CONTEXT-DEPENDENT PLASTICITY IN SOCIAL SPECIES: FEEDBACK LOOPS BETWEEN INDIVIDUAL AND SOCIAL ENVIRONMENT

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Editorial: Context-Dependent Plasticity in Social Species: Feedback Loops Between Individual and Social Environment

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Keywords: social behavior, ethology and behavioral ecology, interactions and social networks, social stress, sociality and complexity, coping style, social umwelt, social niche construction

Editorial on the Research Topic

Context-Dependent Plasticity in Social Species: Feedback Loops Between Individual and Social Environment

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INTRODUCTION

Behavioral sciences cover a wide range of research fields, such as ethology, behavioral ecology, behavioral genetics, and behavioral physiology. In all these fields, individuality in behavior is now widely recognized and thus the focus of many studies is shifting from population averages to individual differences (Wolf and Weissing, 2012). Studies of inter-individual behavioral differences, although descriptive and functional in the beginning (Sih et al., 2004), start once again to address the four fundamental questions of ethology (Tinbergen, 1963), and to focus on developmental and mechanistic aspects (Jeanson and Weidenmüller, 2014). Some attempts also integrate both, inter and intra-individual variations in a more general framework of research (Dingemanse et al., 2010). Given this renewed interest in understanding whether or not changes in individual behavioral decisions occur, it is more important than ever to elucidate how plasticity (developmental, contextual, etc.) combines with non-plastic inter-individual variation, and how norms of individual reaction are essential to elicit the diverse individual behaviors in different contexts.

Social interactions constitute a significant part of an individual's experience (Hinde, 1976; Sachser et al., 2020). As such, these interactions are both immediate contextual factors and selective pressures on the expression of adapted behavioral responses. Behavioral decisions greatly depend on what can be considered a "social umwelt" (von Uexküll, 1921; Yamagishi and Hashimoto, 2016), which is both part of the perceptual environment as well as a way of perceiving the environment, allowing individuals to act upon a diversity of cues and signals. This potential richness in contextual variation has certainly shaped the individual behavior of social species, having consequences on decision mechanisms, such as the cognitive mechanisms associated with social life.

Recent studies have shown how social context and experience can change behavioral decisions of a variety of social species (Yagound et al., 2012; Fragaszy et al., 2017). Ultimately, the social environment can even create such an intense stress response that animals have difficulties showing sufficient plasticity or adaptive responses, a current and relevant problem in a period of accelerated ecological changes (Harlow et al., 1965; Koolhaas et al., 2017; Takahashi et al., 2018; Balasubramaniam et al., 2020). This new focus on how plasticity and inter-individual differences influence social behavior makes it timely to join different perspectives and aggregate new findings of various fields. Experimental evidence of the context-dependent plasticity from diverse organisms can lead to the elaboration of a common research framework, bringing back comparative psychology and ethology in the understanding of social behavior, its expression, development, ecology and evolution in an overt fashion.

In this Research Topic, we addressed the mechanisms behind inter and intra-individual variation and/or consistency in behavioral expression focusing on social interactions. Our goal was to explore how experience affects all levels of behavioral complexity, from molecular to population-level approaches.

THE SOCIAL ENVIRONMENT SHAPES BEHAVIORAL PROFILES

Social interactions profoundly influence behavioral development and expression. For instance, it has long been shown that social isolation during development can induce behavioral disturbances in group-living species (e.g., primates: Harlow et al., 1965; insects: Lihoreau et al., 2009). Here several mechanisms by which the social environment influences behavioral flexibility are highlighted.

Behavioral flexibility can depend on group composition. Hemelrijk et al. analyzed a seven years dataset of wild vervet monkeys (*Chlorocebus pygerythrus*) and found that female dominance to males varies relative to the number of males in the group: the more males, the higher the proportion of fights won by females. In this species, intersexual dominance presumably emerges through a winner-loser effect whereby winners of an aggressive interaction tend to win more and more (Dugatkin, 1997). Mutwill et al. showed that behavioral flexibility can also depend on social status. Domestic guinea pigs (*Cavia aperea* f. *porcellus)* live in large mixed-sex groups with a dominance and queuing system that gives older males an advantage for accessing females. By conducting paternity analyses on different colonies, Mutwill et al. demonstrated that both young and old males can nevertheless attain comparable reproductive success. Thus, younger males reproduced irrespective of queuing and their low social status. Males may use different reproductive tactics (sneaking, fighting, bonding with a specific female), which are flexibly applied with the onset of sexual maturity. Kraus et al. performed cross-fostering experiments in guinea pigs of wild origin demonstrating that behavioral and physiological differences between pups were plastic. This study illustrates the combined influence of the social environment and pre and post-natal experience as determinants of adaptive flexibility.

Interestingly however, these effects of the social environment are not expressed in every context. Yoshida and Koda investigated the behavior of goats (*Capra hircus*) facing an unsolvable task (i.e., in which food reward was kept in a sealed transparent bucket in the presence of a human), and observed that the social rank of the goats did not influence their behavior. In this context, inter-individual differences in sociability toward humans best predicted the behavioral responses, as only the most sociable goats sleeked help from humans to solve the task.

