ANTHROPOLOGY

Vocal signals facilitate cooperative hunting in wild chimpanzees

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Cooperation and communication likely coevolved in humans. However, the evolutionary roots of this interdependence remain unclear. We address this issue by investigating the role of vocal signals in facilitating a group cooperative behavior in an ape species: hunting in wild chimpanzees. First, we show that bark vocalizations produced before hunt initiation are reliable signals of behavioral motivation, with barkers being most likely to participate in the hunt. Next, we find that barks are associated with greater hunter recruitment and more effective hunting, with shorter latencies to hunting initiation and prey capture. Our results indicate that the coevolutionary relationship between vocal communication and group-level cooperation is not unique to humans in the ape lineage and is likely to have been present in our last common ancestor with chimpanzees.

INTRODUCTION

A notable feature of the human species is our proclivity for flexible cooperation on both small and large scales. This is virtually impossible without vocal communication because complex coordination of actions requires individuals to relate to each other in space and time (*1*, *2*). A prevailing hypothesis is that human language and cooperation coevolved, with advances in communication facilitating more complex cooperative behavior, which, in turn, selected for more sophisticated linguistic skills (*3*–*5*). Such an interdependence between group-level cooperation and communication seems to have evolved convergently, albeit more simply, in distantly related species including Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), shedding light on the shared selection pressures driving this social behavior (*1*, *6*–*8*). What remains unclear, however, is whether, within the primate order, the coevolution of communication and cooperation is a derived feature of the hominin lineage or whether its basic building blocks may be found in our closest living primate relatives.

There is ample evidence that wild primates produce communicative signals to initiate and regulate dyadic affiliative interactions, such as play, grooming, and reconciliation (*9*–*15*). However, more explicit investigations into dyadic cooperation in captive apes (e.g., tasks to obtain food rewards) have reported either no overt communication between the two partners or the occasional exchange of short-range, nonvocal gestures (*2*, *16*–*18*). Furthermore, much of what makes human cooperation extraordinary is the high frequency of polyadic cooperation (i.e., involving more than two individuals) (*19*). This type of group-level cooperation is evolutionarily less stable than dyadic cooperation due to the emergence of collective action problems. Specifically, an increasing group size dilutes individual payoffs and generates more opportunities to free ride on the efforts of others (*20*). Therefore, polyadic cooperation might particularly benefit from facilitation by means of overt communication (*1*, *6*, *8*). Studies of monkeys (and other species) have shown that communicative signals are important in mediating collective predator deterrence such as mobbing, as well as intergroup conflict (*21*–*24*). However, to date, little is known about the coordination of polyadic cooperative behavior in great apes, data that are key to a phylogenetic reconstruction of the intimate link between cooperation and communication in humans.

Group hunting by chimpanzees is an iconic example of polyadic cooperative behavior. In line with a long tradition of chimpanzee hunting research, we define cooperation as a behavior involving multiple individuals, where joint participation increases success (*25*, *1*). A basic form of cooperation, known as by-product mutualism, does not require that individuals relate to each other in space and time, but rather involves independent, simultaneous actions that incidentally increase the chances of others' success. By contrast, the term coordination is used to describe a more complex form of cooperation, whereby participants respond to each other's communicative behaviors and movements, thus actively modifying their behavior depending on the actions of others. There is disagreement over the extent to which coordination is involved in chimpanzee group hunting. While some research indicates that chimpanzee hunting represents a case of by-product mutualism, where the actions of participants are effectively independent efforts geared toward individual success (*26*–*28*), other studies suggest that there is coordination involved, including the existence of specific roles and tasks both before and during the hunt, which rely on interdependent action for success (*25*, *29*, *30*). It has recently been suggested that cooperative acts may be best conceptualized as falling on a graded continuum that includes intermediate forms between by-product mutualism and full-blown teamwork (*1*). Chimpanzee group hunting may vary along this continuum both within and between populations. Some hunts are potentially well described as a socially influenced collaboration, where individuals' actions are influenced by others but no intentional strategies to coordinate are in place (*1*). This debate notwithstanding, from a descriptive perspective, chimpanzee hunts typically involve the pursuit of arboreal group-living monkeys, most

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often red colobus monkeys (*Procolobus tephrosceles*), by multiple chimpanzees (*29*, *31*). When one or more monkeys are killed, the captors frequently share meat with others (*26*). At our research site (Kanyawara, Kibale National Park, Uganda), chimpanzees do not appear to actively search for monkeys [c.f. Ngogo and Taï (*32*, *33*)]; instead, they see or hear troops opportunistically as they travel through their range.

