Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2020), 31(5), 1120–1128. doi:10.1093/beheco/araa059

Original Article

Acorn woodpeckers vocally discriminate current and former group members from nongroup members

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Received 27 December 2019; revised 19 May 2020; editorial decision 19 May 2020; accepted 26 May 2020; Advance Access publication 18 June 2020.

In species with long-term social relationships, the ability to recognize individuals after extended separation and the ability to discriminate between former social affiliates that have died and those that have left the group but may return are likely to be beneficial. Few studies, however, have investigated whether animals can make these discriminations. We presented acorn woodpeckers (*Melanerpes formicivorus*), a group-living, cooperatively breeding bird, with playbacks of current group members, former group members still living nearby, former group members that had died or left the study area, and familiar nongroup members. Subjects responded more quickly to the calls of nongroup members than to the calls of current group members or former group members still living in the study area but did not discriminate between nongroup members and former group members that had died or disappeared. This suggests that acorn woodpeckers can vocally recognize both current group members and former group members that have dispersed to nearby groups and that they either forget former group members that no longer live in the vicinity or classify them differently from former group members that still live nearby. This study suggests an important role for vocal recognition in maintaining valuable relationships with social affiliates postdispersal.

Key words: **cooperative breeding, long-term recognition, *Melanerpes formicivorus*, sex differences, social cognition, vocal recognition.**

INTRODUCTION

In many long-lived animals, individuals interact repeatedly with the same conspecifics for protracted periods, and interactions may be separated by long intervals without contact (Connor et al. 1992; Wittemyer et al. 2005; Kerth et al. 2011; Schuttler et al. 2014). An ability to remember individual conspecifics after extended periods of separation can thus be critical to maintaining long-term social relationships as has been documented in a number of species. Male hooded warblers (*Setophaga citrina*), for example, recognize the songs of territorial neighbors not seen for 8 months because of winter migration (Godard 1991). Some otariid pinnipeds (Insley 2000; Pitcher et al. 2010) and primates (Matthews and Snowdon 2011; Keenan et al. 2016) remember the calls of individual conspecifics for at least several years, and captive bottlenose dolphins (*Tursiops truncatus*) can recognize the whistles of former tank mates two decades after separation (Bruck 2013). Captive common ravens (*Corvus corax*) not only recognize individual conspecifics based on vocal cues for several years but also remember the nature of the former relationship (Boeckle and Bugnyar 2012).

In other sensory modalities, domestic sheep (*Ovis aries*) can remember the faces of at least 50 conspecifics for over 2 years (Kendrick et al. 2001), and orangutans (*Pongo pygmaeus*) can recognize the faces of former social affiliates for at least 10 years (Hanazuka et al. 2013). Yearling Belding's ground squirrels (*Urocitellus beldingi*) recognized the scent of former littermates after hibernation, which could be explained by either long-term social memory or phenotype matching, but they failed to recognize the scent of previously familiar nonkin (Mateo and Johnston 2000).

Despite the benefits of long-term recognition, remembering other individuals indefinitely without updating knowledge about them is likely costly. Long-term memory capacity can be limited

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(Cook et al. 2005), and there could be additional costs to retaining outdated information as former alliance partners that have died or permanently left the area can no longer be relied upon for assistance. Thus, animals may be under selection to distinguish between those former group members that still live nearby and those that do not or to simply forget former social affiliates once a threshold of time has passed with no interaction (Keenan et al. 2016). However, experimental evidence is lacking as to whether animals discriminate between former group members that currently live nearby and former group members that have died or disappeared.

Cooperatively breeding species offer unique opportunities for studying complex social recognition. Many territorial animals discriminate between neighbors and strangers (Christensen and Radford 2018), but cooperative breeders face the additional tasks of discriminating group members from neighbors and discriminating among multiple group members with different social roles. Cooperative breeders also sometimes rejoin and help kin postdispersal, which may require long-term recognition (Hatchwell et al. 2001; Akçay et al. 2013). Thus, cooperative breeders have evolved a variety of mechanisms for recognizing kin and other group members. Stripe-backed wrens (*Campylorhynchus nuchalis*), for example, learn the songs of their same-sex parents and can recognize even unfamiliar kin on the basis of a shared song repertoire (Price 1998, 1999). By contrast, superb starling (*Lamprotornis superbus*) flight calls contain a learned signature of group identity that is independent of genetic relatedness and are also individually distinct (Keen et al. 2013). Meerkats (*Suricata suricatta*) can individually recognize group members by their "close calls" (Townsend et al. 2012).

Acorn woodpeckers (*Melanerpes formicivorus*) in California live in family groups on stable, year-round territories (MacRoberts and MacRoberts 1976). Groups consist of one to four breeding females and one to eight breeding males, all mating with one another and cooperatively raising offspring in a single nest (Koenig et al. 2016). Cobreeders of the same sex are typically close relatives, but opposite-sex breeders are unrelated (Koenig et al. 1998). Because suitable breeding locations are limited, offspring of both sexes may also remain in their natal territory for many years as nonbreeding helpers (Koenig et al. 2011). Opportunities for helpers to disperse and breed occur when all the breeders of a particular sex have died or disappeared from another group, creating a breeding vacancy. Helpers (and sometimes breeders) from multiple groups engage in "power struggles" to claim such vacancies, and individuals form coalitions with same-sex kin to improve their chances of competing successfully (Koenig 1981a; Hannon et al. 1985).