FROM INTER-INDIVIDUAL TO INTER-GROUP DIFFERENCES

Inter-individual behavioral variance can also shape the social environment and the behavior of groups. This is, for instance, the case in colonies of social insects that rely on division of labor between physiologically, morphologically and behaviorally distinct classes of individuals (Hölldobler and Wilson, 2009). Recent studies put forward the critical importance of behavioral heterogeneity for collective behavior (Jolles et al., 2020).

Kolay et al. reviewed growing evidence of personality within castes of ants. Foragers, in particular, can show persistent inter-individual variability in their incentive to start foraging after receiving food, deposit trail pheromone, be aggressive, be attracted by light, respond to sucrose, or learn. Many of these traits likely influence how individuals perceive and use information, prioritize personal or social information, and learn, which may influence task specialization. The distribution of personalities in a colony can ultimately determine variability in group behavior, for instance with some colonies that are consistently more aggressive than others (Pinter-Wollman, 2012). Japyassu et al. discuss whether the detection of repeated group differences across a population deserves to be considered as a "social personality." Using an epistemological approach, they argue that socially self-organized systems, such as isolated ant trails and bee recruitment groups, are too simple to have personalities. They advocate social personality should be used as a metaphor rather than a real transposition of a psychological phenomenon, highlighting the great care that should be taken when trying to apply concepts derived from human psychology to non-human cognition (Baracchi et al., 2017). This limitation of the cross-talking between psychology and ethology is also exemplified by Oberhauser et al. who explored cognitive biases in value perception by ant colonies. In humans, expectations are a strong driver of perceived value causing an undervaluation of a given option if a better option was expected, and an overvaluation if a poorer one was expected (e.g., Jayles et al., 2017). Oberhauser et al. tested whether the presence of a pheromone trail influenced the perceived value of a food source in foragers of the black garden ant (*Lasius niger*) navigating a Y-maze. Their results clearly show that trail pheromone, a source of social information, does not distort the value of food sources in these ants.

PERSPECTIVES

Contributions in this Topic Research illustrate the importance of the social environment in shaping behavior and social interactions across taxa (e.g., insects, rodents, ungulates, primates) and contexts (e.g., mating, dominance, collective decisions). However, it also questions about the relevance and care that needs to be taken when applying psychological concepts to non-human animals, and changing scales of observations.

We believe that much progress into research on the causes and consequences of behavioral flexibility will greatly benefit from recent technological advances to record and analyse behavior from large numbers of individuals and over long periods of times (Châline et al., 2017; Brown and de Bivort, 2018; Marchal et al., 2020).

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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High Reproductive Success Despite Queuing – Socio-Sexual Development of Males in a Complex Social Environment

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The start of actual breeding in male social mammals can occur long after individuals attain sexual maturity. Mainly prevented from reproduction by older and dominant males, young males often queue until strong enough to compete for favorable social positions and, in this way, to obtain access to females. However, to what extent maturing males also apply tactics to reproduce before this time is largely unknown. Therefore, the aim of the present study was to elucidate male socio-sexual development from onset of sexual maturity through first mating success until the achievement of a stable social position in a complex social environment. For this purpose, guinea pigs were used as a model system and reproductive success of males living in large mixed-sex colonies was assessed during their first year of life. As a reference, males in a mixed-sex pair situation were examined. Pair-housed males reproduced for the first time around the onset of sexual maturity whereas colony-housed males did so much later in life and with a considerably higher variance. In colonies, reproductive success was significantly affected by dominance status. Dominance itself was age-dependent, with older males having significantly higher dominance ranks than younger males. Surprisingly, both younger and older colony-housed males attained substantial reproductive success of comparable amounts. Thus, younger males reproduced irrespective of queuing and already before reaching a high social status. This mating success of maturing males was most likely achieved via several reproductive tactics which were flexibly applied with the onset of sexual maturity. The period of socio-sexual development before a stable social position is established may, therefore, be a time during which male mammals use flexible behavioral tactics to achieve reproductive success more frequently than commonly is presumed. In addition, the findings strongly indicate that high behavioral plasticity exists well beyond sexual maturity.

