Original Article

Experimental evidence that acorn woodpeckers recognize relationships among third parties no longer living together

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Triadic awareness, or knowledge of the relationships between others, is essential to navigating many complex social interactions. While some animals maintain relationships with former group members post-dispersal, recognizing cross-group relationships between others may be more cognitively challenging than simply recognizing relationships between members of a single group because there is typically much less opportunity to observe interactions between individuals that do not live together. We presented acorn woodpeckers (*Melanerpes formicivorus*), a highly social species, with playback stimuli consisting of a simulated chorus between two different individuals, a behavior that only occurs naturally between social affiliates. Subjects were expected to respond less rapidly if they perceived the callers as having an affiliative relationship. Females responded more rapidly to a pair of callers that never co-occurred in the same social group, and responded less rapidly to callers that were members of the same social group at the time of the experiment and to callers that last lived in the same group before the subject had hatched. This suggests that female acorn woodpeckers can infer the existence of relationships between conspecifics that live in separate groups by observing them interact after the conspecifics in question no longer live in the same group as each other. This study provides experimental evidence that nonhuman animals may recognize relationships between third parties that no longer live together and emphasizes the potential importance of social knowledge about distant social affiliates.

Key words: **cross-group relationship, long-term recognition, *Melanerpes formicivorus*, social cognition, triadic awareness, vocal recognition**

INTRODUCTION

The ability to recognize relationships between other individuals, known as triadic awareness or third-party knowledge, is vital for navigating complex social interactions such as alliances and coalitions (Seyfarth and Cheney 2015). Triadic awareness has been studied most extensively in primates (Cheney and Seyfarth 1980; Cheney et al. 1995; Perry et al. 2004; Crockford et al. 2007; Kubenova et al. 2017), and has also been documented in a variety of other vertebrates, including carnivores (Engh et al. 2005), cichlid fish (Grosenick et al. 2007), and birds (Massen et al. 2014). Most work, however, has focused narrowly on knowledge of third-party relationships between the subject's close

social affiliates, potentially ignoring other important social contexts in which triadic awareness may be used. Many taxa interact regularly with individuals outside their core social unit or territory, so an ability to recognize third-party relationships among these more peripheral social affiliates is likely beneficial. For example, family groups of African elephants (*Loxodonta africana*) maintain close social bonds with other family units, so knowledge about third-party relationships within this wider social network could be important for negotiating social interactions when groups meet (Moss and Poole 1983; Wittemyer et al. 2005). Similarly, cooperatively breeding cichlid fish (*Neolamprologus pulcher*) visit other territories prior to dispersal, and knowledge about the social relationships among individuals living on these territories likely improves the probability of successful integration (Jungwirth et al. 2015).

While the boundaries of a social group can be difficult to define (Aureli et al. 2008; Boucherie et al. 2019), here we use the term to

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Table 1

Predicted responses to each treatment under each hypothesis

Hypothesis	Related callers—currently live together	Related callers—last together after subject fledged	Related callers—last together before subject hatched	Related callers—never lived together	Unrelated callers—never lived together
Subjects only recognize relationships between individuals that currently live together	Slow response, no close approach	Fast response, close approach	Fast response, close approach	Fast response, close approach	Fast response, close approach
Subjects use vocal kin signatures to infer kin relationships between others	Slow response, no close approach	Slow response, no close approach	Slow response, no close approach	Slow response, no close approach	Fast response, close approach
Subjects only recognize relationships between others if they observed the callers living together	Slow response, no close approach	Slow response, no close approach	Fast response, close approach	Fast response, close approach	Fast response, close approach
Subjects recognize relationships between callers that no longer live together by observing them visit one another post-dispersal	Slow response, no close approach	Slow response, no close approach	Slow response, no close approach	Fast response, close approach	Fast response, close approach

Columns represent treatment categories and rows represent different hypotheses. A slow response and no close approach to the speaker was expected if the subject recognized the relationship between the callers and, therefore, perceived the playback stimulus (two callers overlapping each other) as congruous. A fast response and close approach to the speaker was expected if the subject did not recognize the relationship between the callers and therefore perceived the playback stimulus as incongruous.

refer specifically to a core social group of individuals who spend significantly more time interacting with one another than with other social affiliates, occupy and defend the same territory in the case of territorial species, and cooperate with one another in the case of cooperative species. Recognition of the relationships among members of other groups could take two different forms. In one scenario, individuals A and B could have a relationship and live in the same group as each other but in a different group from individual C, and C could recognize the relationship between A and B. In another scenario, A and B could live in separate groups but still maintain a relationship, and individual C could live in a third group, but recognize the relationship between A and B. Because some animals maintain lifelong relationships with former group members by visiting them post-dispersal (Dickinson et al. 1996; Boeckle and Bugnyar 2012), an ability to recognize relationships among third parties that used to live in the same group as each other but no longer do so, hereafter termed "cross-group relationships," could be highly beneficial. However, such an ability is likely more cognitively demanding than simply recognizing relationships between closely affiliated third parties that currently belong to the same core social unit. Individuals that maintain relationships across core social units or territories presumably interact less frequently than those that co-occur in the same core social unit on the same territory, so there are likely fewer opportunities for animals to learn about cross-group relationships between third parties than intragroup relationships between third parties.

