

Positive Emotional Contagion in a New Zealand Parrot

Schwing, Raoul^{1,2,3}, Nelson, Ximena J.⁴, Wein, Amelia^{1,2}, and Parsons, Stuart^{3,5}

1 Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, University of Vienna, Vienna, Austria

2 Haidlhof Research Station, University of Veterinary Medicine Vienna and University of Vienna, Bad Vöslau, Austria

3 School of Biological Sciences, University of Auckland, Auckland, New Zealand

4 School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

5 School of Earth, Environmental and Biological Sciences, Queensland University of Technology, Brisbane, Australia

Corresponding author: Raoul Schwing, PhD

Veterinary Medical University Vienna (Vetmeduni Vienna)

Veterinärplatz 1, 1210 Wien

T +43 664 60257-2695

raoul.schwing@vetmeduni.ac.at

Positive emotional contagions are outwardly emotive actions which spread from one individual to another, such as glee in preschool children [1] or laughter in humans of all ages [2]. The play vocalizations of some animals may also act as emotional contagions. For example, artificially deafened rats are less likely to play than their non-hearing-impaired conspecifics, while no such effect is found for blinded rats [3]. As rat play vocalizations are produced in anticipation of play, they, rather than the play itself, may act as a contagion, leading to a hypothesis of evolutionary parallels between rat play vocalizations and human laughter [4]. The kea parrot (*Nestor notabilis*) has complex play behaviour and a distinct play vocalization. We used acoustic playback to investigate the effect of play calls on wild kea, finding that play vocalizations increase the amount of play among both juveniles and adults, likely by acting as a positive emotional contagion. Kea have high cognitive abilities [5] and complex play behaviour (SI), often associated with a characteristic warble call [6] which may signal the sender's playful state. Such a signal would help receivers discriminate social play fighting from aggression. However, as these calls are also associated with solitary play and social play not requiring an interpretation of potentially aggressive signals, they might have an affective origin and could act as an emotional contagion. We tested this hypothesis by performing playback experiments consisting of a 5 min experimental period during which a stimulus was played to the birds, and pre- and post-experimental periods lasting 5 min each (total trial length 15 min). In addition to a play call, four control sounds were played as stimuli: two other types of non-play kea call, a call of the South Island robin (*Petroica australis australis*, a common bird in the area), and a standardised tone. Scored behaviours included social interactions and play (see SI for description).

The play call elicited significant increases in both the number of instances of play and play length when compared with pre- or post-experimental periods, and when compared with the other sound stimuli (Figure 1; GLMM play length: $F_{10,110}=4.398$, $p<0.001$; GLMM play instance: $F_{14,117}=3.77$, $p<0.001$). Upon hearing the play call, many birds did not join in play that was already underway, but instead started playing with other non-playing birds, or in the case of solitary play, with an object or

by performing aerial acrobatics (for a conservative measure of spontaneous play occurrence see SI). These instances suggest that kea weren't 'invited' to play, but this specific call induced playfulness, supporting the hypothesis that play vocalizations can act as a positive emotional contagion. In anthropomorphic terms, kea play calls act as a form of infectious laughter, as suggested for play calls in primates [2] and rodents [4]. Alternatively, heightened mood could increase play in conspecifics. However, moods are a persistent state [7], whereas emotions are brief, intense reactions [8], and play behaviour in the post-experimental period did not differ from that of the pre-experimental period.

Social play behaviour is rare in mature animals of opposite sex [9]. Although the erratic nature and fast pace of aerial play made it impossible to track individual participants with certainty, kea of all ages, including adult males and females, were engaged in play. While intersexual adult play is seen among primates and canids, it is generally associated with courtship behaviour or with other immediate social benefits, such as access to food [9]. Bonobos (*Pan paniscus*) [10] are believed to test potential mates through play, while African hunting dogs (*Lycaon pictus*) and timber wolves (*Canis lupus*) play to strengthen social bonds before a hunt [9]. In contrast, play between adults of the opposite sex in kea occurred spontaneously under the same circumstances as play in juveniles.