Keywords: behavioral development, reproductive success, dominance, reproductive tactic, paternity, behavioral plasticity, guinea pigs

INTRODUCTION

In many social mammals, the start of effective breeding in males can occur months or even years after individuals reach sexual maturity. This includes a wide range of carnivores (e.g., lions, *Panthera leo*: Packer et al., 1991; spotted hyenas, *Crocuta crocuta*: East and Hofer, 2002; meerkats, *Suricata suricatta*: Spong et al., 2008), ungulates (e.g., red deer, *Cervus elaphus*: Clutton-Brock and Albon, 1979), rodents (e.g., wild cavies, *Cavia aperea*: Asher et al., 2008; guinea pigs, *Cavia aperea* f. *porcellus*: Sachser, 1986; striped mice, *Rhabdomys pumilio*: Schradin et al., 2009) as well as different primate species (e.g., mandrills, *Mandrillus sphinx*: Charpentier et al., 2005; mountain gorillas, *Gorilla beringei beringei*: Bradley et al., 2005). The exclusion of younger males from reproduction within a social group is mainly caused by intrasexual selection, in particular male-male competition. Especially in situations where reproductive skew is high and breeding is mostly monopolized by only one or few alpha males, younger males are prevented from mating as they are unable to compete with the stronger dominant males (Bradley et al., 2005). In general, a high social status facilitates the access to resources including mating partners (Ellis, 1995; Spong et al., 2008; Alberts, 2012). However, such alpha positions are often constrained by a certain age, size, and weight (Haley et al., 1994; Schuett, 1997; Asher et al., 2008) or specific weaponry like horns and antlers (Lincoln, 1994; Kruuk et al., 2002) that bring about the necessary fighting abilities. As a consequence, maturing males often queue until strong enough to compete successfully and thereby obtain access to mating partners (East and Hofer, 2002; Alberts et al., 2003; Sachser et al., 2011, 2013).

The duration of breeding lifespan or tenure (i.e., period between the age when a male starts to breed effectively and the age when it stops) has a large influence on lifetime reproductive success and thus fitness. Therefore, queues of short duration in males might still be paid off by later benefits of reproduction, while long-term queues might already disadvantage the young males and promote "queue-jumping" (Wiley and Rabenold, 1984; Alberts et al., 2003). Because the time until favorable social positions are reached can be rather long in many species (East and Hofer, 2002; Alberts et al., 2003), counter tactics by maturing males against reproductive suppression might be expected. The period of socio-sexual development in male social mammals, beginning from onset of sexual maturity until the establishment of a stable social position, may therefore offer more opportunities in terms of reproduction than just queuing.

The domestic guinea pig (*Cavia aperea* f. *porcellus*) is a group-living rodent with a complex social bonding and dominance system (Sachser, 1986). In the natural habitat, its ancestor the wild cavy (*Cavia aperea*) is characterized by different forms of social organization (Asher et al., 2004, 2008). At low population densities the animals live in small groups, consisting of either mixed-sex pairs or small harems. At high population densities, wild cavies form larger harems which can be associated by male satellites (Asher et al., 2008). In addition, roaming males range over the whole area without stable spatial or social associations (Asher et al., 2008). These density-dependent social organizations can also be found in a comparable way in the domestic form (Sachser, 1986). Furthermore, male guinea pigs show high developmental plasticity during socio-sexual development. In particular, based on the social environment encountered during adolescence, they form completely different adaptive reproductive tactics (Sachser et al., 2011, 2013). More specifically, males raised in mixed-sex pairs develop a high-aggressive tactic of mate defense. In contrast, males growing up in large mixed-sex colonies establish a low-aggressive adolescent phenotype that precludes costly agonistic encounters with older and dominant males (Lürzel et al., 2010, 2011a,b; Zimmermann et al., 2017a). This queuing of maturing males seems to be adaptive in this complex social situation (Zimmermann et al., 2017b) as colony-housed males appear unable to effectively compete for high ranking positions with other males until an age of about 7 months, when they are fully adult (Sachser, 1986). However, paternity data are required to unequivocally clarify whether colony-housed males fail to reproduce before this time or whether they apply other reproductive tactics while queuing to reach an alpha position in adulthood.

The aim of the present study was therefore to elucidate the socio-sexual development of male guinea pigs from onset of sexual maturity through first mating success until the attainment of a stable social position in full adulthood in large mixed-sex colonies. For this purpose, reproductive success of colony-housed males was assessed over this phase of life and as a reference a mixed-sex pair situation was examined. It was hypothesized that owing to the social situation, colony-housed males would reproduce for the first time later in life (hypothesis 1, H1) and show a higher variance in time of first reproduction (H2) than pair-housed males. It was further assumed that reproductive success in colonies would be affected by dominance status (H3) and that according to previous work (Sachser, 1986), dominance itself would be age-dependent. Explicitly, we expected higher dominance status (H4) as well as a higher variance of statuses (H5) in older than in younger males. Accordingly, we predicted that reproductive success would be higher in older than in younger males (H6). Proportions of multiple paternities (= litters fathered by more than one male) were expected to be higher in younger than in older males as indication for potential sneaking tactics (H7). For the same reasons it was further assumed that proportions of multiple paternities would be affected by dominance status (H8).

