

## Research



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# Joint attention skills in wild Arabian babblers (*Turdoides squamiceps*): a consequence of cooperative breeding?

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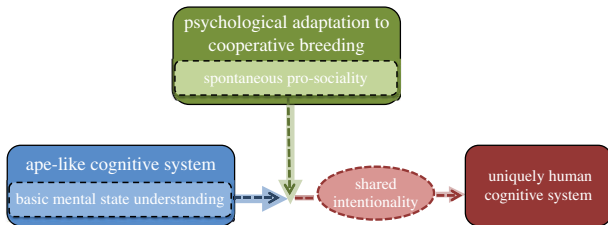
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Human cooperation strongly relies on the ability of interlocutors to coordinate each other’s attentional state: joint attention. One predominant hypothesis postulates that this hallmark of the unique cognitive system of humans evolved due to the combination of an ape-like cognitive system and the prosocial motives that facilitate cooperative breeding. Here, we tested this hypothesis by investigating communicative interactions of a cooperatively breeding bird species, the Arabian babbler (*Turdoides squamiceps*). The behaviour of 12 wild social groups was observed focusing on two distinct communicative behaviours: OBJECT PRESENTATION and BABBLER WALK. The results showed that both behaviours fulfilled the criteria for first-order intentional communication and involved co-orientation of recipients’ attention. In turn, recipients responded with cooperative and communicative acts that resulted in coordinated joint travel between interlocutors. These findings provide the first evidence that another animal species shows several key criteria traditionally used to infer joint attention in prelinguistic human infants. Furthermore, they emphasize the influence of cooperative breeding on sophisticated socio-cognitive performances, while questioning the necessity of an ape-like cognitive system underlying joint attentional behaviour.

## 1. Introduction

The extraordinary degree of cooperation exhibited by humans seems unrivalled in the animal kingdom [1,2]. Theorists have implicated a specific cognitive capacity, joint attention, as one of the essential building blocks for the evolution of the cooperative abilities of humans [1,3]. Traditionally, joint attention has been defined as the ability to attract and coordinate the attention of a recipient towards a locus of mutual interest (e.g. an object/event in the environment [4]). Precursors of this cognitive capacity can already be found in human infants at the age of approximately six months, who respond to joint attention by following the direction of a caretaker’s gesture [5]. At the age of 9–12 months, infants are capable of initiating joint attention with a social partner by gesturing towards a locus of mutual interest [4]. Consequently, the development of joint attention skills is seen as a fundamental milestone in the ontogeny of human cooperative communication [5,6]. Some scholars even see joint attention as the ‘small difference that made a big difference’ in the cognitive evolution of our species [3].

One predominant hypothesis about the evolution of human sophisticated social cognition, the ‘cooperative breeding’ hypothesis [2], postulates that cooperative breeding installed prosocial psychological functioning supporting systematic alloparental care. This, in turn, resulted in immediate consequences for socio-cognitive performance [7]: Caretakers of cooperative breeders evolved specific cognitive capacities for understanding the needs of others’ offspring. In parallel, the offspring developed elaborate communicative signalling to



**Figure 1.** The hypothesized role of cooperative breeding in the transition from ape-like to uniquely human cognition (after [2, p. 177]).

attract attention and care from caretakers other than their mothers [8]. Concerning humans, it has been argued that the exceptional co-occurrence of an existing ape-like cognitive system together with humans' systematic reliance on alloparental care [9,10] gave rise to unique socio-cognitive capacities such as joint attention (figure 1) [2,7].

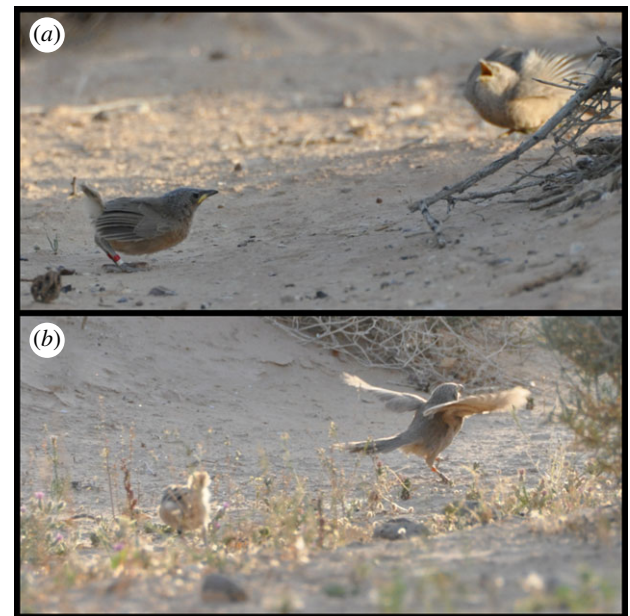
However, are joint attentional skills indeed uniquely human and is the combination of an ape-like cognitive system and cooperative breeding a crucial prerequisite?

To date, relatively little is known about joint attentional skills and the acting selection pressures in other animal species. Furthermore, whether specific behaviours of non-human animals towards human caretakers (e.g. gaze alternation in chimpanzees, *Pan troglodytes* [11]; pointing in bottlenose dolphins, *Tursiops truncatus* [12]; and vocal learning in grey parrots, *Psittacus erithacus* [13]) qualify as joint attentional skills in the human sense is subject to a contentious debate [3,14,15].