When chimpanzees encounter a monkey troop, one or more individuals may immediately climb in pursuit, or there may be a period of minutes to hours during which individuals appear to assess their chances of success by scanning the canopy from the ground. Males are more likely than females to hunt arboreal monkeys (*34*), and while occasionally an individual will hunt alone, the majority of hunts at most sites involve multiple hunters (*35*). The probability of a kill increases with the number of active hunters, although there is debate over the per capita benefits of hunting in groups (*29*, *36*). Overall, as hunts may unfold over a large forested area with potentially poor visibility, the vocal expression of motivation to hunt would arguably improve the efficacy of group hunts (*31*). Vocalizations could provide valuable information, such as the number, location, identity, and/or motivation of hunters, which individuals can use to make their own decision about whether to participate.

Chimpanzee bark vocalizations occur in the context of group hunting (*31*, *37*), and previous research has shown this vocalization to be acoustically distinct from barks produced in other contexts (*37*). If acoustic communication is truly tied to the evolution of large-scale cooperation as the literature suggests (*3*–*5*), then multiple features render chimpanzee hunting a likely case in which to observe context-specific vocal behavior. First, hunts are energetically costly and associated with variable success and risk of injury (*26*, *34*), representing a selective pressure on hunter performance. Next, hunt success is known to be dependent on factors that might be most efficiently detected via vocalizations, such as the number and identity of hunters (*26*, *28*, *31*, *36*). Last, barks produced in hunting contexts are generally emitted before active pursuit of prey, reflecting a likely communicative function (*31*). Here, we tested the hypothesis that these "hunting barks" facilitate cooperation by increasing participation or efficacy in hunts. First, we tested the prediction that a bark signals an individual's motivation to hunt by examining the relationship between bark production and hunt participation at the individual level. As hunting success is related to the number and identity of hunters, this information should be useful to individuals who are undecided about whether to hunt. Accordingly, we next predicted that, at the level of hunting events, barks would be associated with increased participation or expedited hunt initiation. Last, we predicted that barks would be associated with increased hunting success in terms of greater kill probability or shorter latency to make a kill. Given the rich social context of hunts, our analyses also controlled for age, sex, and party size and composition ("party" refers to a temporary subgroup of chimpanzees belonging to the same community; see Materials and Methods for the operational definition used).

To study hunting in chimpanzees, specific aspects of this complex behavior must first be operationally defined. Given that it is empirically intractable to unambiguously establish when the chimpanzees themselves perceive the hunt to have started, we instead rely on a criterion that has been frequently applied across multiple field sites, defining the start of a hunt as the time at which the first chimpanzee climbed to the height of the lowest monkey (see Materials and Methods) (*28*, *33*). This represents a standardized way to describe the initiation of prey pursuit, a key feature required to designate a hunt as such. We examined the production of barks during a total of 307 hunting events over a 23-year period (1996–2018) in the Kanyawara chimpanzee community of Kibale National Park, Uganda. To exclude ambiguous events, we removed a subset of data consisting of incomplete records and events where the identity of barkers was unknown ($n = 75$) from further analysis. In the remaining 232 events, we found that barks were produced in 39% of events (91 of 232), with a total of 343 individuals producing barks (mean of 3.7 individuals per event; SD = 2.3; see Materials and Methods for further information about model-specific sample sizes). In 93% of events with barks (85 of 91), barks occurred before the start of the hunt. Barkers started to vocalize, on average, 47 s (SD = 157 s) before hunt initiation, although it was not feasible to record the duration of barking bouts in real time. Henceforth, all references to barking indicate single barks or bouts of barks that commenced before hunt initiation. We classified individuals as hunt participants only when they actively pursued monkey prey, not merely if they produced a hunting bark.