Two studies have demonstrated that some animals have the capacity to recognize relationships or associations among individuals that live in the same group as each other but not the same group as the subject. When two mixed-sex groups of common ravens (*Corvus corax*) were housed in adjacent cages, the males recognized simulated reversals in dominance status between members of the neighboring group (Massen et al. 2014). Similarly, wild female acorn woodpeckers (*Melanerpes formicivorus*) were able to determine whether two individuals from outside the subject's social group belonged to the same group as each other (Pardo et al. 2018). No prior study, however, has apparently documented whether animals can recognize relationships between third parties that no longer live together (i.e., cross-group third party relationships).

Acorn woodpeckers in California are territorial, permanent residents that live in cooperatively breeding family groups with 1–4 joint-nesting females, 1–8 cobreeding males, and up to 10 nonbreeding helpers of either sex, which are the adult offspring of the breeders (Koenig 1981a). Group members cooperate to raise offspring in a single nest, to store acorns in specially drilled holes in a "granary" tree, and to defend this resource from outsiders, making a "group" easy to identify in this species (Koenig 1981a; Mumme and de Queiroz 1985; Koenig and Walters 2016). Cobreeders of the same sex are close relatives, but opposite sex breeders are unrelated (Haydock et al. 2001). Suitable breeding territories are limited (Koenig et al. 2011; Barve et al. 2019), and thus when all the breeders of a particular sex die or disappear from an existing group, helpers (and sometimes breeders) from other groups agonistically compete to fill the vacancy in dramatic "power struggles" (Koenig 1981b; Hannon et al. 1985). To improve their chances of competing successfully, individuals form coalitions with same-sex relatives, and these coalition members often share the breeding position as cobreeders upon winning the power struggle (Hannon et al. 1985; Barve et al. 2020). Both males and females make frequent extraterritorial forays to other groups, which may help them become familiar with a large number of individuals from other groups and identify breeding vacancies (Koenig et al. 1996; Barve et al. 2020).

Acorn woodpeckers discriminate between the calls of former group members that have dispersed to a nearby group and the calls of familiar individuals with whom they have never shared a group, suggesting that they maintain relationships with, or at least recognize, some of their former group members several years postdispersal (Pardo et al. 2020a). Moreover, individuals sometimes return to their natal group many years after dispersal, and same sex, related former groupmates that currently live on separate territories sometimes join to form a coalition during power struggles for breeding vacancies, strongly suggesting the existence of cross-group relationships among former groupmates (Hagemeyer N, personal communication). If acorn woodpeckers can recognize such long-term, cross-group relationships between third parties, it could potentially help them assess the number of allies that a rival could recruit during a power struggle. However, while acorn woodpeckers

have been shown to recognize the association between members of another group that *currently* live with each other (Pardo et al. 2018), whether they can also recognize third-party relationships between individuals that *formerly* lived together on the same territory has not previously been tested.

Acorn woodpeckers could potentially learn about the relationships of conspecifics occupying other territories by observing interactions among them during extraterritorial forays (Barve et al. 2020). If acorn woodpecker vocalizations contain a vocal signature of kinship, woodpeckers might also use this putative cue to infer the existence of relationships among others (Price 1998; Yurk et al. 2002). We investigated whether female and male acorn woodpeckers can recognize relationships between members of other groups that occupy separate territories, and if so, by what mechanism. Specifically, we tested the following competing hypotheses:

(A) acorn woodpeckers only recognize relationships between members of other groups that currently live together;
(B) acorn woodpeckers can determine if two individuals living in separate groups are genetically related to one another via a putative vocal signature of kinship;
(C) acorn woodpeckers can recognize relationships between members of other groups that no longer live together only if they observed those individuals living together in the past;
(D) acorn woodpeckers can recognize relationships between members of other groups that no longer live together, even if the subject never observed the focal individuals living in the same group, by observing the focal individuals visit one another after those individuals dispersed into separate groups.

Based on previous work (Pardo et al. 2018), we expected subjects to respond more strongly (i.e., shorter latency and/or closer approach) to playback of an overlapping chorus between callers that were *unrelated* to each other and *never* lived in the same group compared to playback of an overlapping chorus between callers that were *related* to each other and lived in the *same* group at the time of the experiment. This is because acorn woodpeckers typically only produce overlapping choruses with their social affiliates, so subjects should perceive a simulated chorus between two unaffiliated individuals as highly anomalous. While the function of these overlapping choruses has yet to be determined, they appear to be an affiliative greeting display (MacRoberts and MacRoberts 1976).

