Male *Anolis* lizards discriminate video-recorded conspecific and heterospecific displays

JOSEPH M. MACEDONIA*‡, CHRISTOPHER S. EVANS* & JONATHAN B. LOSOS†

*Animal Communication Laboratory, University of California, Davis, CA 95616-8761, U.S.A.
†Department of Biology, Washington University, St. Louis, MO 63130-4899, U.S.A.

The conspicuous head-bobbing and dewlap-pulsing signals of male *Anolis* lizards have long intrigued ethologists. With over 250 species, this large genus exhibits striking variation in body size, coloration, and display pattern (see Crews & Williams 1977; Jenssen 1977; Williams & Rand 1977; Fleishman 1992 for reviews). It has, however, proved difficult to identify the display components mediating species recognition, because attributes such as size, shape, coloration, and head-bobbing pattern often covary (e.g. Williams & Rand 1977). There have been very few attempts to conduct playback experiments with visual displays, although Jenssen (1970) successfully evoked responses using 16-mm film loops. The technique has not been widely adopted, perhaps because film images are inherently difficult to manipulate. In contrast, recent advances in video technology provide considerable flexibility in defining stimulus attributes (e.g. Evans et al. 1993). This approach shares with film the advantage of allowing controlled playback experiments. Here we report an initial study on species recognition in anoles using video-recorded stimuli.

We selected a pair of Hispaniolan 'sibling species' (see Losos 1985b): *Anolis cybotes* and *A. marcanoi*. Adult males were collected in the Dominican Republic in August 1991. Prior to experimental tests, they were maintained for 60 days on a 14:10 h light:dark cycle, at a temperature of 32°C and a relative humidity of 65%, to bring them into breeding condition (Licht 1967).

We obtained stimulus footage by placing pairs of conspecific males in a 38-litre aquarium, which was fitted with perches at each end and lined with grey card to eliminate reflections. The

‡Present address: Department of Anthropology, University of Michigan, Ann Arbor, MI 48109-1382, U.S.A.

ensuing agonistic interactions were video-recorded through the end wall of the tank, using a Panasonic PV-S350D S-VHS camcorder (resolution >400 lines) with a shutter speed of 1/250 s. We focused on the more distant of the two males, as he was consistently oriented toward the closer male, and hence toward the camera. Focal length was adjusted so that the image obtained on the Panasonic CT-1331Y 33 cm colour monitor subsequently used for playbacks was precisely life-sized.

Stimulus sequences were assembled using professional video editing equipment, together with a microcomputer system that allowed us to overlay a 'mask' on each frame, creating a window in which only the more distant male was visible (see Evans et al. 1993 for details). Two matched pairs of stimuli were created. All four sequences began and ended with 3-min 'baseline' periods, during which a digitized image of the branch on which the stimulus lizard had been perched was visible. We scored head-bobbing movements and dewlap extensions, which are essentially synchronous in both *A. cybotes* and *A. marcanoi*, as aggressive displays. The chronological order of these displays was preserved, and a temporal escalation in display rate was simulated by systematically decreasing the inter-display interval from 60 s to 20 s in 10-s increments (Fig. 1a,c).

Only *A. marcanoi* males were used as experimental subjects because the aggressive displays of *A. cybotes* lack a progressive hierarchical structure (Jenssen 1983; Losos 1985b). We conducted tests in a room with the same light, temperature and humidity settings as that in which the lizards were housed. Subjects were transferred from their home tanks to a 38-litre test tank 46–50 h before testing began. This tank contained a single horizontal perch, positioned 38 cm from a video monitor abutting the end wall.

Each male was randomly assigned a conspecific or heterospecific stimulus for the first test trial, and was then presented with the paired alternative stimulus at the same time on the following day. All males were subsequently re-tested with the two exemplars that they had not seen during the first test session, and with the stimulus sequence reversed. Playbacks were initiated only when the subject lizard was sitting calmly on the perch. All tests were video-recorded.

Fifteen of the 16 subjects responded to the video sequences of displaying males with aggressive displays of their own. All of the components of normal aggressive display were elicited, including head-bobbing, dewlap extension, crest erection, 'pointing' and intention movements for leaping toward the video screen.

We examined the distribution of display activity over the course of the test session by reviewing test session videotapes, frame by frame (temporal resolution 33 ms), and noting the duration and onset time of each aggressive display by each of the subject males. Display durations were then summed for successive 1-min intervals and log-transformed to reduce positive skew.

