



Food, audience and sex effects on pinyon jay (*Gymnorhinus cyanocephalus*) communication

C.R. Dahlin^{a,*}, R.P. Balda^a, C. Slobodchikoff^b

^a Department of Biological Sciences, Northern Arizona University, Avian Cognition Laboratory, Flagstaff, AZ, USA

^b Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA

Received 26 November 2003; received in revised form 29 September 2004; accepted 30 September 2004

Abstract

Pinyon jays (*Gymnorhinus cyanocephalus*) have a complex social system that may require a complex communication system. They need to interact with multiple flock members, and they form life-long pair-bonds. We researched whether pinyon jays would selectively vocalize depending on the presence or absence of food and certain flock members. We recorded the vocalizations of nine pinyon jays (four pair-bonds and one single male) in response to different audience types. The calls of the test bird were recorded after it was given either an empty food cup or one containing 50 pinyon pine (*Pinus edulis*) seeds, and the bird was in the presence of one of the following audience types: (1) two males and two females including subject's mate; (2) two males and two females excluding subject's mate; (3) four males excluding mate; (4) three females excluding mate; and (5) no audience. Birds gave fewer calls when there was food. When alone, birds called in a manner that may maximize long-distance transmission. Trends indicate that birds call differently to their mate. A sex effect was also found in that males and females called in a distinct manner, possibly reflecting differences in dominance status. Overall, birds responded to the presence or absence of an audience. © 2004 Elsevier B.V. All rights reserved.

Keywords: Audience; Avian; Communication; Corvids; Sex differences

1. Introduction

Animals require a suite of abilities in order to thrive in their environment, one of which is the ability to communicate. This is particularly true for social

animals, because they need to recognize large numbers of individuals and often maneuver within a social hierarchy (Balda et al., 1996). Sociality, in addition to environmental factors, may therefore play an important role in promoting communication abilities (Balda et al., 1996; Bond et al., 2003; Cheney and Seyfarth, 1990; Humphrey, 1976). One area of interest is whether animals exhibit an audience effect, that is, do they vocalize selectively depending on the conspecifics that are present. This raises the question of whether animals

* Corresponding author. Present address: Department of Biology, MSC 3AF, New Mexico State University, Las Cruces, NM 88003, USA. Tel.: +1 505 522 7197.

E-mail address: crdahlin@yahoo.com (C.R. Dahlin).

are aware of which conspecifics are present, and use that information to modify their communication. Food and predators are frequently used as stimuli, because both have a direct impact on an animal's fitness. Calling or abstaining from calling in response to food can impact the resources animals control for themselves or their mates. Alarm calling can lead to increased rates of predation, but can also enhance an animal's indirect fitness by warning kin (Dunford, 1977; Hauser, 1998a; Smythe, 1977; Trivers, 1972; Williams, 1966). Due to these and other factors, individuals may alter their calling depending on the audience that is present. Audience effects on food and predator calling have been shown in a variety of social species in the avian and mammalian world, including cockerels (*Gallus gallus*), vervet monkeys (*Cercopithecus aethiops*), and ground squirrels (*Spermophilus tereticaudus*) (Gyger and Marler, 1988; Cheney and Seyfarth, 1985; Cresswell, 1994; Dunford, 1977; Evans and Marler, 1992; Gyger et al., 1986; Marler et al., 1986).

This study examined audience effect on pinyon jay (*Gymnorhinus cyanocephalus*) calling. Pinyon jays are members of the family Corvidae, and live in highly complex societies composed of 50–500 birds (Balda, 2002). Flocks consist of extended family and non-related individuals, with a well-developed social hierarchy (Balda and Bateman, 1971, 1972). They do everything as a flock, including feeding, roosting and nesting. Consequently, we hypothesized that they would have complex communicative abilities.

Pinyon jays also form life-long, monogamous pair-bonds, and factors such as plumage color, bill size, weight, dominance status and age, all play a role in mate selection (Johnson, 1988a,b; Marzluff and Balda, 1988a, 1992). Extra-pair copulations have never been observed, and in over 100 pairs of pinyon jays only three were known to have divorced (Marzluff and Balda, 1988b, 1992). Of the species previously studied for audience effect, only pinyon jays exhibit such strong bonds between non-related individuals.

Previous studies over a span of 15 years indicate that pinyon jays do exhibit some complex communicative abilities, although it has not been researched whether jays give different types of calls in response to different flock members or situations. Berger and Ligon (1977) identified 16 types of calls in an earlier study. Playbacks indicate that they recognize individuals, discriminate between non-flock and flock members, and between

call types (Marzluff and Balda, 1992). Pinyon jays also recognize the calls of their mates and young (Balda and Balda, 1978; Berger and Ligon, 1977; Marzluff, 1988; McArthur, 1982). Additionally, pinyon jays are specialized seed cachers, and cache thousands of pine seeds each year (Balda, 1980). Mated jays recover their mate's caches significantly more than non-mated birds (Chen, 2000), and this activity is accompanied by an increased rate of vocalizations between mated birds (Shulzitski, 1999).

The purpose of this research was to determine whether pinyon jays call differently in response to different flock members. A second goal was to examine whether pinyon jays respond differently to the presence or absence of food. Pinyon pine seeds (*Pinus edulis*) were chosen as the food stimulus because they are an important resource in pinyon jay life (Balda, 1980; Ligon, 1971, 1978; Vander Wall and Balda, 1981). Our general hypothesis is that pinyon jays have abilities that enable them to discriminate among members of a social flock, and call differently according to the flock members that are present or absent. This may be done by using different calls, by altering the structure of their calls, or by calling more or less. They may also respond differently depending on whether they receive food. The specific hypotheses include the following.

Food hypothesis

Pinyon jays will call differently depending on whether food is present or absent. Pinyon jays feed as a flock, so we hypothesize that they will call to alert their flock to the presence of food. Although calling could potentially attract predators, we predict that the benefits of increased security in a flock would outweigh that risk. In the wild pinyon jays are always observed feeding as a group, never individually (Balda and Bateman, 1972; Marzluff and Balda, 1992). Indirect fitness is also increased when related flock members gain access to food.

Audience hypotheses

1. Pinyon jays will call more, or in a different manner when their mate is present in the audience. The pair-bond in pinyon jays is exceptionally strong and lasts for life, so the success of one bird depends on the success of his/her mate.

