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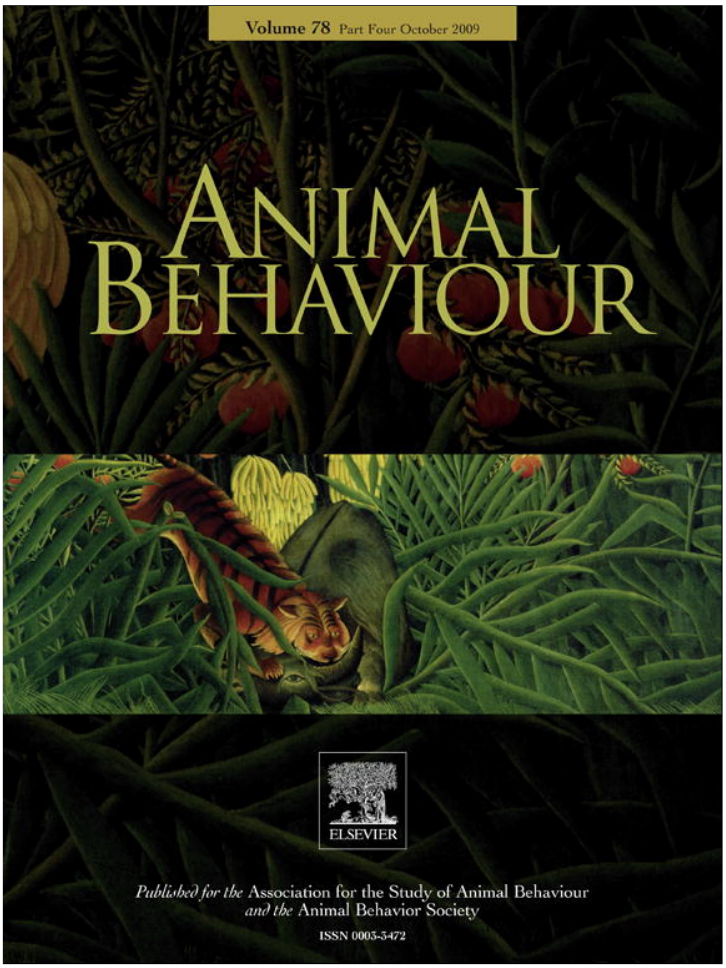

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Video playback and social foraging: simulated companions produce the group size effect in nutmeg mannikins

Guillaume Rieucau*, Luc-Alain Giraldeau

Groupe de Recherche en Écologie Comportementale et Animale, Département des Sciences Biologiques, Université du Québec à Montréal

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The use of video playbacks may provide a promising technique for the study of social behaviour because it allows experimenters to present a diverse set of behavioural patterns while precisely controlling what the observer experiences. However, in order to validate this technique for social foraging contexts, we must first show that video playbacks can effectively simulate foraging in the presence of foraging groups. A well-documented behavioural response of group-living animals to an increase in group size is a decline in individual levels of vigilance coupled with an increase in foraging rate: the so-called group size effect. We investigated this in captive nutmeg mannikins, *Lonchura punctulata*, by noting the vigilance and foraging behaviour of focal birds exposed to different numbers of either real or video-simulated companions. Similar patterns of changes in scanning and foraging were observed with changes in both real and simulated group sizes; the birds increased their feeding rate and decreased the time devoted to scanning. The video playback technique therefore provides an effective and appropriate technique for investigating social foraging questions.
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Many animals forage in groups, a condition that requires foraging responses that are specific to these social circumstances (Giraldeau & Caraco 2000). A well-documented behavioural response to an increase in foraging group size is a decline in scanning accompanied by an increase in foraging rate: the so-called group size effect. The function of these behavioural responses has been the focus of a number of studies (Lima & Dill 1990; Lima 1998). Generally, the reduction in vigilance is thought to be an adaptive response to an increasing number of conspecifics within the group, providing multiple eyes, and hence, increased detection power despite individual reduction in vigilance effort (Pulliam 1973; Lima 1990, 1995). The increased foraging rate is thought to follow passively, as individuals reallocate the time saved on antipredatory vigilance towards foraging behaviour (Lima et al. 1999). However, in some cases, the increased foraging rate may also be attributed to competition. Increasing group size may impose an adaptive increase in feeding rate to allow individuals to maximize their share of the resource (Beauchamp & Livoreil 1997; Beauchamp 2003). A key to unravelling the adaptive function of each response of the group size effect may lie in an investigation of the cues that animals use to adjust their behaviours. However, experimental manipulation of these cues may prove challenging and often involves the use of simulated companions.

