

Female Japanese quail affiliate with live males that they have seen mate on video

ALEXANDER G. OPHIR & BENNETT G. GALEF, JR Department of Psychology, McMaster University

(Received 12 April 2002; initial acceptance 14 August 2002; final acceptance 21 October 2002; MS. number: A9332R)

A female Japanese quail, *Coturnix japonica*, will increase her tendency to affiliate and mate with a conspecific male after seeing him court and mate with another female. In the present study, we found that female quail increased the time they spent near a live target male after seeing that same male court and mate with another female in a 5-min video displayed on an active-matrix TFT monitor. However, female quail that were shown 5-min video sequences of either a target male standing alone or a randomly selected male courting and mating did not subsequently increase the time they spent near a live target male. These findings provide the first demonstration of which we are aware of birds transferring individual identification from a video sequence to a real animal.

© 2003 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour.

Replacing live stimulus animals with video recordings can facilitate research by increasing control of stimuli while reducing: (1) variability inherent in direct interactions between living individuals, (2) disruption of normal behaviour caused by handling and (3) the number of subjects needed for experiments. Video sequences have been used to study a range of topics and species, including social facilitation (domestic fowl, Gallus gallus domesticus: Keeling & Hurnik 1993), social learning (Burmese junglefowl, G.g. spadecius: McQuoid & Galef 1993), theory of mind (chimpanzees, Pan troglodytes: Premack & Woodruff 1978), motion perception (domestic fowl: Lea & Dittrich 1999), audience effects (domestic fowl: Evans & Marler 1991), predator recognition (domestic fowl: Evans et al. 1993), foraging behaviour (anuran sp.: Roster et al. 1995), aggressive interactions (anoles, Anolis grahami: Macedonia & Stamps 1994; jacky dragons, Amphibolurus muricatus: Ord et al. 2002), song learning (zebra finches, Taeniopygia guttata: Adret 1997; northern cardinals, Cardinalis cardinalis: Yamaguchi 1999), and, most relevant to the present studies, mate choice (jumping spiders, Maevia inclemens: Clark & Uetz 1990, 1992; wolf spiders, Schizocosa ocreata: Uetz & Smith 1999; Uetz & Roberts 2002; three-spined sticklebacks, Gasterosteus aculeatus: McKinnon 1995; guppies, Poecilia reticulata: Kodric-Brown & Nicoletto 1997; Nicoletto & Kodric-Brown 1999; green swordtails, Xiphophorus helleri: Rosenthal et al. 1996; Rosenthal & Evans 1998; Amazon

Correspondence: A. G. Ophir, Department of Psychology, McMaster University, Hamilton, ON, Canada L8S 4K1 (email: ophirag@ mcmaster.ca). mollies, *P. formosa*: Landmann et al. 1999; fiddler crabs, *Uca pugilator*: Pope 2000).

As might be anticipated in work involving such a wide variety of species and issues, as well as equipment of varying degrees of sophistication, some studies have not found exposure to video sequences as effective as exposure to living animals in evoking behaviour (species identification in chickens and pigeons, *Columba livia*: Ryan & Lea 1994; social recognition in domestic fowl: D'Eath & Dawkins 1996; individual and species recognition in domestic fowl: Patterson-Kane et al. 1997; and tutoring in African grey parrots, *Psittacus erithacus*: Pepperberg 1994; Pepperberg et al. 1998). Such relative failures have been reported in the literature particularly often when birds have been used as subjects, perhaps as a consequence of properties of both avian visual systems and video playback.

D'Eath (1998) described five features of video playback that might be responsible for failure of subjects to respond to such stimuli in the same way that they respond to live conspecifics: (1) failure to match spectral characteristics (Fleishman et al. 1998; Cuthill et al. 2000) and (2) depth cues (Zeil 2000), (3) presence of flicker, and (4) reduced acuity (Fleishman & Endler 2000) and (5) absence of interaction (Ord & Evans 2002). The first four of these five potential causes of relative lack of efficacy of video playbacks in eliciting normal behaviour can be ameliorated by improving video equipment itself.