MATERIALS AND METHODS

Animals and Housing Conditions

The guinea pigs used for this study were descendants of a heterogeneous shorthaired and multicolored breeding stock of 40 founder animals obtained from a professional breeder in 1975. To counteract inbreeding, individuals from other breeders were regularly crossbred into the stock. All animals were born and reared in a total of four mixed-sex colonies, each consisting of 7–12 males, 11–16 females and their pre-weaned offspring. Each colony was kept in a wooden enclosure of approximately 6 m^2 with wood shavings on the floor and three shelters. In each group, a graduated age structure was maintained by introducing young females (21 ± 1 days of age) every 4–6 weeks and young males (29 ± 2 days of age) every 6–8 weeks. Offspring routinely were taken out of the groups at 21 (±1) days of age, and adult guinea pigs removed at an age of about 20 months. For this study, 29-(±2)-day-old males from different litters were either moved from the natal colony to one of the other colonies (colony housing) or individually placed together with a 20-to-30-day-old unfamiliar female (pair housing). Pairs were kept in wooden enclosures of 0.5 m^2 with wood shavings on the floor and one shelter. All animals were housed under controlled conditions with 12 h:12 h light/dark cycle (lights on at 7 am) at a temperature of about 22°C and a relative humidity of about 50%. Commercial guinea pig diet (Höveler Meerschweinchenfutter 10700, Höveler Spezialfutterwerke GmbH & Co. KG, Langenfeld, Germany) and water were available *ad libitum*. Vitamin C was provided in the water twice a week. This diet was daily supplemented with hay. Date of birth was known for all animals and natural markings in fur color patterns allowed distinctive identification of each individual.

Experimental Approach

In colony and pair housing conditions, age at first mating success was determined for all males. In colonies, paternities and dominance status were additionally assessed. An overview of the procedure is depicted in **Figure 1**.

Assessment of Mating Success

In the four colonies, paternities of the offspring were determined over a period of about 17 months. For each male the dates of mating success (i.e., when copulation resulted in fertilization) were estimated by subtracting the median gestation period of 69 days from the date of birth of respective offspring. By this means, time of first mating success could be assessed for 27 colony-housed males. In 15 pair-housed males, time of first mating success was calculated on the basis of first offspring of the partner female. For litters in colonies of which parentage could be determined for all pups, it was examined whether offspring were sired by a single male or by multiple males (= multiple paternity litters).

Assessment of Dominance Status

In colonies, dominance status was determined for all males of an age between 60 and 359 days over a period of about 4 months. Every focal animal was monitored live in its respective home colony for 3 × 10 min per week by use of the software The Observer XT (Observer XT 7.0, Noldus Information Technology BV, Wageningen, Netherlands). Observations were carried out in the morning and in the afternoon by a trained observer (CR) applying focal animal sampling and continuous recording (Martin and Bateson, 2007). The order of colonies and focal animals for the observations was randomized. To assess dominance status, the outcome of agonistic encounters was scored by means of retreats (= subject moves to at least one body length from opponent within 3 s following agonistic interaction or approach by an opponent). The animal provoking a retreat was regarded as the winner. On this basis, dominance index was calculated for each male by the ratio of wins to the total number of scored agonistic interactions (minimum = 5 interactions). The index ranges from 0 to 1, with high values denoting dominant and low values denoting subordinate individuals (Sachser, 1986). Reproductive success was analyzed for all males that resided in the colonies over this period of 4 months (*n* = 11) to assess whether it was affected by dominance status.

Assessment of Age Effects

When testing for effects of age, data of males were divided into "younger males" (60–209 days of age) and "older males" (210–359 days of age). The cut-off at 210 days was chosen as colony-housed males begin to obtain high ranking (= alpha) positions around this age (Sachser, 1986). In a first step, we analyzed whether younger (*n* = 11) and older (*n* = 12) males differed in their dominance status. For this, those males of which dominance indices were determined over at least 5 weeks were taken into account. In a second step, we examined those males observed for at least 90 days in each age group (*n* = 19) to determine age differences in reproductive success and the proportion of multiple paternities. To account for different lengths of observation periods, relative measures of reproductive success (proportion of sired to possible offspring or litters) were used for this analysis.

Paternity Analysis

Ear tissue samples were collected from pups as well as all potential parents and stored in 70% ethanol until analyzed. Genomic DNA was purified by first digesting the tissue samples using Proteinase K, followed by phenol/chloroform extraction and DNA precipitation with ethanol. DNA pellets were washed with 70% ethanol several times and re-suspended in TE-buffer. Fourteen microsatellites were amplified by PCR and sequenced. See Asher et al. (2008) and Kanitz et al. (2009) for further details on microsatellite loci and amplification procedures. Alleles were analyzed using GeneMarker (version 2.6.2, SoftGenetics LLC, State College, PA, United States) and all potential parents as well as all pups which were included in subsequent analyses were genotyped at a minimum of 6 loci.

