundred meters with robot in tow. SMER. (Photo courtesy of S. Joshi.)

tail flagging if present, while a second observer would monitor the behavior of the snake in response to the presentation (Figure 8). A trial consisted of three 120-s presentations, each separated from the others by 120-s periods during which the stimulus was withdrawn. After completion of a successful trial (a full 12-min cycle of presentations without the snake withdrawing), video recorders were left in position to monitor the snake's behavior for up to 24 h afterward. Such extended posttrial monitoring of the snake's behavior is crucial for evaluating the impact of the robot encounter on the target snake. Rattlesnakes wait in ambush for long periods of time to successfully forage for prey (six to seven days in the case of some individuals); so observation of the long-term effects of the robot on a snake is critical to fully understand its impact.

Collaboration between scientists from robotics and biology has created a number of important new directions in research for both the fields.

Since the number of trials with the original field robot was small, statistical data concerning the impact of the robot on the rattlesnakes are unavailable. When presented with the robot, the target snakes responded in ways similar to their reactions to natural squirrel encounters, through tongue flicking and very slight head reorientation. In contrast, target snakes showed no response to the control presentation of the metal enclosure alone. This suggested that the robot was doing a suitable job of impersonating a real ground squirrel (although more trials would have to be completed for statistical conclusions).

More importantly, the field testing provided experience with deploying the robot in the field and indicated ways to improve the robot in future iterations. Our most important discovery was that the prototype outdoor robot was heavy and cumbersome to transport and present to snakes (both the robot itself and the requisite power pack and heating controls toolbox, Figure 6). Transportation was a real issue as the robot had to be carried by researchers in very rough terrain that included wading through thick brush, hiking up cliffs, and scaling large rocks. In addition, the researchers had to be vigilant to avoid the myriad of other venomous snakes, tarantulas, and mountain lions common to the area. Two to three people were required to carry the equipment from one snake site to another.

Figure 8. Presentation of robotic squirrel involves positioning squirrel in front of the snake and then remotely operating the robot. Separate researcher videotapes snake movements. SMER. (Photo courtesy of S. Joshi.)

Presentation of the robot to the snakes was another critical issue. The snakes chose a variety of ambush sites at SMER, including the underside of large rocks, brush, the edge of cliffs, and on tree branches. Each site presented unique challenges in simulating a squirrel approach (with the humans hiding) and recording the snake's behavior (Figure 8). It became clear that extended field experimentation would require that we redesign the robot to reduce the complexity of connecting all the component boxes every time the robot was to be used (power pack, heating toolbox, and actual squirrel), reduce the number of components to be carried around (as well as the size and weight of the robot), provide additional means to record snake behavior through advanced video capability, make the robot as durable and simple to use as possible, and simplify the task of repairing the robot and associated electronics.

Outdoor Robot Redesign and Features

Once we confirmed the feasibility of field deployment of a robotic squirrel, a completely new version was designed. This required that we abandon all the 110-V electronics, create custom electronics, and reduce the overall bulk and weight to be transported. All previous features were retained (albeit with new designs), such as the body and tail heaters, tail flagging, and remote user control. In addition, new features were added, including onboard cameras and data logging to a removable SD card. Most dramatically, all power sources, heaters, control processors, and onboard cameras were fitted into a small mounting box underneath the squirrel itself (Figure 1). This made deployment and operation of the robot substantially easier in rough terrain and met all the requirements identified by the initial field testing described previously. Figure 9 shows a block diagram of the entire electronic hardware layout of the robot.

The new robot design was based around an ATmega128 microprocessor, with 4 kB of data memory and 128 kB of program memory. The microcontroller was mounted on a custom two-layer printed circuit board (PCB) that included a DB9 serial port for RS232 communication, an SD card slot for data storage, a Joint Test Action Group port for programming/debugging, radio control hardware, and all the requisite discrete electronics (Figure 10). The main program of the microcontroller functioned fairly simply: it ran in a permanent while loop that constantly checked for user input from the remote control.

Every second, however, an internal timer interrupt triggered the microcontroller to sample the temperature of the squirrel body and tail, run a proportional-integral (PI) heating control loop for each, and log the current time and temperature to the SD card. After the interrupt was finished, the controller resumed checking for user input until the next timer interrupt was triggered 1 s later. This continued indefinitely until the power was removed or a hard reset was triggered.