Relative to cathode ray tube (CRT) monitors, used in almost all previous studies of responses to video sequences, active matrix, thin-film transistor (hereafter TFT) video monitors that have recently become available for use in research, enhance contrast and brightness and increase the likelihood of producing percepts of lifelike, continuous motion. Consequently, video sequences presented on TFT monitors might be expected to be more effective than those presented on CRT monitors in eliciting natural behaviours, especially in birds whose visual acuity, colour perception and high maximum critical flicker-fusion frequencies may make them particularly susceptible to the inadequacies of CRT displays. Consistent with such a view, Ikebuchi & Okanoya (1999) found that male zebra finches, Taeniopygia guttata castanotis, and Bengalese finches, Lonchura striata domestica, directed song towards live conspecific females or towards video sequences showing conspecific females when they were presented on TFT video monitors, but not when they were presented on CRT video monitors.

We undertook the experiments described here to determine whether female Japanese quail, *Coturnix japonica*, would copy the mate choices of female conspecifics seen courting and mating on a TFT video monitor. Female quail show an increased probability of affiliating and mating with males they have seen court and mate with other females (reviewed in White & Galef 2000), a strategy hypothesized to reduce costs associated with mate choice and increase the accuracy of assessment of potential mates (Gibson & Höglund 1992).

'Focal' female Japanese quail increase the time that they spend near a previously nonpreferred 'target' male after seeing him court and mate with another female (Galef & White 1998; White & Galef 1999). If female quail perceive moving TFT video images of conspecific males as they perceive live individuals, then they should show a similar increase in time spent affiliating with nonpreferred males whether they see them court and mate with other females live or on a TFT video monitor.

We conducted the same basic experiment twice to confirm the results of our investigation of female Japanese quails' use in mate selection of information acquired from video sequences. In experiment 1, a live nonpreferred male was always on the same side of the experimental apparatus where we had shown a female a video clip of that male courting and mating with another female. Although this procedure avoided any disruption of behaviour that might have been caused by moving live males, it also produced an obvious confound between where females had previously seen movement on a video monitor and where a nonpreferred male was to be found. In experiment 2, we moved the live nonpreferred male to the opposite side of the apparatus from where a video clip of him courting and mating had been displayed. We thus controlled for alternative explanations of any bias induced in mate preferences of female subjects in experiment 1 while repeating our basic observation.

EXPERIMENT 1

We examined effects on affiliative preferences of focal female Japanese quail of seeing digital video sequences presented on a TFT monitor that showed a previously nonpreferred target male quail courting and mating with a model female.

Methods

Subjects

Subjects were 30 male and 30 female 52-day-old Japanese quail acquired from a local commercial breeder (Speck's Poultry Farm, Vineland, Ontario, Canada). After we transported subjects to our laboratory, we placed them in individual, commercial quail cages ($55 \times 55 \times 110$ cm; Berry Hill, St Thomas, Ontario).

Throughout the experiment, the cages resided in a temperature- and humidity-controlled colony room illuminated for 16 h/day. We maintained all subjects on ad libitum Mazuri Pheasant Starter 5637 (PMI Feeds, St Louis, Missouri, U.S.A.) and tap water. For environmental enrichment, twice each week, we provided each bird with a handful of autoclaved hay. All procedures were approved by the McMaster University Animal Research Ethics Board (Animal Utilization Proposal No. 99-05-26).

To allow birds to come into breeding condition, we waited 40 days before starting the experiment. We considered a female ready to breed when she started to lay an egg at least once every other day. To determine whether a male was in breeding condition, as soon as he began to call regularly, we paired him for 5 min daily with a series of sexually mature females. We considered a male to be sexually mature when he mounted and made cloacal contact with females on 2 successive days. One male subject failed to reach criterion for sexual maturity after 10 days of pairing with females, and we did not use him in the experiment.

We randomly assigned sexually mature subjects to 23 trios, each consisting of one 'focal' female and two 'target' males. Seven females served only as 'model' subjects.

Apparatus

Filming. We recorded each male subject in a 10-gallon (37.9-litre) glass aquarium ($41 \times 21 \times 27$ cm), both while he courted and mated with a female and while he stood alone. We made video recordings of males using a CCD digital camcorder (Panasonic Digital Palmcorder, PV-DV910) with EIA Standard (525 lines with 60 fields) NTSC colour signal and optical resolution in the CCD of 680 000 pixels. Such digital video images have greater intensity bandwidth and reproduce spatial detail substantially better than the VHS analogue equipment used in most similar experiments in the past (Ord et al. 2002).