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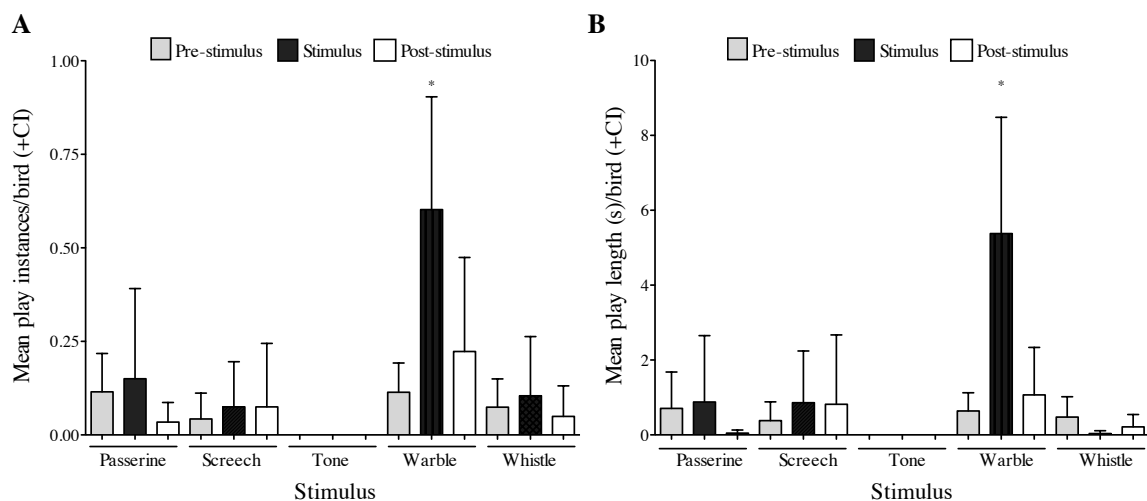


Figure 1 Mean (+95% CI) kea play response before, during and post-stimulus playback periods for five auditory stimuli. **(A)** Number of play bouts per bird. **(B)** Play bout length produced per bird (s). Warble play calls were the only stimulus to significantly increase both the instances of play and the length of play bouts during playback (indicated by an asterisk), when compared to the pre- and post-experimental periods. No other comparisons were significant.

Supplemental Information

Supplemental Experimental Procedures

Location and Subjects

Experiments were carried out in May 2012 and April 2013 at the Death's Corner lookout in Arthur's Pass National Park, in the Southern Alps of the South Island of New Zealand (42°56.72383'S 171°33.94056'E). The site has a steep rise in elevation that creates consistent updrafts of air, which the kea exploit for aerial play. Many of the birds at this location can be identified by unique coloured leg bands. A small number of resident kea were present on most days over the experimental period (see table 1). Between years, however, there was an almost complete turn-over of resident birds; only one bird was seen in both years. There were usually no more than 4-5 resident birds present in each year, with small groups of banded and unbanded non-residents joining for a few hours at a time to form larger temporary groups of 4 to 12 birds.

Experimental Setup

Playback experiments consisted of a 5 min experimental period, during which a stimulus was played to the group of birds present, and pre- and post-experimental periods lasting 5 minutes each, which directly preceded and followed the experimental period. In addition to a play call, four control sounds were played as stimuli: two other types of kea calls, a call of the South Island robin (*Petroica australis australis*, a common bird in the area), and a standardised tone. The two other kea calls were the screech contact call, the most common kea call, and the whistle, which is the rarest and is associated with intimate social interactions [S1]. The robin vocalisation was a territorial call [S2], and the standardised tone was at a frequency of 1000 Hz, which is within the bandwidth and region of peak energy of most kea calls [S1]. Stimuli ranged in duration from 1 to 1.5 s, and were played once every 30 s for the 5 min experimental period. Kea and robin calls were recorded from birds resident at or within 10 km of Death's Corner lookout during the previous two years; none of the kea calls used were from birds present during the experiments, as verified by leg band identification. All bird call stimuli used 3 different recordings, semi-randomized in order (not occurring more than twice in direct succession), during the playback. For the kea these were from 3 different individuals (as verified at the time of recording by leg bands), while for the passerine it was not possible to verify the identity of the individual (no leg bands present).