Acorn woodpeckers have individually distinctive calls and can discriminate vocalizations of their current group members from those of other groups (Yao 2008). Several observations further suggest that former group members may still recognize one another several years after one of them has dispersed. First, individuals that have already attained a breeding position may temporarily leave their territory to help relatives with which they have not lived for a year or more to fight for a breeding vacancy elsewhere (Hagemeyer N, personal communication). Second, individuals may rejoin their natal group many years after dispersing (Koenig W, Walters E, unpublished data). Third, individuals may disperse into a group with established breeders if the breeders of the same sex as themselves are their former group mates (Koenig W, Walters E, unpublished data).

If acorn woodpeckers recognize former group members, it could be beneficial for them to discriminate between former group members living in nearby groups with whom they are likely to interact and former group members that have died or permanently left the area. For example, helpers seeking to join same-sex kin that have already attained breeder status in another group require up-to-date knowledge about which of their former group members are still alive and present in the vicinity. Similarly, anecdotal evidence suggests that individuals may sometimes actively recruit kin living in other territories to form coalitions, in which case they would need to know which individuals are still alive and able to offer assistance (Hannon et al. 1985).

We conducted two playback experiments to investigate vocal discrimination in acorn woodpeckers. In Experiment 1, we investigated whether acorn woodpeckers could discriminate among the calls of current group members, former group members, and nongroup members. In Experiment 2, we investigated whether acorn woodpeckers could discriminate among the calls of former group members currently present in the study area, former group members absent from the study area for at least a year, and nongroup members.

We predicted that both sexes would react more quickly and approach the speaker more closely in response to playbacks of nongroup members and former group members that are no longer observed in the study area compared to playbacks of current group members or former group members that still live in the study area. As acorn woodpeckers compete with same-sex rivals for breeding vacancies and rely on same-sex kin for assistance in coalitions (Hannon et al. 1985), we predicted that both males and females would react more quickly and approach more closely in response to callers of the same sex as themselves compared to callers of the opposite sex. Moreover, given that females engage in power struggles more than males (Koenig 1981a), we predicted that females would react more quickly and approach more closely than males in response to same-sex callers.

MATERIAL AND METHODS

Study site and population monitoring

All data were collected on wild acorn woodpeckers at Hastings Natural History Reservation in central coastal California (36.387°N, 121.551°W). This population has been the subject of a long-term study since 1968 (MacRoberts and MacRoberts 1976; Koenig 1981b), and >95% of the individuals are color-banded. Most individuals are banded in the nest at 21 days of age, and unbanded adults immigrating into the population are captured and banded whenever possible. As of 2019, there are approximately 50 social groups within the study area, and each group is censused approximately every 8–10 weeks using spotting scopes to resight color-banded individuals.

Experiment 1: vocal discrimination of current, former, and nongroup members

We conducted Experiment 1 from 14 April to 19 June 2017 and 2 May to 14 June 2018. Subjects were seven females and seven males from eight social groups, and all but one were of breeder status. We presented each subject with three different playback stimuli on different days: 1) a call of a current group member; 2) a call of a former group member that had died, left the group, or remained on the natal territory after the subject had dispersed 1.1–6.4 years prior to the experiment (median = 2.8 years); and 3) a call of an unrelated individual from a nearby territory that had never lived

in the same group as the subject. The distance between the territory centroids of the subject and the nongroup member caller was 40–862 m (median = 167 m) and, in 9 of 14 nongroup member trials, the caller and subject shared a territorial boundary. As acorn woodpeckers make frequent forays to other territories with a mean foray distance of 500–600 m, subjects were likely familiar with all of the nongroup member callers (Barve et al. 2020).

The order of the presentation was balanced according to a Latin square design (Table 1). The three stimuli played to a given subject were always recorded from callers of a single sex such that each subject received either three male or three female calls. The sex of the subject matched the sex of the callers in 7 of 14 cases. Successive playbacks to the same group or to groups <250 m from each other were spaced by 6.0 ± 4.8 days on average (minimum 3 days to same group and 2 days to groups closer than 250 m).

Testing the difference in response to callers living in the study area (hereafter "nearby") versus callers that had died or left the study area (hereafter "absent") was not an a priori goal of Experiment 1. However, because of the difficulty of obtaining playback-quality recordings from known individuals, we used the call of an individual that was no longer observed on the study area at the time of the experiment as the former group member stimulus for two female and four male subjects (Table 1). None of the former group members that were classified as "absent" had been observed on the study site for at least a year prior to the experiment and none were seen at least a year postexperiment (as of September 2019). For two of the males that received a former group member stimulus from an absent caller, the nongroup member stimulus was also from an absent caller (not seen for 7 months prior to the experiment). Among the subjects that received the call of a nearby former group member, the distance between the territory centroids of the subject and the caller was 121–1587 m (median = 228 m) and, in 5 of 8 nearby former group member trials, the caller and subject shared a territorial boundary

Experiment 2: vocal discrimination of nearby and absent former group members

We conducted Experiment 2 from 6 April to 12 July 2019 using five female and six male subjects from eight different groups (Table 2). Six individuals were used as subjects in both Experiment 1 and Experiment 2 and, among the 11 subjects used in Experiment 2, all but 2 were members of a social group that was exposed to playbacks in Experiment 1. Experiment 2 was designed as a follow-up to Experiment 1 to investigate whether acorn woodpeckers could vocally discriminate between nearby and absent former group members. We presented each subject with the call of a former group member living on a neighboring territory within the study area (nearby), the call of a former group member that had not been observed in the study area for 1.1–7.3 years before the experiment (median absence = 3.0 years), and the call of an unrelated individual from a nearby territory that had never lived in the same group as the subject.