During filming, we disabled the auto-focus, set the zoom lens to its widest angle, and placed the camera 52 cm from the centre of the front wall of the aquarium that held the male and elevated it 14 cm above the surface on which the aquarium rested. The result was both to fill the total viewing area of the camera with an image of the aquarium wall and to provide life-size images of target male quail for presentation to focal females.

To visually isolate the aquarium from its surroundings while filming, we covered the aquarium floor with white absorbent liners (Tray Liners, Lilo Products, Hamilton, Ontario) and lined three of its walls with white Bristol board. We positioned lights to minimize reflection and glare from the walls of the aquarium (Fig. 1).



Figure 1. Illustration of the apparatus used to produce video clips of male quail either mating or standing alone. The positions of 60-W incandescent lamps and 150-W halogen floodlights (H) were arranged to avoid glare and reflections, and the distance from camera to aquarium was selected to give life-size images of quail during the observation phase of experiments. Shading indicates transparent surfaces. DV-R=Digital video recorder.



Figure 2. Illustration of the apparatus configured for presentation of video sequences during the observation phase of experiments 1 and 2. Shading indicates transparent surfaces. TFT=Active matrix, thin-film transistor video monitor; HC=holding cage.

We edited video sequences to 5.17 min using Apple iMovie 2.0.3 software. Each video clip opened with 5 s showing a black background with white text that identified the male subject. Thus each stimulus lasted a total of 5.25 min. (Portions of the video clips can be found at http://www.science.mcmaster.ca/Psychology/ophir/ago_research_video.html.) When we presented video sequences to subjects, we muted the sound so that females were exposed solely to the visual information presented on the TFT monitor.

Testing. We tested subjects in an apparatus consisting of three aquaria (Fig. 2): two 'end tanks' $(41 \times 21 \times 27 \text{ cm})$ and a 'central tank' $(61 \times 32 \times 41 \text{ cm})$ all with floors covered with absorbent paper liners. White Bristol board covers on two walls of the central tank restricted the view from within it, and a CCTV video camera (Panasonic WV-CP230) mounted above the central tank and connected to both a video monitor and video-cassette recorder (Panasonic PV9664) permitted observation and recording of behaviour. Each end tank was lined on three

sides with white Bristol board and had its transparent wall located 56 cm from the nearer end wall of the central tank.

A holding cage, constructed of transparent Plexiglas $(18 \times 18 \times 30.5 \text{ cm})$ with a removable opaque shell constructed of white Bristol board, could be placed at the midpoint of the central tank.

Using a firewire cable, we transferred each video stimulus in DV format from the camcorder to an Apple G4, 733-MHz computer. We used iMovie 2.0.3 to display these video clips in DV format without compression on a 15-in active-matrix, TFT monitor (VG-151, ViewSonic, Walnut, California, U.S.A.) with RGB display set at 16.7 million colours. The monitor's resolution was 1024×786 pixels and the viewable area was 30.5×23 cm.

To reduce extraneous visual stimuli, we placed in front of the monitor a white Bristol board shield $(71 \times 56 \text{ cm})$ into which we cut a 30.5×23 -cm window. Whenever the monitor was used as a stimulus, we placed both it and a Bristol-board barrier $(71 \times 56 \text{ cm})$ 25.5 cm from each of the end tanks (Fig. 2).

Testing

Design

Each test trial consisted of three phases, a 10-min pretest, a 5.25-min observation phase, and a 10-min post-test. During the pretest, we determined a 'focal' female's preference between a pair of males. During the observation phase, each focal female viewed: (1) a video clip of the male that she did not prefer during the pretest standing alone, (2) a video clip of the nonpreferred male mating with another female, or (3) her nonpreferred male mating live with another female. We counterbalanced across focal females the order in which they participated in the three test conditions, and no focal female ever encountered any male in more than one test condition.

Because we were concerned with effects of viewing video sequences of males' mating on females' subsequent affiliative behaviour, we did not assign focal females to view live males standing alone during the observation phase. In previous studies in our laboratory we have repeatedly found that females that see a live, non-preferred male mating during the observation phase show an increase from pretest to post-test in the time that they spend with their nonpreferred male. To the contrary, females who see a nonpreferred male standing alone during the observation phase show no change from pretest to post-test in the time that (Galef & White 1998; White & Galef 1999, 2000).