Our predictions for how subjects would respond to a pair of callers that did not live together at the time of the experiment but lived together in the past and/or were genetically related differed under each of our hypotheses (Table 1). We also predicted that if any sex differences existed in triadic awareness, females would be better able, or more motivated, than males to keep track of relationships between members of other groups, given that females are more likely to disperse and compete for breeding vacancies in other groups (Hannon et al. 1985; Koenig et al. 1996).

MATERIALS AND METHODS

Study site and population monitoring

We collected all data at Hastings Natural History Reservation in central coastal California, where the acorn woodpecker population has been the subject of a long-term study since 1971 and >95% of the individuals are color-banded (MacRoberts and MacRoberts 1976; Koenig 1981a). Each year, approximately 50 social groups are monitored, and a census is conducted of each group

approximately every 8–10 weeks. Subjects for this experiment were 26 wild adult acorn woodpeckers, including 9 breeder females, 5 helper females, 7 breeder males, and 5 helper males from 18 social groups. Experimental trials were conducted from 19 Jul to 27 Nov 2017 and from 6 May to 8 Jul 2018.

Experimental design

We conducted a playback experiment with a violation-of-expectation paradigm following a previously published protocol (Pardo et al. 2018). Woodpeckers were presented with playback stimuli consisting of *waka* calls recorded from two different individuals, overlapped artificially to simulate two birds calling simultaneously. *Waka* calls are individually specific, affiliative vocalizations that are frequently given in an overlapping chorus between two or more members of the same group, but rarely given between individuals with no affiliative relationship (MacRoberts and MacRoberts 1976; Yao 2008). If the two overlapping callers in a playback stimulus had no affiliative relationship that the subjects recognized, the playback stimulus was expected to violate the expectations of the subjects and the subjects were expected to respond more strongly by reacting more rapidly and approaching the speaker more closely. Conversely, if the two overlapping callers in a playback stimulus had an affiliative relationship that the subjects recognized, the subjects were expected to respond less strongly (Pardo et al. 2018).

We presented subjects with playbacks from the following five treatment categories and attempted to present each subject with all five treatments, although this was not always possible (Supplementary Table S1). In all cases, the callers used in each playback stimulus were unrelated to and had never lived in the same group as the subject. The order of presentation was balanced using an incomplete Latin square design (Supplementary Table S1), and playbacks to the same group were spaced apart by 2–48 days (median = 4 days) to avoid habituation. Playbacks to groups within 250 m of one another were also spaced apart by at least 2 days.

(T1) *Related callers—currently live together:* two related callers that lived in the same social group at the time of the experiment.
(T2) *Related callers—last together after subject fledged:* two related callers that formerly lived in the same social group but ceased to do so because of dispersal or death of one individual 1.0–5.8 years (mean: 2.1 years) prior to the experiment, but *after* the subject had fledged. Thus, the subject would have had the opportunity to observe the callers living together in the past during extraterritorial forays to the callers' group (Barve et al. 2020).
(T3) *Related callers—last together before subject hatched:* two related callers that formerly lived in the same group, dispersed into separate groups before the subject hatched in the nest 2.2–6.4 years (mean: 4.5 years) prior to the experiment, and were both confirmed to be alive after the subject had fledged. Thus, the subject would not have had the opportunity to observe the callers living together but could have observed them visiting one another post-dispersal.
(T4) *Related callers—never lived together:* two genetically related callers that never lived in the same group and were both confirmed to be alive after the subject fledged.
(T5) *Unrelated callers—never lived together (control):* two unrelated callers that never lived in the same group and were both confirmed to be alive after the subject fledged.

Because of the difficulty of obtaining playback-quality recordings from a canopy-dwelling species with unpredictable calling patterns, for some playback stimuli we were forced to use the calls of individuals that had died or disappeared from the study area prior to the experiment. Preliminary analyses indicated that subjects responded more quickly to playback stimuli containing the call of a dead or missing individual (Supplementary Table S2 and Figure S1). Therefore, we excluded all trials that used the call of a dead or missing individual from the analyses presented here (see Supplementary Materials for analyses including both live and dead callers). Most (19 of 24) playback stimuli for treatment T2 (related callers—last together after subject fledged) contained the call of a dead or missing individual, so this treatment was excluded from analysis. After excluding the aforementioned trials, there remained 24 playbacks of related callers—currently live together, 11 playbacks of related callers—last together before subject hatched, 13 playbacks of related callers—never lived together, and 13 playbacks of unrelated callers—never lived together, with a total sample size of 25 subjects (8 breeder females, 5 helper females, 7 breeder males, and 5 helper males) from 17 different groups (Supplementary Table S1).

Playback stimuli contained only recordings from callers of the same sex as the subject to increase the likelihood that the subjects would respond (Hannon et al. 1985). For the three treatment categories consisting of a pair of related callers, relatedness between the two callers in each playback stimulus was calculated using a pedigree, which was constructed from parentage assignments based on microsatellite markers (Haydock J, unpublished data). Mean relatedness ($r_{(T1)} = 0.36$, $r_{(T3)} = 0.38$, $r_{(T4)} = 0.38$) did not differ significantly across these three treatment categories (ANOVA, $F_{2,45} = 0.10$, $P = 0.91$).