The interterritorial distance of subjects and nearby former group members was 102–257 m (median = 132 m), and all nearby former group members shared a territorial boundary with the subject. The interterritorial distance of subjects and nongroup members was 102–734 m (median = 257 m), and 5 of 11 nongroup members shared a territorial boundary with the subject. Thus, as in Experiment 1, subjects were likely familiar with all nearby former group member and nongroup member callers. As of September 2019, none of the absent former group members had been observed in the study area since their last sighting 1.1–7.3 years before the experiment.

We ensured that the amount of time since the subject and caller last lived together did not statistically differ between nearby former group member and absent former group member playback stimuli (Paired *t*-test, $t_{10} = -1.2$, $P = 0.25$). As in Experiment 1, order of presentation was balanced according to a Latin square design (Table 2), and the three playback stimuli presented to a given subject were recorded from three callers of a single sex, which matched the sex of the subject in 6 of 11 cases. Successive playbacks to the same group or to groups <250 m apart were separated by 6.6 ± 6.5 days (minimum 2 days).

Playback stimuli

In both experiments, the calls used as playback stimuli were *waka* calls, an individually distinctive, affiliative call typically produced when members of the same group approach one another after a short period of separation (MacRoberts and MacRoberts 1976; Yao 2008). All playback stimuli were recorded at Hastings Reservation

Table 1

Experimental design for Experiment 1, investigating responses to the calls of current group members, former group members, and nongroup members. *Order* refers to the order in which a given subject received the three playback stimuli (*C*urrent group member, *F*ormer group member, and *N*ongroup member). As much as possible, *order* was balanced with respect to *subject sex*, *caller sex*, and whether the caller used for the former group member stimulus was nearby or missing from the study area at the time of the experiment. *Nearby or absent* was not balanced with respect to *subject sex* or *caller sex*

Subject ID	Group	Year	Order	Subject sex	Caller sex	Former group member nearby or absent
4672	1500	2017	C-F-N	F	F	Nearby
5007	KNOL	2017	C-F-N	F	F	Nearby
5945	PLQE	2018	C-F-N	F	M	Absent
4754	MLF2	2017	C-F-N	M	M	Nearby
4935	CAVI	2018	C-F-N	M	F	Absent
5389	ROBH	2017	F-N-C	F	M	Nearby
5103	PLQE	2017	F-N-C	F	M	Nearby
5006	PLQE	2017	F-N-C	M	M	Absent
3399	KNOL	2018	F-N-C	M	F	Absent
5715	KNOL	2018	N-C-F	F	F	Absent
4629	CAVI	2017	N-C-F	F	M	Nearby
5378	Y	2017	N-C-F	M	M	Nearby
5082	1500	2018	N-C-F	M	M	Nearby
5251	LHAY	2017	N-C-F	M	F	Absent

Table 2

Experimental design for Experiment 2, investigating responses to the calls of nearby former group members, absent former group members, and nongroup members. *Order* refers to the order in which a given subject received the three playback stimuli (*N*earby *f*ormer group member, *A*bsent *f*ormer group member, and *N*ongroup member). As much as possible, *order* was balanced with respect to *subject sex* and *caller sex*

Subject ID	Group	Year	Order	Subject sex	Caller sex
4629	CAVI	2019	Nf-Af-Ng	F	F
5007	KNOL	2019	Nf-Af-Ng	F	F
4751	MLF2	2019	Nf-Af-Ng	M	M
5880	WIMA	2019	Nf-Af-Ng	M	M
5103	PLQE	2019	Af-Ng-Nf	F	M
5945	PLQE	2019	Af-Ng-Nf	F	M
5082	1500	2019	Af-Ng-Nf	M	M
5698	UPBA	2019	Af-Ng-Nf	M	F
5700	PLAN	2019	Ng-Nf-Af	F	M
5006	PLQE	2019	Ng-Nf-Af	M	F
5085	1500	2019	Ng-Nf-Af	M	M

from 19 March 2015 to 26 May 2017 using a Sennheiser ME67 or ME62 microphone (Wedemark, Germany) and a Marantz PMD661 (Kanagawa, Japan), Fostex FR-2 (Akishima City, Tokyo, Japan), or Roland R26 (Hamamatsu, Shizuoka, Japan) digital recorder (48 kHz, 16 or 24 bits). Prior to constructing the playback stimuli, the calls were high-pass filtered (200 Hz cutoff, 6 dB roll off) and normalized to −3 dB in Audacity® 2.1.1, and any calls originally recorded at 24 bits were converted to 16 bits.