There was clearly a close correspondence between the display activity of the subject males (Fig. 1b,d) and that of the video-recorded lizards (Fig. 1a,c). No displays occurred during the pre-stimulus period. Males began displaying shortly after the stimulus male appeared and continued to do so as long as he was visible. Display activity then declined rapidly during the post-stimulus period. These responses are reflected in robust main effects for time in repeated-measures ANOVAs (stimulus pair 1: $F_{13,195}=6.95$, $P=0.0001$; stimulus pair 2: $F_{9,126}=6.17$, $P=0.0001$).

We observed an unexpected difference in the distribution of display activity elicited by the two sets of video-recorded stimuli. While display responses to the first pair of matched sequences increased monotonically and then remained at a high level for the duration of the playback (Fig. 1b), there was a transient drop in display rates after the initial response to the second pair of sequences (Fig. 1d). We speculate that the subject males may have had difficulty matching the relatively rapid escalation in display rate characteristic of the second pair of video-recorded stimuli (compare Fig. 1a and Fig. 1c). Further playback experiments will be necessary to verify that
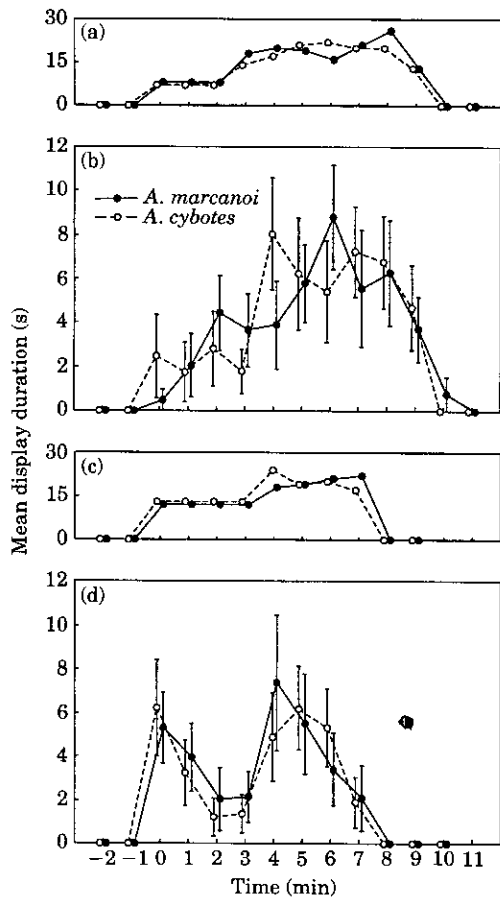

Figure 1. Display activity by male *A. marcanoi* subjects in response to matched video-recorded sequences of conspecific and heterospecific (*A. cybotes*) aggressive displays. Stimulus characteristics for (a) sequence pair 1 and (c) sequence pair 2. Mean (± SE) duration of displays evoked (b) in response to sequence pair 1 and (d) in response to sequence pair 2.

A. marcanoi males are capable of assessing the display rates of video-recorded conspecifics.

We also explored the moment-to-moment correspondence between video-recorded stimulus displays and those of subject males, by calculating a 'display synchrony index' for each test trial as follows: DSI=Total duration of subject displays during stimulus display/(total duration of all subject displays × proportion of playback sequence containing display).

This measure summarizes the timing relationship between subject displays and those of the

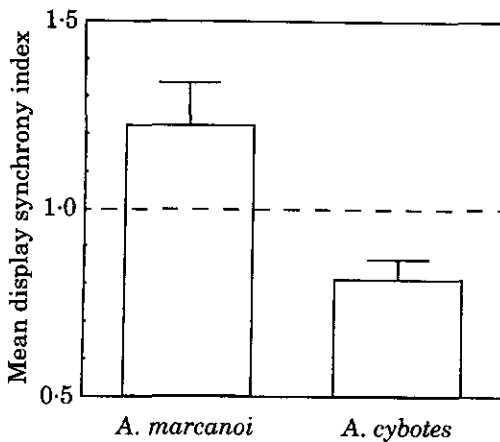**Figure 2.** Mean (± SE) display synchrony scores. Values less than 1·0 reflect a tendency to inhibit display while the video-recorded male was displaying, scores greater than 1·0 reflect a tendency to display preferentially at the same time as the video-recorded male (see text for details).

video-recorded stimuli and is independent of the absolute level of display elicited. It is thus particularly valuable when there is marked individual variation in responsiveness. The index has a value of 1·0 when the subjects' behaviour is independent of the video stimulus, a value between 0·0 and 1·0 if they inhibit their own displays when the stimulus lizard is displaying, and a value greater than 1·0 when they display synchronously with the stimulus.