Ethologists have long championed the use of simulated companions by conducting experiments over the years using dummies (Noble 1934; Tinbergen & Perdeck 1950), mirrors (Gallup & Capper 1970; Cohen & Looney 1973), audio playback (McGregor et al. 1992), animated robots (Fernandez-Juricic et al. 2006), video playback of real animals (D'Eath 1998; Hebets 2005; Bird & Emery 2008) and digitally created computer animations (Rosenthal 2000; Peters & Evans 2007). The main goal of all these methods has been to ensure strict experimental control of the stimuli presented to focal animals. The use of video playbacks appears to provide a particularly promising technique for the study of social behaviour and social foraging in particular because it allows experimenters to present a large range of behavioural patterns while controlling precisely what the observer gets to see or experience in terms of resource competition.

Reviews of the video playback technique's increasing use in behavioural studies have pointed out the importance of taking into account a number of technical points (D'Eath 1998; Fleishman et al. 1998; Oliveira et al. 2000) such as the use of thin film transistor (TFT) liquid crystal display (LCD) screens instead of common cathode screens to accommodate the higher critical flicker–fusion frequency of some avian species (e.g. diurnal birds species have a flicker–fusion frequency in the 105–140 Hz range). Other points that must also be considered are brightness (Fleishman & Endler 2000), size (Zeil 2000) and motion of the broadcasted elements (Fleishman & Endler

* Correspondence: G. Rieucau, Groupe de Recherche en Écologie Comportementale et Animale, Département des Sciences Biologiques, Université du Québec à Montréal, CP 8888, Succ. Centre-ville, Montréal, Québec H3C 3P8, Canada.
E-mail address: rieucau.guillaume@courrier.uqam.ca (G. Rieucau).

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2000; Peters et al. 2002; Woo & Rieucau 2008), as well as colour perception (Fleishman & Endler 2000) and depth (Cuthill et al. 2000).

Video images induce natural behavioural responses in many taxa; however, most studies have been done in contexts of mate choice (Clark & Uetz 1993; McDonald et al. 1995; Rosenthal et al. 1996; Adret 1997; Ikebuchi & Okanoya 1999; Witte & Klink 2005; Hebets et al. 2006), intraspecific aggression (Rowland 1995; McKinnon & McPhail 1996) or recognition of predators (Evans & Marler 1991; Evans et al. 1993) and conspecifics (Mottley & Heyes 2003; Bird & Emery 2008). The validity of the video playback approach in social foraging studies remains uncertain, especially because of the problems posed by broadcasting realistic images of groups. Few studies have questioned the recognition of simulated groups and fewer still have reported conclusive results (McQuoid & Galef 1993, 1994).

In studies of social foraging, video playbacks often require presentation of groups of several individuals. Therefore, if this technique is to be useful in addressing social foraging questions, we must first establish whether it can effectively simulate the presence of foraging groups. For this reason, we compared the effect of changing group sizes on the foraging responses of focal nutmeg mannikins, *Lonchura punctulata*, when the group was composed of real companions and when the group was composed of an equivalent video playback of these companions. Similar patterns of response in vigilance and foraging in both conditions would indicate that the video playback approach is valid as an experimental tool for investigating social foraging questions and especially the functional interpretation of the group size effect.

