







Predicting Prosociality in Primates: Socio-Ecological Influences and a Framework of Inter-Brain Neural Synchronization

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ABSTRACT: Prosocial co-operation is critical for evolution and survival on Earth and has crucially shaped the development of *Homo sapiens*. Inter-brain neural synchronization (IBNS) has been shown to enhance prosocial co-operation in mammals and avians. The selection pressures which led to the development of IBNS throughout primate evolution are currently unknown. This paper aims to expand the understanding of IBNS in non-human primates by reviewing the literature on various primate populations that display prosocial behaviors that could correlate with IBNS. Binary logit modelling using machine learning methods was applied to social, ecological, morphological, and biological (SEMB) variables correlated with prosocial behaviors to obtain probabilities of prosociality. Our results suggest that select SEMB variables such as daily socialisation, food-sharing and hierarchy structure are strong predictors of prosocial behaviors in primates. We provide a framework that offers testable hypotheses for the existence of IBNS in primates based on the correlations between SEMB variables and prosocial behaviors. We also offer ideas of the ecological/behavioral forces that may correlate with neural activation patterns of primate IBNS. Through comparison to *Homo sapiens* models, these findings suggest IBNS in primates may exist beyond cercopithecids and may be evoked by similar socio-ecological contexts. However, some key neurological distinctions between the two groups exist, influencing which distinct patterns of behavior may evoke IBNS (relative to their socio-ecological context).

KEYWORDS: prosociality, comparative behavior, inter-brain neural synchronization, neural systems, machine learning



Original article

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Introduction

When analysing the evolution of life on Earth, a common trend prevails – co-operation can become a vital key to reproductive success. From the smallest amoeba to *Homo sapiens*, co-operation birthed longevity (Kreider et al. 2022; Zhu et al. 2023). In retrospect, if co-operation in the Hominidae clade disappeared some 3 million years ago, *H. sapiens* could not have evolved. Our hominin ancestors needed co-operation as a survival tool to combat harsh environments that posed risks to their small population numbers (Townsend et al. 2023). Evolution of the *Homo* genus was dependent on the cooperative behaviors of our ancestors, who evolved from Miocene primates. Most extant primates still rely on cooperation to survive (Boyd and Richerson 2009).

From this point forward, when we refer to primates we exclude the tribe Hominini of which *H. sapiens* and their immediate ancestors are members. Primates are faced with a myriad of unique threats to their survival in various environments including predators, terrain, food security, and so on. However, using co-operation as a tool to protect against these forces is a common strategy used in prosocial behaviors such as unified defence against predators or foraging as a group to increase food collection (Garber 1987; Treves 2000; Boinski and Garber 2001). Though co-operative behaviors can be quite varied, all can be collectively classified as prosocial behaviors as they benefit the group instead of (or as well as) the individual primate (De Waal and Suchak 2010). The nature of primate prosocial behavior is different when compared to *H. sapiens*. Prosociality in *H. sapiens* is distinguished by a stronger empathic drive that employs a wider range

of enforcement mechanisms, allowing for more stable cooperation to form in larger groups of unrelated individuals (Melis and Semmann 2010). This enabled *H. sapiens* to flourish in the late Pleistocene (Sterelny 2021; Townsend et al. 2023), leading to the large population size increase seen today. How then do extant non-human primates sustain prosocial behavior without the usage of complex enforcement mechanisms cognate to *H. sapiens*? One answer to this question may be found in inter-brain neural synchronization (IBNS).

Inter-brain neural synchronization is an unconscious mechanism; where neural oscillatory activity is synchronized between people, so that recorded neural behavior across brain regions and bandwidths associated with prosocial tasks is identical (Valencia and Froese 2020; Lotter et al. 2023). Observational and experimental studies in mammals (including *H. sapiens*) describe IBNS as a neural behavior pattern evoked by prosocial behaviors such as alloparenting, physical co-ordination and group tasks serving a common goal (Tseng et al. 2018; Kingsbury et al. 2019; Rose et al. 2021; Zhang et al. 2022; Ogawa and Shimada. 2023). A distinction between mirror neuron activity and IBNS must be made here, with implications to identify IBNS as a facilitative process for the achievement of social goals. As mirror neurons are grounded in motor-based behavior (inter-personal motor synchrony) it is difficult to generalise their synchronization effect to abstract situations between people (e.g. conversational turn-taking) (Hasson and Frith 2016). However, IBNS does result in cortical synchronization between areas representing abstract processes and even correlates to enhancements of abstract cognition (e.g. shared intention-

ality) (Fishburn et al. 2018; Gvartz-Provolovski and Perlmutter 2021). Thus, IBNS is distinct from mirror neurons as there is no proof that it is a static process; it is more likely that IBNS fluctuates between synchronized and desynchronized periods (Froese et al. 2024). Wang et al. (2025) demonstrate that by separating the effects of motor synchronization (mirroring) from genuine IBNS, brain activity synchronized specifically to abstract cognition (e.g. emotion) can be isolated. Therefore, IBNS is characterized by the synchronization of neural activity underpinning abstract cognition. Prosociality often requires abstract cognition as it involves understanding and acting on shared goals, beliefs, or expectations; considering the perspectives or needs of others (Houwelingen and Dijke 2023). Considering this, IBNS is more than a computed correlation of synchronized brain regions, as previous hyper-scanning studies strongly indicate that prosociality mediates the IBNS process.

In *H. sapiens*, IBNS is a typical response associated with prosocial activity requiring shared intention and is suggested to enhance co-operation and cohesion in prosocial tasks, especially when compared to the same scenarios where IBNS is weak or not evoked between people (Rennung and Goritz 2016; Hu et al. 2017; Lu et al. 2023; Wass et al. 2020; Wang et al. 2025). Considering these benefits, IBNS could play a crucial, facilitative role in the co-operation of primates where there is an absence of similar levels of enforcement mechanisms which motivate stable prosocial behavior in *H. sapiens* (Koski and Sterck 2009; Melis and Semmann 2010).

Little information on IBNS in primates exists (Ramakrishnan et al. 2015; Tseng et al. 2018). It should be noted

that the current IBNS literature in primates is based solely on macaques (cercopithecids). None of these studies examine IBNS elicited through natural engagement in prosocial behaviors, and thus overlook aspects of the socio-ecological contexts that select for such behaviors. In this paper, it is proposed that our IBNS framework in primates will help researchers identify populations where IBNS may be easily observed. These assumptions are based on predictive correlations using the overarching socio-ecological contexts of primates, which are likely to elicit displays of prosociality. The proposed framework could also be made falsifiable by fieldwork that reports consistent prosocial behavior in primates that does not evoke IBNS. Both outcomes would provide distinct insight into the evolution of IBNS in *Homo sapiens*.