Stimuli were played using a custom-made portable sound system comprising speaker with a 5" woofer / midrange speaker (CW2192, woofer driver, frequency response 70 Hz – 7 kHz) and a 2.5" tweeter horn (CT1930, tweeter driver, frequency response 1 kHz - 20 kHz) powered by a 2 x 80 W RMS amplifier (AA0420, all Jaycar Electronics, Rydalmere, Australia). The speaker was set up in plain sight of the birds before the start of the pre-experimental period, and direct interaction with the speaker was inhibited by the close proximity of the researcher to the equipment. Sessions were conducted in the morning (8-10 am) and in the late afternoon (5-7 pm), as those are the times of highest activity for kea [S3]. Sessions consisted of at least two trials and up to six, dependent on the presence of the birds and/or other factors such as human disturbance which masked the playback; Death's Corner lookout is frequented by tourist, and trials were only conducted when there was no human disturbance. Trial order alternated between the focal stimuli (play call) and control stimuli,

with the latter semi-randomized (not the same stimulus twice in immediate succession). In total 60 trials were conducted: 19 play call, 10 screech call, 12 whistle call, 10 passerine call, and 9 tone.

Behaviour was recorded using a Sony Handycam HDR-XR550V (SONY Corporation, Tokyo, Japan) during the pre, experimental and post periods, and included audio commentary about behaviour occurring off-screen (commentary provided simultaneously by two experimenters with extensive kea behaviour experience). Behaviours were scored from video recordings using JWatcher 1.0 (Copyright 2006–Daniel T. Blumstein, Janice C. Daniel & Christopher S. Evans).

Interactions were scored as ‘play’, ‘other-social’, and ‘antisocial’ behaviours; play could also occur as individual object or aerial play (see descriptions below) although for the analysis no such distinction was made. The total length of time birds were engaged in play was extracted using the ‘state analysis’ function in JWatcher. All behaviours other than play duration were scored as binary events (yes or no). Non-behavioural data noted were: number and identity of birds present during the experiment, time-of-day, wind strength (light, heavy, none), rain strength (light, heavy, none), and general weather (sunny, overcast, fog, rain). Scoring was done by the two observers present during the sessions and inter-observer reliability was found to be excellent (Kappa 0.938 [4]) on the basis of the coded behaviours from three trial periods.

Table S1 Birds present at Death’s Corner during the playback experiments with different stimuli. Only one banded bird was seen in both years (whJgr). Within unbanded birds, only fledglings from different years or multiples from the same age-sex category present in the same session could be differentiated with certainty. Unbanded birds made up between 13 and 46 of the participants depending on how one estimates the number of repeat visits (e.g. for low estimate (13 unbanded birds) all unbanded adult females present in different sessions are the same bird, while for high estimate (46 unbanded birds) all unbanded adult females present in different sessions are different birds).

Individual	age sex	2012					2013				
		passerine	tone	warble	screech	whistle	passerine	tone	warble	screech	whistle
rdAwh	jf	0	0	0	0	0	3	3	9	0	2
whXor	am	0	0	0	0	0	1	3	13	4	4
rmm	af	0	0	0	0	0	0	3	10	4	4
whJgr	jm	0	0	1	1	0	0	1	4	0	4
whCrd	jm	0	0	0	0	0	1	1	7	1	2
bkSwh	af	0	0	0	0	0	1	0	3	0	1
bkFwh	jf	0	0	0	0	0	0	0	2	0	1
bkGgr	am	0	0	0	0	0	0	0	1	0	1
yeCbl	jm	0	0	0	0	0	0	0	1	0	0

whOors	af	0	0	0	0	0	0	0	1	0	0
Imm	am	0	0	0	0	0	1	0	1	0	0
whbl	ff	0	0	0	0	0	1	0	1	0	0
rdwh	am	0	0	0	0	0	0	0	3	1	0
Norman	am	7	3	3	6	5	0	0	0	0	0
Jesse	am	5	1	2	3	4	0	0	0	0	0
rdFwh	ff	2	0	1	1	3	0	0	0	0	0
Eva	af	4	3	2	4	1	0	0	0	0	0
bkFors	am	4	3	3	5	2	0	0	0	0	0
whZgr	fm	2	2	1	3	1	0	0	0	0	0
yeRbl	jm	0	0	1	1	0	0	0	0	0	0
unknown	am	2	2	2	2	3	2	1	1	0	0
unknown	af	0	1	0	1	0	0	0	0	0	0
2 unknown	af	0	0	0	0	0	1	0	1	0	0
unknown	jm	0	1	0	1	1	2	3	8	4	1
2 unknown	jm	0	1	1	1	0	0	0	0	0	0
unknown	fm	0	0	1	1	0	3	2	6	0	1
2 unknown	fm	3	3	2	4	2	0	0	0	0	0
unknown	ff	3	2	2	4	1	0	3	8	3	5
2 unknown	ff	0	1	0	0	0	3	3	6	1	1
3 unknown	ff	0	0	0	0	0	0	0	1	0	1

Supplemental Analysis

Behaviours Coded

Play call: a highly variable call associated with play behaviour, must include an element with frequency modulations covering a large bandwidth, see [S1] for full description of kea calls.