To increase the likelihood that subjects had the opportunity to become familiar with all the callers, we presented subjects with callers from territories as near as possible to the subject's territory. The mean ± standard deviation (SD) distance between the territory centroids of the subjects and the callers was 435 ± 233 m and did not differ significantly across treatment categories (ANOVA, $F_{3,57} = 0.43$, $P = 0.73$). As acorn woodpeckers make daily forays to the territories of other groups with a mean foray distance of 500–600 m (Barve et al. 2020), subjects were likely familiar with all or most of the callers with which they were presented.

Whenever possible, we constructed each playback stimulus from a unique pair of call exemplars to minimize pseudoreplication (Supplementary Table S1). All of the playback stimuli for the treatments "related callers—last together before subject hatched" and "unrelated callers—never lived together" consisted of a unique pair of call exemplars that was only used once, although we sometimes used multiple different exemplars of the same callers. However, only 14 of 24 stimuli for "related callers—currently live together" and 8 of 13 stimuli for "related callers—never lived together" consisted of a unique pair of call exemplars.

The speaker was placed in a tree 40–50 m away from the focal bird, and playback volume was standardized at 100.1 ± 1.3 dB re 20 μPa at 1 m, which is near the upper end of the range of natural *waka* calls (Pardo et al. 2018). Playback stimuli consisted of 1 min of background noise with a fade-in, followed by the two overlapping calls, then 30 s of background noise, then the same two overlapping calls again, and a final 10 s of background noise with a fade-out. The trial was aborted if the focal bird flew away before the first set of overlapping calls began. As *waka* calls consist of a variable number of repeated notes, we could not standardize the duration

of the playback stimuli without heavily modifying the calls. The duration of the overlapping call chorus within each playback stimulus ranged from 3.7 to 7.0 s and did not differ significantly among treatments (ANOVA, $F_{3,57} = 0.21$, $P = 0.89$).

Measuring response to playback

We videotaped the subject during each trial and measured the following six response variables within a 3-min period beginning with the onset of the first pair of overlapping calls in the playback stimulus: latency to the first "reaction" (vocalizing, flying to higher vantage point, or flying toward speaker), latency to the first "positive flight" (flying to higher vantage point or toward 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 to the speaker. For latency variables, if the behavior of interest did not occur within the allotted 3 min, the latency was assigned the maximum possible value of 180 s and marked as "censored." We were blind to the experimental condition in each trial until all the videos had been scored. Before the trials, we measured distances between the speaker and various nearby landmarks using a transect tape and used these measurements to estimate approach distances to the nearest 5 m during the playbacks.

We used only *latency to react*, *latency to positive flight*, and *distance of first approach* in the analysis, as the other response variables were highly correlated (Pearson's $r > 0.80$) with at least one of these variables. We used both *latency to react* and *latency to positive flight* because it was unclear whether reaction strength was best measured by flight behaviors and vocalizations or by flight behaviors alone. We could not measure *latency to vocalize* as a stand-alone variable because there were many trials in which the subject flew toward the speaker and out of sight before the first vocalization was heard, and thus it was impossible to know whether the vocalization was produced by the subject or another individual.

Statistical analyses

All analyses were conducted in R 3.6.3 (R Core Team 2020), and the significance level was set to 0.05 for all tests. We used mixed-effects Cox proportional hazards regression, which accounts for censored observations, in the package *coxme* (Therneau 2019) to analyze *latency to react* and *latency to positive flight*, and a linear mixed model in the packages *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2017) to analyze *distance of first approach*.

The residuals for *distance of first approach* were not normally distributed (Shapiro–Wilk test, W = 0.95, $P = 0.02$), so we rank transformed *distance of first approach* before running the linear model (Shapiro–Wilk test on rank-transformed model: W = 0.97, $P = 0.11$). Each model contained *treatment*, *sex*, *treatment*sex*, *order of presentation*, and *days since previous playback* as fixed effects, and *individual ID* as a random effect. *Days since previous playback* represented the number of days since the last playback to the same group and was coded as 0 for the first playback to a given group. We compared all treatments to the control (unrelated callers—never lived together) separately for females and males in the package "*emmeans*" (Lenth 2019) using Dunnett's method to adjust for multiple comparisons within a given model.