Parentages were assigned at a 95% confidence level based on simulations of 100,000 cycles using the likelihood-based approach implemented in Cervus (version 3.0.7, Kalinowski et al., 2007). Allele frequency analysis of all potential parents (*n* = 212) revealed a significant deviation from Hardy–Weinberg equilibrium and an increased number of null alleles at two loci (ap13, ap16) that were hence discarded. As pups may suckle from lactating females other than their own mother under colony housing conditions, maternities could not be clearly determined by observation in some cases. Accordingly, offspring were assigned to potential parents consisting of all sexually mature males (at least 60 days of age) that resided in the respective colony at the estimated date of fertilization (±3 days) and either the known mother or up to three candidate mothers. The proportion of genotyping errors was estimated in two ways (see Hoffman and Amos, 2005): First, mismatches in repeatedly genotyped samples (*n* = 35) were counted, resulting in 18 allele mismatches in 378 loci and

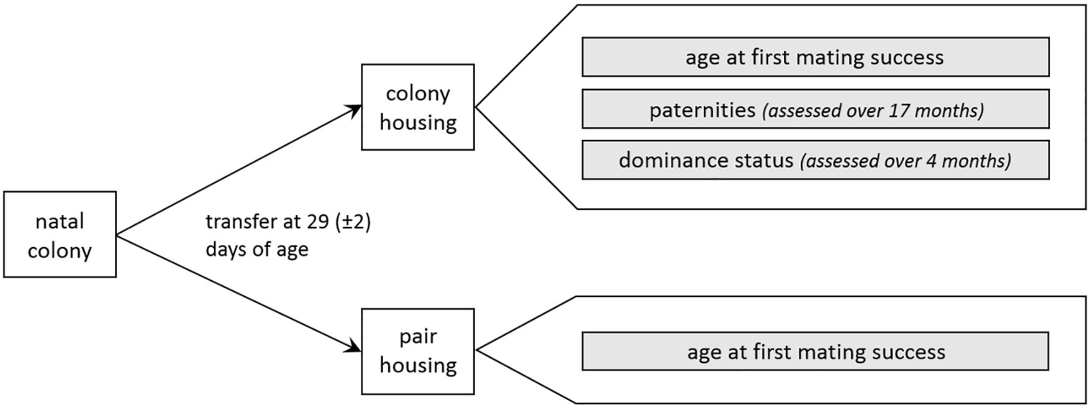

FIGURE 1 | Experimental approach (for details see text).

an error rate of 0.048 per locus. Second, known mother-offspring pairs with a single pup randomly chosen from each mother with multiple offspring (n = 94) were checked for allele mismatches, yielding a mean error rate across loci of 0.0078. The assigned paternities based on the more conservative error rate estimate of 0.048 per locus were chosen for all subsequent analyses.

Statistics

From a statistical viewpoint, data were analyzed as a series of ordered hypotheses (H1–H8, see section "Introduction"). To control the familywise error-rate, null hypotheses were tested in this pre-specified order, and the $(i + 1)$-th null hypothesis was tested only if the i-th null hypothesis had been rejected. This so-called "gate-keeping procedure" allows testing of each of the hypotheses with the help of a level-α-test, without level adjustment, see e.g., Dimitrienko et al. (2010). Since H5 was the first hypothesis where the null hypothesis could not be rejected, we had to stop the gate-keeping procedure at this point. Hence, the gate-keeping procedure came to the conclusion that null H1, H2, H3, and H4 can be rejected, while null H5, H6, H7, and H8 have to be accepted. However, from a descriptive viewpoint, formal tests were calculated for H6–H8, to see whether there were hints of possible effects.

For analysis of first mating success (H1 and H2) a model was developed (see **Supplementary Material** for details) and as test statistics the Wald test (mean) and F-test (variance) were applied, respectively. As proposed by a referee, an additional analysis of the coefficient of variation was performed to correct for the fact that variance increases with the mean. To test the effect of dominance index on reproductive success (H3) a generalized linear model (GLM) was used on basis of a Poisson distribution. Analysis of whether younger and older individuals differed in dominance indices (H4 and H5) was performed with a Wilcoxon–Mann–Whitney test together with a Permutation test. For testing whether younger and older individuals differed in reproductive success or proportion of multiple paternities (H6 and H7) a Wilcoxon signed-rank test was used. To analyze the effect of dominance index on the proportion of multiple paternities (H8) a general linear model (LM) was applied. Our statistical analyses took account of the fact that colony-housed males lived in four different colonies.

One of the referees had reservations against the gate-keeping procedure. As an alternative, it was proposed to use the Benjamini–Hochberg procedure (Benjamini and Hochberg, 1995) to control the false discovery rate (FDR). This procedure requires that we have only one p-value for each hypothesis. For H3, however, we have used two possible responses. If we use the number of sired offspring, the Benjamini–Hochberg procedure (controlling the FDR at $q = 0.05$) leads to exactly the same result as the gate-keeping procedure. If we use the number of sired litters, the Benjamini-Hochberg procedure still provides a significant result for H1 and H2, while no significance can be achieved for the other hypotheses. We indicate statistical significances based on the consistent result of the gate-keeping procedure and the Benjamini–Hochberg procedure when using the number of sired offspring as a parameter for reproductive success. For a description of the detailed methods used to test the single hypotheses, see **Supplementary Material**.