In Experiment 1, the playback stimuli consisted of 60 s of background noise with a 10-s fade-in, followed by a single *waka* call, followed by 30 s of background noise, followed by the same *waka* call, followed by a final 10 s of background noise with a fade-out applied to all 10 s. Repeating the call increased the likelihood that the subjects would respond to the playback, and the 30-s interval between calls followed previously published protocols (Yao 2008; Pardo et al. 2018). While natural *waka* calls are most commonly produced singly, they are sometimes repeated at an interval close to 30 s (Pardo M, unpublished data). The playback stimuli for Experiment 2 were constructed in the same way except that the initial period of background noise only lasted 30 s. We made this change to reduce the chance that the subject would fly away before the call began.

Playback protocol

Playback trials for both experiments followed a similar protocol to Pardo et al. (2018). In brief, we placed a Yamaha PDX 11 loudspeaker (Hamamatsu, Shizuoka, Japan) characterized at 100.1 ± 1.3 dB re 20 µPa at 1 m in a tree 1–1.5 m off the ground and 40 m away from a tree near the center of the group's territory ("center tree"). This volume was at the upper end of the range of natural *waka* calls produced by a captive adult male acorn woodpecker (Pardo et al. 2018). The speaker was always placed in the same location during successive trials to a given group. Once the subject was located in the center tree, an observer began filming the subject using either a Canon PowerShot SX510 digital camera (Ota City, Tokyo, Japan) or a Sony Handycam DCR-SX45 Camcorder (Minato, Tokyo, Japan) and immediately played the appropriate playback file.

Measuring response to playback

Based on video and audio recordings of each playback trial, we measured the following aspects of the focal bird's response: latency to the first "reaction" (defined as vocalizing, flying up to a higher vantage point, or flying toward the speaker), latency to the first "positive" flight (defined as flying up to a higher vantage point or toward the speaker), latency to the first approach to the speaker, latency to the closest approach to the speaker, distance of the first approach to the speaker, and distance of the closest approach. For the latency variables, if the focal bird did not exhibit the behavior of interest within 3 min after the start of the playback, latency was assigned the maximum possible value of 180 s and marked as censored. Distances were estimated by eye to the nearest 5 m using landmarks of known distance to the speaker, measured before the experiment with a 50-m tape. The authors involved in scoring the videos were blind to the experimental condition in each trial until all scoring was complete.

Statistical analyses

We conducted statistical analyses in R 3.6.1 (R Core Team 2019). Because of limited sample sizes, we pooled the results of both experiments. For Experiment 1, we rescored each former group member trial as either nearby former group member or absent former group member, according to whether the caller was still living in the study area at the time of the experiment. Thus, in the pooled data set, there were four treatment categories (current group member, nearby former group member, absent former group member, and nongroup member), and each subject only received three of these four treatments within a given experiment. We used 13 unique call exemplars from 13 different callers as playback stimuli for the current group member category (n = 14), 17 unique exemplars from 13 different callers for the nearby former group member category (n = 19), 12 unique exemplars from 8 different callers for the absent former group member category (n = 17), and 19 unique exemplars from 17 different callers for the nongroup member category (n = 25).

We limited our model set to *latency to react*, *latency to positive flight*, and *distance of first approach* as response variables as all other responses measured were highly correlated (Pearson's $r > 0.75$) with at least one of these. We analyzed *latency to react* and *latency to positive flight* using Cox regression in the R package *coxme* (Therneau 2019) to account for the fact that some of the latencies were censored. We analyzed *distance of first approach* using linear mixed models in the R packages *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2017). For each response variable, we ran a model with *treatment*, *subject sex*, *caller sex*, and the interaction of *subject sex* by *caller sex* as fixed effects and *individual ID* as a random effect. As the goal of the experiment was to determine whether subjects could discriminate current and former group members from nongroup members, we compared the responses to nongroup members with the responses to each remaining treatment category using Dunnett's method in package *emmeans* to adjust for multiple comparisons (Lenth 2019). We also conducted pairwise comparisons for the interaction of *subject sex* × *caller sex* using Tukey's method in *emmeans*.

To determine if the time since the subject last lived with a former group member affected the subject's response to that former group member's call, we ran an additional model for each response variable using only the present and absent former group member trials. These models included *time since together* as a fixed effect and *individual ID* as a random effect.

RESULTS

Differences among playback treatments

Subjects vocalized or flew up or toward the speaker (*latency to react*) more quickly in response to nongroup members than to nearby former group members (Dunnett's test, hazard ratio = 0.33,

$P = 0.01$; Figure 1a; Table 3). Subjects showed no significant difference in *latency to react* between nongroup and current group members (Dunnett's test, hazard ratio = 0.52, $P = 0.22$), nor between nongroup and absent former group members (Dunnett's test, hazard ratio = 0.82, $P = 0.86$).