RESULTS

Latency to react

Subject latency to vocalize, fly up, or fly toward the speaker (*latency to react*) differed among treatments (Figure 1; Table 2). Pairwise
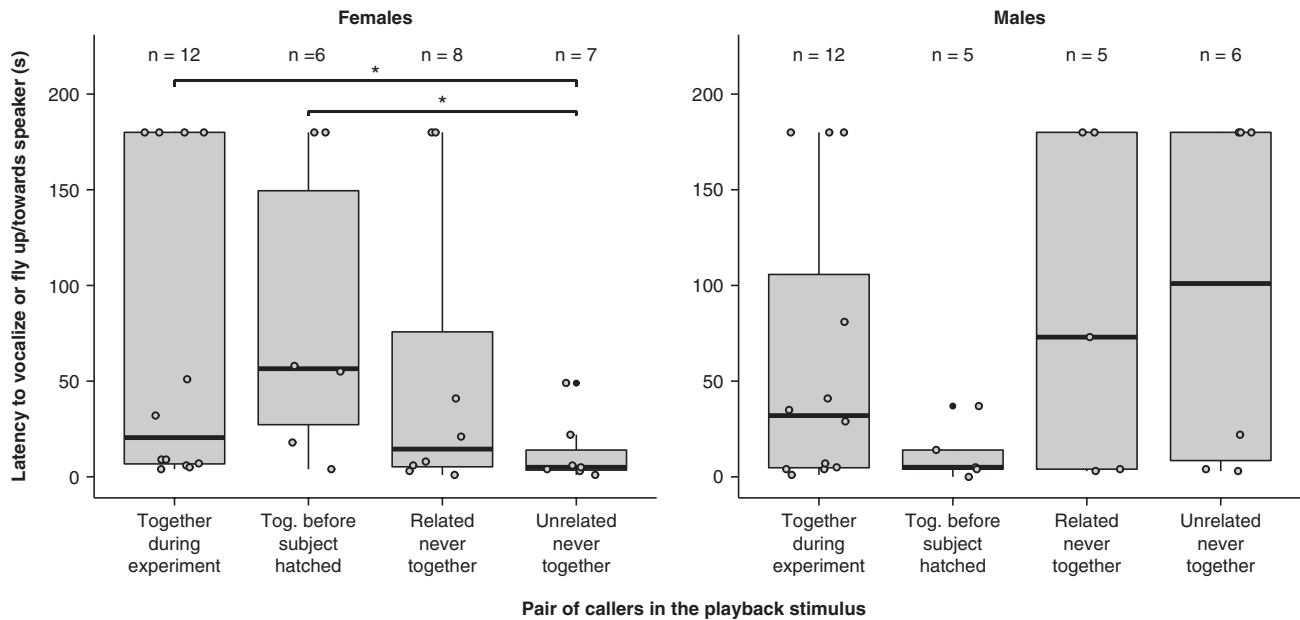
Figure 1

Latency to react (vocalize, fly up to higher vantage point, or fly toward speaker) as a function of *treatment*, with females and males presented separately. 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. Asterisk indicates $P < 0.05$ (Dunnett's test on Cox regression model).

Table 2

Output for each model

Model type	Response variable	n	Fixed effects	Chi-square	df	P-value
Cox regression	Latency to react	25 subjects, 61 trials	Treatment	13.3	3	**0.00**
			Sex	1.7	1	0.19
			Treatment × Sex	5.9	3	0.12
			Order	2.6	4	0.62
			Days since previous playback	1.6	1	0.21
Cox regression	Latency to positive flight	25 subjects, 61 trials	Treatment	6.9	3	0.08
			Sex	0.7	1	0.41
			Treatment × Sex	2.3	3	0.51
			Order	3.4	4	0.50
			Days since previous playback	0.6	1	0.42
Linear regression	Distance of first approach (rank transformed)	25 subjects, 59 trials	Treatment	3.5	3	0.33
			Sex	0.03	1	0.86
			Treatment × Sex	8.3	3	**0.04**
			Order	2.1	4	0.72
			Days since previous playback	0.71	1	0.40

Latency to react = latency to subject's first vocalization or flight up to a higher vantage point or toward the speaker; *latency to positive flight* = latency to subject's first flight up to a higher vantage point or towards the speaker; *distance of first approach* = closest distance between the subject and the speaker during subject's first approach toward the speaker. *Distance of first approach* was rank-transformed to correct for non-normality of the residuals. Each model contained all five fixed effects listed plus *individual ID* as a random effect. Statistically significant *P*-values are in bold.

comparisons separated by sex (Table 3) showed that females reacted more quickly to a pair of unrelated callers that never lived together (T5) than to a pair of related callers that lived together at the time of the experiment (T1). Females also reacted more quickly to a pair of unrelated callers that never lived together (T5) than to a pair of related callers that last lived together before the subject hatched (T3), but they exhibited no difference in *latency to react* between a pair of unrelated callers that never lived together (T5) and a pair