We provide more descriptive details on general hunting dynamics in the Supplementary Materials. We modeled our data in a Bayesian framework, and, where possible, we presented a Bayesian version of the R^2 statistic and summarized its posterior probability distribution by its mean (R^2_{μ}) and associated 95% credible interval (R^2_{CI}). We offer biological interpretations for model parameters of fixed effects that do not feature in any higher-order effects, and, for which, the posterior 95% credible interval did not include 0. See Materials and Methods for more details on model specification and validation.

RESULTS

To investigate whether the production of barks was associated with an increased probability of individual participation, we constructed a generalized linear mixed-effects model (binary GLMM) using 2398 observations on 74 chimpanzees across 227 hunting events. The slight variation in sample size among the five different models reflects the availability of response variables for extraction (see Materials and Methods). This model ($\Delta_{elpd} \pm SE_{elpd} = -212.8 \pm 18.9$; table S3), which controlled for individual characteristics and social context, explained a substantial amount of variation in the probability of individual participation in a hunting event ($R^2_{\mu} = 0.465$, $R^2_{CI} = 0.442$ to 0.486). The probability of participation was considerably higher for an individual that had barked than one that had not ($b_{\mu} = 5.70$, $b_{CI} = 3.80$ to 7.76) (Fig. 1). This finding suggests that the bark vocalization used in a hunting context was an honest signal of hunting motivation (*31*).

In line with previous research (*28*), our first model also found that hunting probability was quadratically associated with age, with a maximum probability of individual participation at an age of ~25 years (b_{μ} quadratic $= -0.39$, b_{CI} quadratic $= -0.55$ to -0.23). In addition, as chimpanzee party size increased, the probability that a given individual participated decreased ($b_{\mu} = 0.04$, $b_{CI} = -0.08$ to 0.00), as would be predicted if chimpanzees were encountering a collective action problem (see the Supplementary Materials). We further found sex-specific effects of both the presence of "impact hunters," i.e., individuals whose presence increases the likelihood of hunt occurrence (see the Supplementary Materials for impact male calculation) (*26*, *28*) and swollen (sexually receptive) females in the hunting party,

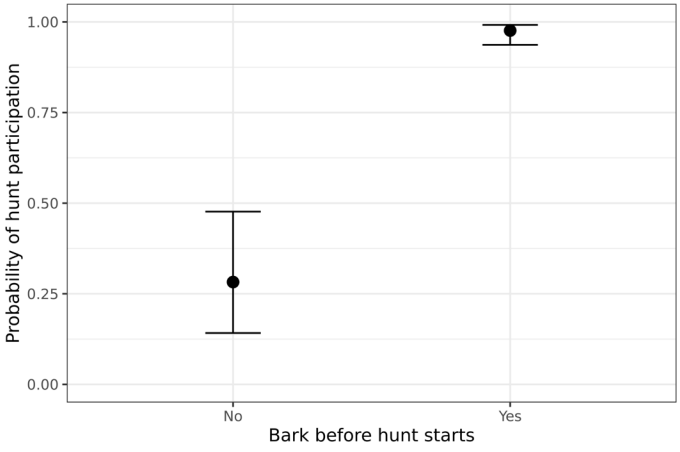

Fig. 1. Illustration of Bayesian model predictions of how individual participation in a hunt is associated with production of barks. Posterior prediction plot of our first binary GLMM (n_{obs} = 2398, n_{ind} = 74, n_{hunts} = 227; R^2_{μ} = 0.465, R^2_{CI} = 0.442 to 0.486), visualizing the effect of bark production on an individual's probability of participating in a hunt. Individuals that barked were consistently more likely to join a hunt than those that did not.

with males overall being more likely to participate than females, particularly in the presence of impact hunters (b_{μ} = 1.59, b_{CI} = 0.76 to 2.40), but becoming less likely to participate whenever swollen females were present (b_{μ} = −0.71, b_{CI} = −1.29 to −0.15).