Subjects flew up or toward the speaker (*latency to positive flight*) more quickly in response to nongroup than to current group members (Dunnett's test, hazard ratio = 0.33, $P = 0.04$; Figure 1b; Table 3). There was also a trend to fly up or toward the speaker more quickly in response to nongroup than to nearby former group members, but this was not statistically significant (Dunnett's test, hazard ratio = 0.41, $P = 0.05$). *Latency to positive flight* did not differ between nongroup and absent former group members (Dunnett's test, hazard ratio = 0.61, $P = 0.43$).

The distance of the subject's first approach to the speaker did not differ among treatments (Figure 1c; Table 3). The time since the subject last lived with a former group member had no effect on the subject's response to that former group member for any of the response variables measured (Table 4).

Sex differences

Females vocalized or flew up or toward the speaker (*latency to react*) more quickly than males in response to female callers (Tukey's test, hazard ratio = 6.2, $P < 0.001$), but males and females did not differ in their *latency to react* to male callers (Tukey's test, hazard ratio = 0.89, $P = 0.72$; Figure 2a; Table 3). Similarly, females vocalized or flew significantly more quickly to female callers than to male callers (Tukey's test, hazard ratio = 3.1, $P = 0.003$). Males did not differ significantly in *latency to react* between male and female callers (Tukey's test, hazard ratio = 0.44, $P = 0.05$).

Females flew up or toward the speaker (*latency to positive flight*) more quickly than males in response to female callers (Tukey's test, hazard ratio = 3.4, $P = 0.01$), but males and females did not differ in *latency to positive flight* to male callers (Tukey's test, hazard ratio = 0.79, $P = 0.57$; Figure 2b; Table 3). Similarly, females flew up or toward the speaker more quickly in response to female than to male callers (Tukey's test, hazard ratio = 3.5, $P = 0.01$), but males showed no difference in *latency to positive flight* between female and male callers (Tukey's test, hazard ratio = 0.81, $P = 0.65$).

Females approached the speaker more closely than males on average, but there was no significant interaction between subject sex and caller sex for *distance of first approach* (Figure 2c; Table 3).

DISCUSSION

Our results suggest that acorn woodpeckers can discriminate between the calls of nongroup members and the calls of both current group members and former group members that currently live on a nearby territory. By contrast, we found no evidence of discrimination between nongroup members and absent former group members that had died or left the study area a year or more before the experiment. These findings build on a previous study with this population, which found that acorn woodpeckers could discriminate between the calls of current and nongroup members but did not investigate discrimination of former group members (Yao 2008).

Many territorial animals exhibit either a "dear enemy" effect, in which they respond less aggressively to neighbors than to strangers, or a "nasty neighbor" effect, in which the converse is true (Radford 2005; Müller and Manser 2007; Draganoiu et al. 2014; Goll et al. 2017; Moskát et al. 2017; Christensen and Radford 2018). In some cases, neighbor-stranger discrimination can be explained by territory holders reacting differently to familiar versus unfamiliar stimuli without necessarily recognizing the neighbors and strangers in question. For example, green woodhoopoes (*Phoeniculus purpureus*) responded less strongly to vocal choruses from neighboring groups than from groups three or more territories away,