RESULTS

First Mating Success

At first successful mating, pair-housed males were on average 76 days old, ranging from 57 to 102 days of age. Colony-housed males sired their first offspring at 151 days of age on average with a range of 56 to 400 days of age. Hence, colony-housed males reproduced significantly later in life ($n_{\text{pair}} = 15$, $n_{\text{colony}} = 27$; Wald test: $t = -2.90$, $p = 0.0038$) and showed a significantly higher variance in the time to their first mating success than pair-housed males ($n_{\text{pair}} = 15$, $n_{\text{colony}} = 27$; F-test: $F = 42.23$, $p \leq 0.0001$) (**Figure 2**). Subsequent testing revealed a higher coefficient of variation for colony-housed males ($n_{\text{pair}} = 15$, $n_{\text{colony}} = 27$; F-test: $F = 7.98$, $p \leq 0.0001$). The larger variance in colony-housed males was therefore not explained by the larger mean alone.

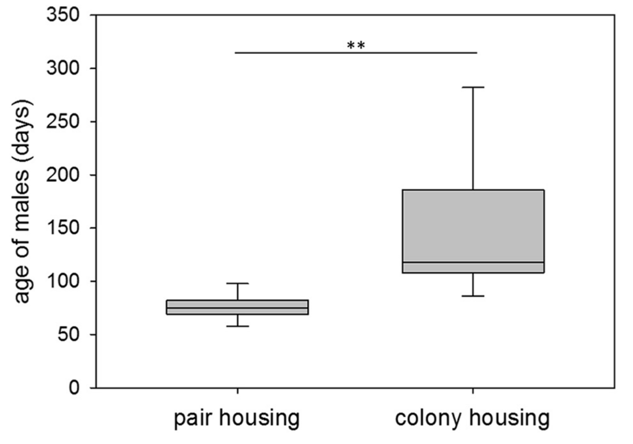

FIGURE 2 | First mating success. Age of male guinea pigs (days) at first successful mating while living in pair or colony housing. Box plots represent the 25–75th percentile with medians (line in box). Whisker lines represent the 10th and 90th percentile. Statistics: $n_{pair} = 15$, $n_{colony} = 27$; Wald test (mean): $t = -2.90$, $p = 0.0038$ (**); F-test (variance): $F = 42.23$, $p \leq 0.0001$.

Dominance Status and Reproductive Success

Colony-housed males between 60 and 359 days of age showed a broad range of dominance indices from 0.13 to 0.93. There was a significant effect of dominance on reproductive success, with a higher dominance status leading to more sired offspring and litters ($n = 11$; GLM (offspring): $z = 4.52$, $p \leq 0.0001$; GLM (litters): $z = 2.02$, $p = 0.0432$) (**Figures 3A,B**).

With respect to age, younger males showed a median dominance index of 0.15, older males a median dominance index of 0.40. Thus, younger males overall had a significantly lower dominance status than older males ($n_{younger} = 12$, $n_{older} = 11$; Wilcoxon–Mann–Whitney test: $W = 165$, $p = 0.025$; Permutation test: $p = 0.0228$) (**Figure 4**). Variance in dominance indices was high in both age groups, but did not differ between them ($n_{younger} = 12$, $n_{older} = 11$; Permutation test: $p = 0.1605$).

Age and Reproductive Success

At younger ages, males sired 11% of possible offspring and contributed to 16% of possible litters on average. At older ages, the same males sired 13% of possible offspring and contributed to 18% of possible litters on average. Thus, there was no difference in male reproductive success between the younger and the older age group [$n = 19$; Wilcoxon signed-rank test (offspring): $V = 70$, $p = 0.2568$; Wilcoxon signed-rank test (litters): $V = 67$, $p = 0.2165$] (**Figures 5A,B**).

Multiple Paternities

Proportions of multiple paternity litters were 54 and 49% of sired litters when males were younger and older, respectively. There was therefore no difference in the proportion of multiple paternity litters between the two age groups ($n = 14$; Wilcoxon signed-rank test: $V = 52$, $p = 0.5251$) (**Figure 6**). Further, there was no effect of dominance status on the proportion of multiple paternity litters ($n = 11$; LM: $t = -0.78$, $p = 0.4563$) (**Figure 7**).