Here, we revisited the claim that joint attentional skills are a uniquely human ability [3,15] and tested whether the combination of an ape-like cognitive system and cooperative breeding represents a necessary requirement for joint attention to unfold [2]. We predicted that if an ape-like cognitive system and cooperative breeding are both necessary for joint attention [2,7], bird species will not exhibit key hallmarks of this trait. However, if an ape-like cognitive system is not necessary, but cooperative breeding does facilitate the performance of joint attention skills [16], cooperatively breeding species will demonstrate hallmarks of joint attention. To test these predictions, we investigated communicative interactions in a cooperatively breeding bird species, the Arabian babbler (*Turdoides squamiceps*), in the wild.

Arabian babblers live in stable social groups [17], consisting of 2–20 kin and non-kin from both sexes [17]. All members provide substantial alloparental care and use elaborate communicative signalling [17]. We focused on two distinct signals, 'OBJECT PRESENTATION' [18] and 'BABBLER WALK', which are frequently used to solicit following behaviour from conspecifics. OBJECT PRESENTATION involves the discreet presentation of an object to attract the recipient's attention without being seen by other group members. The goal is to lead the recipient towards a hidden location for copulation [18] (see electronic supplementary material, video S1). BABBLER WALK is a multi-modal signal that involves conspicuous wing waving and vocalizations, and is used to solicit a conspecific to follow the signaller (figure 2).

We paid special attention to two distinct issues that have hampered comparative research on joint attention. First, disagreement on an applicable definition of joint attention has so far prevented valid quantitative comparisons between human and other animal species [19–21]. For example, some define joint attention as the 'intentional co-orientation of two or more organisms to the same locus' [21]. Others



**Figure 2.** Adult caretaker (right) performing **BABBLER WALK** by (a) waving its wings and vocalizing in front of a fledgling; then (b) turning and hopping away while waving its wings, resulting in a following response. (Online version in colour.)

(e.g. [3]), by contrast, require complex mind reading and define it as 'the mutual awareness of having attended to the same entity between two (or more) individuals. Mutual awareness is established through communication by at least one individual during mutual gaze' [20]. To overcome this lack of consensus, we refrained from testing whether communicative episodes between Arabian babblers fit a specific definition. Instead, we investigated whether communicative interactions that were initiated by OBJECT PRESENTATION and BABBLER WALK fulfilled distinct hallmarks that have traditionally been used to infer joint attention in prelinguistic human infants: (i) intentional communication (e.g. [21,22]), (ii) co-orientation of attention (e.g. [4,15]) and (iii) mutual awareness (e.g. [20,23]). By applying this approach, we aimed to instigate a constructive discussion on joint attentional skills that provides useful tools to pinpoint the different degrees of joint attention and cognitive capacities involved [19].

Second, research on joint attention in non-human species has been strongly biased towards interactions with objects (e.g. [12,20]). However, joint attention can revolve around any type of locus [15] such as, for instance, the interlocutors themselves, or the activity they are performing at the time [4,24]. Hence, we examined whether signallers acted to attract and co-orient recipients' attention to their joint travel.

We thus investigated whether communicative episodes initiated by OBJECT PRESENTATION and BABBLER WALK fulfil the following three key hallmarks of joint attention (see table 1 and methods for detailed operational criteria).

### (a) First-order intentional communication

To investigate the presence of first-order intentionality (in which the signaller intends that the signal produces a specific response in the recipient without necessarily requiring the recipient to recognize this intention [22]), we tested the following key markers [6,22,28]: (i) voluntary signalling, (ii) recipient-directed signalling, (iii) whether signalling elicits responses that are conducive to realizing the signaller's goal