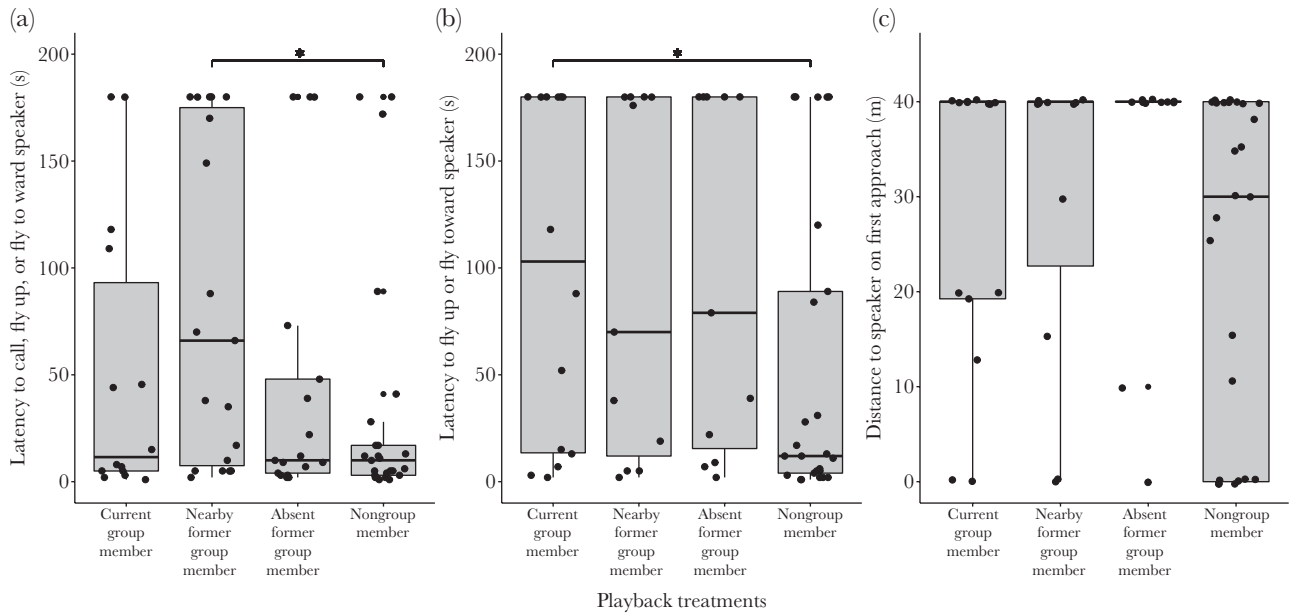

Figure 1

Responses to the calls of current, nearby former, absent former, and nongroup members. The gray boxes indicate interquartile ranges (IQR), the horizontal bars indicate medians, the upper whisker indicates the largest value ≤ the third quartile + 1.5 × IQR, and the lower whisker indicates the smallest value ≥ the first quartile − 1.5 × IQR. Data points are jittered horizontally to improve readability. (A) represents the subject's latency to vocalize, fly up to a higher vantage point, or fly toward the speaker, (B) represents the subject's latency to fly up or toward the speaker, and (C) represents the distance of the subject's first approach to the speaker, with shorter distances indicating a closer approach. * indicates $P < 0.05$.

Table 3

Summary of each of the models for *treatment*, *subject sex*, and *caller sex*. Values shown are chi-square statistic (*P*-value) for fixed effects and variance for *individual ID*. *Latency to react* is defined as the latency to the subject's first vocalization, flight to a higher vantage point, or flight toward the speaker; *latency to positive flight* is defined as the latency to the subject's first flight up to a higher vantage point or toward the speaker; and *distance of first approach* is defined as the closest distance between the subject and the speaker during the subject's first approach toward the speaker. For latency response variables, we used Cox regression models, which account for the fact that some of the observations were censored; that is, no response within the allotted 3 minutes. For *distance of first approach,* we used a linear model. Significant *P*-values are in bold

Model type	Response	Treatment (df = 3)	Subject sex (df = 1)	Caller sex (df = 1)	Subject sex × Caller sex (df = 1)	Individual ID
Cox	Latency to react	10.2 (**0.02**)	14.7 (**0.00**)	8.8 (**0.00**)	10.9 (**0.00**)	0.00
Cox	Latency to positive flight	8.6 (**0.03**)	6.3 (**0.01**)	7.8 (**0.01**)	5.2 (**0.02**)	0.05
Linear	Distance of first approach	1.3 (0.74)	7.7 (**0.01**)	2.7 (0.10)	1.6 (0.20)	0.00

df, degrees of freedom.

Table 4

Summary of each of the models for *time since together*. Values shown are chi-square statistic (*P*-value) for *time since together* and variance for *individual ID*. *Latency to react* is defined as the latency to the subject's first vocalization, flight to a higher vantage point, or flight toward the speaker; *latency to positive flight* is defined as the latency to the subject's first flight up to a higher vantage point or toward the speaker; and *distance of first approach* is defined as the closest distance between the subject and the speaker during the subject's first approach toward the speaker. For latency response variables, we used Cox regression models, which account for the fact that some of the observations were censored; that is, no response within the allotted 3 minutes. For *distance of first approach*, we used a linear model

Model type	Response	Time since together (df = 1)	Individual ID
Cox	Latency to react	0.77 (0.38)	0.23
Cox	Latency to positive flight	0.40 (0.53)	0.00
Linear	Distance of first approach	2.0 (0.16)	99.5

df, degrees of freedom.

which could result from habituation to familiar choruses (Radford 2005). In other cases, however, vocal discrimination cannot be explained by familiarity alone. Group-living superb starlings and tropical mockingbirds (*Mimus gilvus*) discriminated between their own group members and territorial neighbors, even though they were presumably familiar with both (Botero et al. 2007; Keen et al. 2013). Similarly, in habituation–dishabituation experiments, noisy miners (*Manorina melanocephala*) and apostlebirds (*Struthidea cinerea*) differentiated between the calls of two conspecifics even when both callers were unfamiliar or both were familiar (McDonald 2012; Warrington et al. 2015).

In acorn woodpeckers, vocal discrimination of current and former group members from nongroup members is unlikely to be based on familiarity. Eighty-four percent of nearby former group members and 56% of nongroup members in our study (Experiments 1 and 2 combined) shared a territorial boundary with the subject. More importantly, automated radio-telemetry has revealed that breeder and helper acorn woodpeckers of both sexes make routine extraterritorial forays to other groups, often multiple times per day, with a mean foray distance of 500–600 m (Barve et al. 2020). In the current study, the mean distance (±standard deviation [SD]) between the territory centroids of subjects and callers was 279 ± 353 m for nearby former group members and 277 ± 219 m for nongroup members, well within the typical foray distance. Thus, subjects were almost certainly familiar with most or all of the callers they were exposed to, including the nongroup members. Moreover, in a previous study, acorn woodpeckers discriminated between the calls of their own group members and members of other groups, but responded equally strongly to the calls of neighbors and strangers, further suggesting that familiarity is not the sole basis for vocal discrimination in this species (Yao 2008).