METHODS

Study Animals

Subjects were 23 wild-caught nutmeg manikins, obtained as adults (2 years old) from a commercial breeder (L'oisellerie de l'Estrie, Thetford Mines, Québec, Canada), that we individually identified from coloured leg bands. These social birds search for and feed on seeds on the ground, show little aggression over food and have no stable priority of access to food hierarchy (Giraldeau et al. 1990). Experimental birds were kept in cages in the animal care facilities at the Université du Québec, at room temperature and under a 12 h day/night lighting regime with ab libitum seeds and water.

Apparatus

The experimental apparatus consisted of two boxes, A and B ($18 \times 13 \times 15$ cm), placed 30 cm apart inside an observation room (Fig. 1a). Each box was equipped with a perch, a drinking trough and a feeder containing a large quantity of mixed millet seeds. One long side of each box was transparent to allow the observer (G.R.) to see inside, and one short side of each box was transparent to allow the birds in one box to see into the other. The top of each box was covered with plastic wire mesh. For the video playback condition, box B was replaced by a 16-inch (41-cm) TFT LCD monitor (Sony DSM-m61: resolution max: 1280 dots $\times$ 1024 lines, operating frequency 48–85 Hz, resolution $>$ 600 lines) placed in front of the

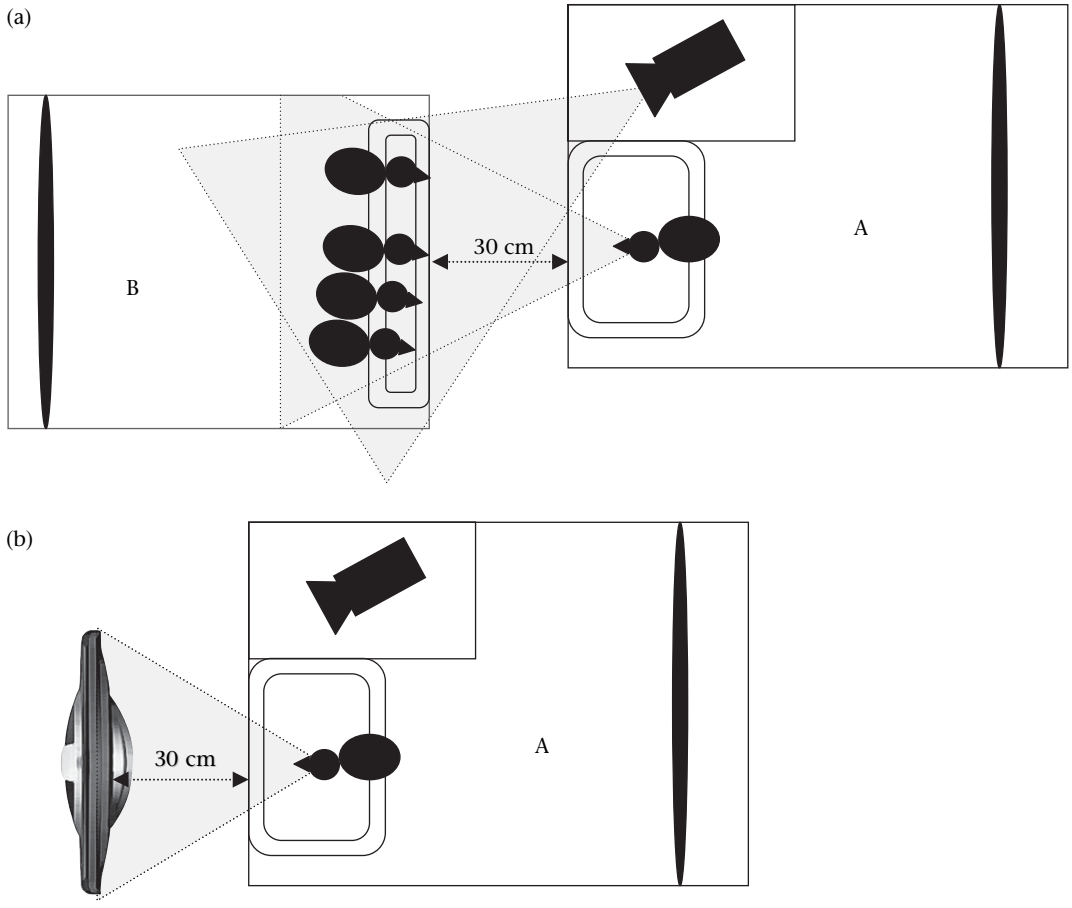

Figure 1. Apparatus for (a) the real companions condition and (b) the simulated companions condition. For the simulated companions condition, box B was replaced by a 16-inch TFT LCD monitor placed in front of the transparent side of box A.

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transparent side of box A 30 cm away (Fig. 1b) and connected to a computer outside the observation room. The birds' behaviour was videotaped using a digital mini DV camera (Canon Optura 30) that recorded the trials from outside the observation room through a one-way mirror. To create the video sequences for the video playback experiment, a digital mini DV camera (Panasonic PV-GS320, shutter speed of 1/250 s, aperture of F 1.8, optical resolution 540 lines, recording at 29.97 frames/s, NTSC video standard) was placed in box A beside the feeder and hidden under a cardboard cover. We adjusted the camera focal length to ensure that the companion birds on the feeder appeared life-sized in the video sequences. The camera recorded the feeding behaviour of companions from a focal bird's level, but at a slight angle, because the camera was not directly in front of the box but slightly to the side. Birds closer to the lens appeared slightly larger than those located on the opposite side of the feeder. The cardboard cover was never removed either during the training session or during the real companions condition. Our design