**Table 1.** Criteria used to infer joint attention in interactions initiated by OBJECT PRESENTATION and BABBLER WALK.

criteria	operational criterion	data coded
<i>first-order intentional communication</i> voluntary signalling (social use) [22]	selective production and withholding of signalling according to the presence of certain recipients and their behaviour	audience composition and behaviour in which signalling started and stopped
recipient-directed signalling [22,25]	the production of signalling behaviour—and its continuous adjustment—to ensure reception by the recipient's sensory perception	(1) did the signaller position itself in front of the recipient before starting to signal (yes/no) (2) was visual contact between interlocutors blocked (e.g. by vegetation) during the joint movement of the interlocutors (yes/no) (2a) If yes, did the signaller re-position itself within sight of the recipient (yes/no, see electronic supplementary material, video S2)
signalling behaviour elicits responses that are conducive to realizing the signaller's goal [22,25]	a change in the recipient's behaviour that (i) is repeatedly followed by the cessation of signalling [22,26] and (ii) does not elicit an aversive response from the signaller	(1) did the recipient stop its pre-signalling behaviour and start a new behaviour during signalling without being physically forced by the signaller to do so (yes/no) (2) the recipient's response type (3) its behaviour when the signaller stopped signalling
goal-directed signalling [22,25]	persistence: the signaller continues to re-signal and/or exaggerate the same signal used at the beginning of the communicative episode until its goal is realised or failure is clearly indicated (see electronic supplementary material, video S3) elaboration: the signaller modifies the signal it used at the beginning of the communicative interaction (i.e. by adding and/or subtracting and/or modifying elements) or performs a different signal until its goal is realised or failure is clearly indicated (see electronic supplementary material, video S4)	(1) the duration of signalling behaviour (2) was the recipient cooperative (i.e. a recipient that bent over in a copulation posture/ followed the signaller within 30 s of receiving the signal) or uncooperative (i.e. a recipient that did not bend over for copulation/ did not follow the signaller within 30 s/ stopped following it after few metres) (3) did the signaller continue or stop signalling following the recipient's response (4) did the signaller elaborate its signal during the communicative interaction (yes/no)
<i>co-orientation of attention to the signaller's activity</i> monitoring the recipient's behaviour [26]	the signaller turns its head from its direction of movement—at least 45°—towards the recipient (i.e. gaze alternation, see electronic supplementary material, videos S5 and S6)	each time the signaller turned its head towards the recipient at least 45° or when it turned its entire body back towards the recipient
co-orientation of the recipient's attention [26]	following its gaze alternation, the signaller continues to move forward if it was followed (electronic supplementary material, video S6) or returns to re-engage the recipient if not (see electronic supplementary material, video S7)	(1) the recipient's behaviour when the signaller gazed towards it (bent over in a copulation posture/ followed the signaller/ did not follow the signaller) (2) The signaller's behaviour following gaze alternation (continued to move forward/ re-signalled from the same location/ returned towards the recipient and re-signalled)
<i>common ground</i> coordinated joint engagement [4,27]	following signalling, the recipient stops its current behaviour and travels with the signaller for at least 3 s (electronic supplementary material, video S6)	joint engagement was recoded from the moment the recipient started approaching the signaller until one of the participants stopped following the other or when body contact was established

(Continued.)

Table 1. (Continued.)

criterion	operational criterion	data coded
understanding the signaller's goal [26]	<p>the recipient follows <i>and</i> moves ahead of the signaller in the same direction (electronic supplementary material, video S6)</p> <p>for OBJECT PRESENTATION:</p> <p>(1) if a signal is produced at an already hidden location, the recipient bends over for copulation</p> <p>(2) upon arrival at a hidden location, the recipient bends over without further signal (electronic supplementary material, video S1)</p>	changes in the recipient's behaviour throughout the communicative interaction
re-communication [23]	following an OBJECT PRESENTATION, the recipient presents an object to the signaller as well (see electronic supplementary material, video S8)	

and (iv) goal-directedness of the behaviour. Since we have shown elsewhere [18,25] that OBJECT PRESENTATIONS qualify as intentionally produced signals, we examined these criteria here with regards to the BABBLER WALK only.

### (b) Co-orientation of attention

To examine whether signallers co-orient recipients' attention to their own activity [4,15], we investigated whether signallers used gaze alternations to monitor recipients' behaviour and whether they tried to re-engage them in the case of non-cooperation [27].

### (c) Common ground

This hallmark is controversial at theoretical and operational levels. At the theoretical level, some argue that awareness of the communication process is not required to achieve intentional co-orientation of attention [4,21]. By contrast, others see it as signature of truly intersubjective sharing [1]. Concerning the operational level, proponents of the mutual awareness criterion consider the communicative quality of sharing looks as the most convincing evidence for this hallmark in human infants [15] (defined as 'looks directed to the [human] tester that could be seen to express a participant sharing experience' [29]). However, such a qualitative evaluation of looks is not testable in animals, thereby resulting in an artificial human–animal divide [20,30]. Hence, we used traditional criteria that can be operationalized across a wide range of species and provide evidence for an establishment of common ground between interlocutors about their joint affair. We tested (i) whether successful communication resulted in coordinated joint engagement between interlocutors [4], (ii) whether recipients' responses indicated an understanding of the signaller's goal [27] and (iii) whether recipients responded communicatively to signallers [20,23].

## 2. Methods

### (a) Study site and population

The study was conducted in the Shezaf Nature Reserve (30.718° N, 35.266° E) in Israel (permit number: 2014/40304, The Israel Nature and Parks Authority). The Arabian babbler population in the reserve has been studied since 1971. Individuals are well habituated to researchers and marked with a unique combination of coloured rings [17]. The majority of individuals' life histories and dominance ranks are known in detail [17,31].

### (b) Behavioural observations

We carried out 86 observation sessions during the breeding season (February–June) of 2014, resulting in a total of 144.7 h of observation. Observations were conducted during the 4 h beginning when the group left its roosting tree at dawn and during the last 2 h of the day until the group roosted again. We observed a total of 80 birds (older than three months of age) from 12 different social groups. To document OBJECT PRESENTATIONS, we followed the dominant female during the days of egg-laying, which is the time period when most copulations occur [32]. OBJECT PRESENTATION was defined as *an individual picking up an object with its beak and holding it in front of an opposite-sex conspecific* [18]. BABBLER WALKS were documented by following fledglings during the three weeks after they had left the nest (recipients' age: 17–35 days). It was defined as *an individual performing wing waving and/or beak gaping while vocalising and*

subsequently hopping or flying away (recording role: continuous recording [33]). Behaviours were recorded from a distance of 2–20 m using an HD camera (Canon Legria HFM 41). Visual recording was accompanied by detailed narration of the observed behaviours.