Rather than simply discriminating between familiar and unfamiliar stimuli, acorn woodpeckers likely recognize their former group members either at the group level, or more likely, individually. Yao (2008) found evidence of individual signatures in acorn woodpecker *waka* calls using Mel-Frequency Cepstral Coefficients and Hidden Markov Models but found no evidence of group signatures using spectrogram cross-correlation. She also found that acorn woodpeckers treated playback of their own call differently from the calls of group members, which is consistent with individual recognition but not with recognition based on a shared group signature. Finally, subjects in our study discriminated between nearby former group members and nongroup members but not between absent former group members and nongroup members, which is also consistent with individual-level, but not group-level, recognition.

One way in which animals can recognize former group members is by maintaining contact with them after they have left the group, even if that contact is as simple as listening to the calls of a former group member now living on a nearby territory. A number of species, such as long-tailed tits (*Aegithalos caudatus*) and western bluebirds (*Sialia mexicana*), interact extensively with kin after dispersal (Hatchwell et al. 2001; Akçay et al. 2013). The regular extraterritorial forays of acorn woodpeckers give them ample opportunity to maintain contact with former group members (Koenig et al. 1996; Barve et al. 2020). Moreover, most of the nearby former group members in this experiment lived on territories within hearing range of the subject's territory, making it highly likely that the subjects maintained contact with these former group members. If acorn woodpeckers rely on continued contact with former group members to recognize them several years postdispersal, then subjects likely responded equally strongly to absent former group members and nongroup members because they perceived them both as intruders from another group and were responding aggressively.

Alternatively, it is possible that acorn woodpeckers can remember former group members for several years even in the absence of continued contact and that they are also aware of which individuals are still alive and which have died or disappeared. Under this scenario, subjects likely responded strongly to absent former group

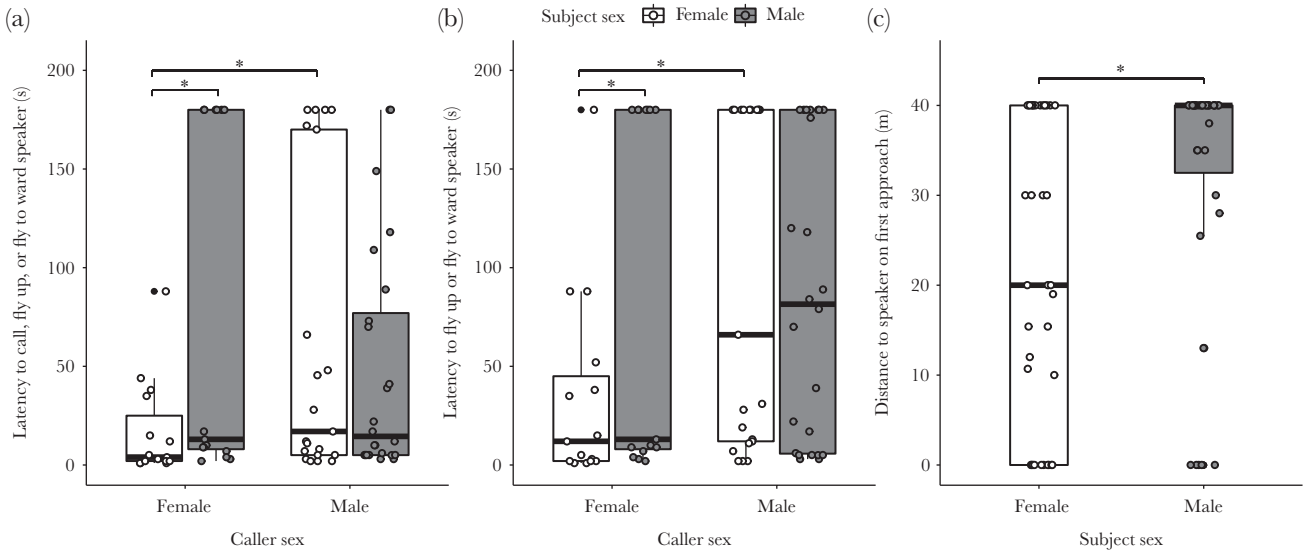

Figure 2

Differences in response between male and female subjects. The boxes indicate interquartile ranges (IQR), the horizontal bars indicate medians, the upper whisker indicates the largest value ≤ the third quartile + 1.5 × IQR, and the lower whisker indicates the smallest value ≥ the first quartile − 1.5 × IQR. Data points are jittered horizontally to improve readability. (A) represents the subject's latency to vocalize, fly up to a higher vantage point, or fly toward the speaker, (B) represents the subject's latency to fly up or toward the speaker, and (C) represents the distance of the subject's first approach to the speaker, with shorter distances indicating a closer approach. White boxes represent female subjects and dark boxes represent male subjects. For (A) and (B), the differences between male and female subjects depended on the sex of the caller. * indicates $P < 0.05$.

members because their expectations were violated by hearing the call of an individual that they had classified as "dead." The mean time (±SD) since a subject and former group member caller last lived together in our experiments was 3.2 ± 1.8 years overall and 3.8 ± 1.9 years among the living former group members (max. = 7.3 years), and the duration of time apart had no effect on the subject's response. Thus, if the acorn woodpeckers in our study recognized their former group members via long-term memory, this would be among the longest examples of social memory yet demonstrated in a bird, with the caveat that no previous study has attempted to identify the upper limit of long-term vocal recognition in birds (Godard 1991; Boeckle and Bugnyar 2012; Draganoiu et al. 2014).