Unlike the previous version of the robot, which had separate heating controllers in addition to a microcontroller responsible for the tail flagging, the new version integrated the heating controls into the microcontroller. Temperatures were sampled by 100-kΩ thermistors located in the body and tail. Data for the PI control loops were stored in two data structures that were updated each time the hardware interrupt was triggered. Control of the Nichrome heating elements was accomplished through pulsewidth modulation (PWM) control of transistors. The duty cycle of the PWM was varied according to how much heating power was required to reach the desired temperature. Depending on ambient conditions, the robot took approximately 5–10 min to reach the steady state temperature.

Control of the tail flagging was handled through a 16-b counter in fast-PWM compare-match mode hooked up to the same Hitec servo from the initial version of the robot. The servo required a PWM signal with a 20-ms period and a duty cycle between 2.5% and 7.5%. The duty cycle varied the angular position of the servo and tail position. When user input was detected, the compare-match value was varied in the timer registers to alter the duty cycle and change the position of the tail. The duty cycle was varied multiple times, with several delays in between to give the appearance of the tail flagging back and forth. Unlike the previous version of the robot that had the tail servo mounted inside the metal enclosure, the new version had the servo mounted inside the robot itself (within the squirrel body), which allowed for a more realistic tail-flagging motion (Figure 1). Power was provided by a single 12-V, 1.4-Ah sealed lead acid battery. The heating elements were driven directly at 12 V, while all the other electronics were regulated at a lower voltage level. Radio control was accomplished using a premade receiver–transmitter kit. This kit consisted of two peripheral interface controller microcontrollers programmed to work as 8-b radios.

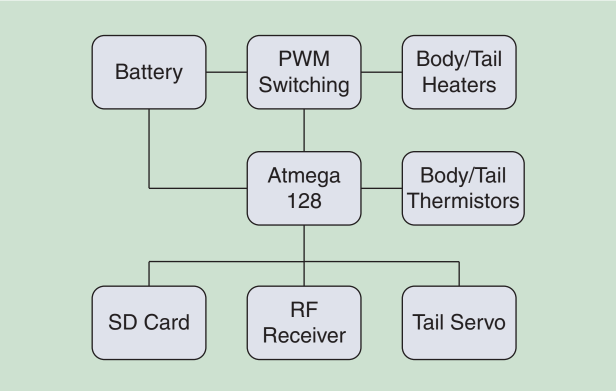

Figure 9. Block diagram of the robot electronic hardware.

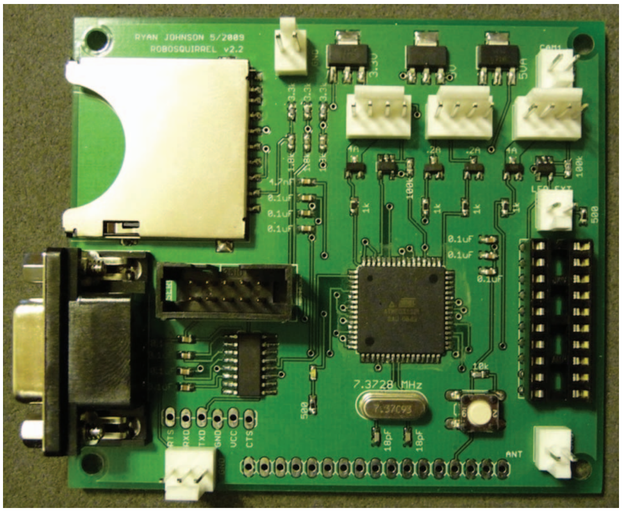

Figure 10. Custom-designed robotic squirrel control board measuring 8.6 cm × 7.6 cm (slightly larger than the face of a deck of cards). (Photo courtesy of R. Johnson.)

A camera provided a live color video feed to the operators of the robot to help aid in positioning the squirrel appropriately relative to the snake and then to monitor the snake itself. The camera provided 640 × 480 resolution in full color, outputted through an RCA receptacle on the rear of the robot enclosure. This allowed a long video cable to tether the robot to a handheld video monitor in the blind and allowed the manipulator of the robot to determine the robot position with respect to the target snake more accurately. Once in the field, handheld portable digital video recorders were available that could capture and record the video feed.