required that some of the focal birds experienced the real companions condition first so that we could record the video sequences to be used in the video playback condition. After recording the companions' foraging, we attempted to reduce the effect of the slight angle of the camera relative to the feeder by using Windows Movie Maker for Vista (Microsoft Corporation) to correct the angle of vision. However, we only succeeded in creating a mirror image of the actual video sequence, which simply reversed the angle of the shot. We then used these mirror images and a video editing software (Pinnacle Studio 9, Avid Technology Inc, Mountain View, CA, U.S.A.) to create four 6 min silent video sequences for each group size. Although the experimental apparatus allowed the transmission of acoustic cues from one box to the other, the video playback condition was conducted without audio.

Training and Experimental Trials

We randomly selected (using random number tables) six nutmeg mannikins from the colony to be used as experimental subjects and housed them together in a cage for 6 day before the trials. The other birds, housed in similar conditions, were used as companions to constitute groups of different sizes. Both focal and companion birds were food deprived before each trial, for 14 h (overnight + 2 h after lights on) between trial days and for 90 min between consecutive trials.

To acclimatize the birds to the feeding apparatus, each focal bird was placed in box A four times per day for 2 consecutive days with access to the feeder. Companion birds in box B were trained following the same procedure with access to a feeder containing a mix of millet seeds. To allow birds to become accustomed to feeding next to the monitor, we placed each bird in box A for 15 min at 90 min intervals four times per day for 2 consecutive days, during which time it could eat from a feeder placed next to a video monitor playing a video sequence of a feeder without companions. A bird was considered trained when upon entering the apparatus it obtained its first seed within the first 30 s.

A trial started when the focal bird landed on the feeder and it ended when the focal bird left the feeder or stopped foraging for 30 s. Trials never exceeded 6 min. Each focal bird was observed twice for each group size (0, 1, 3, 5 companions) and for each companion type (real or simulated). The experimental condition was randomly chosen before introducing a focal bird into the apparatus.

For the real companions condition, the combination of birds making up each group size was randomly selected immediately before introducing the birds into the apparatus. For the simulated companions condition, we used multiple randomly chosen exemplars of each group size during experimental trials to avoid pseudoreplication (McGregor 2000).