A study of IBNS in *Macaca mulatta* dyads performing a socio-motor task where one member came into the vicinity of a food item while the other observed, showed that *M. mulatta* exhibited IBNS that was dependent on specific aspects of social interaction and cognition (Tseng et al. 2018). Ecological conditions such as the food reward (and its location) and the presence of conspecifics influenced the IBNS response, underpinned possibly by dopaminergic reward-response pathways critical to social learning and adaptation in primates (Murray et al. 2011; Beeler and Dryer. 2019; Wise 2020). Tseng et al. (2018) present a possible relationship between primate IBNS and specific stimuli/co-operative behaviors influencing IBNS activation patterns (with socio-ecological forces potentially acting as a mediating factor). An identical framework for IBNS is found in *H. sapiens* (Valencia and Froese 2020). However,

this paper offers a broader hypothetical framework for primate IBNS that derives from analysis of potential differences in the elicitation and manifestation of this function across a wide range of primate species. We suggest that future research based on hypotheses proposed here may lead to the verification of IBNS in a wide range of primates.

Inter-Brain Neural Synchronization in animals extends beyond the primates; bats, rats and birds also demonstrate IBNS concomitant with increased cooperation and social adaptation (Hoffman et al. 2019; Kingsbury et al. 2019; Zhang and Yartsev 2019; Rose et al. 2021; Zhang et al., 2022). Notably, no modern reptile has been documented to exhibit IBNS, though social complexity influenced by ecological variables has been recorded (Brattstrom 1974). Though reptiles are stereotypically labelled as non-social, both current and ancient reptilians present valid cases of prosocial behavior (Doody et al. 2012; Titus et al. 2021). Therefore, their potential for IBNS should not be overlooked, which raises two important considerations: 1. Ecology influences the emergence of prosociality and 2. The absence of a prosocial behavior does not preclude any species from having a latent aptitude for IBNS. Considering this, we cannot say whether IBNS may exist as a homoplasy or homology in evolution (in part due to the absence of IBNS research in reptiles and other non-mammalian vertebrates such as fish). So far IBNS has been recorded in some animals of mammalian ancestry; within this lineage there also exist animals who display little prosociality. The naturally solitary *Pongo abelli* is a prime example, though they are still capable of prosocial behavior and even display con-

flict resolution skills under crowded living conditions with conspecifics (an example of prosocial behavior influenced by socio-ecological forces) (Kopp and Liebal 2018). This fact could further the argument of IBNS as a homoplasy; a latent ability of all vertebrates with a central nervous system and the capacity for abstract cognition, where socio-ecological selective pressures for prosociality evoke the IBNS response. Future research into vertebrates outside the class Mammalia will provide further insight so assumptions made here are tentative. Generally, however, social adaptation to environmental cues appears to be the crux of IBNS. Therefore, by creating a framework where socio-ecological forces predicting prosocial behavior are a necessary condition to evoke IBNS, we offer a predictive model of IBNS which can be applied to all primates.

Past research in primates exploring the link between prosociality and environment mainly used cause-and-effect models of explanation (Tennie et al. 2016; Kuroshima and Fujita 2018; Shultz and Dunbar 2022). However, there is a lack of predictive correlational modelling and machine learning within this research area. This type of method would allow for a broader understanding of prosociality and IBNS in primates by creating probability estimates of prosocial behavior predicted by correlated socio-ecological variables. Predictive modelling and machine learning can use natural observations to calculate these probabilities and their stability when generalized from the model, which may broaden our knowledge of factors influencing the evocation of prosociality and IBNS in primates. In comparison, cause-and-effect models cannot predict behavioral relationships in the absence of an inter-

vention and are restricted to explanatory analyses in niche or laboratory environments, detracting from generalizability (De Waal & Suchak 2010, Lopresti-Goodman & Villatoro-Sorto 2022). In behavioral research, establishing causality for a specific behavior requires a complete understanding of context and record of all environmental variables which is beyond the scope of the current study. Correlational models are therefore more effective at predicting outcomes as the statistical relationship between variables can be analysed and validated without a causal link (Allison 1999). Our exploratory study aims to achieve a broader conceptualization of IBNS in primates by using predictive modelling techniques to outline which generalizable prosocial behaviors could theoretically evoke IBNS (mediated by socio-ecological factors). Our findings may provide a foundation for both natural and experimental IBNS research in primatology, where so far, the topic has been neglected.

Method

We used data from existing literature to demonstrate the likely presence of IBNS in primates in multiple socio-ecological contexts. We first measured select prosocial behaviors. Forms of prosociality vary greatly and can become niche behaviors, reducing their generalizability between primate species and resulting in non-standardized measurements (Polit and Beck 2010). Accordingly, six prosocial behavioral traits that can be generally measured in primates were chosen: (i) consolation behavior, (ii) group-hunting, (iii) group-foraging, (iv) formation of coalitions, (v) food-sharing, and (vi) alloparenting. These prosocial variables are distinct behavioral markers of so-

cial cooperation and have been previously studied across primates (Boesch 2009; Burkart et al. 2014; De Waal and Van Roosmalen 1979; De Waal, Luttrell, and Canfield 1993; De Waal et al. 2008; De Waal and Suchak 2010; Hohn et al. 2024; Fuente et al. 2021; Van Leeuwen et al. 2021). We feel it is necessary to note here that we are not analysing specifically proactive prosociality, as all forms of prosocial behavior are currently theorized to evoke IBNS in *H. sapiens*. We correlated these six variables against forty-nine variables measuring social, ecological, morphological, and biological (SEMB) conditions.

The sample consisted of 41 primate species from a random stratified collection, representing approximately 8% of total extant primate species (NB: logit modelling only requires a sample of at least $N = 20$ for model stability; Concato et al. 1995). Stratification was necessary as information on individual primates is unbalanced; more popularly studied primates, such as the great apes or macaques, retain far more information on SEMB variables over less studied primates such as the *Cacajao calvus* or *Galago senegalensis*. Regardless, missing observations still occurred and were marked "N.A." for easy translation into the R programming language. Power analyses are not necessary for this sample as there is no specific hypothesis that we are aiming to test, the data are non-explanatory, and we only aim to predict the occurrence of prosocial traits and IBNS based on associations between prosocial and SEMB variables. However, we offer hypotheses for further investigation based on the results of these predictions.

We gathered data on each primate species primarily from the Wisconsin

National Primate Centre Primate Information Network (2023) and San Diego Zoo Wildlife Alliance Library (2023), two open-access databases which record primate information on behavior, biology, and ecology from observational studies. If no information on a specific variable existed in either of these databases, primary sources such as journal articles, academic books and textbooks were used to gather information on SEMB variables. These sources were accessed through keyword searches within the Zoological Record database. Objective, observational recordings of all primate data were dummy coded into arbitrary classifiers (ordinal or binary), while observations of variables on a continuous scale (e.g., amount of daily socialization) were not recoded as they need no categorical classification for statistical analysis. Some ordinal variables were dummy coded based on quartile distribution analyses. Predation pressure and resource competition variables were calculated from existing models which were used as predictive equations and were coded into the data table (van Schaik 1989; Hart 2007). A list of recodes can be found in Supplementary File 1 (Supplementary materials Table S1). A significant limitation of this dataset lies in the disparate observational sources used to inform it. There is no specific, standard reporting practice for observational studies of primates to follow, with varying quality and quantity of information between sources. This caveat introduces possible biases into the dataset, such as errors in reporting and lower reporting reliability based on more subjective interpretations of behavior.