2. Pinyon jays will call more when alone, regardless of food availability. The flock provides security from predators, so birds are more at risk when alone. Therefore, they are likely to call in an attempt to locate their flock.

Audience–sex difference hypotheses

Sex ratios are skewed toward males in the majority of flocks. The skewed sex ratio may promote sex differences in calling. Although pinyon jays can live beyond 10 years, mortality is high in females, possibly due to higher risks during dispersal and nesting (Marzluff and Balda, 1989, 1992). Therefore it is likely that males will need to acquire a new mate during their lifetime. Since excess males are nearly always available, a female should be able to find a mate more readily than a male if her own mate dies. We hypothesize that males will call more than females to non-mated individuals of the opposite sex. That is, males will call to an all female audience even if their mate is not present, while females will only call to their mate.

2. Methods

The subjects were nine captive pinyon jays that were housed at the Avian Cognition Laboratory on the campus of Northern Arizona University, in Flagstaff, AZ. All birds were captured as adults and had been in captivity for over 5 years. Birds were banded, weighed, and sexed using blood samples (Mullenbach et al., 1989; Griffiths et al., 1996). The birds had all been used in previous experiments, but none had been exposed to these experimental procedures. When the study began, birds had been free-flying in an aviary (5.72 m × 4.72 m) for at least 2 years, where they experienced natural sunlight and temperature.

The birds included five males and four females. The pair-bonds were redetermined for all birds at the onset of the study during three 2-h sessions (Chen, 2000; Shulzitski, 1999). We recorded courtship behaviors, which are used to establish and maintain pair-bonds (Chen, 2000; Marzluff and Balda, 1992). Birds only fed or participated in nest building activities with their mate, and the observations confirmed the pair-bonds of birds used in previous experiments.

2.1. Habituation sessions

After pair-bonds were determined, birds were housed in 0.51 m × 0.51 m × 0.72 m cages. When trials were not in progress, paired birds were allowed to interact with their mates. Before beginning testing, habituation sessions were conducted to ensure that the birds adjusted to the experimental apparatus. The apparatus consisted of a plaster food cup that rested on a small platform, which was attached to one side of the test bird's cage. Birds had to reach their heads through the bars of their cage to obtain the food. They were presented with five mealworms (*Tenebrio larva*), a preferred food. Birds were considered habituated when they consumed all five mealworms in the cup in 2 min or less. We withheld mealworms from the birds' normal food allotment during the habituation period.

2.2. Experiment

We withheld pinyon pine seeds from the birds for the duration of the experiment except during experimental trials. To ensure food was an effective stimulus, we did not feed birds until after trials were finished for the day. We designed the experiment to examine the birds' calls in response to audiences composed of different members of their flock. There were five audience types including:

1. Mate, mixed sex: two males and two females, one of which was the test bird's mate;
2. no mate, mixed sex: two males and two females, without the test bird's mate;
3. no mate, male: four males, without the test bird's mate;
4. no mate, female: three females, without the test bird's mate (three individuals were used because there were only four females in the flock);
5. no audience: the test bird was alone.

All audience tests were conducted when the test bird was given either 50 pinyon pine seeds, or no food. Thus, two stimuli × five audience types resulted in 10 stimulus/audience trial combinations. Test birds were provided with more seeds than could be consumed in the allotted time to encourage calling to the audience. Henceforth, the stimulus/audience types will be abbreviated, where F = food, N = no food, and the audience types are referred to by the numbers listed above. For

example, no-food, male audience without mate will be referred to as N-3.

The experimental room consisted of the aviary cell with a wall that divided the cell in half (Fig. 1). The test bird was placed in a gap in the wall and the audience was placed in the corner. A transparent, Plexiglass lid could be placed on the food cup, so the birds could observe the contents of the food cup, but not have access to the food. Theoretically, the test animal could signal what it observed (i.e., presence/absence of food) with calls and/or behavior. A trial consisted of a 7.5 min habituation period, 1 min pre-period (food lid on), and a 2 min post-period (food lid off). During the habituation the test bird was positioned on the platform, and the audience was in place. At the end of the habituation period, the platform with the food cup was attached to the test bird's cage, thus beginning the pre-period. During the pre-period birds could see what was in the cup, but could not reach inside, which enabled us to record the bird's initial reaction prior to eating. The first 30 s were not recorded because the bird's calls may have been biased by the experimenter approaching the cage and attaching the apparatus. After the pre-period ended, the lid was quickly removed by the experimenter, beginning the post-period. The entire post-period was recorded,

because birds began eating immediately after the food lid was removed. We recorded all vocalizations with a directional, Dan Gibson parabolic microphone (model P-200) and a Sony tape recorder (TC-D5 Pro II). The microphone was placed approximately 1.5 m from the test bird's cage and was aimed at the cage. As this was a directional microphone, the test bird's calls were much louder than the audience calls in the recording. Trials were conducted during the months of September and October. In nature, this is the time of intense seed caching (Marzluff and Balda, 1992). The order of test subjects, audience types and audience members were randomly determined. Each bird was run three times per trial type, because individual response was variable. Each bird was run once on each experimental day.

2.3. Call type discrimination

Discriminant function analyses (DFA) were used to determine the number and types of calls that birds gave during this study. The call types and methodology used by Berger and Ligon (1977) were mainly ignored, to avoid classification bias. Spectrograms of the calls were created using the signal RTS software (version 3.0) using fast Fourier transforms that had a sampling rate of 44 kHz, a frequency resolution of 48.4 Hz and a transform length of 256 points that used a Hanning window. All birds were used in determining the call types. Prior to running the DFA, the call types were visually discriminated in a subjective manner. This was done using print-outs of 1 s spectrograms of the calls, with examples from each individual that gave the call. Birds gave single calls and groups of calls composed of temporally separated, discrete calls. We considered calls to be single if they were separated from adjacent calls by >0.35 s, while we considered calls to be within groups if they were separated by <0.35 s. We chose the 0.35 s selection criteria because analyses indicated that the majority of single calls were separated by more than 0.35 s. It appeared that there were 13 types of calls that were given singly. There were two types of call groups: groups consisting of the same type of call repeated (uniform sequence), and groups consisting of different types of calls (compound sequence).