Pretest

To begin a test trial, we placed a focal female in the holding cage in the central tank with the opaque shell in place, and then placed a target male in each end tank. Next, we removed the holding cage and opaque shell and waited until the focal female took her first step. For the next 10 min, we recorded the time that the focal female spent closer to each of the two end tanks, each containing a target male, and defined the target male that a female spent less time closer to as her 'nonpreferred male'.

Observation phase

To begin the observation phase, we returned the focal female to the holding cage with its opaque shell in place. We then placed the Bristol-board barrier between the end tank housing a focal female's preferred male and the central tank. When a focal female was assigned to either the 'video-mating' or 'video-alone' conditions (see below), we placed the TFT monitor between the central tank and the end tank containing a focal female's nonpreferred male. We then removed the opaque shell from the holding cage and allowed the focal female to observe a 5.25-min video clip of her nonpreferred male either courting and mating (video-mating condition) or standing alone (video-alone condition). When a focal female was assigned to the 'live-mating' condition, we placed a model female in the end tank with the focal female's nonpreferred male, and allowed the focal female to observe him court and mate for 5.25 min.

Post-test

We conducted the post-test exactly as we had conducted the pretest, allowing a focal female to choose for 10 min between the same two target males that she had chosen between during the pretest. We left both males in the same positions that they had occupied during the pretest.

Data Analysis

We calculated the difference between pretest and posttest in the time that each focal female spent with her nonpreferred male when in each of the three test conditions. We used a one-way, repeated measures analysis of variance (ANOVA) and planned-comparison, Bonferroniadjusted, paired t tests to analyse the data.

Results

Data from eight of the 23 focal females were not used. Five focal females did not approach both males during one or more pretests, one focal female laid an egg during a pretest and two focal females were severely disturbed during observation periods by loud noises associated with construction under way in the building.

Interobserver reliability

A naïve observer, unaware of the condition in which a subject was being run, scored a random sample of 15 videotapes of focal subjects' behaviour during pretests and post-tests. Her scoring was highly correlated with that of one of the authors (A.G.O.; Fisher's exact test: r_{13} =0.92, *P*<0.0001).

Pretest

During pretests focal females in the video-mating, video-alone and live-mating conditions spent a mean \pm SE of, respectively, 6.4 ± 0.3 , 7.0 ± 0.4 and 7.0 ± 0.4 min closer to their preferred than nonpreferred target



Figure 3. Mean±SE change in time (min) between pretest and post-test that focal female subjects assigned to video-mating, videoalone and live-mating conditions spent nearer to the target subject they had not preferred during the pretest (experiment 1).

males (repeated measures, one-way ANOVA: $F_{2,14}$ = 1.29, NS).

Observation phase

During the observation phase all males assigned to the live-mating condition courted and successfully copulated with their model females.

Post-test

There was a significant effect of the type of stimulus to which we exposed focal females during the observation phase on their change in response from pretest to posttest towards nonpreferred target males (repeated measures ANOVA: F2,14=8.23, P<0.01; Fig. 3). After females had observed a video clip of a nonpreferred target male courting and mating on a TFT monitor, they showed a significantly greater increase in time spent closer to that target male than when they observed a video clip of a nonpreferred target male standing alone (Bonnferoni-corrected paired t test: t_{14} =3.16, P<0.01). Furthermore, seeing a video clip of a nonpreferred target male court and mate had the same effect on the change between pretest and post-test in the time that the female spent closer to a nonpreferred target males as did seeing a live male court and mate (t_{14} =0.56, NS).

Discussion

The results of experiment 1 are consistent with the hypothesis that focal females, when assigned to the video-mating condition, recognized target males that they had observed courting and mating on a TFT monitor, just as they recognized target males seen mating live when in the live-mating condition. In both cases, focal females increased the time that they spent near nonpreferred target males significantly more than when they saw such males in the video-alone condition. There are, however, alternative interpretations of the results of experiment 1. For example, during the post-test, focal females may have spent increased time at the end of the central tank closer to where, during the observation phase, they had seen any male courting and mating, two quail doing nothing at all, or any motion.