of related callers that never lived together (T4). Males showed no significant differences in *latency to react* among any of the treatments (Table 3).
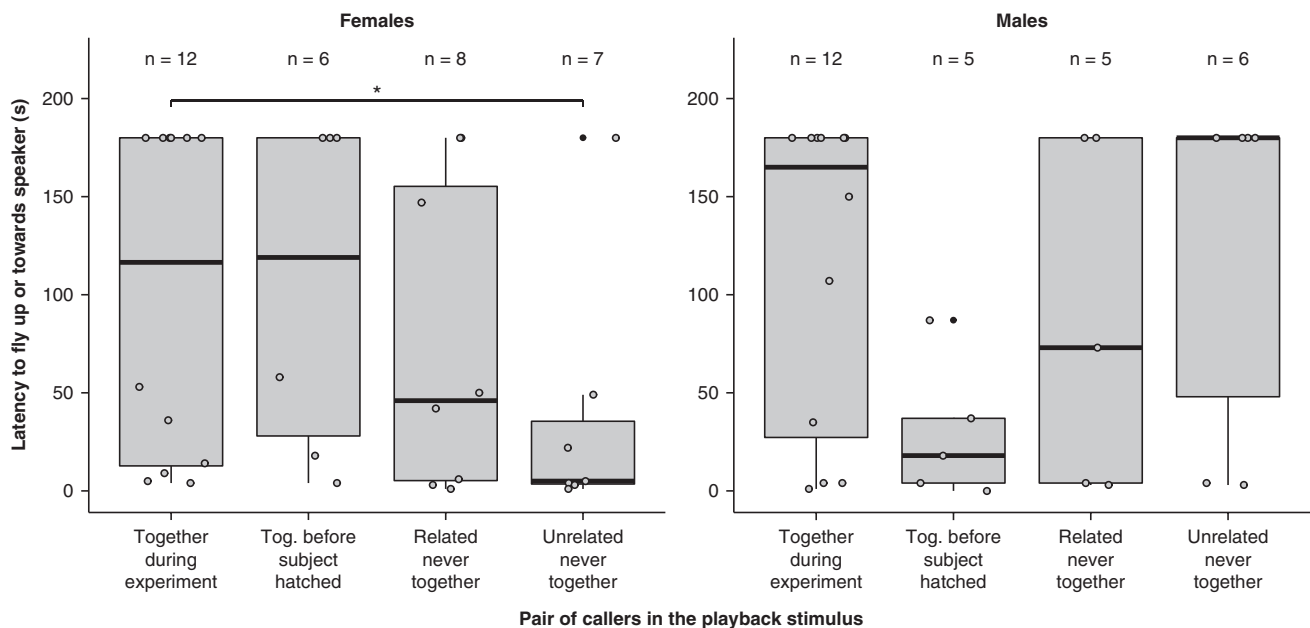
Latency to positive flight

Subject latency to fly up or toward the speaker (*latency to positive flight*) differed among treatments (Figure 2; Table 2). Pairwise comparisons

Table 3

Pairwise comparisons (separated by sex) of the control treatment (T5: Unrelated callers—never lived together) with each other level of *treatment* using Dunnett's test

Sex	Model	T1: Currently live together		T3: Last together before subject hatched		T4: Related but never together	
		Z	*P*-value	*Z*	*P*-value	*Z*	*P*-value
Females	Latency to react	−3.3	**0.00**	−2.9	**0.01**	−2.1	0.11
	Latency to positive flight	−2.5	**0.04**	−1.7	0.23	−0.99	0.62
	Distance of first approach	$t_{35.5} = -0.87$	0.70	$t_{38.6} = 0.44$	0.92	$t_{37.3} = -1.2$	0.51
Males	Latency to react	−0.21	0.98	0.57	0.86	−0.25	0.98
	Latency to positive flight	−0.71	0.79	0.54	0.88	0.03	1.00
	Distance of first approach	$t_{36.9} = 0.00$	1.00	$t_{45.2} = -1.9$	0.16	$t_{30.9} = -0.07$	1.00

Test statistics (*Z*-ratio or *t*-ratio$_{\text{df}}$) and *P*-values are presented for each contrast. For the latency models, a positive *Z*-ratio indicates that subjects responded more quickly to the treatment in question than to the control; a negative value indicates the opposite. For the distance model, a positive *t*-ratio indicates that subjects approached less closely to the treatment in question than to the control. *Distance of first approach* was rank-transformed to correct for non-normality of the residuals. Statistically significant *P*-values are in bold.

Figure 2

Latency to positive flight (fly up to higher vantage point or toward speaker) as a function of *treatment*, with females and males presented separately. 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. Asterisk indicates *P*<0.05 (Dunnett's test on Cox regression model).

separated by sex (Table 3) revealed that females exhibited their first flight up or towards the speaker more quickly in response to unrelated callers that never lived together (T5) than in response to related callers that lived together at the time of the experiment (T1). However, they showed no difference in *latency to positive flight* between unrelated callers that never lived together (T5) and either of the other treatments. Males showed no significant differences in *latency to positive flight* among any of the treatments (Table 3).

Distance of first approach

Females and males differed in how *treatment* affected the rank-transformed distance of their first approach to the speaker (Table 2). However, none of the pairwise comparisons between unrelated callers—never lived together (T5) and any of the other

treatments were statistically significant for either sex (Figure 3; Table 3).