We then addressed the role of barks in augmenting group participation and expediting hunt initiation and asked whether barks influenced the outcome of a hunt. These analyses were conducted at the level of hunting event rather than individual. We expected events in which barks were produced before hunt initiation to be associated with greater group participation and reduced delay in hunt initiation, compared to events with no barks. We also predicted an increase in the probability of making a kill and a reduction in the delay to make it, in association with bark production.

The first model (binomial GLMM; n_{obs} = 232; $\Delta_{elpd} \pm SE_{elpd}$ = −38.2 ± 8.4) accounted for more than half of the variation in the proportion of individuals recruited (R^2_{μ} = 0.614, R^2_{CI} = 0.518 to 0.696). Bark occurrence (i.e., at least one individual barked) was associated with an increase in the proportion of individuals in the party that participated in the hunt (b_{μ} = 0.45, b_{CI} = 0.22 to 0.69; Fig. 2A and table S4). We also detected a positive effect of impact hunter presence on the proportion of individuals that participated (b_{μ} = 0.37, b_{CI} = 0.03 to 0.71) and a negative effect of party size (b_{μ} = −0.11, b_{CI} = −0.13 to −0.08).

We ran a second model to explain the variation in the latency from the first predatory interest in monkeys to hunt initiation (Cox proportional hazards LM; n_{obs} = 230; $\Delta_{elpd} \pm SE_{elpd}$ = −0.3 ± 11.5). Bark occurrence increased the hazard ratio of hunt initiation (b_{μ} = 0.36, b_{CI} = 0.08 to 0.63; Fig. 2B and table S4): Delays were shorter if at least one individual barked. Conversely, swollen female presence decreased the hazard ratio (b_{μ} = −0.56, b_{CI} = −0.88 to −0.25), corresponding to longer delays.

A third model examined variation in hunting success (binary GLM; n_{obs} = 232; $\Delta_{elpd} \pm SE_{elpd}$ = −3.0 ± 4.4, R^2_{μ} = 0.085, R^2_{CI} = 0.032 to 0.144) and indicated that kill probability did not increase with the occurrence of barks (b_{μ} = 0.26, b_{CI} = −0.35 to 0.90; Fig. 2C and table S4). Kills were less likely when swollen females were present (b_{μ} = −0.89, b_{CI} = −1.65 to −0.19), whereas when either independent individuals' party size (b_{μ} = 0.06, b_{CI} = 0.00 to 0.13) or the number of hunters (b_{μ} = 0.19, b_{CI} = 0.03 to 0.35) was larger, kill probability increased, corroborating previous findings (*30*, *31*, *35*, *36*).

A final model investigated variation in the latency from hunt initiation to the first kill (Cox proportional hazards LM; n_{obs} = 157; $\Delta_{elpd} \pm SE_{elpd}$ = −5.3 ± 4.7). Kills occurred more quickly in hunting events preceded by barks than in those without barks (b_{μ} = 0.63, b_{CI} = 0.28 to 0.96; Fig. 2D and table S4). We also found that the time to obtain a kill was greater when impact males were present (i.e., the hazard ratio decreased: b_{μ} = −0.69, b_{CI} = −1.17 to −0.20). The reasons for this counterintuitive finding demand further investigation, but impact males may be more likely to persevere under difficult conditions rather than to abandon the endeavor, leading to a longer interval between hunt initiation and success. Measuring individual-level latencies from joining a hunt to perpetrating a kill and comparing impact and nonimpact hunters would contribute to clarifying this.

DISCUSSION

By examining the association between barks and subsequent hunting dynamics in chimpanzees, we provide evidence that vocal signals are associated with more efficient cooperative resource acquisition in a wild ape. Specifically, we show that individuals who barked before hunt initiation could be reliably expected to pursue prey in the hunt. Next, we demonstrate that the occurrence of barks before hunt initiation was associated with (i) a greater proportion of party members participating in the hunt, (ii) a reduced latency to initiate hunting, and (iii) a reduced latency to make a kill.