EXPERIMENT 2

The hypothesis that focal females in the video-mating condition of experiment 1 experienced increased attraction to the nonpreferred male that they saw court and mate on video leads to two predictions. First, exchanging the locations of preferred and nonpreferred target males between the observation phase and post-test should have no effect on the behaviour of focal females during the post-test. Focal females should continue to show an increased preference between pretest and post-test for nonpreferred target males seen courting and mating in video clips. Second, seeing video clips of an unfamiliar male courting and mating during the observation phase should have no effect on focal females' response to their respective nonpreferred target males during the post-test.

In experiment 2, during the observation phase, we allowed focal females, when assigned to the 'switch condition' to see a video clip of their nonpreferred target male courting and mating during the observation phase, then reversed the locations of the two target males before starting the post-test. During the observation phase, focal females when assigned to the 'third-male condition' observed a video clip of an unfamiliar male courting and mating. We then conducted the normal post-test, allowing focal females to choose for 10 min between the same two target males that they had chosen between during the pretest.

Methods

Subjects and Apparatus

The same 30 male, 15 focal female and 7 model female subjects in experiment 1 also served in experiment 2. We assigned focal females and target males to trios in experiment 2 so that no female was in a trio with either male that she had seen in experiment 1. We used the same apparatus for testing and the same video stimuli as in experiment 1 (Fig. 2).

Procedure

The procedure was the same as that used in experiment 1, except that we assigned each of the 15 focal females to both switch and third-male conditions. When a focal female was in the switch condition, at the end of the observation phase, we placed the opaque shell around the holding cage, reversed the locations of her two target males, and, to reduce any effects of handling on behaviour, waited 3 min before starting the post-test. When in the third-male condition, each focal female saw a video of an unfamiliar male, rather than of her nonpreferred target male, courting and copulating during the observation phase. We counterbalanced across focal females the order in which they participated in the two con-

Figure 4. Mean±SE change in time (min) between pretest and post-test that focal female subjects assigned to switch and third-male conditions spent nearer to the target subject they had not preferred during the pretest (experiment 2).

ditions, and no focal female ever encountered any male in more than one test condition.

Results

5

Data from three focal females were excluded when they failed to approach both males during a pretest.

Pretest

Focal females assigned to switch and third-male conditions spent, respectively, an average of 6.6 ± 0.3 and 6.7 ± 0.3 min closer to their preferred than to their non-preferred males (Student's paired *t* test: $t_{11} = -0.74$, NS).

Post-test

When assigned to the switch condition, focal females showed a significant increase between pretest and posttest in the time that they spent closer to their respective nonpreferred males (t_{11} =3.14, P<0.01; Fig. 4). To the contrary, when assigned to the third-male condition, focal females showed no increase between pretest and post-test in the time they spent closer to their nonpreferred male (t_{11} =0.93, NS; Fig. 4), and when in the switch condition, focal females showed a significantly greater increase in the time they spent nearer their respective nonpreferred males than when in the third-male condition (t_{11} =3.02, P<0.02).

Discussion

The results of experiment 2 are consistent with the hypothesis that, during the post-test, focal females in experiment 1 did not remain nearer the end of the central tank closer to where they saw courting and mating during the observation phase. Rather, during the post-test, focal females increased the time that they spent near the end of the central tank closer to a nonpreferred male that they saw court and mate during the observation phase.



GENERAL DISCUSSION

A female Japanese quail that sees a conspecific male court and mate with another female subsequently shows an enhanced tendency to affiliate with the male she saw courting and mating (Galef & White 1998; White & Galef 2000). The results of the present experiments indicate that a female quail who views a video clip of a conspecific male courting and mating on a TFT monitor subsequently shows a similar increase in her tendency to affiliate with the nonpreferred male that she saw courting and mating on video. This increased attraction is specific to the male seen mating and is not a result of a general tendency on the part of females to approach areas where they have seen conspecifics either standing alone or engaged in reproductive behaviours.