### (c) Data coding and inter-observer reliability

The coding of videos was based on established coding schemes of bird [34] and great ape signalling [35] (see table 1 for the parameters coded). A second observer, blind to the hypotheses tested, coded 25% of OBJECT PRESENTATION and 17% of BABBLER WALK episodes. Inter-observer reliability was tested by using Cohen's kappa for categorical variables [36] and Spearman's rank correlation for duration measurements. Due to tied observations,  $p$ -values of Spearman's rank correlations were estimated using 10 000 permutations. All inter-observer reliability tests were significant ( $p < 0.005$ ). Cohen's kappa ranged from 0.80 to 1.00 and correlation coefficients from 0.86 to 0.93 (see electronic supplementary material, table S1 for results of inter-observer reliability tests).

### (d) Statistical analyses

Statistical analyses were conducted using the program R v. 3.2.3 with the packages irr [37], parallel [38] and lme4 [39] (v. 1.1–11). All tests were two-tailed, and the significance level was set to  $\alpha = 0.05$ . Due to vegetation cover and the mobile nature of the examined behaviours, data for some criteria were not always available. In these cases, we report a different sample size. Linear mixed models (LMMs) or generalized linear mixed models (GLMMs) [40] were used to account for pseudo-replication [41]. For each criterion tested, we used separate models for OBJECT PRESENTATION and BABBLER WALK. Models included the signaller, recipient (both nested in a social group) and social group identities as random effects. The significance of each full model as compared to its corresponding null model (containing only the intercept and random effects) was examined using a likelihood ratio test (R function 'anova' with argument test ' $\chi^2$ ' [42]). We assessed the models' stability by excluding levels of the random effects one at a time from the dataset and comparing model estimates derived from these data with those derived from the full dataset. This did not reveal influential levels of random effects to exist. To keep type I error rate at the nominal level of 5%, we included random slopes which were likely to be identifiable [42,43] (see electronic supplementary material, table S2 for the random slopes included).

#### (i) Signalling elicits responses that are conducive to realizing the signaller's goal

To examine whether the behaviours of fledglings after the production of BABBLER WALKS were responses to these signals (rather than being fixed responses to the sight of a conspecific), they were compared to the behaviours of fledglings when an adult group member passed by without signalling. For this purpose, 10 adults were each observed for 20 min. We recorded the fledgling's response when the focal individual passed within 50 cm without performing a BABBLER WALK (see electronic supplementary material, video S9). For a GLMM analysis, each episode was coded such that it included all six behaviours that were observed in the two conditions, and the response then indicated which was actually performed during an episode (zero for the behaviours not performed and one for the behaviour performed). The model included the fixed effect of condition, a random intercept for the particular episode, a random intercept for the behavioural responses (factor with six levels) and random intercepts for signaller and group identity. The key term in the model was the random slope [42,43] of condition within the response

type, which accounts for the possibility that certain response types would be particularly likely in only one of the conditions. To account for the possible choices of the responses within an episode not being independent (i.e. only one could be performed), significance was established by means of a permutation test [44]. For this purpose, the chosen response type was randomized within episodes. A total of 1000 permutations in which we included the original data as one permutation were used. The standard deviation estimated for the random slope of condition-within-response-type was used as a test statistic. The  $p$ -value was finally estimated as the proportion of permutations that revealed a test statistic at least as large as that of the original data. Sample size was 1236 possible behaviours (i.e. six behaviours multiplied by 206 BABBLER WALKS and control events) involving 42 actors, 11 groups and six behaviours. The recipient's identity was not included as a random effect since it was not always available in the control sessions.

#### (ii) Persistence of signalling

Persistence of signalling was examined from two perspectives. First, the duration of signalling behaviour towards cooperative versus uncooperative recipients was compared. We set an LMM with the duration of signalling behaviour (seconds) as the response variable and the recipient's behaviour (cooperative/uncooperative) as fixed effect. Since the duration of signalling had a right-skewed distribution, it was log transformed to meet the assumptions of normally distributed and homogeneous residuals and to avoid influential cases. Sample size was a total of 114 BABBLER WALKS involving 38 signallers and 26 recipients from 11 groups.

Second, the probability that a signaller would re-signal or quit signalling was compared between episodes with cooperative versus uncooperative recipients. For this purpose, a GLMM with binomial error structure and logit link function [40,45] was used. The model included the signallers' behaviour (continue/quit signalling) as the response variable and the recipients' behaviour (cooperative/uncooperative) as a fixed effect. BABBLER WALKS often involved several fledglings as recipients and in two out of 114 episodes not all recipients responded in the same way. We thus removed these two episodes from the data of this analysis to avoid ambiguity with regard to which behaviour the signaller responded. We then randomly selected one of the recipients from each of the remaining episodes to be included into the data. To obtain results unconditional on any particular random selection, we conducted 1000 random selections and report average model estimates. Sample size was a total of 112 BABBLER WALKS involving 28 signallers and 23 recipients from ten groups.