Subject males spent more time displaying synchronously with conspecific video sequences than with heterospecific video sequences (Fig. 2). This difference was significant both when we considered only those males that responded to all four stimuli ($z=2.20$, $N=7$, $P=0.028$) and when we included all males that responded to at least one stimulus of each kind ($z=2.29$, $N=10$, $P=0.022$).

In summary, video sequences of displaying anoles were sufficient to evoke the full gamut of aggressive visual responses characteristic of agonistic interactions with live opponents. The display synchrony analysis demonstrates that males discriminated conspecific video sequences from heterospecific ones, even though these stimuli were matched for overall display rate. This suggests that species recognition is mediated by display pattern and/or morphological cues (e.g. Fleishman 1992). We speculate that synchronous

displays may function to signal a higher degree of threat to intruding conspecifics, as has been suggested for analogous changes in the timing of acoustic signals in frogs (e.g. Narins 1983) and birds (e.g. McGregor et al. 1992).

The results of these video playback experiments differ from those obtained from staged agonistic interactions (Losos 1985a), in that conspecific stimuli did not elicit a greater overall level of aggression than heterospecific stimuli. This difference may be attributable to the lack of stimulus-subject interaction in the present study. Several recent playback experiments have demonstrated that animals are sensitive to the moment-to-moment relationship between their behaviour and stimulus presentations (e.g. Dabelsteen & Pedersen 1990; Evans 1991; McGregor et al. 1992) and such contingencies may assume particular importance during aggressive dyadic interactions.

REFERENCES

Crews, D. & Williams, E. E. 1977. Hormones, reproductive behavior, and speciation. *Am. Zool.*, **17**, 271–286.

Dabelsteen, T. & Pedersen, S. B. 1990. Song and information about aggressive responses of blackbirds, *Turdus merula*: evidence from interactive playback experiments with territory owners. *Anim. Behav.*, **40**, 1158–1168.

Evans, C. S. 1991. Of ducklings and Turing machines: interactive playbacks enhance subsequent responsiveness to conspecific calls. *Ethology*, **89**, 125–134.

Evans, C. S., Macedonia, J. M. & Marler, P. 1993. Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. *Anim. Behav.*, **46**, 1–11.

Fleishman, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *Am. Nat.*, **139**, S36–S61.

Jenssen, T. A. 1970. Female response to filmed displays of *Anolis nebulosus* (Sauria, Iguanidae). *Anim. Behav.*, **18**, 640–647.

Jenssen, T. A. 1977. Evolution of anoline lizard display behavior. *Am. Zool.*, **17**, 203–215.

Jenssen, T. A. 1983. Display behavior of two Haitian lizards, *Anolis cybotes* and *Anolis distichus.* In: *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams* (Ed. by A. G. J. Rhodin & K. Miyata), pp. 552–569. Cambridge: Museum of Comparative Zoology.

Licht, P. 1967. Environmental control of annual testicular cycles in the lizard *Anolis carolinensis.* I. Interaction of light and temperature in the initiation of testicular recrudescence. *J. exp. Zool.,* **165,** 505–516.

Losos, J. B. 1985a. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. *Copeia,* **1985,** 905–910.

Losos, J. B. 1985b. Male aggressive behavior in a pair of sympatric sibling species. *Breviora,* **484,** 1–30.

McGregor, P. K., Dabelsteen, T., Shepherd, M. & Pedersen, S. B. 1992. The signal value of matched singing in great tits: evidence from interactive playback experiments. *Anim. Behav.,* **43,** 987–998.

Narins, P. M. 1983. Synchronous vocal response mediated by the amphibian papilla in a neotropical treefrog: behavioural evidence. *J. exp. Biol.,* **105,** 95–105.

Williams, E. E. & Rand, A. S. 1977. Species recognition, dewlap function and faunal size. *Am. Zool.,* **17,** 261–270.