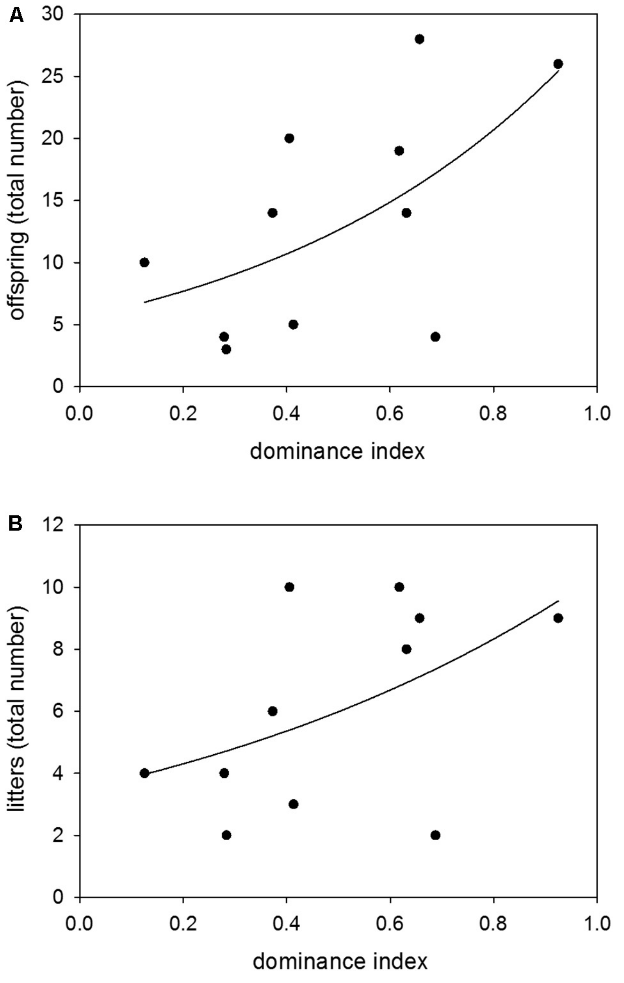

FIGURE 3 | Dominance and reproduction. Effects of dominance index on **(A)** the total number of sired offspring and **(B)** the total number of sired litters. Data were based on observations of colony-housed males (60–359 days of age) over about 4 months. Statistics: $n = 11$; GLM (offspring): $z = 4.52$, $p \leq 0.0001$; GLM (litters): $z = 2.02$, $p = 0.0432$.

DISCUSSION

The aim of the present study was to elucidate the socio-sexual development of males from onset of sexual maturity through first mating success until full adulthood in a complex social environment. For this purpose, reproductive success of guinea pigs living in large mixed-sex colonies was assessed during their first year of life. As a reference condition, a mixed-sex pair situation was used. The main findings were that males living in colonies sired their first offspring much later in life and showed a significantly higher variance in the time to their first mating success than pair-housed males. Furthermore, reproductive success in colonies was significantly affected by

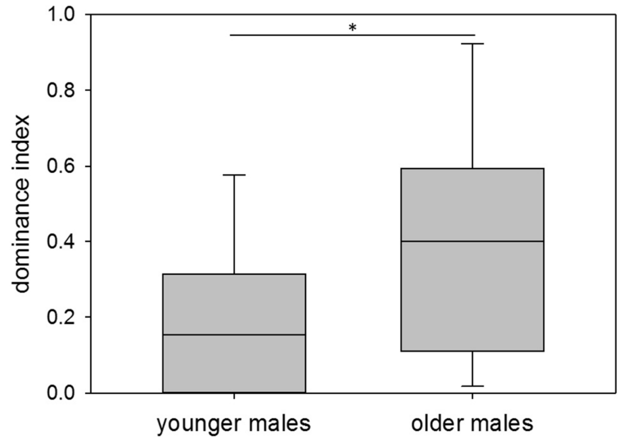

FIGURE 4 | Age and dominance. Dominance indices of younger (60–209 days of age) and older (210–359 days of age) colony-housed males. Box plots represent the 25–75th percentile with medians (line in box). Whisker lines represent the 10th and 90th percentile. Statistics: $n_{younger} = 12$, $n_{older} = 11$; Wilcoxon–Mann–Whitney test (mean): $W = 165$, $p = 0.025$ (*), Permutation test: $p = 0.0228$; Permutation test (variance): $p = 0.1605$.

dominance status. Dominance itself was age-dependent with older males (7–12 months of age) having significantly higher dominance status than younger males (2–7 months of age). Interestingly, there were no indications of differences in male reproductive success between the two age groups.

First mating success of pair-housed males was achieved at 76 days of age on average with relatively low variance. This is in line with the literature, reporting that male guinea pigs usually reach sexual maturity around this time, indicated by a significant increase in testosterone levels between 50 and 90 days of age (Rigaudière et al., 1976; Sachser and Pröve, 1988) and coinciding with first sperm production around 55–60 days of age (Rigaudière et al., 1976). Thus, first mating success fell exactly in the period around which males became physiologically able to reproduce. At this time, partner females were already sexually mature, as first vaginal opening (estrus) occurs at an age of about 3–4 weeks (Sachser, 1994; Trillmich et al., 2006). Unless interrupted by pregnancy, female guinea pigs then show periodic estrus cycles of about 16 days (Ediger, 1976; Kaiser et al., 2010). Taken together, average age and age range of first mating success in pair-housed males could be fully explained by the onset of male sexual maturity and by the female reproductive cycle.