All statistical analyses took place in R Studio (R Core Team 2024); all variables were imported from an initial CSV

worksheet (Sevastidis, 2024). Naturally, the size of this dataset cannot be properly fitted into a binary logit model for each dependent variable (Harrell 2015). Thus, Kendall's correlations were performed correlating each prosocial variable with all 52 independent SEMB variables. We used Kendall's Tau (τ) for all correlations due to its flexibility in measuring non-normal variables of continuous, ordinal, and binary scales (Newson 2006). The lower τ -coefficient margin was set at 0.3 (fair association) to select associations between prosocial and SEMB variables that were suitable for predictive analyses using machine learning models. Variable selection through correlative analysis also assists in preventing the analysis of redundant variables where associations are multicollinear, which avoids over-fitting regression models (Montesinos-López, Montesinos-López and Crossa 2022). We set alpha (α) to 0.05 as the level of significance for all statistical analyses. Within binary predictive modelling of natural data, the confidence estimates of probability performance models are more relevant to identifying whether modelled values have occurred by random chance (Gardner and Altman 1986; Du Prel et al. 2009). Additionally, explicit testing of false positives using dedicated algorithms (e.g. AUROC) trumps the usage of an arbitrary p-value benchmark that is most applicable to two-tailed hypotheses, which are not investigated in this manuscript (merely offered for future research) (Kim and Bang, 2016; Jafari and Ansari-Pour 2018).

After we screened variable pairs via both correlation and significance measures, binary logit modelling using the prosocial variables could begin. Binary logit models were used for predictive modelling of binomial prosocial behavior.

ral traits as dependent variables (Harrell 2015). We input each prosocial variable into its own logit regression with all SEMB traits that were significantly correlated to that prosocial variable. Generally, logit model equations cannot contain more than one predictor variable per ten observations in the dataset or they incur significant risk of overfitting the model and increasing Type 1 Error rates (Concato et al. 1995; Peduzzi et al. 1995). Since the dataset contains 41 total observations, it was only suitable to include four predictor variables in every model equation for each prosocial dependent variable. Thus, we used a combination of a priori knowledge of variable associations and step-AIC (Akaike Information Criterion) algorithm to remove excess predictor variables. We recommend that any step-wise method is used in conjunction with a priori analysis, as automatic functions can remove critical predictors from model equations (Heinze et al. 2015). Therefore, we formed models based on predictors previously associated with prosocial variables and comparisons between AIC values between-models, resulting in a best-fit model with the most relevant predictors. It should be noted here that removed predictors were significant, but less relevant than others. We checked models for multicollinearity through variance inflation factor (VIF) scores with an exclusion cut-off of 5; only variables below the exclusion cut-off were included in models (Marcoulides and Raykov 2019).

We used the initial model output to calculate the predicted probability of each prosocial behavior occurring in relation to its correlated socio-ecological (SEMB) variables. We obtained probabilities through exponentiation of modelled odds ratios. In models with

more than one predictor variable, we used the full variation of all predictor value combinations to create predicted probabilities of prosocial behaviors associated with correlated socio-ecological (SEMB) variables. In models where two or more continuous predictor variables were present, separate model outputs were produced where each continuous predictor was variably held at its mean. This allowed deeper insight into each continuous variable's association with a prosocial behavior by modelling its full range. We then plotted predicted probabilities of prosocial variables with associated SEMB variables using the *ggplot2* package (Wickham 2016) in R Studio (R Core Team 2024). Where multiple variable values were missing or removed in a model predictor (due to statistical incompatibility), we used imputational binary logit modelling to establish estimates of likelihood and significance using the MICE package (Van Buuren and Groothuis-Oudshoorn 2011).

We reported McFadden's pseudo- R^2 -values summarising the overall fit of each model using guidelines from Hensher and Stopher (1979), where McFadden reports ρ^2 -values between 0.2 and 0.4 a good fit (above 0.4 is considered an excellent fit). We also used confusion matrices to identify the ratio of false negatives and positives output by binary logit models, the results of which were displayed through fourfold plots for ease of interpretation.

Based on these values, we created an Area Under the Receiver Operating Characteristic Curve (AUROC) to display the overall accuracy of model predictions, comparing AUC scores with leave one out cross validation (LOOCV) computations for each model. Comparison to each model's LOOCV AUC

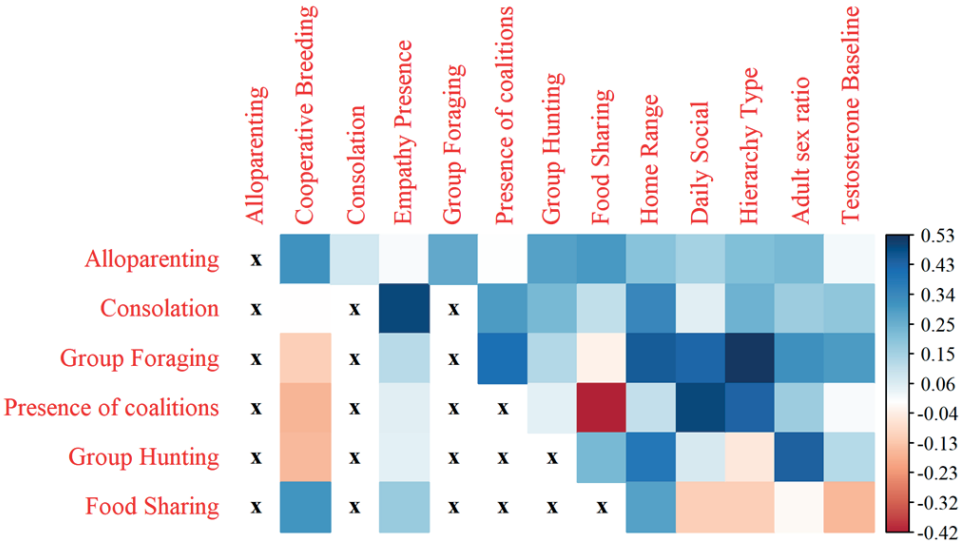
allows us to validate that predictive performance should remain stable when applied to similar populations external to the model. LOOCV uses N-1 iterations of the sample size for each model (40 iterations for each model) to train the model on all data points. The AUC output ranges within a 0-1 scale (compared against a random model at 0.5) and is a commonly used performance metric for model discrimination between specific classifiers. Confidence estimates of probability within the AUROC were distribution-independent as approximations on the link (logit) scale are unlikely to yield valid results for non-normal data, and binary data intervals have coverage equal to 0 (Cortes and Mohri

2005). Therefore, confidence estimates were avoided in binary logit models and were instead the focal point of AUROCs which reflect model accuracy of predicting true positives.

Results

Correlation coefficients of selected SEMB variables to prosocial behaviors were all statistically significant ($p = <0.05$) (Sevastidis 2025). Due to the size of the correlation table, only variables included in modelling were displayed in the following heatmap (Figure 1).

All results of original AUROC comparisons to LOOCV models can be seen below in Figure 2.