If bark vocalizations serve to catalyze hunting as our data suggest, then it is pertinent to ask why these vocal signals are produced only in a subset of hunts. Although we do not explicitly test this question, it is likely that hunting bark production is influenced by a number of social and environmental factors. One possibility is that environmental visibility plays a role, with barks being more likely to be produced in settings with low visibility, where vocal communication may be more important to allow hunters to gauge participation and/or maintain cohesion. A targeted study quantifying vegetation density during hunts would be instrumental in evaluating this hypothesis. Another potential predictor of bark occurrence might be favorable conditions for hunting, including, for example, certain prey demographics (e.g., presence of vulnerable juveniles or infant monkeys) and/or canopy structure (e.g., sparse canopy offering fewer escape routes). Increased arousal in the face of these favorable conditions may then induce hunting-specific vocal behavior in chimpanzees.

It is important to consider whether favorable hunting conditions could offer an alternative explanation for our results, acting as a confound that may be independently driving both bark production and hunting success. Although, in correlational analyses, it is impossible to rule out unmeasured confounding factors, it seems unlikely that favorable hunting conditions can explain our findings. Favorable hunting conditions are difficult to objectively quantify, but they should result in a higher likelihood of a successful kill. Critically, if favorable conditions were confounding the relationship between barking and hunting success, then barks should reliably predict the likelihood of a kill. However, kill success was not strongly influenced by bark vocalization production in our study, making it unlikely that our pattern of results was confounded by favorable hunting conditions. Ultimately, future research should strive to move