We ran a DFA using variables we measured on 1-s sonograms, to determine whether the variability within each call type was less than the variability between call

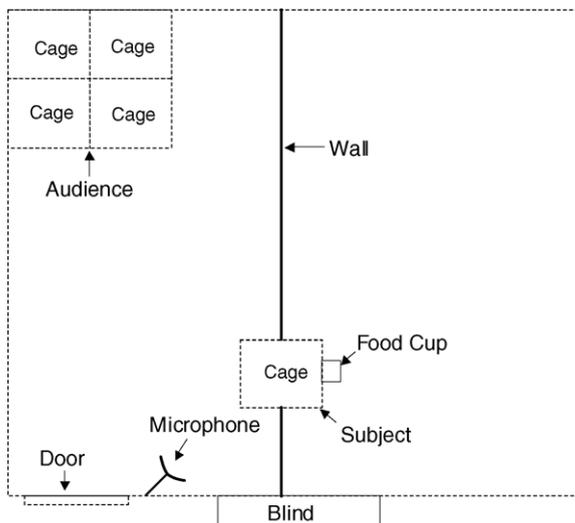


Fig. 1. Aviary cell showing the experimental apparatus (approximate, not exact scale). Birds were observed through the blind. The test bird's cage was placed on a platform in the gap in the wall. The test bird could observe the audience and the contents of the food cup, while the audience could not observe the food cup.

Table 1
Three-way ANOVA (repeated-measures design)

Fixed/random	Factor	Degrees of freedom	Mean square	F-test
Fixed	Stimulus	1	MS 1	MS 1/MS 5
Fixed	Audience	4	MS 2	MS 2/MS 9
Fixed	Sex	1	MS 3	MS 3/MS 4
Random	Individual (sex)	5	MS 4	MS 4/MS E
Fixed	Stimulus × audience	4	MS 5	MS 5/MS 11
Fixed	Stimulus × sex	1	MS 6	MS 6/MS 7
Random	Stimulus × individual (sex)	5	MS 7	MS 7/MS E
Fixed	Audience × sex	4	MS 8	MS 8/MS 9
Random	Audience × individual (sex)	20	MS 9	MS 9/MS E
Fixed	Stimulus × audience × sex	4	MS 10	MS 10/MS 11
Random	Stimulus × audience × individual (sex)	20	MS 11	MS 11/MS E
	Error	141	MSE	

Stimulus refers to pinyon vs. no-food, audience refers to the five audience types, and sex refers to male vs. female.

homogeneity of variance and a normal population, so it was log-transformed. Post hoc, Tukey–Kramer honestly significant difference (HSD) tests were run for pair-wise comparisons (Zar, 1999).

DFAs were also used to look for stimulus, audience and sex differences in pinyon jay calling. The variables used in the DFAs were the number of calls birds gave of each type (e.g., two racks, three valleys). These were averaged over the three trials ran for each bird for each stimulus/audience combination. To determine whether a DFA was significant, exact F and p values were provided when the sample was generated from two groups (d.f. = 1). For any analyses with more than two groups (d.f. > 1), the exact approach could not be used, and both an approximate F and a chi-square value were provided. Both provide virtually the same p values. Exact F values are listed for analyses of two groups, and chi-square values are listed for any other analyses.

3. Results

3.1. Call type results

Birds delivered calls in two general ways; single calls and call groups. Call groups were further classified into uniform sequences and compound sequences (see Section 2). DFA was run on 13 types of calls that were originally visually discriminated, using variables measured on sonograms of the calls. A minimum discriminatory accuracy rate of 70% was required before a call type was considered distinct. The probability that the

calls would randomly be placed in the correct groups was 8%, so the criterion was high. The overall discriminatory accuracy for the 13 call types was 84.3% (DFA: $X^2_{144} = 3569.87, p < 0.0001$), and the individual discriminatory percentages ranged from 73.3 to 100%. Therefore, all 13 of the call types were considered distinct for all further analyses. The most important discriminatory variables were the length of call time, the number of harmonics, the number of peaks and the high harmonic frequency. For further analyses, the 13 call types were also classified based on their mode of delivery (Table 2).

In general, calls that were given during compound or uniform sequences had more harmonics than did calls given singly. The group mean for all call types was 9.51 harmonics. Seven of the 13 call types had 11 or more harmonics, on average. Six of these seven call types were given during compound sequences or as multiples, including racks, small racks, steep racks, small steep racks, valley-bumps and rackas.

3.2. Stimulus results

General trends indicate that birds gave more calls during no-food trials than during pinyon-pine seed trials, but interactions complicated the results. There were significant stimulus × audience interactions for the ANOVA results concerning the total number of calls, the number of call groups and the number of call types. That is, birds may have given more types of calls during no-food trials than pinyon-pine seed trials in response to some audience types, but not to

Table 2
Mode of delivery for calls discriminated using DFA

DFA call type	Single call	Uniform sequence	Within compound sequence	Final call categories (excluding compound sequences)
SR		X	X	Double small rack
Fl	X	X		Flat
Ra	X	X	X	Rack, multiple rack
Ri	X			Rise
SmSTR			X	Small steep rack
S-1	X			Soft-1
S-2	X			Soft-2
STR			X	Steep rack
Va	X		X	Valley
VB	X		X	Valley-bump
Rr		X	X	Multiple rackra
Ro			X	Round
Bu			X	Bump

X signifies the delivery method. Compound calls were grouped into one category in later analyses, so the final call categories designate the categories that were used in further DFAs, only after considering their delivery as single or multiple calls. Racks and flats were both given as single and multiple calls. Racks were differentiated into two categories (single and multiple), but flats could not because they were not given frequently enough to warrant further division.

other audience types (Table 3). For example, Table 3 shows that N-5 is different than P-1, P-2, P-3, P-4 or P-5, but N-4 is only different than P-2, P-3 and P-4. Only the analysis for the number of single calls had no interaction.