Experimental Testing and Results

Field testing of the new redesigned robot was done at Camp Ohlone in the Sunol Regional Park in Sunol, California. We performed field tests at that site from the months of April 2009 to July 2009. The field site was selected because of the large populations of both California ground squirrels and northern Pacific rattlesnakes. Camp Ohlone features a large walnut orchard with a sizable squirrel colony as well as several other large colonies located nearby. The terrain at Camp Ohlone is generally less severe and has a lower density of vegetation than SMER, making it an attractive site for field work. Our goal was to carry out a preliminary test of the pursuit-deterrence hypothesis. This hypothesis predicts that rattlesnakes should abandon their ambush sites if a squirrel tail-flagging visit verifies that they have lost the advantage of surprise [32].

Robot trials were initially scheduled for mid-May to coincide with the newly born squirrel pups coming above ground for the first time, as the new pups are the primary prey target for the rattlesnakes during this time. In the days leading up to pup emergence, 17 snakes were captured and radio tagged (in the same method as the red diamond snakes at the Santa Margarita field site) so that they could easily be tracked and located. Snakes were selected for robot trials based upon their location and accessibility. Only snakes that were actively foraging in or on the outskirts of an active squirrel colony were selected to receive presentations of the robot. Additionally, the snakes had to be in an accessible position where the robot could be easily presented to them. Snakes that were hiding deep within burrows were not accessible for effective presentations and did not receive trials unless they emerged from their ambush location. The goal is to present each snake with a full suite of three trials. These included the robot with heating and tail flagging, the robot with just heating, and a control trial of just the enclosure. Video footage from both the robot and an external handheld camera was taken to monitor the response of the snake to the stimulation. In addition, video cameras were left at the snake site afterward to observe the long-term effects of the interaction with the robot, such as abandoning its location.

The robotic model was controlled entirely by a computer during the duration of the testing.

The robot was operated by a researcher hidden from view behind a large field blind. Trials lasted 5 min and involved five presentations of the robot. Each minute began with a 10-s robot or control presentation and ended with a 50-s period during which the robot was withdrawn from the snake's view. Eleven such presentations were conducted in all: five with a full defensive display, two with just body and tail heating, and four with just the control box. These 11 presentations were spread among seven unique rattlesnakes, which were all in ambush hunting positions in a ground squirrel colony. Both immediate (during trial) and delayed (after trial) responses were quantified.

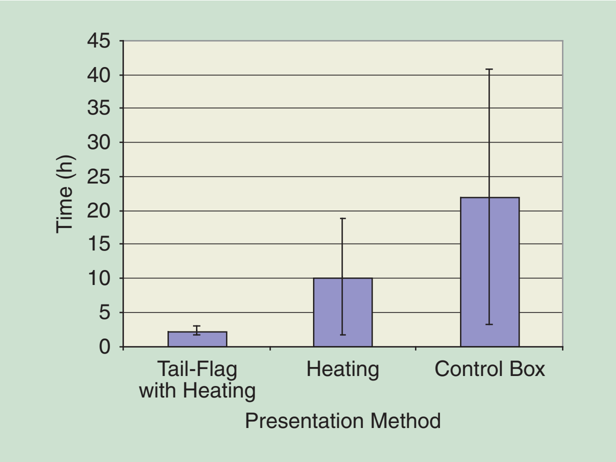

Figure 11. Time to abandonment of snake ambush site versus presentation method (means ± standard deviation).

Our small sample size and nonindependent data points did not permit a rigorous statistical analysis, but our results were consistent with the pursuit-deterrence hypothesis. Rattlesnakes appeared to abandon ambush sites sooner after receiving the tail-flagging robot trial than after both the non-tail-flagging robot and box trials (Figure 11). The results from the control trials also suggest that the enclosure on which the robot is mounted has little effect on how the snake perceives the robot. Although the relatively lengthy delay between tail-flagging trials and abandonment (mean = 2.3 h) seems long, there are other variables that have strong effects on snake movement, such as how recently the snake has eaten, and the snake's body temperature [32]. In general, snake behaviors transpire over a longer temporal scale than humans are used to and what may seem like a long delay to a human observer may not be so for a foraging snake (see [31]).

Unfortunately, statistically significant data about how snakes respond to the robot will take multiple seasons to amass. The probability of a successful robot presentation depends heavily on the location and orientation of the snake. The robot requires a clear approach to the snake that is free of excessive vegetation and substrate. In addition, the target snakes are often found in ambush positions inside squirrel burrows, which are too small for presentation of the robot. Consequently, the rate of accumulation of successful trial data is quite low; acquisition of sufficient data for rigorous statistical analyses will require either multiple field seasons (years) or larger sample sizes of radio-implanted snakes. However, we now have the tools to conduct such a study.