X = Perfect Correlation or Duplicates

Figure 1. Correlation Heatmap of Modelled Variables. Prosocial variables of interest are displayed on the y-axis and social, environmental, morphological and biological (SEMB) variables on the x-axis. The side legend represents correlation statistics for each variable pair on a gradient colour scale. Both the upper and lower triangles contain unique combinations of prosocial/SEMB variables

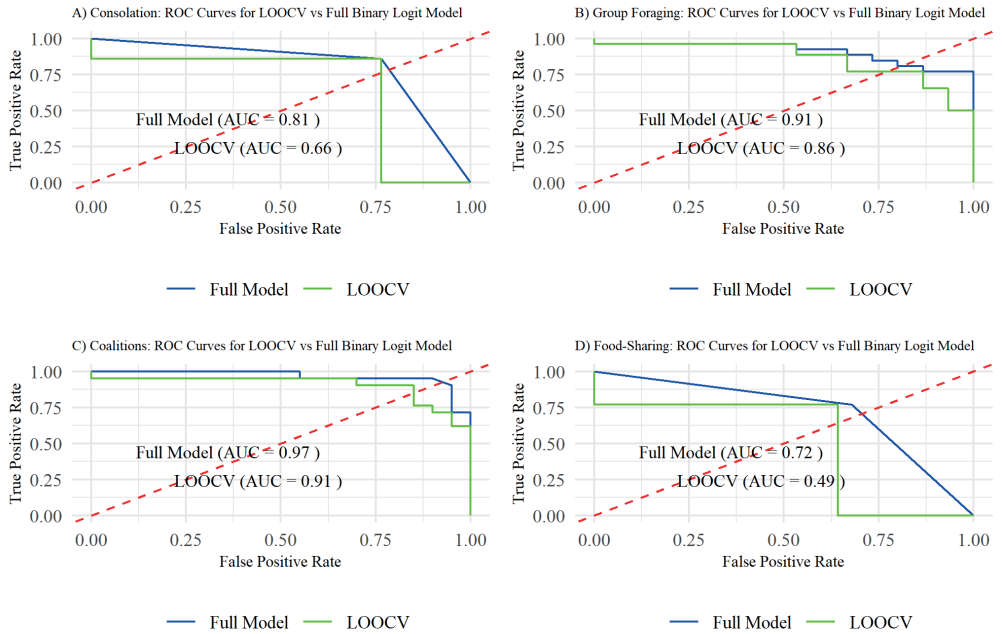


Figure 2. A collated figure of all Area Under the Receiver Operating Characteristic curve (AUROC) models analysed. AUROC of full model is presented in blue, while AUROC of Leave One Out Cross Validation (LOOCV) is presented in green. An AUROC score above 0.5 indicates that the model predicts more accurately than random chance. Plotline represents the ability of classifiers within the model to distinguish between sensitivity/specificity at all possible thresholds (values beyond those which belong to a particular class). AUROC is plotted against a random model (red diagonal dashed line). 2A) AUROC of empathy predicting consolation compared to a random model (LOOCV vs Full Model). 2B) AUROC of home range and daily socialising predicting group foraging compared to a random model (LOOCV vs Full Model). 2C) AUROC of hierarchy type, food-sharing & daily socialising predicting coalitionary behavior (LOOCV vs Full Model), and 2D) AUROC of coalitionary behavior predicting food-sharing (LOOCV vs Full Model)

Alloparenting

Recorded observations of co-operative breeding in primates were not significantly predictive of alloparenting behavior ($p = >0.05$) (Supplementary materials Table S2). Perfect separation was detected between the variables, where all recorded co-operative breeding societies also displayed alloparenting behavior (Supplementary materials Figure S1). McFadden's pseudo- R^2 ($\rho^2 = 0.11$), indicated poor model fit (Table B3).

Consolation

Consolation behavior in primate species was significantly predicted by observations of empathetic behavior; variables showed an excellent fit for the model ($p = 0.01$, $\rho^2 = 0.26$) (Supplementary materials Tables S3 and S4). Observed empathetic behaviour was defined as any behaviors that are recorded in the literature as empathetic or observations of behaviors which are commonly described as empathetic (e.g.

social contagions, targeted helping and so on) (Campbell and De Waal, 2014; Yamamoto, 2016). We did not include observations where empathy was assumed through abstract terms e.g. perspective taking, that did not accompany an accepted form of empathetic primate behavior. The absence of observed empathetic behavior resulted in a 3.7% probability that any given primate species would display consolation behaviors, while displays of empathy resulted in a 43% likelihood of consolation behaviors being present (Supplementary materials Table S5).

A four-fold plot displayed the rates of Type 1 and 2 Errors for the model (Supplementary materials Figure S2). Full model AUROC results indicated that the model has good predictive accuracy, outputting a true positive rate of 81% before producing any false positives (AUC = 0.81) (Figure 2A). However, once cross validated the AUC estimate was reduced to 0.66, indicating that while within-model prediction is excellent, applied to external populations predictions may only result in true positives 66% of the time. While confidence estimates for the full model are slim (95% CI = 0.8 to 1), the LOOCV model retains a wide interval (95% CI = 0.4 to 0.9) (Supplementary materials Table S6; generalizations from this model should be made cautiously).

Group Foraging

Both home range and daily socialising (as a % of a 24-hour day) significantly predicted the probability of group foraging behavior in primate species; model fit was excellent (home range $p = 0.03$, daily social $p = 0.02$, $\rho^2 = 0.48$) (Supplementary materials Table S7). At their means, home range ($M = 7.83\text{km}^2$) ex-

ceeded 7km^2 and daily socialising ($M = 5.84\%$) exceeded 5% of total time in the day, where primate species had a 93.4% probability of being group foragers. Since home range and daily socialising are continuous variables with a binary response, two separate plots were produced where one variable was held at its mean and vice versa (Supplementary materials Figure S3).

The AUROC for the full group foraging model inferred excellent predictive performance of the SEMB variables on group foraging behavior, outputting a true positive rate of 90.8% before encountering any Type 1 Errors (AUC = 0.908, 95% CI = 0.81 to 1) (Figure 2B, Supplementary materials Table S6). A Four-Fold plot of the binary confusion matrix showed that the model output four Type 1 and four Type 2 Errors out of 41 total predictions (Supplementary materials Figure S4). The LOOCV AUC comparison yielded a similar result (AUC = 0.86), validating the excellent predictive performance of this model when generalized to similar populations (95% CI = 0.74 to 0.96) (Supplementary materials Table S6).

Presence of Coalitions

Societies with no indication of strict despotism and egalitarianism were used as reference for these analyses. We aimed to measure predictive correlations of coalitionary behavior to distinct hierarchy types for clarity of analyses, but recognise that such behaviors are not universal to all primates. Daily socialising, food-sharing and despotic hierarchies were modelled with a statistically significant relationship to coalitionary behavior (daily social $p = 0.04$, food-sharing $p = 0.04$, hierarchy type 2 (despotic) $p = 0.01$,

$\rho^2 = 0.51$). Hierarchy type 3 (egalitarian) was not significantly related to coalitionary behavior in the model ($p = 0.22$), however is still important to be included in the model to classify data accurately (Supplementary materials Table S8). AUROCs displayed an excellent predictive accuracy for both full-model and the LOOCV model (full model AUC = 0.96, LOOCV AUC = 0.91) (Figure 2C) with high confidence estimates (full model 95% CI = 0.88 to 1, LOOCV 95% CI = 0.80 to 1) (Supplementary materials Table S6).