#### (iii) Elaboration of signalling

A GLMM with a binomial error structure and logit link function was used to compare the probabilities of signal elaboration in episodes with uncooperative versus cooperative recipients. It included the signallers' behaviour (elaborated/did not elaborate the signal) as the response variable and the recipients' behaviour (cooperative/uncooperative) as a fixed effect. We excluded from the data a single episode in which recipients responded differently from one another. We randomly selected one recipient for each episode and ran 1000 selections as described above. In addition, as the response variable did not include episodes of elaboration towards a cooperative recipient, the model suffered from complete separation [46]. To cope with this, we adopted the approach of Goodale *et al.* [47]: we modified the data to make it include all possible results (i.e. also cases of elaboration towards cooperative recipients). Thus, for each of the 1000 selections described above, we altered one instance of the response. This was randomly chosen out of those 24 episodes in which the recipient was cooperative and the signaller did not elaborate its signalling behaviour to indicate a signaller that elaborated its

**Table 2.** Responses to OBJECT PRESENTATION, BABBLER WALK and their corresponding control behaviours. Data for OBJECT PRESENTATION are amended from [25].

recipient's response	number of responses for			
	OBJECT PRESENTATION	control <sup>a</sup>	BABBLER WALK	control
follows the actor	27 <sup>b</sup>	0	87 <sup>b</sup>	2
follows and moves ahead of the actor in the same direction	10 <sup>b,c</sup>	0	30 <sup>b,c</sup>	0
bends over in a copulation posture (if OBJECT PRESENTATION produced at a hidden location)	3 <sup>b,c</sup>	0	—	—
moves away from the actor	3	14	2	0
waits for actor to approach and opens beak	0	84	0	0
waits for actor to approach and refuses to open beak	0	10	0	0
other responses	2	0	6	0
no response (continues previous behaviour)	8	0	13	71
total	53	108	138	73
on arrival at a hidden location the recipient bends over for copulation posture without further signalling	15 <sup>b,c</sup>	—	—	—
total	18	—	—	—

<sup>a</sup>Allofeeding attempt: individual standing and later moving towards another adult with a food item in its beak.

<sup>b</sup>Responses that were in line with the signaller's goal.

<sup>c</sup>Responses that promoted the signaller's goal beyond passive following.

signalling. We then fitted a model to this modified dataset and conducted a full-null model comparison. Note that this is a conservative approach since the difference between the two conditions (i.e. the number of cases in which the signaller elaborated its signal when communicating with a cooperative versus uncooperative recipient) is made slightly smaller than it actually was. We report average model estimates. Sample size was 100 BABBLER WALKS involving 23 signallers and 20 recipients from eight groups.

#### (iv) Co-orientation of attention

We examined whether gaze alternations were used to monitor the partner's behaviour and re-engage it when necessary. We used GLMMs that included the signaller's behaviour following its gaze alternation as the response variable (move further/return to signalling in front of the recipient or continue signalling from the same location) and the recipient's behaviour at the time of gaze (approached/did not approach the signaller) as a fixed effect. As communicative episodes usually involved several acts of gaze alternation, episode IDs were included as a random effect. A further random effect of signalling event identity was included in the BABBLER WALK model to account for the fact that episodes often involved several recipients. Sample size for the OBJECT PRESENTATION model was a total of 157 gaze alternations during 50 episodes involving nine signallers, eight recipients and five groups. Sample size for the BABBLER WALK model was a total of 299 gaze alternations during 116 episodes involving 40 signallers, 454 fledgling responses made by 26 recipients from ten groups.

### 3. Results

We documented a total of 55 OBJECT PRESENTATIONS. These were performed by six alpha males ( $n = 49$  episodes), three subordinate males ( $n = 4$  episodes) and one alpha female ( $n = 2$ ) from six social groups.

We recorded 138 BABBLER WALKS that were performed by 42 caretakers from 11 social groups (21 males, 12 females and

nine young birds that could not be sexed [17]). Signallers were older than two months of age and included dominant and subordinate group members.