Discussion and Conclusions

Results from our laboratory study suggest that our infrared playback technique was tapping into an infrared-based communicative system between ground squirrels and rattlesnakes, as we reported in [29]. The addition of an infrared component clearly shifted rattlesnakes from hunting to defensive behavior. Such an impact would not only protect pups but might also be expected to encourage rattlesnakes to leave the area, an effect that similar tail-flagging confrontation by chipmunks and gray squirrels appears to have [32]. Future versions of the robotic squirrel models designed to accompany infrared-reinforced tail flagging with substrate throwing and looming (as done by squirrels in natural environments) could provide a more complete understanding of the dynamics of interactions involving infrared signaling.

Experiments with our robot could also allow us to assess the responses of other squirrels to tail-flagging displays. Antipredator displays have been hypothesized to deter predators not only by signaling to the predator that it has been detected but also by advertising the presence of the predator to others [33]. In the current version of the robot, tail flagging is done with fairly noisy servos. Initial tests of the robot with live squirrels tended to startle the live squirrels (unpublished data), possibly because of the servo noise, or some other facet of the squirrel that indicated it was not a real squirrel.

We learned several more general lessons with robosquirrels in the laboratory and field, which may extend to other robotic models as well. First, close collaboration between roboticists and biologists is very important during robot design. Engineers need a clear understanding of both the robot features important to biologists and the conditions in which the biologists are conducting their experiments. As mentioned earlier, in our studies, the biologists contributed to robot design and building, and engineers contributed to behavioral data collection in the field and laboratory. However, ultimately it was the goal to have the biologists use the robots without the need for constant support from the engineers. Even the most advanced robotics tools are useless unless they can be used easily and effectively.

Second, the robot designers need to consider not only the features that the robot must possess to interact with the live animals but also the entire experiment cycle, from transport to calibration and setup, to deployment, to actual interaction, and cleanup. Major difficulties in any of these facets could lead to rejection of the robot as a research tool. Third, durability and robustness of the robot systems are very important. If a robot fails midway through an interaction experiment, not only are those particular interaction data invalid, but the live subject with which the failed robot interacted could be called into question for future interaction trials. This can seriously compromise the study, as live subjects are difficult to obtain and expensive to maintain. In the field, if the robot breaks, it must be replaceable or repairable quickly and effectively. If the robot fails in the field, then that entire field season could be wasted, including the human researchers' time, travel costs, and housing costs. Therefore, the most complex robot is not necessarily the best robot. It may be best to limit the number of moving parts or limit the number of components that are left exposed to the weather.

The field of biorobotics/biomechatronics is in its infancy, and there are a number of fundamental issues that must be studied including: what makes a robot believable to another animal, what are the kinds of studies in which a robot is the best choice as a research tool, and what kind of training is needed for the next generation of researchers to effectively design and incorporate these new research tools. The answers to all these questions will guide the field in the future.

Dedication

This article is dedicated to our friend, colleague, and mentor, Prof. Donald Owings (1943–2011). He will be missed by many.

Acknowledgments

The authors acknowledge the undergraduate students who contributed to the building of the robosquirrel models over the years, including Erin Chin, Nick Giannini, Travis Kupp, and Chris Sullivan. Funding for the first-generation model was provided by grants from the American Society of Mammalogists, the Sigma Xi, the Animal Behavior Society, the American Museum of Natural History, and the Chicago Herpetological Society to support the graduate work of A. Rundus. Funding for the outdoor models was provided by the Department of Mechanical and Aerospace Engineering, University of California, Davis, to support the graduate work of R. Johnson. Funding for field research on rattlesnakes was provided by the National Geographic Society Waitts Grant W17-08, the Animal Behavior Society, and the American Museum of Natural History. Additional funding is provided by the National Science Foundation (NSF) grant 0951010. The authors also thank SMER and the East Bay Regional Park District's Camp Ohlone for the use of their facilities. Finally, they thank Valerie J. Clark for helpful suggestions during the final preparation of this manuscript.

References

[1] B. Webb and T. Consi, *Biorobotics: Methods and Applications*. Cambridge, MA: MIT Press, 2001.

[2] P. Dario, B. Hannaford, and A. Takanishi, "Special issue on biorobotics," *IEEE Trans. Robot.*, vol. 24, no. 1, pp. 1–244, 2008.

