Video and computer technology have emerged as a powerful tool for controlling visual stimuli and investigating questions about perception in a variety of animal taxa, including spiders (Clark and Uetz, 1990, 1992, 1994), birds (Evans and Marler, 1991; Evans et al., 1993a, 1993b), lizards (Macedonia et al., 1994; Macedonia and Stamps, 1994), anuran amphibians (Roster et al. 1995), and teleost fishes (Rosenthal et al., 1996; Rowland et al., 1995a, 1995b). Video playback and computer animation of test stimuli afford several benefits over presentation of live stimuli. In particular, the researcher can match or vary attributes of appearance and movement and determine the repetition rate or the sequence of the behaviors performed by the test stimulus. Although this technique has proven successful under laboratory conditions, in which lighting and testing environments can be controlled, it has not previously been used under natural field conditions.

For many studies, it may be more feasible to use video playback in the laboratory. Nonetheless, laboratory studies frequently elicit questions regarding the behavior of animals in nature. Field studies may provide additional information, unobtainable in a laboratory environment, and thus serve to complement laboratory experiments (Jenssen et al., 1995). Territorial animals in nature typically have fought to obtain and retain access to their parcel of habitat. Such animals in natural settings therefore may exhibit stronger responses to certain stimuli (e.g., conspecifics) than those in laboratory experiments.

The purpose of this research was twofold. First we sought to determine how Anolis grahami (Lacertilia: Iguanidae), a Jamaican species naturalized on Bermuda since 1905 (Wingate, 1965), would respond to video stimuli in the field. Second, because previous studies used analog video stimuli only (Macedonia et al., 1994; Macedonia and Stamps, 1994), we wanted to ascertain A. grahami response to computer-animated versions of a displaying conspecific male.

Materials and methods.—The analog video and computer-animated versions of A. grahami display used as stimuli were generated in the laboratory prior to testing in the field. Analog video sequences of male A. grahami display behavior used in a previous study (see Macedonia and Stamps, 1994) were used as a stimulus tape for field playbacks and as a template to generate a computer-animated sequence using an Amiga 3000 computer. Each frame of the display sequence was captured with a VideoToaster (Newtek, Inc.) frame grabber and rendered as a 64-color, 320 × 400 pixel image using Art Department Professional software (ASDG, Inc.). Single frames were sequenced together in an animation file using the batch processing software program, ProControl (ASDG, Inc.). Next, the animation was loaded into a video paint and animation program (Deluxe Paint IV, Electronic Arts), which allowed clearing of the background and manual tuning of the sequence to simulate actual male display behavior. This animation sequence was then downloaded from the computer to VHS tape using a Panasonic AG-1970 videotape recorder. Both the analog video and computer-animated stimulus tapes ran for a total playing time of 60 min and were edited such that each A. grahami headbob/dewlap display lasted approximately 12 sec and was separated by 1 min of nondisplay. Each headbob/dewlap display started and stopped on a frame in the sequence where the stimulus was motionless.

Field sites were chosen by first surveying the local A. grahami populations in Warwick Parish, Bermuda, for actively displaying territorial males. Video playbacks were conducted between 0900 h and 1900 h on 6 and 7 June 1994. Weather conditions were partly sunny, with an average temperature of 27–28 °C throughout the day.

For video playback in the field, a DC-powered video cassette recorder (Panasonic NV-8420; 12-volt rechargeable Nicad battery; 90 min average playback time) and playback monitor (Sony PVM-8044Q; 20.3 cm diagonal screen; 400 lines of resolution) powered by a 12-volt rechargeable battery (Innotec, Portable Power Station, #SB152; 2.5 h average playback time) were used (Fig. 1). The VCR was attached to the video monitor with a 7 m long cable, allowing control of the playback from a distance that did not appear to disturb the resident lizards. The playback monitor was placed in a shady location and camouflaged with vegetation (to avoid screen glare) but where it would be conspicuous to the resident male and females. The re-
Fig. 1. Schematic representation of the video setup in the field. (A) Battery-powered video cassette recorder; (B) portable battery power source for television monitor; (C) television monitor camouflaged with vegetation; (D) Anolis lizard observing conspecific video stimulus.

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Responses of lizards toward the test stimuli were videotaped with a Sony Handycam 8 mm Camcorder. All video equipment was set up approximately 1 h before the test session began.

Results.—The first playback session was conducted using the analog video stimulus, on 6 June 1994 at 1510 h. After 15 min, the resident male was observed facing the monitor from a distance of approximately 3 m. He was oriented toward the monitor screen and moved steadily toward the video stimulus. When within 2 m of the monitor, he began to headbob and to extend his dewlap. The male displayed intermittently for about 10 min toward the stimulus and then suddenly charged the playback monitor, veering off just to the right of it at the last moment. He then stopped, extended his dewlap, and circled the apparent boundaries of his territory for approximately 5 min while periodically looking at and displaying toward the playback monitor. The male then retreated and disappeared from view into thick vegetation.

Ten minutes after the resident male departed, a female approached the video stimulus to about 35 cm, turned perpendicular to the monitor, gave two headbob displays, and then remained motionless until the stimulus tape was completed (approximately 35 min). Five minutes later, a second female approached from an angle of approximately 45° above and to the left of the monitor. From a distance of approximately 35 cm, she jumped to the top of the monitor, walked forward and peered over the front edge at the displaying video male on the screen. Subsequently, she perched motionless on top of the monitor until the end of the test session. The two females did not interact with each other but appeared focused on the display behavior of the video male.

On the following morning at 0900 h, a playback trial using the computer-animated stimulus was initiated in the territory of a different male. After about 10 min of playback, the male began to display toward the monitor from a distance of approximately 2 m. He approached and stopped about 1 m from the monitor to display again, then turned and ran directly away from the monitor along a railing on which the monitor was placed. The male stopped 3–4 m from the monitor and engaged in a series of pushup displays before jumping off the railing into the adjacent vegetation. Like the first male, this second male then patrolled the apparent boundaries of its territory for about 10 min, intermittently displaying toward the monitor before disappearing into the vegetation.

In the final video presentation on 7 June 1994 at 1900 h, the computer-animated male stimulus was played in the territory of a third male subject. This male did not display toward the video stimulus but retreated from the monitor and disappeared into the vegetation shortly after the stimulus tape began. The stimulus tape was allowed to continue, however, and a female appeared. Like the other females, this subject approached the monitor while continuously fixating on the stimulus. At a distance of approximately 30 cm, she headbobbed, erected her small dewlap, and then remained motionless in front of the monitor until the stimulus tape ended 20 min later.

Discussion.—These results demonstrate that video playback of either analog or computer-animated stimuli holds potential for behavioral studies of lizards in nature. Lizards may respond to video stimuli of conspecifics with greater intensity in the field than in the laboratory. For example, in several years of conducting video playbacks to A. grahami in the laboratory, we never have observed males responding to a video stimulus with pushup displays involving all four limbs, where the body was lifted entirely off the substrate. In addition, field experiments may elicit a broader range of responses than those in the laboratory, because some behaviors may be suppressed or insufficiently stimulated in highly artificial settings. The territorial patrol behavior of the A. grahami males we observed would be difficult to elicit in the lab, where space is limited.

In summary, with the advent of portable video equipment and computers, much of the visual stimulus control possible in the laboratory
can now be brought into a larger ecological and evolutionary context of an organism's natural habitat. Just as the field sound playback studies have contributed enormously to our understanding of animal acoustic communication (McGregor, 1992), video playback can now be used to broaden our understanding of animal visual communication and perception under natural conditions.

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