The experimenter noted foraging and scanning behaviour from playbacks of the video recordings of the trials using Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands). We distinguished between vigilant and nonvigilant behaviour according to the birds' head vertical orientation. When an imaginary line projected from a bird's eyes through its nares was parallel to the horizon, the bird was considered vigilant. A bird was considered to be foraging when its head was oriented down into the feeder as well as when it was manipulating a seed while holding its head in an upward position.

Granivorous birds can visually scan their surrounding environment while manipulating seeds. When food manipulation can be done in an upright posture, handling is not exclusively a foraging activity; it often allows animals either to scan for predators or to attend to social cues to gain social information. For this reason, we focused on the part of the vigilance that is concomitant with food-handling: the food-handling scan (Lima et al. 1999). A food-handling scan starts when a bird's head is held upright while its mandibles are husking a seed and it ends once the seed is swallowed. The feeding rate is defined as the number of seeds eaten/min spent foraging. The mean food-handling scan duration is the mean of all focal birds' mean scan durations while manipulating a seed averaged over the trial's duration. Scanning rate is the number of scans/min spent foraging.

Statistical Analysis

We used repeated measures ANOVA to examine the effect of real and simulated group size on feeding rate, mean food-handling scan duration and scanning rate. Focal birds experienced each combination of the three fixed within-subject-factors treatments: real or simulated companions, group sizes (0, 1, 3, 5 companions) and replicates (two for each treatment and group size). Sphericity was tested for conditions with more than two factors using the Mauchley test. In cases where the sphericity assumption was violated, we used adjusted P values with the Huynh–Feldt correction. We investigated the potential interactions between the two treatments and group size for each behavioural variable. All analyses were conducted with SPSS 10 (SPSS, Inc., Chicago, IL, U.S.A.), and results are expressed as means ± SE.

RESULTS

We found that feeding rates increased in both companion conditions with increasing group size, consistent with the group size effect hypothesis. Feeding rates did not significantly differ between the two companion conditions ($F_{1,5} = 0.67$, $P = 0.45$; Fig. 2a). The absence of a significant interaction between the type (real or simulated) and the number of companions ($F_{3,15} = 2.76$, $P = 0.11$; Table 1) indicates that focal birds modified their feeding rate in the same way for both types of companions when group size increased. An increase in the number of companions, either real or simulated, induced an increase in the feeding rate of focal birds.

Also consistent with the group size effect hypothesis, food-handling scan durations decreased when group size increased. The companion type did not significantly affect food-handling scan durations ($F_{1,5} = 0.15$, $P = 0.71$; Fig. 2b). Moreover, the interaction between companion type and group size was not significant ($F_{3,15} = 0.35$, $P = 0.78$; Table 1) indicating that scanning while handling was affected in the same way by group size in both treatments. When the number of companions of either type increased, focal birds lowered their food-handling scan durations.