Figure 3 shows that food-sharing was a mediating variable influencing the ability of daily socialising to predict if primate species display coalitionary behavior. Food-sharing primates required higher levels of socialising to reach higher probabilities of coalition formation compared to primates where food-sharing has not been recorded. Additionally, rates of daily socialising reflecting similar predicted probabilities of coalition formation vary between hierarchy types and could indicate an

inferential relationship to coalition formation in a despotic hierarchy. A Four-Fold confusion plot showed that the model produced two Type 1 and one Type 2 Errors (Supplementary materials Figure S5).

Group Hunting

Due to validity issues caused by missing values of testosterone baseline and adult sex ratio, imputational data were used to model both variables when predicting group hunting in primates. The imputed data resulted in both adult sex ratio and testosterone not being significant predictors of group hunting (adult sex ratio, $p = 0.22$; testosterone baseline, $p = 0.60$) shown in Table S9 (Supplementary materials). Density plots comparing iterations of imputed data showed that simulated values variably followed the general trend of real values within the original dataset (Supplementary materials Figure S6). A discussion on improving this model can be found in the Supplementary File 2.

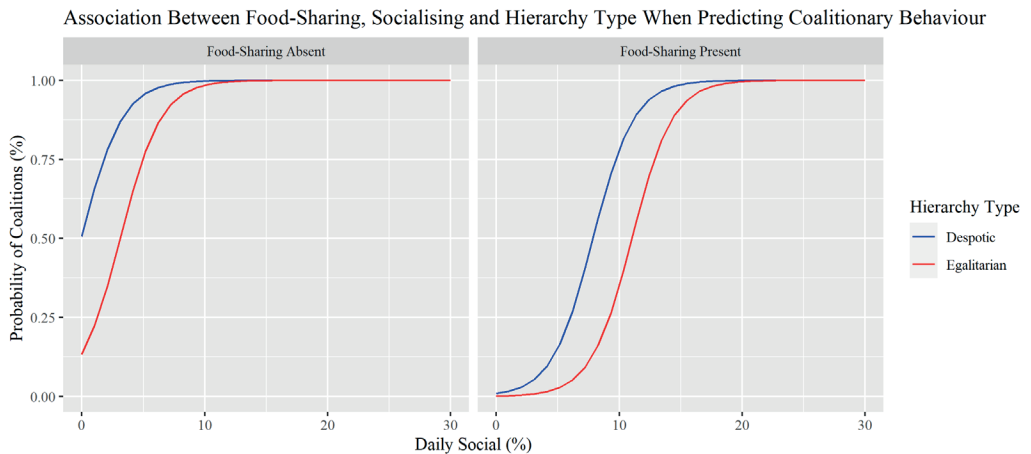


Figure 3. Food-Sharing Mediates the Relationship Between Daily Socialization and Probability of Coalitions. Egalitarian hierarchies displayed more socialization in each food sharing condition to achieve higher probabilities of coalition presence compared to despotic hierarchies

Food Sharing

Food-sharing in primates was significantly predicted by the presence of coalitions ($p = 0.01$, $\rho^2 = 0.14$) (Supplementary materials Table S10). Primates who display coalitionary behavior had a 13.6% probability of being food-sharing species, whereas the absence of coalitions resulted in a 52.6% probability of food-sharing in primates (Supplementary materials Table S11). AUROC results of the full model in Figure 2D displayed a good level of predictive accuracy ($AUC = 0.72$), however the LOOCV AUC displayed poor predictive accuracy for the model ($AUC = 0.49$). Confidence estimates for the full model and LOOCV AUC are wide (95% CI = 0.57 to 0.87, LOOCV 95% CI = 0.28 to 0.7) (Supplementary materials Table S6), indicating a low reliability of predictions made both within and external to the model. A Four-Fold confusion plot showed that the model produced eleven Type 1 and three Type 2 Errors (Supplementary materials Figure S7).

Discussion

This research suggests that certain socio-ecological contexts may predict prosocial behaviors in primates. We proceed to discuss possible inferential relationships within our models and explore how prosociality within these contexts could provide a framework to test IBNS generally within this taxon. While the discussions on IBNS presented here are theoretical, it is hoped that our findings and hypotheses are tested through future IBNS research in primates, especially in species that naturally fulfil socio-ecological conditions that select for prosocial behaviors.

We note that alloparenting and co-operative breeding are erroneously used as interchangeable terms in much of the current primate literature. While the two are semantically similar, in this paper alloparenting is defined as a society with non-restrictive breeding and care provided by non-parents, whereas co-operative breeding is used for societies where alloparents are a by-product (or possibly forced consequence) of reproductive skew to dominant breeders (Lukas and Clutton-Brock 2012). However, the definitive usage for each term is still debated (Mocha et al. 2023).

The predictive relationship between co-operative breeding and alloparenting was not significant; considering the logical and frequently observed relationship between the two, this result seems surprising. However, the raw data suggest a perfect separation between the two variables. No co-operative breeding was recorded in primate societies without alloparenting; the statistical model could not calculate a significant difference between the two variables as no variance between them existed. Therefore, no predictive modelling could be extracted from these data, though readers should note that logically, a co-operative breeding society will always alloparent; otherwise, the purpose of co-operative breeding is lost and the behavior would likely not exist. Based on this assumption, we can infer that primate species which practice co-operative breeding also practice alloparenting. Future studies should consider exploring if distinct behaviors associated with alloparenting (which vary between primate species) have any correlations to SEMB variables and potentially IBNS (Cerrito and Spear 2022; Isler and van Schaik 2012).

Interplay Between Home Range and Daily Socialization When Predicting Group Foraging

Our study found that the likelihood of a primate being a group forager increased to nearly 100% when the daily time spent socialising was at 10% or more (Supplementary materials Figure S3a). Group or social foraging is a cohesive action that depends on physical and temporal co-ordination, making it an optimal variable to discriminate between primates that could hypothetically display IBNS. This also provides an opportunity for researchers to investigate if cortical synchronization is varied during IBNS in different co-operative tasks. While group foraging is a widespread and effective behavior in the animal world, its presence in primate species is variable (Swedell 2012). Group foraging behaviors can display uniquely in each primate and can depend on the decision of leading party members to secure vegetation (Strandburg-Peshkin et al. 2015; Williams et al. 2022).