[3] B. Webb, "Can robots make good models of biological behavior?" *Behav. Brain Sci.*, vol. 24, no. 6, pp. 1033–1050, 2001.

[4] C. J. May, J. C. Schank, S. S. Joshi, J. Tran, R. J. Taylor, and I. E. Scott, "Rat pups and random robots generate similar self-organized and intentional behavior," *Complexity*, vol. 12, no. 1, pp. 53–66, 2006.

[5] A. J. Ijspeert, A. Crespi, D. Ryczko, and J.-M. Cabelguen, "From swimming to walking with a salamander robot driven by a spinal cord model," *Science*, vol. 315, no. 5817, pp. 1416–1420, 2007.

[6] J. Schank, C. J. May, J. Tran, and S. S. Joshi, "A biorobotic investigation of Norway rat pups (*Rattus norvegicus*) in an arena," *Adaptive Behav.*, vol. 12, no. 3/4, pp. 161–173, 2004.

[7] A. Michelsen, B. B. Andersen, W. H. Kirchner, and M. Lindauer, "Honeybees can be recruited by a mechanical model of a dancing bee," *Naturwissenschaften*, vol. 76, no. 6, pp. 277–280, 1989.

[8] J. Halloy, G. Sempo, G. Caprari, C. Rivault, M. Asadpour, F. Tache, I. Said, V. Durier, S. Canonge, J. M. Ame, C. Detrain, N. Correll, A. Martinoli, F. Mondada, R. Siegwart, and J. L. Deneubourg, "Social integration of robots into groups of cockroaches to control self-organized choices," *Science*, vol. 318, no. 5853, pp. 1155–1158, 2007.

[9] S. D. A. Leaver and T. E. Reimchen, "Behavioural responses of *Canis familiaris* to different tail lengths of a remotely-controlled life-size dog replica," *Behaviour*, vol. 145, no. 3, pp. 377–390, 2008.

[10] G. L. Patricelli, J. A. C. Uy, G. Walsh, and G. Borgia, "Sexual selection: Male displays adjusted to female's response," *Nature*, vol. 415, no. 415, pp. 279–280, 2002.

[11] G. L. Patricelli, S. W. Coleman, and G. Borgia, "Male satin bowerbirds, *Ptilonorhynchus violaceus* adjust their display intensity in response

to female startling: An experiment with robotic females," *Animal Behav.*, vol. 71, no. 1, pp. 49–59, 2006.

[12] R. C. Taylor, B. A. Klein, J. Stein, and M. J. Ryan, "Faux frogs: Multimodal signalling and the value of robotics in animal behaviour," *Animal Behav.*, vol. 76, pp. 1089–1097, 2008.

[13] R. G. Coss, "Effects of relaxed natural selection on the evolution of behavior," *Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms*, S. A. Foster and J. A. Endler, Eds. Oxford: Oxford Univ. Press, 1999, pp. 180–208.

[14] C. Black, *A Review of North American Tertiary Sciuridae*. Bulletin of the Museum of Comparative Zoology of Harvard University, vol. 130. Cambridge, MA: Harvard Univ., 1963, pp. 109–248.

[15] J. A. Holman, *A Review of North American Tertiary Snakes*. Publications of the Museum of Michigan State University Paleo Series, vol. 1. East Lansing, MI: Michigan State Univ., 1979, pp. 203–260.

[16] H. S. Fitch, "Study of snake populations in central California," *Amer. Midland Naturalist*, vol. 41, no. 3, pp. 513–579, 1949.

[17] H. S. Fitch, "Ecology of the California ground squirrel on grazing lands," *Amer. Midland Naturalist*, vol. 39, no. 3, pp. 513–596, 1948.

[18] J. E. Biardi, "The ecological and evolutionary context of mammalian resistance to rattlesnake venoms," *The Biology of Rattlesnakes*, W. K. Hayes, M. D. Cardwell, K. R. Beaman, and S. P. Bush, Eds. Loma Linda: Loma Linda Univ. Press, 2008, pp. 557–568.

[19] J. E. Biardi, D. C. Chien, and R. G. Coss, "California ground squirrel (*Spermophilus beecheyi*) defenses against rattlesnake venom digestive and hemostatic toxins," *J. Chem. Ecol.*, vol. 31, no. 1, pp. 2501–2518, 2005.

[20] D. F. Hennessy and D. H. Owings, "Rattlesnakes create a context for localizing their search for potential prey," *Ethology*, vol. 77, no. 4, pp. 317–329, 1988.