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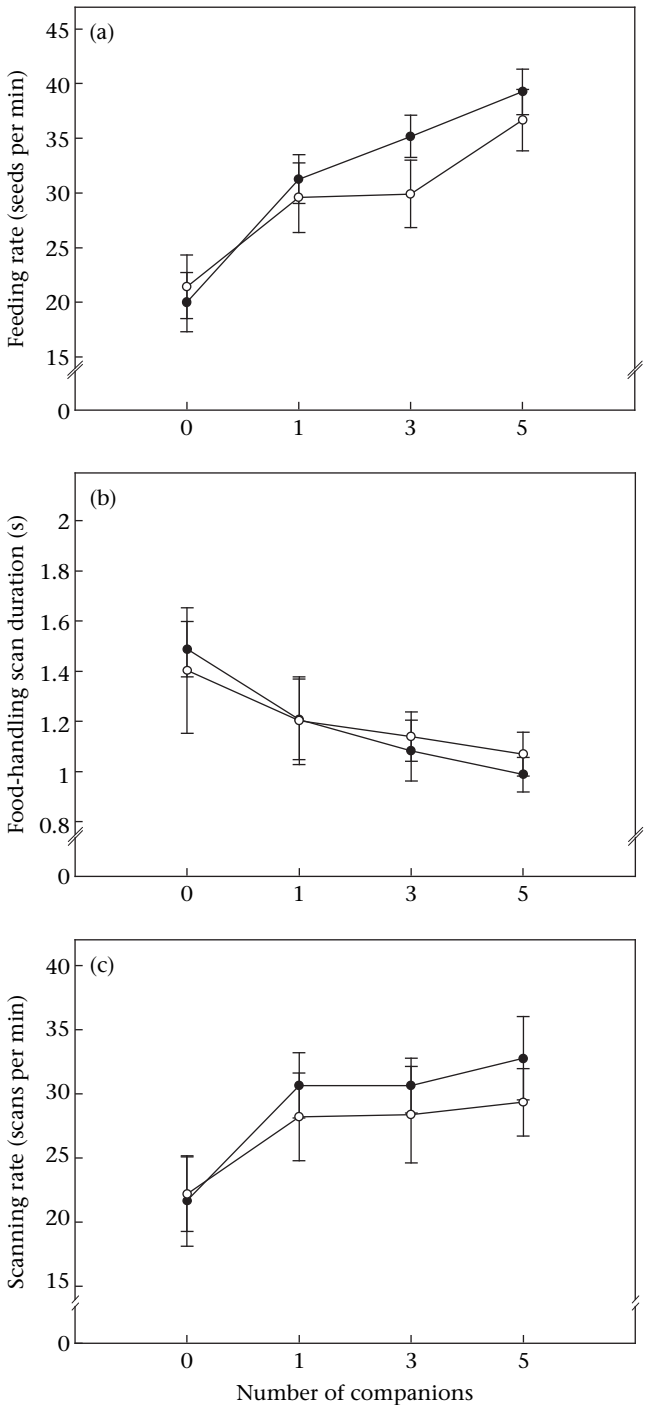

Figure 2. Variation in (a) feeding rate, (b) food-handling scan duration and (c) scanning rate of focal nutmeg mannikins as a function of group size with real companions (●) and simulated companions (○). Values are means ± SE.

Scanning rates did not significantly differ between the two companion types ($F_{1,3} = 1.15$, $P = 0.33$; Fig. 2c). Also, the interaction between the type and the number of companions was not significant ($F_{3,15} = 0.47$, $P = 0.71$; Table 1). When group size increased, either with real or simulated companions, focal nutmeg mannikins increased their scanning rates.

DISCUSSION

Nutmeg mannikins responded in the same way to an increase in group size with either real or simulated companions, suggesting that the video playback technique can provide an effective means of investigating social foraging problems. Birds showed classic behavioural responses in terms of vigilance and foraging to changes in group size, irrespective of whether companions were real or simulated. For both types of companions, birds had shorter food-handling scan durations and increased their feeding rate. Our results provide evidence that nutmeg mannikins show the group size effect common to many other species. However, detailed analysis of the behavioural responses to group size raises some questions about the functional interpretation of the effect.

We found that food-handling scan durations were shorter as group size increased. This result is consistent with a number of previous studies arguing that predation danger decreases with increasing group size (Lima et al. 1999). However, scanning rate increased with group size and nutmeg mannikins used shorter and more frequent scans as group size increased. This pattern cannot be derived simply from a hypothesis of reduced predation hazard with increasing group size.