#### (a) First-order intentional communication

##### (i) Voluntary signalling

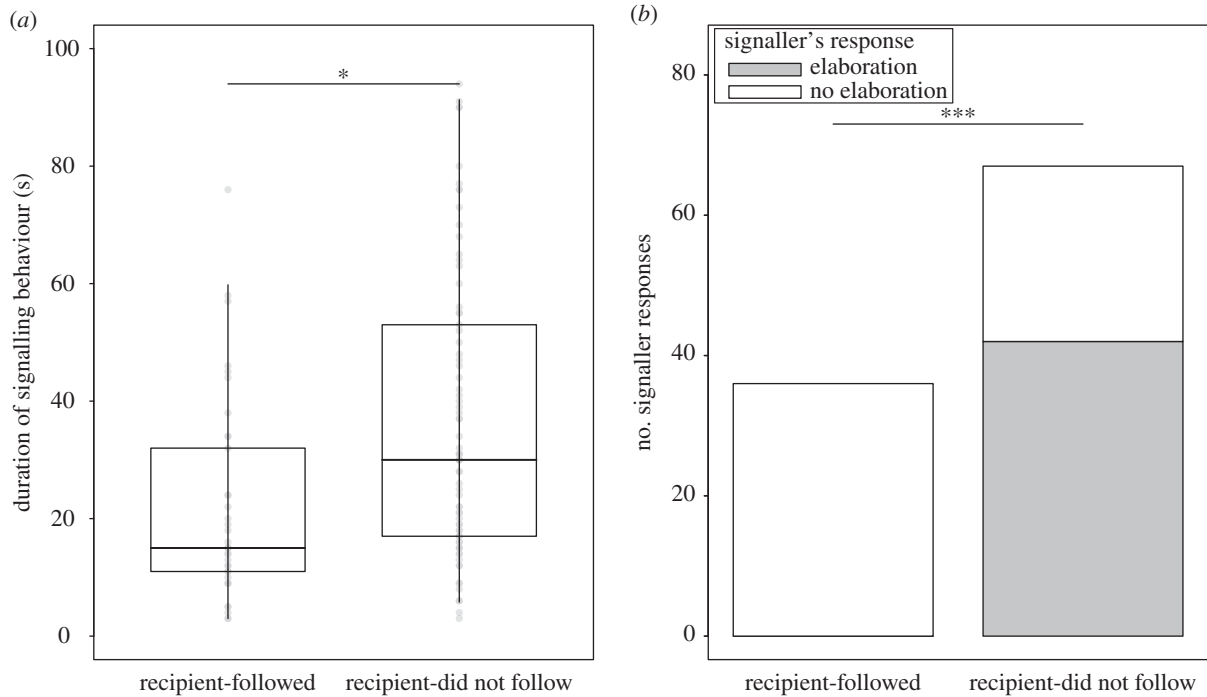
BABBLER WALKS were systematically performed in the presence of dependent fledglings (less than 35 days old; 100%,  $n = 138$ ). Our anecdotal observations suggest that the signal is occasionally used to solicit an adult conspecific to follow the signaller under 'urgent' conditions (for further information, see electronic supplementary material, table S3). Caretakers frequently moved close to fledglings without signalling (see control behaviour in table 2; electronic supplementary material, video S9). We could not identify any distinct behaviours performed by the fledglings that induced the production of this signal.

##### (ii) Recipient-directed signalling

All BABBLER WALKS started when the signaller and recipient were already in sight of each other or after the signaller had actively repositioned itself to be within the recipient's sight (100%,  $n = 116$ ). Moreover, whenever the signaller moved forward during signalling and left the recipients' visual field due to vegetation, it returned to re-signal in front of the recipient (100%,  $n = 87$ ; see electronic supplementary material, video S2).

##### (iii) Response to BABBLER WALK

Ninety-one per cent of BABBLER WALKS elicited a voluntary response from the recipient ( $n = 138$ ). The majority of first responses consisted of travelling with the signaller (94%). These responses were not fixed responses towards conspecifics as BABBLER WALKS elicited different responses compared to those



**Figure 3.** (a) Median, quartiles and quantiles (0.025 and 0.975) of the duration of *BABBLER WALKS* towards following and non-following recipients. (b) Number of episodes in which a signaller elaborated its *BABBLER WALK* depending on whether the recipient followed it or not.

elicited during the control condition in which a caretaker walked nearby a fledgling without signalling (permutation test: standard deviation of the random slope of condition within behaviour = 4.062,  $p = 0.001$ ; see table 2; electronic supplementary material, video S9).

#### (iv) Inferring the signaller's goal

As *OBJECT PRESENTATIONS* stopped after copulation [18,25], we considered the signaller's goal as 'to be followed for copulation'. As the majority of *BABBLER WALKS* stopped upon the recipient following the signaller to a new shelter (table 2), the signaller's goal was considered as 'to be followed'.

#### (v) Goal-directedness

The duration of signalling was shorter towards a cooperative recipient than an uncooperative recipient (estimate  $\pm$  s.e. =  $-0.62 \pm 0.17$ ,  $\chi^2 = 5.75$ , d.f. = 1,  $p < 0.02$ ; figure 3a).

Signallers were less likely to persist with their signalling and also less likely to elaborate it when communicating with a cooperative than with an uncooperative recipient (persistence (means of 1000 GLMMs): estimate  $\pm$  s.e. =  $-26.7 \pm 27.1$ ,  $\chi^2 = 106.17$ , d.f. = 1 all  $p$ -values  $< 0.001$ ; elaboration (means of 1000 GLMMs): estimate  $\pm$  s.e. =  $-6.38 \pm 3.9$ ,  $\chi^2 = 39.74$ , d.f. = 1, all  $p$ -values  $< 0.001$  (see figure 3b; electronic supplementary material, tables S4 and S5 for the mean estimates of these models). Elaboration of *BABBLER WALKS* included one or more of the following modifications ( $n = 48$ ): gaping the beak in front of the recipient (37 episodes; electronic supplementary material, video S4), producing long-lasting vocalizations (eight episodes), or adding wing movements to the vocalization (three episodes).

### (b) Co-orientation of attention to the signaller's activity

#### (i) Monitoring the recipient's behaviour

While signalling, the signaller alternated its gaze from its own direction of movement to the recipient and back at least once during a communicative episode (*OBJECT*

*PRESENTATION*: 98%,  $n = 51$  episodes; *BABBLER WALK*: 99%,  $n = 126$  episodes; electronic supplementary material, video S5).