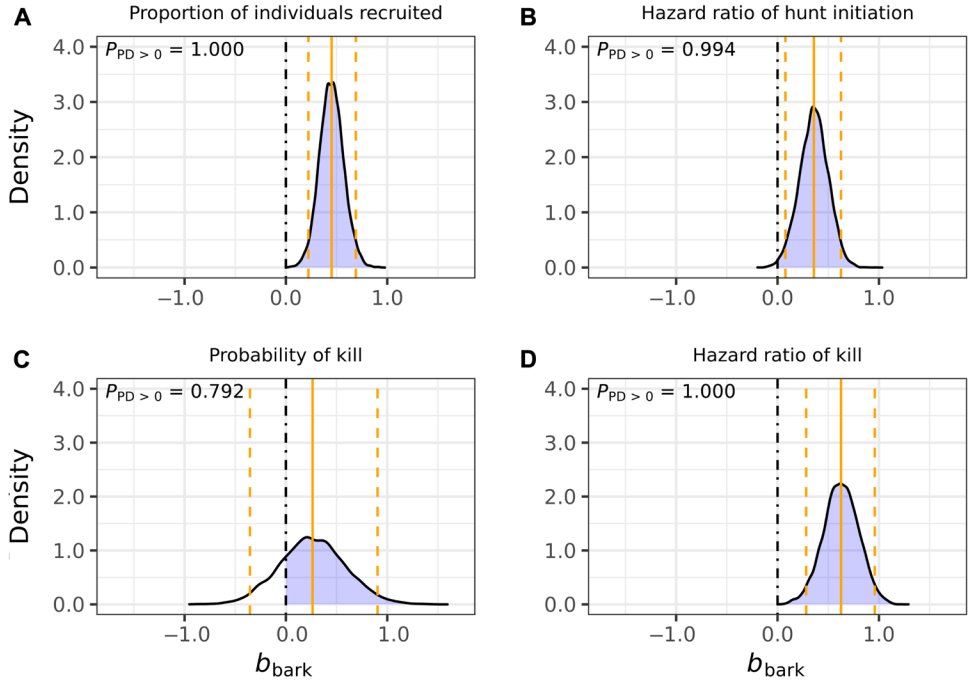

Fig. 2. Parameter estimates from Bayesian analyses showing a positive effect of barks on subsequent hunting dynamics. Displayed are the posterior density distributions of the estimated effect that the occurrence of barks had on four different aspects of group hunts. Distributions are represented by black curves, with solid and dashed orange lines depicting the mean (μ) and 95% credible interval (CI), respectively. In (**A**) to (**D**), the proportion of the distribution greater than zero ($P_{PD} > 0$, i.e., in support of a positive effect of barks on the outcome) is highlighted by purple shading and printed in the top left corner. Models provide compelling evidence that, compared to hunts where no barks were given before hunt initiation, in hunts where barks were produced before hunt initiation, (A) a larger proportion of animals in the party was recruited (binomial GLMM); (B) the proportional hazard of hunt initiation increased, i.e., the latency between the first sign of predatory interest and the onset of a hunt was shorter (Cox proportional hazards LM); and (D) the proportional hazard of a kill increased, i.e., the latency between the onset of a hunt and the time of the first kill was shorter (Cox proportional hazards LM). In contrast, regarding the probability of achieving a kill (C), we found no strong association between bark production and kill likelihood.

beyond the observational, correlational patterns we found to probe causal relationships through playback experiments (*38*). For instance, in areas where monkeys are not present, monkey calls could be broadcast in combination with either chimpanzee hunting barks or chimpanzee vocalizations, which do not occur in the hunting context. If barks catalyze hunting responses as the observational data suggest, then playbacks of monkey calls with barks should elicit more sustained hunting preparation behaviors (e.g., canopy-oriented searching) than when monkey calls with nonhunting vocalizations are broadcast.

Previous work has illustrated how the advertisement of behavioral motivation critically underpins active forms of group coordination (*1*, *39*). For example, olive baboons (*Papio anubis*) and wild dogs (*Lycaon pictus*) base decisions related to group movement on the number of individuals who communicate their readiness to initiate a group departure (*40*, *41*). Because the production of a bark vocalization by a chimpanzee, in the presence of monkey prey, was a strong predictor of the individual actively participating in prey pursuit, this vocalization potentially allowed receivers to reliably assess the extent of participation and, thus, the costs and benefits associated with hunting. Increased participation has previously been shown to be associated with greater success (*26*) and may potentially reduce individual risks (e.g., attacks from male monkeys), so assuming that receivers are sensitive to these factors, they may be more motivated to hunt when barking occurs. In line with a previous observation (*31*), we detected a positive relationship between barks and subsequent participation, showing that receivers are sensitive to barks and may use the occurrence of barks to make informed decisions regarding when it is favorable to join a hunt. Furthermore, we observed a decrease in the delay between the first sign of predatory interest and hunt initiation in events where barks occurred. When barks were produced, individuals had more information available regarding how many others were likely to hunt. When barks did not occur, party members may have required more time to obtain the same information, through direct observation of conspecific movements. Hence, while barks are not necessary for individuals to make decisions about joining a hunt (as they are only produced in ~40% of hunting events), when they are present, they may represent a valuable source of information to expedite such decisions.

Barks provide a potentially valuable source of information for receivers, and our data show that listeners are sensitive to the occurrence of barks. However, it is unclear which cognitive mechanisms are involved in driving receiver behavior in relation to barks. It is possible that simple mechanisms are involved, with barks potentially increasing arousal or excitement in receivers, making subsequent action and participation more likely. Alternatively, as outlined above, receivers may use barks to make informed decisions about the likelihood of success as well as costs and benefits of joining the hunt. This seems feasible given that artificial cooperation paradigms in captivity have shown chimpanzees to be sensitive to the likelihood

of success with partners of varying skill and tolerance (*42*–*44*). Whether driven by arousal or information, receiver sensitivity to barks shows social influence over hunting behavior, rendering the actions of hunters nonindependent (*1*). In addition, if increased participation following bark production arises from a perceived increment in the chances of success, then this would presuppose a knowledge of the causal role of hunting partners in achieving a kill, which constitutes a criterion for attributing an even further degree of coordination complexity (*1*). Future research should probe the cognitive mechanisms that mediate the relationship between calls and hunt participation in receivers, and this may help us better understand the extent of coordination involved in chimpanzee hunts.