Birds gave a higher total number of calls when there was no food than when there were pinyon pine seeds (ANOVA: $F_{1,5} = 47.6$, $p = 0.001$). There was a significant stimulus \times audience interaction (ANOVA: $F_{4,20} = 4.2853$, $p = 0.011$). Birds gave more calls in

Table 3
Results of stimulus comparisons

Variable	Audience type	P-1	P-2	P-3	P-4	P-5
# Total calls	N-1	<0.05	<0.05	<0.05	<0.05	<0.05
	N-2	NS	<0.05	<0.05	<0.05	NS
	N-3	NS	<0.05	<0.05	<0.05	NS
	N-4	NS	<0.05	<0.05	<0.05	NS
	N-5	<0.05	<0.05	<0.05	<0.05	<0.05
# Call groups	N-1	NS	NS	NS	NS	NS
	N-2	NS	NS	NS	NS	NS
	N-3	NS	NS	NS	NS	NS
	N-4	NS	NS	NS	NS	NS
	N-5	<0.05	<0.05	<0.05	<0.05	<0.05
# Call types	N-1	NS	NS	NS	<0.05	NS
	N-2	NS	NS	NS	NS	NS
	N-3	NS	NS	NS	NS	NS
	N-4	NS	NS	<0.05	<0.05	<0.05
	N-5	<0.05	<0.05	<0.05	<0.05	<0.05

All three variables shown (# Total calls, # Call groups, # Call types) had a significant interaction and the table illustrates the results of the Tukey HSD pair-wise comparisons. Significant tests are indicated by $p < 0.05$, while NS indicates a non-significant result. For all significant tests, the response was higher during no-food trials. N—refers to no-food trials, P—refers to pinyon trials. Numbers 1–5 refer to the audience types: type 1 = 2 males, 2 females including mate; type 2 = 2 males, 2 females no mate; type 3 = 4 males; 4 = 3 females; and type 5 = no audience.

each no-food trial as compared to its equivalent pinyon pine seed trial (HSD: Q range = 7.86–12.18, $p < 0.05$). For example, N-1 was greater than P-1, and N-2 was greater than P-2. Birds also gave more call groups during no-food trials than during pinyon pine seed trials (ANOVA: $F_{1,5} = 7.63$, $p = 0.039$). There was a significant stimulus \times audience interaction for call groups (ANOVA: $F_{4,20} = 8.66$, $p = 0.0003$) (Table 4). N-5 was significantly different from all pinyon pine seed trials (HSD: Q range = 13.11–14.64, $p < 0.05$). Otherwise there were no significant differences (HSD: Q range = 2.55–6.79, $p > 0.05$).

Birds gave more types of calls during no-food trials than during pinyon pine seed trials (ANOVA: $F_{1,5} = 10.95$, $p = 0.021$). There was a significant stimulus \times audience interaction (ANOVA: $F_{4,20} = 3.61$, $p = 0.022$) (Table 4). N-5 was significantly higher than all pinyon pine seed trials (HSD: Q range = 12.17–14.96, $p < 0.05$). N-4 was significantly higher than P-3, P-4 and P-5 (HSD: Q range = 11.69–11.82, $p < 0.05$). Otherwise there were no significant differences between no-food and pinyon pine seed trials (HSD: Q range = 6.64–11.57, $p > 0.05$). Birds also gave more single calls during no-food trials than during pinyon pine seed trials (ANOVA: $F_{1,5} = 31.38$, $p = 0.003$), and the stimulus \times audience interaction was not significant (ANOVA: $F_{4,20} = 0.66$, $p = 0.629$).

DFA found significant differences between no-food and pinyon pine seed trials, which supports the results found by the ANOVAs (DFA: $F_{6,7} = 5.87$, $p = 0.017$).

The overall discriminatory accuracy was 92.9%, and 100% of no-food trials were placed in the no-food category, while 85.7% of pinyon pine seed trials were placed in the pinyon pine seed category. Generally, more calls were given during no-food trials than during pinyon pine seed trials. The call types that DFA used to discriminate were, in order of importance, valleys, multiple racks, compound sequences, double small racks, soft-2s, and flats.

3.3. Audience results

Overall, birds gave more calls when they were alone as compared to when there was an audience present. Differences were commonly found in no-food trials rather than pinyon pine seed trials. All analyses showed a trend where subjects called more during mate trials than non-mate trials, but these differences were not significant at $p > 0.05$. When there were significant stimulus–audience interactions, no-food and pinyon pine seed trials were considered separately.

There was a significant stimulus \times audience interaction for the total number of calls (ANOVA: $F_{4,20} = 4.29$, $p = 0.011$). During no-food trials, birds gave more calls when there was no audience than during all trials with an audience (HSD: Q range = 7.8–9.41, $p < 0.05$) (Fig. 3A). There were no significant differences between audience types in pinyon pine seed trials (HSD: Q range = 0.97–4.98, $p > 0.05$) (Fig. 3B). There was also a significant stimulus \times audience interaction for the number of call groups (ANOVA: $F_{4,20} = 8.66$, $p = 0.001$). For no-food trials, birds gave more call

Table 4
Calls given by male and female pinyon jays

Call type	Male, female or both	Number of individuals	Used in DFA?	Male mean	Female mean
Valley-bump	Both	7	Yes	0.078	0.983
Compound calls	Both	6	Yes	0.6	0.729
Rack	Female	3	Yes	0	0.25
Multiple rack	Both	6	Yes	0.7	1.008
Valley	Both	5	No	2.417	0.458
Soft-2	Both	3	No	1.778	1.617
Soft-1	Male	3	No	0.567	0
Rise	Male	1	No	1.667	0
Flat	Male	2	No	0.178	0
Double small rack	Male	1	No	0.022	0
Vibration	Female	1	No	0	0.016
Chatter	Female	1	No	0	0.017

Male, female or both refers to the sexes that gave each call type; number of individuals refers to the number of birds who gave each call; male mean refers to the mean number of calls given by males; and female mean refers to the mean number of calls given by females.