Lea & Dittrich (2000, page 156) suggested that, in birds 'There are as yet no experiments successfully testing transfer of learned discriminations between moving video images and real objects, and there are some well documented failures'. As far as we know, the present studies provide the first such demonstration. Although McQuoid & Galef (1993) showed that Burmese junglefowl transferred CRT images of distinctively coloured food dishes from video to their real counterparts, such a transfer is considerably less difficult than that demonstrated here from video sequences of an individual male to the male himself.

Our success, despite the failure of others to provide similar demonstrations in birds, may be attributable to our use of TFT rather than CRT video displays (but see Yamaguchi 1999), our using quail as subjects (Cuthill et al. 2000; Fleishman & Endler 2000) or our use of mate choice as a dependent variable (Hunt et al. 2001). In a pilot study, male Japanese quail were attracted to a TFT monitor showing a video of a moving female, but not to a CRT monitor displaying the same video images (A. G. Ophir, J. Tangen & B. G. Galef, Jr, unpublished data; see also Ikebuchi & Okanoya 1999). It seems reasonable to hypothesize that birds may perceive video sequences presented on a TFT monitor as more lifelike than the same sequences presented on a CRT monitor.

Acknowledgments

This research was supported by a Natural Sciences and Engineering Research Council of Canada operating and equipment grants to B.G.G., Jr. We thank Jason Tangen and Nav Mangat for technical assistance and Chris Evans for his extensive and most useful comments on an earlier draft of the manuscript.

References

- Adret, P. 1997. Discrimination of video images by zebra finches (*Taeniopygia guttata*): direct evidence from song performance. *Journal of Comparative Psychology*, **111**, 115–125.
- Clark, D. L. & Uetz, G. W. 1990. Video image recognition by the jumping spider, *Maevia inclemens* (Araneae: Salticidae). *Animal Behaviour*, 40, 884–890.

- Clark, D. L. & Uetz, G. W. 1992. Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour*, 43, 247–254.
- Cuthill, I. C., Hart, N. S., Partridge, J. C., Bennett, A. D. T., Hunt, S. & Church, S. C. 2000. Avian colour vision and avian video playback experiments. *Acta Ethologica*, **3**, 29–37.
- D'Eath, R. B. 1998. Can video images imitate real stimuli in animal behavior experiments? *Biological Reviews*, **73**, 267–292.
- D'Eath, R. B. & Dawkins, M. S. 1996. Laying hens do not discriminate between video images of conspecifics. *Animal Behaviour*, 52, 903–912.
- Evans, C. S. & Marler, P. 1991. On the use of video images in birds: audience effects on alarm calling. *Animal Behaviour*, **41**, 17–26.
- 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. *Animal Behaviour*, **41**, 1–11.
- Fleishman, L. J. & Endler, J. A. 2000. Some comments on visual perception and the use of video playback in animal behaviour studies. *Acta Ethologica*, **3**, 15–27.
- Fleishman, L. J., McClintock, W. J., D'Eath, R. B., Brainards, D. H. & Endler, J. A. 1998. Colour perception and the use of video playback experiments in animal behaviour. *Animal Behaviour*, 56, 1035–1040.
- Galef, B. G., Jr & White, D. J. 1998. Mate-choice copying in Japanese quail, Coturnix coturnix japonica. Animal Behaviour, 55, 545–552.
- Gibson, R. M. & Höglund, J. 1992. Copying and sexual selection. Trends in Ecology and Evolution, 7, 229–232.
- Hunt, S., Cuthill, I. C., Bennett, A. T. D., Church, S. C. & Partridge, J. C. 2001. Is the ultraviolet waveband a special communication channel in avian mate choice? *Journal of Experimental Biology*, 204, 2499–2507.
- Ikebuchi, M. & Okanoya, K. 1999. Male zebra finches and Bengalese finches emit directed songs to the video images of conspecific females projected onto a TFT display. *Zoological Science*, 16, 63–70.
- Keeling, L. J. & Hurnik, J. F. 1993. Chickens show socially facilitated feeding behaviour in response to a video image of a conspecific. *Applied Animal Behaviour Science*, **36**, 223–231.
- Kodric-Brown, A. & Nicoletto, P. F. 1997. Repeatability of female choice in the guppy: response to live and videotaped males. *Animal Behaviour*, **54**, 369–376.
- Landmann, K., Parzefall, J. & Schlupp, I. 1999. A sexual preference in the Amazon molly, *Poecilia formosa. Environmental Biology of Fishes*, 56, 325–331.
- Lea, S. E. G. & Dittrich, W. H. 1999. What do birds see in moving video images? *Current Psychology of Cognition*, **18**, 765–803.
- Lea, S. E. G. & Dittrich, W. H. 2000. What do birds see in moving video images? In: *Picture Perception in Animals* (Ed. by J. Fagot), pp. 143–180. Philadelphia: Taylor & Francis.
- Macedonia, J. M. & Stamps, J. A. 1994. Species recognition in *Anolis grahami* (Sauria, Iguanidae): evidence from responses to video playback of conspecific and heterospecific displays. *Ethology*, **98**, 246–264.
- McKinnon, J. S. 1995. Video mate preference of female three-spined sticklebacks from populations with divergent male coloration. *Animal Behaviour*, **50**, 1645–1655.
- McQuoid, L. M. & Galef, B. G., Jr. 1993. Social stimuli influencing feeding behaviour of Burmese red junglefowl: a video analysis. *Animal Behaviour*, **23**, 13–22.
- Nicoletto, P. F. & Kodric-Brown, A. 1999. The use of digitallymodified videos to study the function of ornamentation and courtship in the guppy, *Poecilia reticulata*. *Environmental Biology of Fishes*, 56, 333–341.