#### (ii) Co-orientation of the recipient's attention

Whether the recipient approached the signaller or not had a significant effect on the signaller's post-gaze-alternation behaviour (*OBJECT PRESENTATION*: estimate  $\pm$  s.e. =  $-10.11 \pm 4.84$ ,  $\chi^2 = 12.82$ , d.f. = 1,  $p < 0.001$ ; *BABBLER WALK*: estimate  $\pm$  s.e. =  $-27.43 \pm 3.38$ ,  $\chi^2 = 148.47$ , d.f. = 1,  $p < 0.001$ ; electronic supplementary material, videos S6 and S7): if the signaller was approached, it was more likely to move forward than to re-signal from the same location or return to the recipient. However, if the signaller was not approached, it was more likely to re-signal from the same location or return to re-signal in front of the recipient than to move forward (figure 4).

### (c) Common ground

#### (i) Coordinated joint engagement

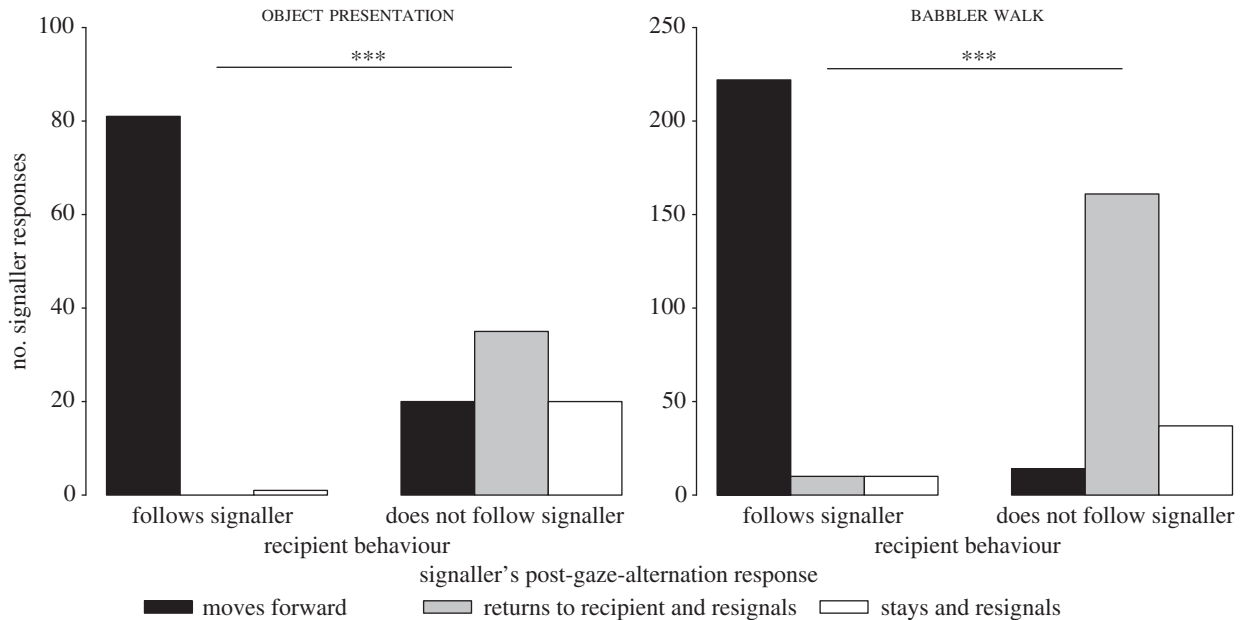
Eighty-two per cent of *OBJECT PRESENTATIONS* ( $n = 38$ ) and 93% of *BABBLER WALKS* ( $n = 103$ ) that elicited a voluntary response were followed by coordinated joint travel of interlocutors (see electronic supplementary material, figure S1). Median coordinated travel following *OBJECT PRESENTATIONS* lasted 22 s (14, 34.5; quartiles;  $n = 31$ ) and 20 s following *BABBLER WALKS* (12, 38; quartiles;  $n = 96$ ).

#### (ii) Understanding the signaller's apparently satisfactory outcome

In response to 40% of *OBJECT PRESENTATIONS* ( $n = 53$ ) and 22% of *BABBLER WALKS* ( $n = 138$ ), the recipient initiated at least one behaviour that contributed to the achievement of the signaller's goal beyond passive following (table 2).

#### (iii) Re-communication

In response to 16% of *OBJECT PRESENTATIONS*, the recipient picked up an object as well and moved together with the signaller ( $n = 55$ , electronic supplementary material, video S8).



**Figure 4.** Effects of the recipient's behaviour on the signaller's post-gaze-alternation behaviours. The number of the signaller's post-gaze-alternation responses according to the recipient's behaviour.

## 4. Discussion

The present study revisited the claim that joint attentional skills are a uniquely human ability and tested whether these abilities require the unique combination of an ape-like cognitive system and intensive cooperative motives (figure 1) [2]. We investigated whether two distinct signals used by a cooperatively breeding bird species were characterized by key hallmarks traditionally used to infer joint attention skills in pre-linguistic human children: first-order intentional communication [21,22], co-orientation of attention [4,15] and common ground [20,23].

Concerning intentional communication, we found that signallers were able to use their signals voluntarily, took into consideration recipients' attentional states, and showed persistence and elaboration of signalling when appropriate. In response, recipients often followed the signallers, who consequently terminated their signalling. Arabian babblers, therefore, demonstrated convergent evidence for first-order intentional communication by fulfilling a number of key markers that have been widely applied to infer intentionality in human [6,27] and non-human species [22]. These results add to the growing evidence that first-order intentional communication is not restricted to the primate lineage [34]. Future studies should therefore develop testable markers to investigate higher-order intentionality in non-human species [48], a capacity that plays a crucial role in enabling the complexity of human communication [48].