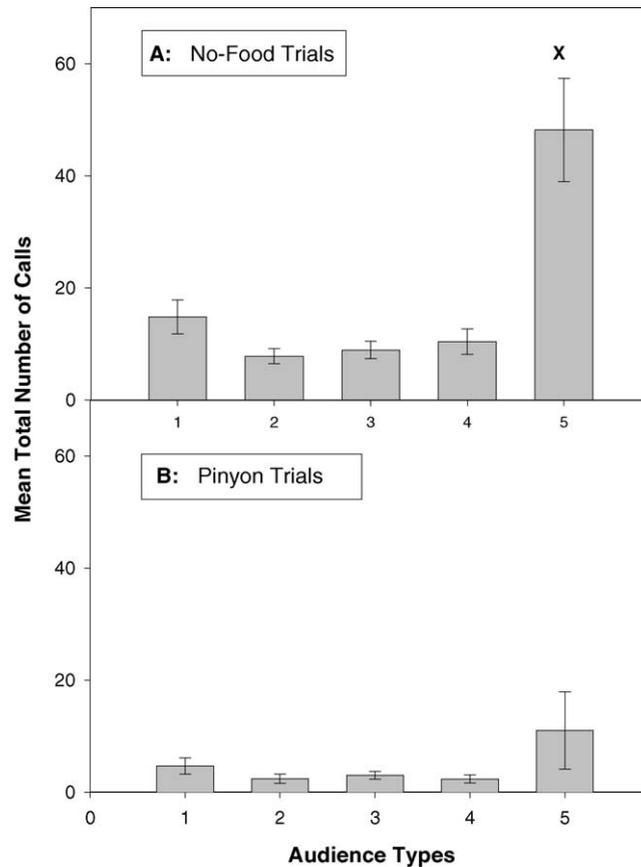


Fig. 3. Mean total number of calls (\pm S.E.) for all audience types for (A) no-food and (B) pinyon pine seed trials. Within stimulus type, X is significantly greater than all other audience types. Numbers 1–5 refer to the audience types: type 1 = 2 males, 2 females including mate; type 2 = 2 males, 2 females no mate; type 3 = 4 males; type 4 = 3 females; and type 5 = no audience.

groups when there was no audience than during all trials with an audience (HSD: Q range = 13.31–14.71, $p < 0.05$) (Fig. 4A). For pinyon pine seed trials, there were no significant differences in the number of call groups (HSD: Q range = 1.05–7.181, $p > 0.05$) (Fig. 4B). In summary, during no-food trials, the trend is that birds gave more individual calls and more call groups when their mate is present and when they were alone. The only significant differences were between no-audience and audience trials.

There were no significant differences in the number of call types birds gave in response to the different audience types (ANOVA: $F_{4,20} = 2.12$, $p = 0.115$). There was a significant stimulus \times audience interaction for the number of call types (ANOVA: $F_{4,20} = 3.61$, $p = 0.022$), but there were no significant differences

within either no-food or pinyon pine seed trials. Since the trends were similar and non-significant we combined the trials in Fig. 5. This figure shows a trend that is similar to the total number of calls and number of uniform sequences, where marginally more types of calls were given during mate trials and no-audience trials.

The main effects test for the number of single calls was significant (ANOVA: $F_{4,20} = 4.60$, $p = 0.008$). The stimulus \times audience interaction was not significant, so pinyon pine seed and no-food trials were not separated (ANOVA: $F_{4,20} = 0.65$, $p = 0.629$) (Fig. 6). This variable shows a different pattern from the previous ones. The trend has been for no-audience trials to be higher than all other trials, followed by mate trials. Although mate trials are still high, birds gave fewer single calls when alone.

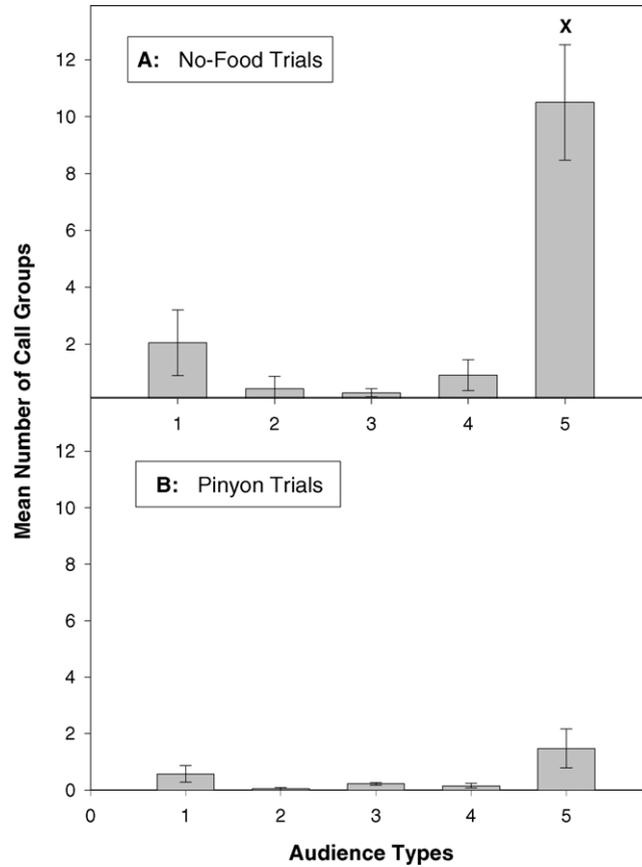


Fig. 4. Mean number of call groups (\pm S.E.) for all audience types for (A) no-food and (B) pinyon pine seed trials. Within stimulus type, X is significantly greater than all other audience types. Numbers 1–5 refer to the audience types: type 1 = 2 males, 2 females including mate; type 2 = 2 males, 2 females no mate; type 3 = 4 males; type 4 = 3 females; and type 5 = no audience.

Audience differences were further analyzed using DFA. No-food trials and pinyon pine seed trials were examined separately. There were significant differences between audience types within no-food trials (DFA: $X_{16}^2 = 40.9$, $p = 0.001$). Despite the significance, the overall discriminatory accuracy rate was only 42.9%, with a range of 0–71.4%. Pair-wise F -tests were calculated to determine which audience types were different from one another, and no-audience trials were significantly different than all other audience types, supporting the ANOVA results (DFA, pair-wise comparisons: F range = 8.62–10.15, $p < 0.0001$). The calls that were most important for discrimination were multiple racks and compound sequences. There were no significant differences

between audience types within pinyon pine seed trials (DFA: $X_{12}^2 = 16.14$, $p = 0.185$).

3.4. Sex results

The main effects tests found no significant differences between males and females for the total number of calls, the number of call groups, the number of call types or the number of single calls (ANOVA, $F_{1,5}$ range = 0.08–0.98, $p > 0.05$).