- Ord, T. J. & Evans, C. S. 2002. Interactive video playback and opponent assessment in lizards. *Behavioural Processes*, 59, 55–65.
- Ord, T. J., Peters, R. A., Evans, C. S. & Taylor, A. J. 2002. Digital video playback and visual communication in lizards. *Animal Behaviour*, 63, 879–890.
- Patterson-Kane, E., Nicol, C. J., Foster, T. M. & Temple, W. 1997. Limited perception of video-images by domestic hens. *Animal Behaviour*, 53, 951–963.
- Pepperberg, I. M. 1994. Vocal learning in grey parrots (*Psittacus erithacus*): effects of social interaction, reference, and context. Auk, 111, 300–313.
- Pepperberg, I. M., Naughton, J. R. & Banta, P. A. 1998. Allospecific vocal learning by grey parrots (*Psittacus erithacus*): a failure of videotaped instruction under certain conditions. *Behavioural Processes*, 42, 139–158.
- Pope, D. S. 2000. Video playback experiments testing the function of claw waving in the sand fiddler crab. *Behaviour*, 137, 1349– 1360.
- Premack, D. & Woodruff, G. 1978. Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1, 515–526.
- Rosenthal, G. G. & Evans, C. S. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proceedings of the National Academy of Sciences, U.S.A.*, **95**, 4431– 4436.
- Rosenthal, G. G., Evens, C. S. & Miller, W. L. 1996. Female preference for dynamic traits in the green sword tail, *Xiphophorus helleri*. *Animal Behaviour*, **51**, 811–820.

- Roster, N. O., Clark, D. L. & Gillingham, J. C. 1995. Prey catching behavior in frogs and toads using video-simulated prey. *Copeia*, 1995, 496–498.
- Ryan, C. M. E. & Lea, S. E. G. 1994. Images of conspecifics as categories to be discriminated by pigeons and chickens: slides, video tapes, stuffed birds and real birds. *Behavioural Processes*, 33, 155–176.
- Uetz, G. W. & Roberts, J. A. 2002. Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. *Brain, Behavior and Evolution*, **59**, 222–230.
- Uetz, G. W. & Smith, E. I. 1999. Asymmetry in a visual signaling character in sexual selection in a wolf spider. *Behavioral Ecology* and Sociobiology, 45, 87–93.
- White, D. J. & Galef, B. G., Jr. 1999. Mate-choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*. *Animal Behaviour*, **57**, 465–473.
- White, D. J. & Galef, B. G., Jr. 2000. Differences between the sexes in direction and duration of response to seeing a potential sex partner mate with another. *Animal Behaviour*, **59**, 1235– 1240.
- Yamaguchi, A. 1999. Auditory experience does not shape sexual preferences for song in female northern cardinals. *Behaviour*, **136**, 309–329.
- Zeil, J. 2000. Depth cues, behavioral context, and natural illumination: some potential limitations of video playback techniques. *Acta Ethologica*, **3**, 39–48.