Screech contact call: the most common call type; also the most common response to all other kea calls, except the play call.

Other call: all call types produced that are neither play calls or screech calls.

Social interaction between two or more birds: one (or more) bird approaches another bird(s) resulting in a social interaction that does not qualify as play, such as allo-feeding or allo-preening.

Antisocial interaction between two or more birds: one (or more) bird approaches another bird(s) not resulting in a social interaction, such as displacement of one or more birds; aggressive interaction.

Look/scan: bird interrupts its current activity and scans the surrounding area or looks at a specific object; often involves an upward stretching of the neck.

Approach speaker: bird moves in a (more or less) straight line towards the speaker used for the playback.

Play (all the following were scored as “play” without further distinction): three categories of play are recognised: tussle ground play, toss ground play and aerial play; play invitations were included in this category (for a definition of play see [S5,S6]).

Social (tussle) ground play: two or more birds are chasing and/or play-fighting on the ground (for full description of tussle ground play see[S7–S10]).

Object (toss) ground play: one or more birds are repeatedly tossing the same object into the air (for full description of toss ground play see[S7–S10]).

Aerial play: two or more birds are performing aerial acrobatics, chasing and/or foot-kicking in the air (see below). More often than not the birds will land in the same spot after playing in the air from where they initially took off.

Aerial acrobatics: one or more birds engage in sinusoid, spiral, loop or other flight paths with high levels of spatial movement without apparent gain in distance or elevation; performed at high relative speeds. One exception to this mostly highly energetic behaviour is when a bird hovers in an updraft at a relatively low elevation (2-3 m above the ground), keeping a consistent spatial position. Often this is the first behaviour in an aerial play bout, with the bird suddenly utilising the updraft to quickly gain elevation and engage in other aerial play behaviour.

Chasing: one or more birds follow the same flight path as a leading bird, which itself is often engaging in aerial acrobatics; often culminates in foot-kicking if/when chaser(s) catches up to chased individual.

Foot-kicking: one or more birds approach another bird and grab(s) at them with its/their feet; this can occur from above or below; if from below the bird is momentarily flying upside down. The bird to be kicked will most often evade (as part of the chase) or will also engage in foot kicking. These encounters are very brief and don't result in two birds grasping each other's feet.

Statistics

The main source of errors for this type of experiment comes from the number and identity of individual birds present and random effects associated with specific playback session (i.e., weather conditions and/or group composition). Therefore, we conducted generalized linear mixed models (GLMMs) with play length or number of play instances as the scale target. Fixed factors added were experimental period x stimulus, session, number of birds, and presence of subjects (unbanded

subjects were added in the most conservative way i.e. all unbanded adult females were considered the same bird, and the least conservative way i.e. each adult female in a different session is a different bird), and covariates were time of day, year, and weather conditions. We ran several reduced models and selected the best fit by comparison of the corrected Akaike Information Criteria (cAIC). For sake of clarity, here we only report the results from the final models with the lowest cAIC. Categorical fixed factors in the final models were examined with multiple pairwise comparisons between the different categories (Holm- Bonferroni correction applied).

The exact number of spontaneous play occurring is impossible to tell as the exact boundaries of play bouts when occurring simultaneously are too vague to quantify. However, as a conservative measure one can look at the first play bout in the experimental period of those trials where no play was recorded in the pre-experimental period, as the first bout would by definition be spontaneous, there being no play to join. This was done by looking at the distribution of a first play bout occurring in an experimental period which followed a pre-experimental period without play using the Mann-Whitney U test.

Analyses were performed in SPSS Version 20.0.0 (IBM Corporation, Armonk, USA). The GLMMs for which results are presented had highly significant corrected model scores, supporting the validity of the model. All reported p-values are two-tailed.

Supplemental Results

There was a significant effect of play increase in the experimental period for the play call stimulus compared to all other stimuli in those trials where there was no play in the pre-experimental phase (Mann-Whitney U, $p=0.002$), when considering only the first play bout (by default a spontaneous act of play).

Supplemental References

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