The DFA was significant, and 100% of all males and females were classified into their proper sex ($F_{4,2} = 52.82$, $p = 0.018$). Males and females differed in two areas: (1) they gave different types of calls, and (2) when both males and females gave a specific

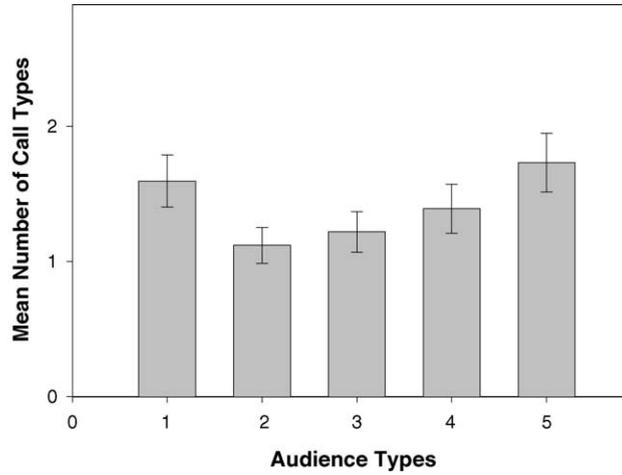


Fig. 5. Mean number of call types (\pm S.E.) for all audience types (no-food and pinyon pine seed combined). There were no significant differences. Numbers 1–5 refer to the audience types: type 1 = 2 males, 2 females including mate; type 2 = 2 males, 2 females no mate; type 3 = 4 males; type 4 = 3 females; and type 5 = no audience.

call type, the sexes differed in the number given of that type (Table 4). The call types used by the DFA were, in their order of importance: valley-bumps, compound sequences, racks, and multiple racks. In general, these call types were given by both sexes, but with different frequencies. Calls given primarily by one sex were not used as discriminating variables.

Only females gave single racks, and females gave more valley-bumps, compound sequences and multiple racks. Males gave more valleys, which was another shared call type, and males were the only sex to give soft-1s, rises, and flats. Valleys, soft-1s, rises and flats were not used as discriminating variables in the DFA.

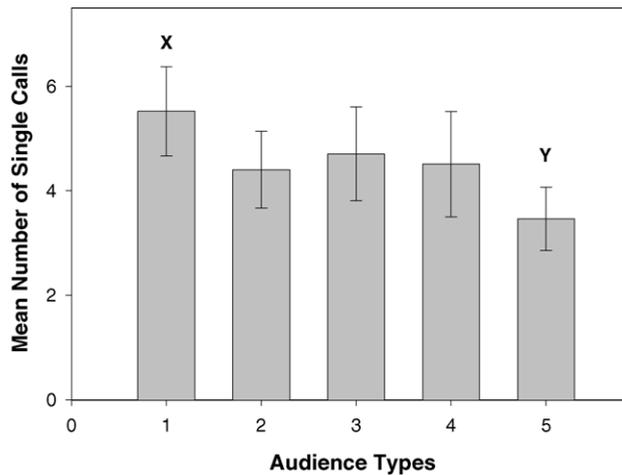


Fig. 6. Mean number of single calls (\pm S.E.) for all audience types (no-food and pinyon pine seed combined). X is significantly greater than Y. Numbers 1–5 refer to the audience types: type 1 = 2 males, 2 females including mate; type 2 = 2 males, 2 females no mate; type 3 = 4 males; type 4 = 3 females; and type 5 = no audience.

4. Discussion

4.1. Stimulus discussion

Pinyon jays called more and with greater complexity during no-food trials than during pinyon pine seed trials. Significant interactions obscured results for some of the ANOVA analyses, but trends were still apparent. The significant differences arose primarily because of N-5 (no audience). Birds gave many more call groups when they were alone and had no food (N-5 mean = 48.2 calls, P-5 mean = 11.0 calls). This lead to significant differences between N-5 trial types and most pinyon pine seed stimulus–audience combinations. The difference between stimulus types for the total number of calls and the number of single calls was unequivocal, however. Birds gave more total calls and single calls during all no-food trials than during the equivalent pinyon pine seed trials.

The hypothesis that pinyon jays would call more when they had food, because they feed as a flock in the wild, was not supported. There are two alternatives that could account for the decreased calling during trials with food. One is that the pinyon pine seeds are an exceptionally strong, non-perishable food stimulus, and time invested in caching the pinyon pine seeds prevented the birds from calling. Indeed, the birds spent the majority of their time eating and/or caching the pinyon pine seeds in their cage during food trials, although this was not quantified. They may have been so engaged in those activities that they simply did not make time to call.

Another possibility is that the birds behaved selfishly, in a way that prevents the audience from realizing they have food. If birds in the wild came upon a valuable food source and did not call, they would have more opportunity to obtain food for themselves and their mate. Behaving selfishly may be more beneficial than having the added security of more individuals. We believe this is unlikely, however, because when birds are observed feeding in the wild, they always vocalize and arrive as a group (Marzluff and Balda, 1992). A selfish behavior pattern is therefore the opposite of observed behavior. The time of the trial may have been the major constraint. If they were given more time to feed they may have begun giving more calls. A perishable food may also have been a better stimulus, because birds would possibly spend less time caching perishable food.

4.2. Audience discussion

There were significant differences within no-food trials, but not within pinyon pine seed trials. Initially, it appears that the birds were not responding to the audiences when they had food. However, even when there was an interaction between audience and stimulus, the pattern of calling was the same during both pinyon and no-food trials. This indicates that the birds are not completely unresponsive to the different audience types when they had food. The total number of calls given and the number of call groups are simply reduced when there was food, and the reduced calling could account for the lack of significance. Since pinyon pine seed trials showed no significant differences, all further discussion concerns no-food trials.

The only audience type that was repeatedly different from all other types was audience type 5. When alone, birds gave more total calls and more call groups. This supports the second audience hypothesis; that pinyon jays will call more when alone. There are several reasons for this reaction. Pinyon jays are very social, and do everything in the flock (Marzluff and Balda, 1992). The flock provides security from predators, so solitary pinyon jays are more at risk. Their strong reaction may be an attempt to reunite with their flock.

Although pinyon jays gave more total calls and call groups when alone, they did not give more single calls. There was either no significant difference between the audience types regarding single calls, or they gave fewer when alone. Birds gave more single calls during audience type 1, when their mate was present, than when they were alone. It appears that in this study, single call notes were relied on more heavily when birds were in close proximity, while call groups were used more when alone, indicating that they may be important for long-distance communication. The DFA results also supports this, because the two most discriminating call types used in the DFA analysis of no-food trials were multiple racks and compound sequences. These were given most often during no-audience trials. Berger and Ligon (1977) found that lone jays frequently gave a call group they termed a falling rack, while a variety of single notes were used when jays were in close contact. Multiple racks are also used when birds are in close contact, however. Multiple racks are alarm calls that function in attracting other birds to mob a predator (Berger and Ligon, 1977;

Marzluff and Balda, 1992). Call groups, including multiple racks, may function in attracting the attention of other birds, both when alone and when there is a predator.