Few previous studies have investigated whether animals cognitively reclassify former social affiliates that have died. In one experiment, a single elephant family (*Loxodonta africana*) gave contact calls and approached the speaker in response to the call of a dead family member played back 23 months after her death, just as they would to a living family member (McComb et al. 2000). This suggests that elephants may remember social affiliates for up to 2 years but does not indicate whether they are aware that a social affiliate has died. Another study found that male chacma baboons (*Papio ursinus*) normally respond to the calls of close female associates but fail to do so if the female's infant has recently died (Palombit et al. 1997). While this might indicate knowledge of the infant's death, it could also be due to a change in the female's behavior following the death of her infant. Currently, there is no evidence either for or against death recognition in acorn woodpeckers. However, given that acorn woodpeckers know the membership of unrelated nearby groups, it is likely that they are at least capable of determining whether a given former group member lives nearby (Pardo et al. 2018).

Subjects flew up or toward the speaker (*latency to positive flight*) significantly more quickly in response to nongroup members than to current group members and marginally more quickly to nongroup than to nearby former group members. Their latency to *vocalize* or fly up or toward the speaker (*latency to react*), however, only differed between nongroup members and nearby former group members. The lack of a difference in *latency to react* between playbacks of current and nongroup members could be because one of the most common vocalizations, the *waka* call, is given in multiple contexts. While acorn woodpeckers often give *waka* calls in response to playbacks of territorial intruders, possibly to rally group members to defend against the threat, they most commonly give *waka* calls as an affiliative display toward members of their own group. Thus, subjects may have vocalized rapidly in response to current group members and nongroup members for different reasons. Alternatively, the more rapid vocal response to playbacks of current group members could be because the individual whose call was played was in the group at the time of the playback and the playback violated the subject's expectations by making it appear as if the caller was in two places at once.

As predicted, females responded more quickly to playbacks of female callers and males exhibited a nonsignificant trend toward responding more quickly to male callers, a pattern commonly seen in other species (Appleby et al. 1999). As extra-group fertilizations are unknown in our study population, this sex-specific aggression is unlikely to be mate-guarding in the typical sense (Mumme et al. 1983; Haydock et al. 2001). Rather, it is likely a response to the threat of being replaced as a breeder by a rival coalition. Acorn woodpeckers may also be more attentive, in general, to the calls of same-sex conspecifics because those are the individuals with which they compete for breeding opportunities (Hannon et al. 1985).

Also, in line with our predictions, females responded more strongly to playbacks than males. Many birds exhibit the opposite pattern, with males being more aggressive than females (Brawn 1990; Fedy and Stutchbury 2005). However, female aggression may be selected for when mating opportunities and resources are constrained and is important in many species

(Rosvall 2011). For example, female crimson finches (*Neochmia phaeton*) were just as aggressive as males (Young et al. 2017) and, in tree swallows (*Tachycineta bicolor*), female aggression was a better predictor of nest-box acquisition than male aggression (Rosvall 2008). In acorn woodpeckers, females are less likely to inherit a breeding position in their natal territory, which creates greater competition for female breeding positions, and female breeders have fewer coalition partners on average to help them defend against intruders (Koenig 1981b; Koenig et al. 2000; Barve et al. 2019). This may select for increased female aggressiveness, which could result in a greater likelihood of both obtaining and defending a breeding position.

One limitation of our study is that we were not always able to use a different call exemplar for each subject, although we did so as much as possible (61 of 75 trials used a call exemplar that was unique to treatment category). Thus, we acknowledge that there is a remote possibility that responses to some playbacks may be attributed to idiosyncratic features of the recordings themselves rather than the identity of the caller per se (Kroodsma 1989).

CONCLUSION

The results of this study not only support earlier findings that acorn woodpeckers can discriminate between the calls of current and nongroup members but also further suggest that these woodpeckers can vocally discriminate between former group members living nearby and nongroup members. Our results also suggest that female and male acorn woodpeckers experience different selection pressures on territorial aggression. Further investigation is required to determine whether acorn woodpeckers recognize former group members via continued contact, long-term memory, or some combination thereof.

FUNDING

This work was supported by a Charles Walcott Graduate Fellowship, an Ivy Graduate Fellowship, and a grant from the Athena Fund from the Cornell Lab of Ornithology, a Graduate Research Fellowship, Doctoral Dissertation Improvement Grant (IOS-1701451), and grants IOS-1455900, IOS-1455881, and DEB-1256394 from the National Science Foundation, and a National Geographic Society Young Explorers Grant.

We thank the Hastings Reserve for the opportunity to conduct fieldwork, S. Pardo for assistance with the experimental design and statistical analyses, L. Johnson for assistance with statistical analyses, S. Barve for blinding the playback stimuli, and V. Voegeli for providing us with a loudspeaker. We are grateful to R. Anderson, S. Heimbach, T. Kuray, and E. Sparks for assistance in collecting the recordings used as playback stimuli, and we thank A. Ridley and two anonymous reviewers for helpful comments on the manuscript.

Conflict of interests: The authors declare no competing interests.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Pardo et al. (2020).

Handling editor: Amanda Ridley

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