Consider the group foraging methods of *Pan paniscus*. Mixed sex groups of five to six conspecifics forage for fruits in tall trees (Janson 1992); when fruits are secured, they can become euphoric and begin to chase, greet, copulate, vocalise, and eat (Kano and Mulavwa, 1984). Though not part of the actual foraging strategy, the process denotes a key part of group foraging behavior – social cohesion (Sterelny 2021; Williams et al. 2022). Consider another group foraging strategy from *P. anubis*; these primates travel and forage in large groups of up to 200 individuals (Kiffner et al. 2022). With such a large population, group foraging operates through party leaders, who decide the direction of the group and time spent at a single foraging site (Strandburg-

Peshkin et al. 2015). Each group member must cooperate with the choices made by leaders of the foraging party to maximise individual foraging efficiency and reward in a species where home ranges can reach 19km² (Barton et al. 1992). All group foraging is dependent on constant socialising and cooperation between group members. It is therefore unsurprising that group foraging forms a strong predictive relationship with daily time spent socialising (Supplementary materials Figure S3a). Group foraging behaviors in primates with high daily rates of socialization indicate an elevated social cohesiveness, thus making them optimal candidates to potentially observe IBNS between conspecifics. However, there are group foraging primates that reflect an inverse of the relationship displayed in (Supplementary materials) Figure S3a.

Lagothrix lagothricha and *Erythrocebus patas* are two examples of the conflicting patterns that emerge when using daily socialising to predict the presence of group foraging in primates. *E. patas* only spends 3% of its day socialising and is a group forager, whereas *L. lagothricha* spends 10% of its day socialising, but does not forage in groups. One explanation for this difference may be found in the home range of each primate; another predictive condition of group foraging behavior in primates. In Figure S3b (Supplementary materials), the model shows that when daily socialising is held at its mean, a wider home range predicts an increased probability of group foraging. *L. lagothricha* lives within a home range of approximately 0.6km² compared to *E. patas* home range of approximately 4km². In Figure S3a (Supplementary materials), a home range of 4km² results in a group foraging probability estimate of 80%. Therefore, even when primates

socialise for 10% or more of their day, their home range can potentially decrease the effect of daily socialising as a predictive condition for group foraging. On the other hand, primates who are not intense socialisers like *E. patas* are certainly not bereft of the ability to act prosocially. To use group foraging as an indicator of IBNS, ecological/behavioral predictive factors of home range and daily socialising must be considered together with the theoretical implications discussed here. These socio-ecological forces predicting group-foraging behaviors may also influence IBNS, potentially altering the number/loci of synchronized cortices between primates where a different motivator (i.e., the presence or absence of regular socialization) spurs IBNS. Specific analysis of the number of loci synchronized between conspecifics should be compared on a gradient from solitary to highly social primates; IBNS most likely exists on such a gradient underpinned by familiarity with conspecifics as seen in humans (Kinreich et al. 2017; Kurihara et al. 2024). Therefore, future research should also consider analysing IBNS within group-foraging primates like *E. patas* that are not highly social.

How Food-Sharing Could Mediate Coalition Formation in Different Primate Hierarchies

Figure 3 suggested that food-sharing may play a mediating role in the probability of primates displaying coalitionary behavior when measured with daily time spent socialising. Higher probabilities of coalition presence in non-food-sharing primates are achieved at lower levels of socialising compared to food-sharing primates. Hierarchical structure was also shown to be significant to this re-

sult. Generally, food-sharing in primates (which is rarely observed) serves one of two functions; to reinforce relationships (through reciprocity or ally consolidation) or to reduce harassment (tolerated theft) (Silk et al. 2013). Both require complex cognitive abilities including the capacity for reciprocity, understanding of social relationships and even anticipatory behavior of conspecifics, suggesting abstract thinking beyond immediate needs (Legg, Ostojić and Clayton 2014). To gain allies, elevated social tolerance between conspecifics (indexed by increased socialization) is required (Tai et al. 2012).

Top-down despotic societies create rigid social boundaries caused by dominance and kinship behaviors, which greatly narrow the opportunities for social relationships and limit socialising in general compared to egalitarian primates (Tombak et al. 2019). Typically, aggression reduces tolerance between conspecifics and forces subordinates in despotic societies to seek coping strategies, especially via social support in the form of coalitions (Sapolsky 2005). Considering this, a likely coalition where food-sharing would take place in despotic societies would be within kin and reciprocal relationships, as bachelor groups are competitive and prone to intra-aggression, and food-sharing is not known to take place during despotic reconciliation (Palagi and Norscia 2015). It must be noted here that food-type alone is not a predictor for any certain behavioral outcome (though it can be associated with certain behaviors) (Jaeggi and Schaik 2011).

Female-cryptic mate choice is an exemplary strategy that mixes both kinship and long-term investment in conspecifics, which can be mediated by food-sharing in both *Pan troglodytes* and *M. mulatta* (Du-

buc et al. 2012; Crick et al. 2013). Firstly, by creating the illusion of paternity through sexual intercourse with variably ranked fathers, cryptic females can theoretically expand their social matrix and acquire multiple mate-guards. This inter-sexual coalition is highlighted by Sapolsky (2005) as a subordinate coping strategy in a despotic society. These relationships are usually prefaced by intense social affiliation such as grooming and physical contact (including sexual engagement), establishing a foundation for reciprocity following Bronsan and De Waal's (2002) proposed three levels of reciprocity. In the highly despotic *M. mulatta*, female consorts are allowed to co-feed more often (Dubuc et al. 2012) at the same site as their male counterpart. In *P. troglodytes*, females receive higher quality food after copulation with a male food possessor even outside of peak fertility; this did not consolidate food-sharing with the same male for the next oestrus period (Crick et al. 2013). Therefore, by participating in bouts of intense socialization, despotic females can temporarily expand their social matrix and consolidate coalitions through transient reciprocal relationships which manipulate paternity, thus using food-sharing as a short-term investment strategy. We note here that the relationship between coalitionary behavior and egalitarian societies was not statistically significant. Accordingly, we discuss the non-relationship between egalitarianism and food-sharing predicting the presence of coalitions.

Primate egalitarianism strives to maintain higher levels of constant social tolerance between conspecifics (Boehm 1993; Pandit and Van Schaik 2003; Tombak et al. 2019; Harrod et al. 2020), thus eliminating the need for intense bouts of socialization to form coalitions. Therefore, should the need for coalitions ever arise

(such as those seen in *P. paniscus* female coalitions against aggressive males) (Tokuyama and Furuichi 2016) preceding socialization (before coalitionary behavior) would theoretically be less intense compared to despotic primates as investment strategies that strengthen cohesion between conspecifics such as food-sharing could permanently exist as a feature of reciprocity in an egalitarian society (Jaeggi and Gurven 2013; Tombak et al. 2019). This makes egalitarian coalitionary support not a matter requiring increased bouts of intense socialising, but a social enforcement mechanism built on long-term investment in conspecifics which maintains egalitarianism. In *H. sapiens*, small-scale egalitarian societies such as the Hadza of Tanzania share food to maintain egalitarianism; with individuals levelling inter-group asymmetries in food income after acquisition (Pinheiro 2021). Therefore, while egalitarian long-term investment in conspecifics using food-sharing could contribute to coalitionary behavior, the basis of coalitions may change dependent on hierarchy type, so much so that a generalized inferential relationship between the two cannot be made. These differences between hierarchical contexts shaping coalition formation and food-sharing between primate populations reiterate that ultimately, prosocial behavior manifests in accordance with the overarching socio-ecological context. This reinforces the previously mentioned notion that IBNS in primates would also uniquely manifest based on the relationship between socio-ecological context and prosocial behavior, like *H. sapiens* (Sáez et al. 2015; Valencia and Froese 2020; Kurihara et al. 2024). We make this assumption in reference to our gradient theory of primate IBNS – social familiarity mediated by

overarching socio-ecological factors will likely influence the manifestation and strength of IBNS in primates.