DISCUSSION

Results support the hypothesis that female acorn woodpeckers can discriminate between pairs of unrelated callers that never lived together and pairs of related callers that last lived together before the subject hatched in the nest, most likely by observing the latter pair of callers visit one another after the callers dispersed into separate groups. Results also support earlier findings that female acorn woodpeckers can discriminate between pairs of callers that never lived together in the same group and pairs of callers that currently live together (Pardo et al. 2018). In the current study, females were presented exclusively with female callers, whereas
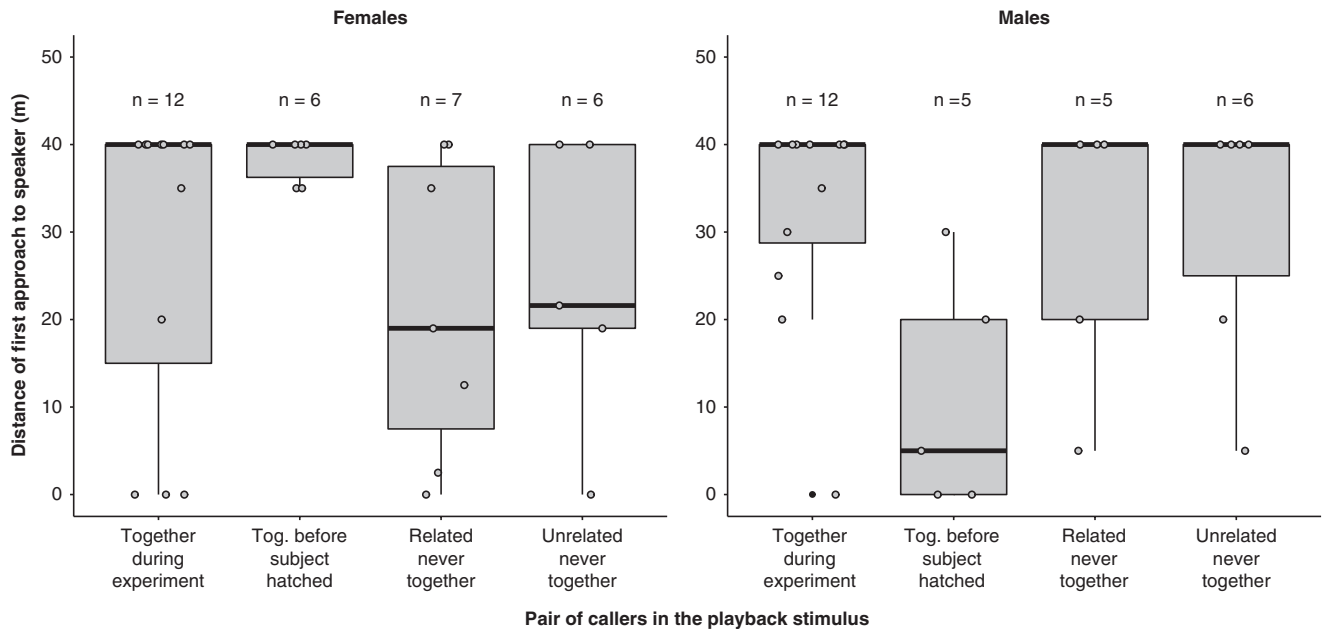
Figure 3

Rank-transformed *distance of first approach* as a function of *treatment*, with females and males presented separately. Shorter distances indicate a closer approach. 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. The sample size for females is smaller for this analysis than for *latency to react* and *latency to positive flight* because of two missing data points.

Pardo et al. (2018) presented females with a mixed-sex pair of callers, suggesting that female acorn woodpeckers can recognize associations between both female–female and female–male dyads from other groups.

Unlike females, males in this study did not exhibit any differences in response among playback treatments. The differences between male and female subjects could be due to caller sex, as subjects only received playbacks of same-sex callers, or due to an overall difference in social knowledge or responsiveness between male and female acorn woodpeckers. Female acorn woodpeckers are more likely to disperse than males, and are more likely to have to compete in a power struggle to secure a breeding opportunity (Hannon et al. 1985; Koenig et al. 2000). Thus, it may benefit females more than males to closely monitor the interactions among individuals on other territories with whom they are competing.

Females, but not males, also responded more quickly to playback stimuli containing the call of a dead or missing individual (see Supplementary Material). Females may have failed to recognize cross-group relationships between dead or missing individuals because they had not observed those individuals interacting with one another recently. Alternatively, females may have responded more quickly to the calls of dead or missing individuals because hearing the call of an individual that no longer lived in the study area violated their expectations. In a previous study both male and female acorn woodpeckers responded more strongly to the calls of dead or missing former members of their own group than to the calls of former group members still living nearby (Pardo et al. 2020a), while in the current study subjects and callers never lived in the same group and only females responded more strongly to dead or missing individuals. One potential explanation for this is that while both sexes may be attentive to the status of their former groupmates, females may be better able or more motivated than males to keep track of non-group members.