Concerning co-orientation of attention, signallers regularly alternated their gaze towards receivers, adjusted their own behaviour in accordance with those of recipients and actively returned to re-signal in front of uncooperative recipients. Whether other avian species engage in active co-orientation of attention is currently unknown. Related findings stem however from captive great apes that co-orientate the attention of human caretakers to third entities [14,21]. A useful candidate to investigate co-orientation of attention is group hunting, which can frequently be observed in wild chimpanzees, spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*) [49]. Though it has been argued that individuals

may only monitor the behaviour of their group members via 'checking looks' [23], rather than actively coordinating each other's attention [3], the existing studies did not (in contrast to the present study) distinguish between checking looks and active co-orientation [50].

Concerning the hallmark of 'common ground', we found that following signalling, interlocutors often engaged in coordinated joint travel. Furthermore, several results show the recipients' understanding of the signallers' goal. First, recipients often responded by moving ahead of the signaller while continuing with the signaller's direction of movement (i.e. recipients not only understood the signaller's goal as to be followed but also the desired direction of joint travel). Second, in the majority of observed OBJECT PRESENTATIONS, it was the recipient who bent over for copulation upon arrival at a hidden location. This indicates an understanding of the signal as an invitation for a copulation in a hidden location. Third, in a sixth of all observed OBJECT PRESENTATIONS, recipients picked up an object and presented it back to the signaller. No further use was documented for these objects and coordinated joint engagements that followed these reciprocal presentations resulted in copulation three times faster than interactions involving presentation by the signaller only. This re-presentation of an object may thus serve as a communicative act used to communicate back [23] the recipient's willingness to engage in mating, thereby fulfilling the third criterion for common ground [23].

Cross-species comparisons of the common ground hallmark have been severely hampered by using markers that are not equally applicable to non-human species [15,20,23], resulting in lively debates [1,14,21]. The parameters applied in the present study may thus convince some scholars [30], while others may question whether interlocutors indeed experience the same thing at the same time and know together that they are doing this [1]. However, the use of criteria that are only testable in humans excludes the study of joint attention in non-human species from scientific inquiry [30,51]. Thus, in addition to the application of criteria that allow valid comparisons across species, we furthermore postulate that joint



attention can be viewed as a layered system involving different cognitive skills. The integration of these approaches will not only enable us to gain a more comprehensive and quantitative view into joint attention skills, but may also shed light on the evolutionary trajectories of the different abilities involved.

In sum, our results show that the hallmarks commonly used to infer joint attention skills in humans also characterize communicative interactions of another cooperatively breeding animal species. These findings suggest that the ability to use joint attention—in its most traditional sense (i.e. the ability to intentionally attract one's attention and co-orient it to a common locus)—does not require an 'ape-like cognitive system' [2]. At the same time, these results do not imply that the processing abilities of an ape-sized brain do not additionally nurture the development of joint attention skills. Nevertheless, as long as complex mind reading, which may underlie human joint attention, is not testable in non-human species, the importance of an ape-like cognitive system for such a 'rich' notion of joint attention [30] will also remain non-testable.

One explanation for joint attention skills in distantly related species that rely on intensive alloparental care such as Arabian babblers and humans is convergent evolution. In both species, the evolution of joint attention may have been driven by selection pressures for systematic attendance to the needs of group members' offspring [2,8]. An alternative explanation may be that joint attention skills represent fundamental communicative capacities that frequently develop in social species. If the latter hypothesis is true, the suggestion that joint attention is uniquely human [1] might be the result of several biases in research: a strong focus on cognitive abilities of captive animals rather than individuals living under active selection pressures [52–54], the paucity of studies on non-primate gestural communication [55], the use of different definitions [15,23] and the neglect of interactions that revolve around entities other than objects. Future research should tackle these alternative explanations by investigating closely related species which differ in their degree of cooperation while using a comparable methodology [7].

## 5. Conclusion

The present study provides the first evidence that crucial hallmarks characterizing joint attention behaviour in

pre-linguistic human infants are not uniquely human. These results provide further support for the hypothesis that intensive cooperative motives affect socio-cognitive performance [2,34,56].

To better understand its evolution, we propose to view joint attention as a layered system involving different components rather than as a single capacity mastered only by a single species: humans. Such a view will enable us to tackle differences and similarities in cognitive skills that underlie co-orientation of attention across species [57].

Furthermore, to reconstruct the changes that paved the way for our sophisticated cognition and communication, we have to view the likely adaptations of early hominins in general, rather than with specific reference to other primates only [58]. In particular, examples of convergent evolution in distantly related species [59] may provide crucial clues to the types of problems that particular cognitive mechanisms were 'designed' to solve [60].

**Data accessibility.** The data on which this study is based are available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.j3s5v66> [61].

**Authors' contributions.** Y.B.M. and S.P. designed the study. Y.B.M. collected the data. Y.B.M. and R.M. analyzed the data. Y.B.M., R.M. and S.P. wrote the paper.

**Competing interests.** We declare we have no competing interests.

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