Why is Food-Sharing more Likely Outside of Primate Coalitions?

When predicting the probability of food-sharing using the presence of coalitions in primate societies, an inverse relationship was found indicating that food-sharing is a prosocial trait more likely to occur in the absence of any coalitional behavior (Supplementary materials Table S11).

Though the model itself was unstable and cannot reliably predict the relationship between these two variables, it is worth noting that instances of food-sharing occur outside of primate coalitions e.g. tolerated theft and kin selection. The inferential relationship between food-sharing occurring outside of primate coalitions still has value to understanding different contexts underpinning prosocial primate behavior. However, it is apparent that food-sharing as a general label is not a suitable classifier to use in predictive analyses and we acknowledge this as a weakness of our model. Instead, we recommend that the food-sharing variable be further operationalized to reflect the distinct contexts in which this behavior takes place. Using a model with a more refined food-sharing variable may increase the accuracy and reliability of predicting the occurrence of this behavior in a general primate population.

Predicting Consolation Behaviors Through Empathy Presence in Primates

The presence of empathetic behavior in primates indicated a 40% likelihood of consolation behaviors being present

within a primate species, whereas the absence of empathy inferred a less than 5% likelihood of any consolation behavior. It should be noted here that the empathy presence variable contained observations which reflected of both cognitive and affective empathy. Though either type of empathetic behavior can still lead to consolation, cognitive empathy has been shown in *H. sapiens* to motivate consolatory behavior to a greater extent (Abraham et al. 2014). Both cognitive and affective empathy have been theorized to underpin sympathetic concern and consolatory behaviors in great apes, but no data explicitly discriminating these factors exist (Clay and De Waal 2013; Webb et al. 2017). To evaluate the correlations/predictive relationships of empathy to consolation behaviors, more detailed data discriminating between cognitive and affective empathic styles in primates are needed. Furthermore, it is recommended that data on empathy are de-centralized from the great apes to achieve a wider perspective of empathic cognition in primates. Numerous studies in *H. sapiens* have detailed the connection between empathetic behavior and IBNS (Valencia and Froese 2020). Therefore, primates that display empathy and consolation behaviors could be optimal candidates to observe IBNS in future research.

Comparing Inter-Brain Neural Synchronization and Key Prosocial Behaviors Between Primates and *Homo sapiens*

So far, we have discussed predicted prosocial behaviors in primates which may guide researchers to species (outside of macaques) that exhibit unique patterns of IBNS in a range of socio-ecological

contexts. We will go on to discuss the theoretical justification of IBNS related to these prosocial behaviors within primates, and identify key similarities and differences between *H. sapiens* and primate IBNS. We do this with the goal to highlight how IBNS may uniquely manifest with distinct prosocial behaviors influenced by environment and neurobiology in a range of primates.

Many of the prosocial variables presented in the discussion were predicted by daily socialising with an overarching theme of co-ordinated group activity. Group foraging and coalition formation are both behaviors that require large-scale co-operation to achieve common goals, underpinned by increased socialization. Similar patterns of prosociality are seen in modern *H. sapiens*, where group behaviors increase the success of common goals and efficiency of co-operation (Sinha et al. 2016; Szymanski et al. 2017). In *H. sapiens*, such group activities are underscored by IBNS elicited through socialization during co-operation (Valencia and Froese 2020). For example, coalitionary scenarios in *H. sapiens* (such as team sports) evoke IBNS via intense socialization (vocal/physical communication) and co-ordination to achieve a common goal of victory over opponents (an example of shared intentionality), potentially mediated by dopaminergic systems (Li et al. 2020; Liu et al. 2021; Probolovski and Dahan, 2021).

Considering the influence of cooperative group scenarios on the cortical manifestation of IBNS within *H. sapiens*, (Tseng et al. 2018; Valencia and Froese 2020) it is plausible that similar scenarios in non-human primates may elicit unique patterns of IBNS. When food-acquisition becomes the primary goal of primate co-operative teams (typically

seen in group foraging primates) identical patterns of co-operation to *H. sapiens* may emerge. A primate group-foraging party may cooperate by synchronising behavior to commands from a party leader, with the common goal to increase foraging efficiency and success (a form of shared intentionality) (Hintz and Lonzarich 2018; Williams et al. 2022). Similar scenarios have been created with *M. mulatta* in a laboratory setting where observer-participant dyads completed motor courses to achieve food rewards (Tseng et al. 2018). Translation of these results to natural group foraging scenarios (where an even greater scale of teamwork is required in response to dynamic environments) would suggest that IBNS is active during group foraging, with activation patterns possibly being influenced by natural socio-ecological contexts.

However, distinct neuroendocrine systems differentially influence *H. sapiens* and primate prosocial behaviors which may evoke IBNS. Levels of dopamine (critical to *H. sapiens* prosociality) are much higher in the nucleus accumbens (NAcc) and striatum of *H. sapiens* compared to great apes (Raghanti et al. 2018; Hirter et al. 2021). Additionally, great apes retain a higher density of acetylcholine receptors (linked to dominance and territorialism) compared to *H. sapiens* (Raghanti et al. 2018). Interactive analyses have shown that dopamine in *H. sapiens* brain is modulated by both acetylcholine and glutamate and is responsible for increases in prosocial behavior (Lester et al. 2010; Sáez et al. 2015). Furthermore, increases in dopamine are rewarded through interaction with oxytocin, creating a distinct neurochemical positive feedback loop for prosociality in *H. sapiens* (Love 2013). Serotonergic systems in the orbito-frontal

region of great apes also show correlation to pro-social behavior and inhibition of anti-social behaviors; comparatively hominins' striatal serotonin levels show marked increases and correlations with prosocial behavior (Saniotis et al. 2021). The function and interaction of up-regulated oxytocin, dopaminergic and serotonergic systems within *H. sapiens* creates distinct enforcement mechanisms for co-operative and prosocial behavior, leading to distinct manifestations of IBNS (though these may not be critical to its elicitation; only cortical activation patterns) (Mu et al. 2016; Lotter et al. 2023).

In comparison, dopamine receptor modulation was shown to have no significant effect on prosociality in *M. mulatta* (Wendland et al. 2006). This suggests that IBNS could potentially be modulated by distinct neuroendocrine systems which selected for increased co-operation in *H. sapiens* (Clark and Henneberg 2021). Notably, cooperation is much less prominent in great apes compared to *H. sapiens*, highlighting a potential implication of differing neuroendocrine systems supporting prosociality (Tomasello 2023). However, the current literature on primate IBNS is extremely limited so far and no studies have presented direct evidence for a relationship between neurohormones and IBNS in primates. Group foraging practices of *P. paniscus* could provide future researchers with a case for dopamine-induced IBNS (in reference to implications of dopaminergic influence on primate IBNS patterns by Tsung et al. 2018) and vitally expand the existing literature on the neuroendocrine systems that could support primate IBNS.