Most studies of triadic awareness assume that animals learn the relationships between others by recognizing individual conspecifics and observing them as they interact with one another (Seyfarth and Cheney 2015). In theory, however, it might be possible to infer the relationships between third parties using simple cues of kinship or status. For example, the calls of killer whales (*Orcinus orca*) from the same matriline are more similar than the calls of whales from different matrilines, which could potentially be used to assess the degree of relatedness between third parties (Yurk et al. 2002). Similarly, paper wasps (*Polistes dominulus*) have facial markings that signal their dominance status, which could potentially be used to assess the relative dominance ranks of third-party dyads (Tibbetts and Dale 2004).

If female acorn woodpeckers use group signatures (genetic or learned) to assess the relationships among others, then inferring the existence of an association between individuals that no longer live in the same group would be no more cognitively demanding than inferring the existence of an association between individuals that currently live together. If, however, they rely on individual recognition and observation of the interactions among others to infer the existence of third-party relationships, then recognizing relationships between individuals that no longer live together may be substantially more difficult than recognizing relationships between individuals that currently live together. Recognizing such cross-group relationships between other individuals without the help of group signatures would require either remembering for several years that the birds involved used to live together, or observing the birds interact with one another post-dispersal, which is presumably a much rarer event than the frequent interactions among members of the same group.

We did not expect acorn woodpeckers to rely on group signatures to recognize third-party relationships for multiple reasons. First, there is no evidence of learned or genetic group signatures

in acorn woodpeckers, and a previous study failed to find evidence that the *waka* calls of groupmates were any more similar in acoustic structure than the *waka* calls of individuals from separate groups (Yao 2008). Moreover, even if learned group signatures exist in acorn woodpeckers, it is unlikely that subjects used them to recognize the relationships between individuals that no longer lived together. Five out of six female playback stimuli in which the callers last lived together before the subject hatched were recorded after the callers were already living in separate groups, and therefore would have been unlikely to share their prior group's learned signature. Genetically determined kin signatures are also unlikely to be the basis for vocal recognition in this species, because in a previous study, female acorn woodpeckers recognized the association between male and female breeders that lived in the same group but were unrelated (Pardo et al. 2018). Our current finding that females did not discriminate between a pair of unrelated callers that never lived together (T5) and a pair of genetically related callers that never lived together (T4) provides further evidence against the genetic kin signature hypothesis.

Females responded more quickly to callers that never lived together (T5) than to callers that used to live together but dispersed to separate groups before the subject hatched (T3). This result should be viewed with caution because of the small sample size. However, it suggests that female acorn woodpeckers may recognize cross-group relationships between third parties without ever having observed the third parties living in the same group. Since group signatures are unlikely, the woodpeckers likely recognized such relationships by observing the third parties in question visit one another after having dispersed into separate groups.

Understanding the relationships between other individuals that no longer live together represents a cognitive leap beyond the forms of triadic awareness documented in previous studies. Great tits (*Parus major*) remembered the dominance relationship between two rival males for at least 15 min after witnessing a single simulated interaction between them (Peake et al. 2002), and chimpanzees (*Pan troglodytes*) remembered their own agonistic encounters for at least 2 h (Wittig et al. 2014). However, acorn woodpeckers may not visit their former group members every day, and even when they do visit one another, a third individual can only witness their interaction if they happen to co-occur in time and space. Therefore, monitoring the relationships between other individuals that live in separate groups likely requires acorn woodpeckers to retain third-party knowledge for considerably longer than has been documented in other taxa.

Social group size is often used as a proxy for social complexity, and it is often assumed that the size of the core social group determines the number of third-party relationships that individuals need to assess simultaneously (Dunbar 1992). However, this view may be biased by the fact that most research on triadic awareness has been conducted with primates, in which the primary function of triadic awareness appears to be to monitor complex competitive interactions within a single social group that occupies the same territory (Seyfarth and Cheney 2015).

In many birds, social group size often fluctuates considerably over time, and the number of differentiated relationships and social interactions that an individual must keep track of is less closely tied to group size than in primates (Boucherie et al. 2019). Acorn woodpeckers live in a social environment in which many complex competitive interactions take place between, rather than within, territorial groups (Koenig 1981b; Hannon et al. 1985). In areas with sufficient suitable habitat, a radius of 435 m (the mean distance between the territories of subjects and callers in the current study) can encompass ~10 acorn woodpecker groups (unpublished data), each group having a mean size of 4.76 ± 2.58 adults (Koenig 1981a). Therefore, although acorn woodpeckers have much smaller social groups than many primates, acorn woodpeckers likely individually recognize and monitor the relationships among at least 40–50 conspecifics, which is comparable to many primate societies (Dunbar et al. 2018).

The observation that brain size decreases with social group size in the woodpecker clade, opposite the pattern found in primates, supports the idea that social group size *per se* is likely not the primary selective force on the evolution of cognition in woodpeckers (Fedorova et al. 2017). Studying social cognition in non-group living woodpecker species, particularly congeners of acorn woodpeckers, could have important implications for our understanding of social complexity and the evolution of intelligence. More broadly, this study highlights the importance of considering extended social environments when investigating social cognition.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

CONFLICT OF INTEREST

The authors declare no competing interests.

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

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