[21] D. H. Owings and R. G. Coss, "Snake mobbing by California ground squirrels: Adaptive variation and ontogeny," *Behaviour*, vol. 62, no. 1/2, pp. 50–69, 1977.

[22] D. H. Owings and R. G. Coss, "Hunting California ground squirrels: Constraints and opportunities for Northern Pacific Rattlesnakes," in *The Biology of Rattlesnakes*, W. K. Hayes, M. D. Cardwell, K. R. Beaman, and S. P. Bush, Eds. Loma Linda: Loma Linda Univ. Press, 2008, pp. 155–168.

[23] M. P. Rowe and D. H. Owings, "The meaning of the sound of rattling by rattlesnakes to California ground squirrels," *Behaviour*, vol. 66, nos. 3–4, pp. 252–267, 1978.

[24] R. R. Swaisgood, D. H. Owings, and M P Rowe, "Conflict and assessment in a predator-prey system: Ground squirrels versus rattlesnakes," *Animal Behav.*, vol. 57, no. 5, pp. 1033–1044, 1999.

[25] D. H. Owings and R. G. Coss, "Social and antipredator systems: Intertwining links in multiple time frames," *Rodent Societies: Ecological and Evolutionary Perspectives*, J. Wolff and P. W. Sherman, Eds. Chicago, IL: Univ. of Chicago Press, 2007, pp. 305–316.

[26] D. H. Owings, D. F. Hennessy, D. W. Leger, and A. B. Gladney, "Different functions of "alarm" calling for different time scales: A preliminary report on ground squirrels," *Behaviour*, vol. 99, no. 1/2, pp. 101–116, 1986.

[27] Z. T. Halpin, "Naturally occurring encounters between black-tailed prairie-dogs *Cynomys-ludovicianus* and snakes," *Amer. Midland Naturalist*, vol. 109, no. 1, pp. 50–54, 1983.

[28] M. J. Hersek, "Behavior of predator and prey in a highly coevolved system: Northern Pacific rattlesnakes and California ground squirrels," Ph.D. dissertation, Univ. of California, Davis, 1990.

[29] A. S. Rundus, D. H. Owings, S. S. Joshi, E. Chinn, and N. Giannini, "Ground squirrels use an infrared signal to deter rattlesnake predation," *Proc. Nat. Acad. Sci. USA*, vol. 104, no. 36, pp. 14372–14376, 2007.

[30] N. S. Poran and R. G. Coss, "Development of antisnake defenses in California ground squirrels (*Spermophilus beecheyi*): I. Behavioral and immunological relationships," *Behaviour*, vol. 112, no. 3/4, pp. 222–245, 1990.

[31] M. J. Hersek and D. H. Owings, "Tail flagging by adult California ground squirrels: A tonic signal that serves different functions for males and females," *Animal Behav.*, vol. 46, no. 1, pp. 129–138, 1993.

[32] R. W. Clark, "Pursuit-deterrent communication between prey animals and timber rattlesnakes (*Crotalus horridus*): The response of snakes to harassment displays," *Behav. Ecol. Sociobiol.*, vol. 59, no. 2, pp. 258–261, 2005.

[33] E. Frankenberg, "The adaptive significance of avian mobbing 4: Alerting others and perception advertisement in blackbirds facing an owl," *Zeitschrift Fur Tierpsychologie*, vol. 55, no. 2, pp. 97–118, 1981.

[34] K. Schwenk, "Of tongues and noses—Chemoreception in lizards and snakes," *Trends Ecol. Evol.*, vol. 10, no. 1, pp. 7–12, 1995.

[35] H. Greene, *Snakes: The Evolution of Mystery in Nature*. Berkeley, CA: Univ. of California Press, 1997.

[36] L. Klauber, *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*. Berkeley, CA: Univ. of California Press, 1972.

[37] N. Ford and G. Burghardt, "Perceptual mechanisms and the behavioral ecology of snakes," in *Snakes: Ecology and Behavior*, R. A. Seigel and J. T. Collins, Eds. New York: McGraw Hill, 1993, pp. 117–164.

[38] D. F. Hennessy, D. H. Owings, M. P. Rowe, R. G. Coss, and D. W. Leger, "The information afforded by a variable signal: Constraints on snake-elicited tail flagging by California ground squirrels," *Behaviour*, vol. 78, no. 3/4, pp. 188–226, 1981.

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