However, prosocial activity does not always have to involve large coalitions or teams striving to achieve a common goal. Co-operation is also realized on a smaller

scale in both the primates and *H. sapiens* in individuals who take on roles as alloparents or carers, sometimes subserved by empathic or socio-cultural motivations. Parenting in modern *H. sapiens* strongly elicits IBNS, mediated by communication and distress between parent and child (Liu et al. 2024), usually in the form of crying and distress vocalizations. Parent responses to infant distress are mediated by empathy in *H. sapiens*, particularly cognitive empathy (Abraham et al. 2014). Cortical areas responsible for cognitive empathy are synchronously activated in parental dyads by IBNS during observation of infant distress, an example of sympathetic concern (Wever et al. 2021). Sympathetic concern is followed by consolatory behavior in *H. sapiens* which evokes IBNS via inter-parental neural coupling (Liu et al. 2024). Consolation behavior motivated by IBNS and empathy has also been documented to increase social closeness in *H. sapiens* (Turner and Turner 2013).

Notably, *H. sapiens* parental concern-consolation reaction can result from several unique social scenarios involving infants and conspecifics; possibly following hominin behavioral adaptations due to erect posture and further development of the Default Mode Network (DMN). Early hominin erection of the trunk may have significantly reduced the tactile relationship between mother and infant, resulting in more frequent bouts of infant distress (via crying or vocalizations) richer in semantic meaning and empathic manipulation compared to great ape predecessors (Falk 2004). This may have led to the distinct behavioral displays of concern-consolation behaviors seen uniquely in *H. sapiens* such as feeding or *motherese* to alleviate distress, as well as the usage of distal communication to

soothe infants (Falk, 2004; Hayashi and Matsuzawa 2017).

Primates also have the capacity for cognitive empathy and show sympathetic concern to socially close conspecifics in distress (De Waal 2008; De Waal 2011; Palagi et al. 2014), which can be followed by engagement in consolatory behaviors for the distressed (e.g., licking, grooming). Consolation behaviors in primates also predict improved social closeness and integration, reflecting the same pattern of empathy-motivated behavior seen in *H. sapiens* (Webb et al. 2017). However, consolation in this sense may occur through two different neuroanatomical pathways between primates and *H. sapiens*. The topography of *H. sapiens* and *P. troglodytes* prefrontal cortex shows distinct anatomical differences in relation to the DMN, namely the absence of the dorso-medial prefrontal cortex (D-MPFC) in *P. troglodytes* (Rilling 2014). The D-MPFC has functional relevance to language and theory of mind behaviors within *H. sapiens*, a distinct form of cognitive empathy which has been shown to facilitate IBNS (Decety 2010; Fishburn et al. 2018).

Although, great apes may lack this specific neuroanatomical pathway, they are still capable of using cognitive empathy that is rudimentary in comparison to *H. sapiens* (Hare et al. 2000). Advances in the anatomical development of the DMN may have occurred in early hominins with the development of language and more advanced forms of tool-making (Rilling 2014). This highlights the importance of Falk's (2004) *motherese* hypothesis and Dissanayake's (1999; 2003; 2004) work in hominin mother-infant interaction, when analysing the potential differences in patterns of cortical activity (during IBNS) between primates and *H. sapiens*. Notably, these works highlight an epoch in the

hominin lineage where unique prosocial behaviors arose from exapted features of increasingly prosocial mother-infant interactions. This idea extends to neuro-hormonal regulation of prosociality (e.g., oxytocin pathways to regulate cohesion) and advancements in socio-cognitive architecture – including the DMN and advanced forms of empathy. Recent studies have compared the superior temporal sulcus (STS) of non-human primates to the temporoparietal junction (part of the DMN) in *H. sapiens*, particularly the circuit connecting the STS, amygdala and lateral intraparietal area in non-human primates which may be a precursor to the evolution of theory of mind in *H. sapiens* (Ong, Madlon-Kay and Platt 2021; Platt, Seyfarth and Cheney 2016). Focus should be given to brain areas showing protracted development correlated to prosocial behaviors as these are hypothesized to subserve increased prosocial interaction (and neural responsivity) in non-human primates and thus may be easier to measure for IBNS during prosocial interaction (Cerrito et al. 2024).

No studies to date have shown a relationship between theory of mind and IBNS in primates. It can be argued that neuroanatomical differences resulting from early hominin selection pressures have influenced the formation of distinct prosocial behaviors unavailable to other primates which elicit IBNS in *H. sapiens*. Considering that both primate and *H. sapiens* consolation behavior is activated via sympathetic empathy, especially towards infants, future studies should aim to investigate the presence of IBNS in alloparental primates who show high investment in the offspring of related individuals. It should be noted here that the current study did not use phylogenetic comparative analysis to correlate

SEMB variables with complex prosocial behaviors, therefore limiting evolutionary tracing and analysis of them. However, we recommend that future research uses trait mapping and predictive modelling of paleoneurology associated with SEMB variables (see Pearson and Polly, 2023; Pearson and Polly 2024) to provide a richer description of behavioral phylogeny.

Using modelled predictions of prosociality in a diverse sample of primate species, we compared prosociality between primates and *H. sapiens* to explore the idea that IBNS may be possible in all primates. Primates behave within similar prosocial contexts that precede IBNS in *H. sapiens*, ranging from empathetic concern and consolation to group-based behaviors that require higher levels of socialising. Additionally, the current studies on primate IBNS clearly demonstrate the existence of this function within this taxon (though limited only to macaques), potentially underpinned by similar neurohormones to *H. sapiens*. However, key differences between these groups may exist in relation to how IBNS is evoked. The factors that differentiate IBNS between primates and *H. sapiens* have likely been shaped by early hominin selection pressures. This research has implications for investigating the presence of IBNS in hominins. In our study, we provide a framework on how IBNS could exist in all primate populations which fulfill socio-ecological conditions that elicit prosocial behaviors, and the potential distinctions of IBNS between primates and *H. sapiens*. We have provided multiple hypotheses for future researchers to test the existence of IBNS in a diverse range of primates; potentially expanding our understanding of IBNS in non-human primates, which could further extend our knowledge on IBNS in *H. sapiens*.

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Conflict of interest

The authors declare that Maciej Henneberg is an Editor of Anthropological Review, but was not involved in the handling of this manuscript.

Author contributions

All authors contributed to study conceptualization, discussed results, and made critical contributions to revisions/editing, resulting in the final manuscript. JS was the lead researcher, conceived the study concept and design, acquired all data for data analysis, performed all data analysis, and wrote the entire manuscript. GC provided many materials for the study. MH contributed to the design of statistical methods.

Ethics statement

Not applicable.

Data availability

Data on primate species used for this study are freely accessible in online repositories (Wisconsin National Primate Research Center and San Diego Zoo Wildlife Alliance Library) or through online literature.

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