Call groups may be particularly useful when alone, because they may maximize long-distance transmission. They are longer and may be easier for a receiver to hear and respond to rather than to a short, abbreviated call. This could help a lone jay contact a distant flock that it has become separated from. Some calls are also flock specific, so a longer call may contain information that helps a flock discriminate between their flock members and other flocks (Marzluff and Balda, 1992). Compound sequences, which were used extensively when alone, are also more complex because they are composed of at least two different call types. Compound sequences may therefore provide more information to a listener. Multiple and compound sequences also had more harmonics on average than calls that were given singly. Studies indicate that broadband sounds such as the calls found in multiple sequences are easier for birds to locate than pure tones (Knudson, 1980; Knudson and Konishi, 1979; Shalter and Schleidt, 1977). Although amplitude was not measured in this experiment, multiple and compound sequences also sounded substantially louder to a listener, and could carry better over longer distances. High-energy frequencies (higher harmonics) also decay with increasing distance (Wiley and Richards, 1978). This decay may provide recipients with information about the distance to a separated flock member (Catchpole and Slater, 1995; Cleveland and Snowdon, 1982; Wiley and Richards, 1978).

Cleveland and Snowdon (1982) found that cotton-top tamarins (*Saguinus oedipus oedipus*) also give long, complex compound sequences when they are isolated. These compound sequences are variable, as are the calls given by pinyon jays. Cleveland and Snowdon (1982) suggested two hypotheses: the variability of the compound sequences may allow an animal to continue signaling to other group members that he/she is still lost, or the variability may be attributed to subtle changes in the animal's behavioral state. Cleveland and Snowdon's first hypothesis is not mutually exclusive with the hypothesis that complex compound sequences may provide more information to a listener. Although cotton-top tamarins and pinyon jays are widely separated evolutionarily, both species are very social, and

similar behaviors may therefore be adaptive for both species.

Trends indicated that birds gave more calls when their mate was present, but none of these differences were significant. We predicted that birds would call more when their mate was present, because of the strength of the pair-bond in pinyon jays. It may be that the stimuli the subjects experienced during the trial did not necessitate that they give their mates select information. During the breeding season, mates feed each other food, which would lead to the hypothesis that they would communicate more or different information about food to their mate. These trials were run in the fall, however, after the breeding season. A further line of research would be to conduct the experiment in the spring, when birds court. Shulzitski (1999) also found that mated birds vocalize more than unmated birds when they were caching food. Therefore, mated birds appear to communicate more under some circumstances. Further tests should be done to determine whether pinyon jays would respond selectively to their mate at other times of the year, or under different conditions.

4.3. Sex discussion

There are distinct differences in the way males and females call, although these differences were not as hypothesized. Our hypothesis was that the skewed sex ratio, with more males than females in a flock, would lead to males calling more frequently to both their mate, and an all-female audience without their mate. We predicted that females would only call more to their mate. These differences did not occur. Despite the skewed sex ratio, males may not invest extra energy into communicating with other females, especially since divorces rarely occur (Marzluff and Balda, 1992).

However, males and females called differently in other ways. They give some call types in different proportions, and some types of calls appear to be male- or female-specific. Males gave three types of single calls that were never given by females: soft-1s, rises and flats. Only females gave single racks. None of the single call types that were given exclusively by males were used in the DFA, however, so the relative importance of the call types is unclear.

These differences raise the question of why males and females may respond with different types and num-

bers of calls to the same set of circumstances. Male and female birds have distinct roles and may experience different challenges, leading to differences in calling. Females are limited in a flock, and therefore may experience undesirable attention from males who are not their mate. Previous observations noted a call used exclusively by females in response to males who sidle too near (Berger and Ligon, 1977; Marzluff and Balda, 1992). That may be one example of a situation where a female would require a specific call not needed by a male.

Another factor may be the dominance hierarchy within a flock. In a wild flock, males are dominant over females (Marzluff and Balda, 1992). Subordinate birds may be more likely to give calls that served an appeasement function. Birds give an appeasement gesture known as a chin-up display in response to a challenge by a dominant bird (Marzluff and Balda, 1992), and they may also have calls that serve a similar function. Marzluff and Balda (1992) also observed clear dominance hierarchies in wild male jays, while dominance hierarchies in females were much more subtle and difficult to discern. Differences in calling may be associated with differences within sex-specific dominance hierarchies. All of these circumstances may have resulted in sex-specific vocalizations, and differential use of shared call types.

5. Conclusion

Pinyon jays are an extremely social species, and for that reason we hypothesized that they would have complex communication abilities. Their communication does have interesting features, although not always in the manner predicted. Birds did not call more in response to pinyon pine seeds, perhaps due to the time spent consuming it. The birds responded to the presence or absence of an audience, but they failed to significantly change their calling in response to different audience members. The presence of consistent yet non-significant trends in the data, such as more calling in response to mate trials, indicates that more testing needs to be done. Birds did appear capable of calling selectively, however, with regards to the call types they used. For example, during no-food trials, when birds were alone, they gave more call groups, but the same or less single calls when compared to trials with an

audience. This indicates that birds do alter their calls depending on the situation, and that call types may be somewhat context-specific. Males and females also call in a different manner, raising interesting questions as to what purposes these differences serve.

Ultimately, factors such as the presence or absence of an audience, presence or absence of food and the sex of a bird all influence pinyon jay communication. Although pinyon jays did not respond selectively to specific members of an audience, their communication still appears to be complex.

Acknowledgements

Funding was provided by the National Science Foundation (NSF 9992883). We are grateful to Lisa Swanson, Bryce Marshall, Aimee Dunlap-Lehtilä and Tom Greene of the Avian Cognition Laboratory at Northern Arizona University. We thank Dr. Paul Keim of Northern Arizona University for sex determination, Dr. Phil Service and Dr. Graydon Bell for statistical assistance and guidance, and Dr. Les Hunt and two anonymous reviewers for valuable insight. Thanks also to the Merriam-Powell Center for Environmental Research for computing and software assistance. Finally, much thanks to our wives, husbands and loved ones, for their emotional support and tolerance.