Granivorous birds can scan and feed simultaneously. Indeed, an important component of the scanning behaviour observed in our nutmeg mannikins also included food-handling time. Food-handling is not necessarily exclusive of vigilance used either to detect predators or to collect social information. Shorter food-handling scan durations with increasing group size have been previously reported in dark-eyed juncos, *Junco hyemalis* (Lima et al. 1999). In an experiment involving the use of an unlimited food supply, Lima et al. (1999) reported similar declines in food-handling and non-food-handling scan durations with group size, suggesting that competition is not the main driving force of the group size effect on vigilance. Ascertaining the antipredatory, competitive and social information components of the response to an increase in group size will require the kind of detailed analysis that video playback techniques can provide by presenting, for instance, video-edited companions that are either never vigilant or always vigilant (Rieucau & Giraldeau 2009). Video playback is useful for precisely controlling the intensity of competition independently of group size, by avoiding possible differences in competitive abilities or hunger states among companions. We think, therefore, that the video playback technique offers a convenient way of unravelling the antipredatory and competitive components of the group size effect.

Table 1
Effects of increasing group size with real or simulated companions on feeding rate, food-handling scan duration and scanning rate in nutmeg mannikins

	Feeding rate			Food-handling scan duration			Scanning rate		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Real vs simulated companions					7				
Treatment	1	0.67	0.45	1	0.15	0.71	1	1.15	0.33
Group size	3	28.91	**0.0001**	3	4.81	**0.01**	3	7.02	**0.008**
Replicate	1	1.15	0.33	1	0.11	0.75	1	0.56	0.48
Treatment × number of companions	3	2.76	0.11	3	0.35	0.78	3	0.47	0.71

Interactions between treatments (type of companions) and group sizes for each behavioural variable are also presented. Significant values are shown in bold.

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Previous video playback studies have addressed whether video images are adequate to elicit natural behavioural responses. Here, we go further by comparing the behavioural responses towards real and simulated companions in a foraging context. Ascertaining the efficiency of the video playback approach also requires consideration of some technical constraints in our experiment, such as (1) the lack of depth information, which may have reduced the value of the video images as signals of increasing levels of competition, (2) the absence of audio information and (3) the fact that simulated companions do not affect the quantity of resources available.

Because of the two-dimensionality of video images, depth cues cannot be transmitted directly to video sequences, and for videos involving several animals, on-screen differences in the spatial arrangement of individuals relative to the camera lens are transmitted at different absolute sizes. We adopted several measures to mitigate the effects of using a two-dimensional image, assuming that it may be less effective than the three-dimensional foraging group provided by the real companions condition. For instance, the apparatus constrained both the simulated and real groups into the same visual plane by preventing individuals from foraging all around the feeder. Instead, companions stood aligned behind the feeder in front of the video camera. In both cases, therefore, all birds were at similar distances from the focal bird and so their images were the same size.

Our video playback treatment was silent. As such it could have prevented important acoustic cues from the simulated companions, cues that were present for the real companions condition. The lack of differences between the two types of companion conditions suggests that acoustic cues were not required to elicit the behavioural responses linked to an increase in group size. Moreover, Bird & Emery (2008) recently showed that silent video sequences were sufficient to trigger individual recognition in rooks, *Corvus frugilegus*. Thus, silent video sequences appear to be sufficient to simulate group foraging.

One issue that can be singled-out with the use of video playback is that simulated companions have zero effect on the amount of food available to the focal individual. Simulated competition has been successfully used in social foraging studies (McQuoid & Galef 1993; Grand & Dill 1999), showing that the direct presence, within a food patch, of competitors that actually affect the quantity of resources available is not required to trigger the behavioural responses associated with competition. We are confident, therefore, that video sequences of foraging conspecifics are appropriate to simulate foraging competitors, and we believe that the video playback technique could be a convenient tool to further investigate questions related to social foraging.

The video playback technique is becoming an increasingly common and powerful technique in behavioural studies. We demonstrate, here, that it provides a reliable means of investigating social foraging questions. In particular, this technique can be promising for studies addressing other social foraging decisions such as the distribution of competitors over several patches (ideal free distribution theory: Fretwell 1972; Milinski & Parker 1991), the concurrent patch exploitation between foragers (patch residence game: Beauchamp & Giraldeau 1997), or when individuals join the food discoveries of others (producer–scrounger game: Barnard & Sibly 1981; Giraldeau & Caraco 2000).

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