Our data also raise questions concerning the cognitive mechanisms underlying bark production. First, the signal could be intentionally produced to communicate readiness to hunt (*45*). As the vocalization is reliably used in a cooperative context and has the potential to influence the decision-making of others, it could represent a first step toward the more intentional forms of communication-enhanced cooperation typical of our species. However, rigorous testing of caller behavior against established markers of intentionality (*45*) is required before we can evaluate this possibility. As mentioned above, a more parsimonious mechanism underlying bark production is excitement or arousal (*46*). Although our data cannot rigorously disentangle emotional versus more intentional mechanisms, which are not mutually exclusive, this represents a promising avenue for future research that will help shed further light on the similarities between human and great ape vocal coordination of cooperative behavior.

The mechanisms underlying the positive effect of barks on hunting success also remain speculative. Barks did not affect kill probability, which increased with the number of hunters and decreased with the presence of swollen females. However, bark occurrence was associated with a reduced latency in making a kill. We show that this effect was not a by-product of a larger number of hunters, but, rather, it was independently driven by the occurrence of barks. This suggests that the use of communication expedited the achievement of the desired outcome, supporting previous findings in distantly related species (*7*, *47*). The mechanisms driving the association between barking and faster kills are unknown but could include (i) the barks facilitating faster decisions in party members to join the hunt and (ii) the barks startling monkey prey and driving them toward their escape routes, making them easier to catch. Acoustically, chimpanzee barks are loud, sharp calls with sudden onsets (*48*), which may have distressed and repelled the monkeys. Future work probing the timing of monkey alarm calls and panic fleeing in relation to the timing of chimpanzee barks would test this possibility.

More generally, these findings have the potential to shed light on the evolutionary roots of the notable human capacity to vocally coordinate cooperative behavior. For example, in modern Ache hunter-gatherer societies in Paraguay, cooperation mediated by verbal communication is critical to successful hunting of nine-banded armadillos (*Dasypus novemcinctus*) and *Cebus* monkeys (family Cebidae) (*49*). Empirical work demonstrates that increased verbal activity in humans enhances coordination efforts (*50*). Our findings suggest that the behavioral dynamics we observed in hunting chimpanzees could represent precursors to a more typically hominin interplay of communication and cooperation. Within the primate order, vocally mediated polyadic cooperation is unlikely to be a de novo–evolved trait unique to humans but, instead, potentially has its origins rooted more deeply in the lineage and was likely present in at least the last common ancestor of humans and chimpanzees. In wild chimpanzees, barks not only possibly facilitate decisions regarding whether and how quickly to join a hunt but also influence the outcome of the group behavior: Hunting is more effective following a bark.

MATERIALS AND METHODS

Study site and subjects

The Kanyawara chimpanzee community is located in Kibale National Park, Uganda. The community inhabits an area of at least ~15 km^2 within the northwestern region of the park, with at an altitude of ~1500 m, within a habitat comprising mainly evergreen forest and swathes of swamp. The population has been the object of long-term study since 1987 (*51*), and for the duration of this study, between 1996 and 2018, the community size ranged between 40 and 57 individuals.

Data collection and extraction

Since 1996, data on hunting behavior have been collected by trained Ugandan field assistants who record handwritten notes while following chimpanzees, documenting group-level information such as party size and composition and the proximity of any monkey species, as well as individual-level data concerning identity, behavior, sexual swellings, etc. At Kanyawara, a party is defined as all individuals within 50 m using a chain rule, and this variable is recorded every 15 min. All occurrences of hunting attempts (successful and unsuccessful) were recorded by the observing field assistants. Predatory interest in monkeys was defined as any overt gaze orientation or movement directed toward monkeys, while the initiation of a hunting event was defined as a chimpanzee climbing up to the height of the lowest monkey (*28*, *33*). While sometimes it may be difficult to pinpoint the exact start of a hunt, this definition is consistent with that used at other field sites such as Taï, where a hunter is any individual that "climbs up to the height in the canopy where the prey live, looking and orienting itself toward them" (*33*), and Gombe, where a hunter is one that is seen "climbing in pursuit of one or more monkeys" (*36*). During hunting, multiple field assistants coordinated to observe the behavior of as many individuals as possible. Behavioral changes were noted chronologically (hh:mm), providing details of actions performed, recipients involved, and outcomes. Immediately after the hunt, the information from all field assistants and other observers was collated into a predation-specific datasheet.