References

- Balda, R.P., 1980. Are seed caching systems co-evolved? Acta Congre. Int. Ornithol. 2, 1185–1191.
- Balda, R.P., 2002. Pinyon jay (*Gymnorhinus cyanocephalus*). Birds North Am. 605, 1–31.
- Balda, R.P., Balda, J., 1978. The care of young piñon jays (*Gymnorhinus cyanocephalus*) and their integration into the flock. J. Ornithol. 119, 146–171.
- Balda, R.P., Bateman, G.C., 1971. Flocking and annual cycle of the piñon Jay *Gymnorhinus cyanocephalus*. Condor 73, 287–302.
- Balda, R.P., Bateman, G.C., 1972. The breeding biology of the piñon jay. Living Bird 11, 5–24.
- Balda, R.P., Kamil, A.C., Bednekoff, P., 1996. Predicting cognitive capacity from natural history: examples from four species of corvids. In: Nolan, V., Ketterson, E. (Eds.), Current Ornithology, vol. 13. Plenum Press, New York.
- Berger, L., Ligon, D., 1977. Vocal communication and individual recognition in the piñon jay *Gymnorhinus cyanocephalus*. Anim. Behav. 25, 567–584.

- Bond, A.B., Kamil, A.C., Balda, R.P., 2003. Social complexity and transitive inference in corvids. *Anim. Behav.* 65 (3), 479–487.
- Catchpole, C.K., Slater, P.J.B., 1995. *Bird Song*. Cambridge University Press, Cambridge.
- Chen, B., 2000. Sex differences in spatial memory ability by mated pinyon jays, *Gymnorhinus cyanocephalus*. MS thesis, Northern Arizona University.
- Cheney, D.L., Seyfarth, R.M., 1985. Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 94, 150–166.
- Cheney, D.L., Seyfarth, R.M., 1990. *How Monkeys See the World*. University of Chicago Press, Chicago.
- Cleveland, J., Snowdon, C.T., 1982. The complex vocal repertoire of an adult cotton-top tamarin. *Zeitschrift für Tierpsychologie* 58, 231–270.
- Cresswell, W., 1994. The function of alarm calls in redshanks *Tringa totanus*. *Anim. Behav.* 47, 736–738.
- Dooling, R.J., 1982. Auditory perception in birds. In: Kroodsmma, D.E., Miller, E.H. (Eds.), *Acoustic Communication in Birds*. Academy Press, New York.
- Dunford, C., 1977. Kin selection for ground squirrel alarm calls. *Amer. Nat.* 111, 782–785.
- Evans, C., Marler, P., 1992. Female appearance as a factor of the responsiveness of male chickens during anti-predator behavior and courtship. *Anim. Behav.* 43, 137–145.
- Griffiths, R., Daan, S., Dijkstra, C., 1996. Sex identification in birds using two CHD genes. *Royal Society of London* 263, 1251–1256.
- Gyger, M., Karakashian, S., Marler, P., 1986. Avian alarm calling: is there an audience effect? *Anim. Behav.* 34, 1570–1572.
- Gyger, M., Marler, P., 1988. Food calling in the domestic fowl, *Gallus gallus*: the role of external referents and deception. *Anim. Behav.* 36, 358–365.
- Hauser, M., 1998a. *The Evolution of Communication*. The MIT Press, Cambridge.
- Humphrey, N.K., 1976. The social function of intellect. In: Bateson, P., Hinde, R. (Eds.), *Growing Points in Ethology*. Cambridge University Press, Cambridge.
- Johnson, K., 1988a. Sexual selection in pinyon jays I: female choice and male–male competition. *Anim. Behav.* 36, 1038–1047.
- Johnson, K., 1988b. Sexual selection in pinyon jays II: male choice and female–female competition. *Anim. Behav.* 36, 1048–1053.
- Knudson, E.I., 1980. Sound localization in birds. In: Popper, A.N., Fay, R.R. (Eds.), *Comparative Studies of Hearing in Vertebrates*. Springer-Verlag, New York, pp. 289–322.
- Knudson, L.E., Konishi, M., 1979. Mechanisms of sound localization in the barn owl (*Tyto alba*). *J. Comp. Physiol.* 133, 12–21.
- Ligon, J.D., 1971. Late summer-autumnal breeding of the piñon jay in New Mexico. *Condor* 73 (2), 147–153.
- Ligon, J.D., 1978. Reproductive interdependence of piñon jays and piñon pines. *Ecol. Monogr.* 48, 111–126.
- Marler, P., Dufty, A., Pickert, R., 1986. Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Anim. Behav.* 34, 194–198.
- Marzluff, J.M., 1988. Vocal recognition of mates by breeding pinyon jays *Gymnorhinus cyanocephalus*. *Anim. Behav.* 36, 296–298.
- Marzluff, J.M., Balda, R.P., 1988a. Pairing patterns and fitness in a free-ranging population of pinyon jays: what do they reveal about mate choice? *Condor* 90, 201–213.
- Marzluff, J.M., Balda, R.P., 1988b. The advantages of, and constraints forcing, mate fidelity in pinyon jays. *Auk* 105, 286–295.
- Marzluff, J.M., Balda, R.P., 1989. Causes and consequences of female-biased dispersal in a flock-living bird, the pinyon jay. *Ecology* 70, 316–328.
- Marzluff, J.M., Balda, R.P., 1992. *The Pinyon Jay*. T & AD Poyser, London.
- McArthur, P.D., 1982. Mechanisms and development of parent-young vocal recognition in the piñon jay (*Gymnorhinus cyanocephalus*). *Anim. Behav.* 30, 62–74.
- Mullenbach, R., Lagoda, J.P.L., Welter, C., 1989. An efficient salt-chloroform extraction of DNA from blood and tissues. *Trends Genet.* 5, 391.
- Shalter, M.D., Schleidt, W.M., 1977. The ability of barn owls *Tyto alba* to discriminate and localize avian calls. *Ibis* 119, 22–27.
- Shulzitski, J., 1999. Sex differences in the spatial memory ability of mated pinyon jays. MS Thesis, Northern Arizona University.
- Smythe, W.J., 1977. The function of mammalian alarm advertising: social signals or pursuit invitation? *Am. Nat.* 111, 191–194.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), *Sexual Selection and the Descent of man*. Aldine Press, Chicago.
- Vander Wall, S.B., Balda, R.P., 1981. Ecology and evolution of food-storage in conifer seed caching Corvids. *Zeitschrift für Tierpsychologie* 56, 217–242.
- Wiley, R.H., Richards, D.G., 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3, 69–94.
- Williams, G.C., 1966. *Adaptation and Natural Selection*. Princeton University Press, Princeton.
- Zar, J., 1999. *Biostatistical Analysis*, fourth ed. Prentice Hall, Upper Saddle River.