Data for subsequent analyses were extracted from the complementary information contained in the handwritten individual accounts and predation-specific datasheets. The full list of variables extracted from these sources is detailed in table S1. These data include variables reported directly on the datasheets by the field assistants, such as the full party size, identity of individuals, hunting party size, timing of when barks started to be produced and by whom, and hunt initiation. Additional variables, such as the delay in hunt initiation and the delay in obtaining a kill, were extracted from the detailed behavioral descriptions.

Statistical analyses

Our sample sizes for the five different statistical models varied slightly. This variation results from the availability of response variables for extraction. In the case of individual participation following a bark, this response variable was unambiguously recorded in 227 events,

resulting in a sample size of 227. In the case of hunt participation, the response variable was unambiguously coded in 232 events. In the case of hunting delay, this specific response variable was unambiguously recorded in 230 events. In the case of kill probability, the response variable was unambiguously coded in 232 events. Last, in the case of delay to obtain a kill, this specific response variable was unambiguously recorded in 157 events. The sample size thus reflects the specific response variables of the different models.

We conducted analyses within a Bayesian framework using the "brms" and "rstan" packages (*52*, *53*) in R 3.6.3 (*54*). Given the naturalistic nature of the data, resulting in sometimes small and unbalanced sample sizes, we only considered up to second-order interaction effects in our first analysis (removing interactions for which model comparisons indicated that they did not enhance posterior predictive accuracy), and only the main effects in the four models composing our second analysis. Pseudo-replication within our first dataset, due to multiple observations on the same individual across multiple hunting events and multiple individuals participating in each event, was accounted for by including both individual ID and hunt ID as partially crossed random effects. An observation-level random effect was included in the first model of our second analysis (modeling the proportion of individuals recruited in each hunt) to absorb the overdispersion in this particular dataset (*55*).

Models were fitted by running four independent Markov chains (based on the Hamiltonian Monte Carlo algorithm with No-U-Turn Sampler) for 2000 warm-up and 2000 post–warm-up iterations each. We specified weakly regularizing priors to restrict the sampled parameter space and defined normal distributions for fixed intercepts ($\mu = 0$, $\sigma = 10$) and predictor variables ($\mu = 0$, $\sigma = 5$) while setting Cauchy distributions for estimates of the variance components representing random intercepts ($x_0 = 0$, $\gamma = 2$). Chain mixing, stationarity, and convergence were confirmed by visual inspection of trace plots and by insisting on scale reduction factor values of 1 (R-hat = 1.00). To achieve this for all estimates across all models, the resolution of the sampler was increased by adjusting the "adapt_delta" parameter in the "brm()" function in R to 0.99. Ensuing concerns about algorithm efficiency were addressed by allowing a maximal tree depth of 15. Effective sample size for all parameter estimates in all models was >2000.

To assess model performance, we conducted graphical posterior predictive checks and calculated a Bayesian version of the R^2 statistic (*56*) whenever possible [note that neither procedure is implemented (yet) for Cox proportional hazards models (*52*)]. Candidate models were compared on the basis of their relative out-of-sample predictive accuracy using approximate leave-one-out cross-validation (*57*). This procedure calculates differences in the expected log pointwise probability density (Δ_{elpd}) of candidate models, in which models with larger values are deemed more plausible than models with lower values, given the data at hand. The full results from all models are shown in tables S3 and S4.

All event-level analyses were also run on the full dataset including events associated with barker uncertainty ($n = 307$) to rule out the possibility that results obtained were driven by the exclusion of certain types of events, e.g., larger hunting parties, where identifying more barkers is more challenging, rather than by the explanatory variables in our models. The pattern of results was consistent with our original set of analyses (see the Supplementary Materials for further details), suggesting that our findings were not driven by the exclusion of events with unidentified barkers.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.abo5553

View/request a protocol for this paper from *Bio-protocol*.

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