In contrast, colony-housed males sired their first offspring at 151 days of age on average and showed a much higher variance in timing of first mating success. The earliest time of reproduction was at day 56 of age, just around the onset of male sexual maturity (see above), similar to pair-housed males. However, most of the males reproduced much later. One influencing factor again was female reproductive physiology. In particular, even though up to 16 females were available in colonies, access was restricted by a post-partum estrus cycle. This means mating with each of the females was only possible every 63–72 days when they became receptive for a few hours immediately after giving birth (Kaiser et al., 2010). An additional factor in the colony situation, generated by competition, was dominance: higher ranking males had higher reproductive success than lower ranking males. Such a positive relationship between dominance status and reproductive success is not only in line with previous work in guinea pigs (Sachser et al., 1998), but can generally be found in a great variety of taxa including different fish, bird, mammalian, and even invertebrate species (Ellis, 1995; Clutton-Brock, 2016). Attaining high ranking positions requires the ability to compete with other males (Alberts, 2012; Zimmermann et al., 2017b). Hence, dominance rank is often associated with age, size, and weight in various species (Haley et al., 1994; Schuett, 1997; Alberts, 2012). Also previous work in guinea pigs showed that males in colonies usually do not reach alpha positions before an age of 7 months (Sachser, 1986), which is well beyond sexual maturity. In agreement with these results, older colony-housed males in the present study achieved significantly higher dominance status than younger males.

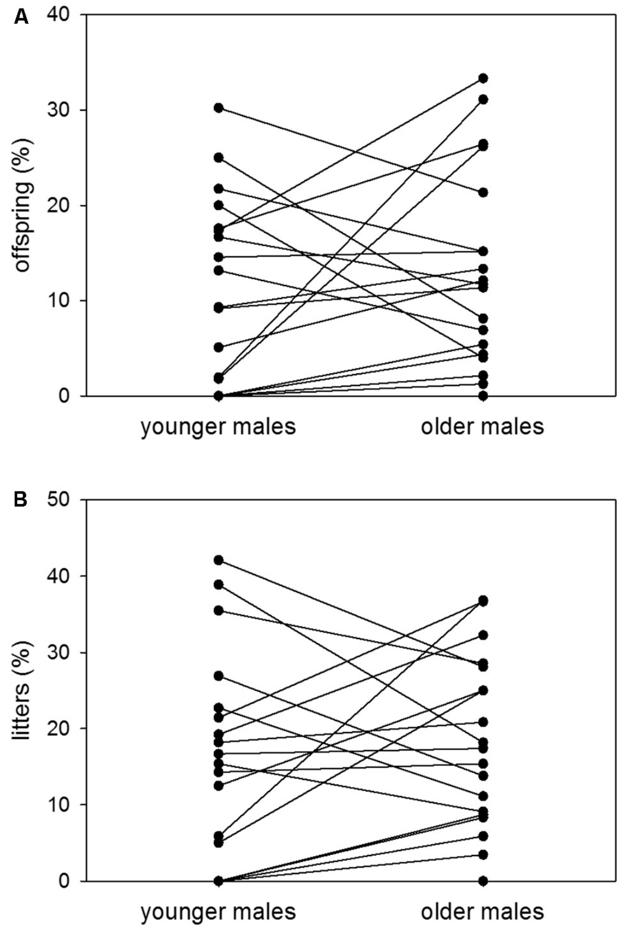

FIGURE 5 | Age and reproductive success. Proportions (%) of **(A)** sired offspring to possible offspring and **(B)** sired litters to possible litters of colony-housed males in the younger (60–209 days of age) and the older (210–359 days of age) age group. Each pair of dots with connecting line represents one individual. Statistics: $n = 19$; Wilcoxon signed-rank test (offspring): $V = 70$, $p = 0.2568$; Wilcoxon signed-rank test (litters): $V = 67$, $p = 0.2165$.

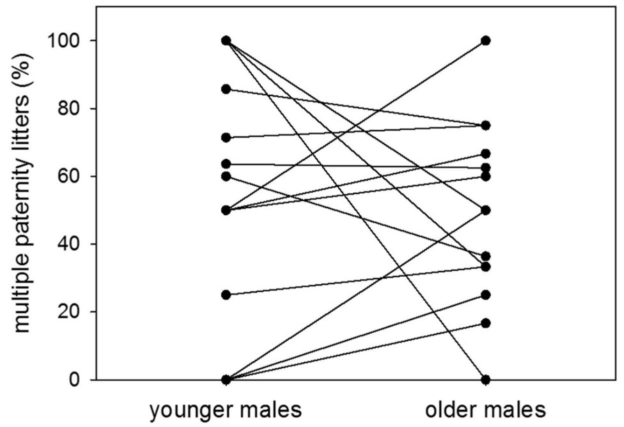

FIGURE 6 | Age and multiple paternities. Proportions (%) of multiple paternity litters to sired litters of colony-housed males in the younger (60–209 days of age) and the older (210–359 days of age) age group. Each pair of dots with connecting line represents one individual. Statistics: $n = 14$; Wilcoxon signed-rank test: $V = 52$, $p = 0.5251$.

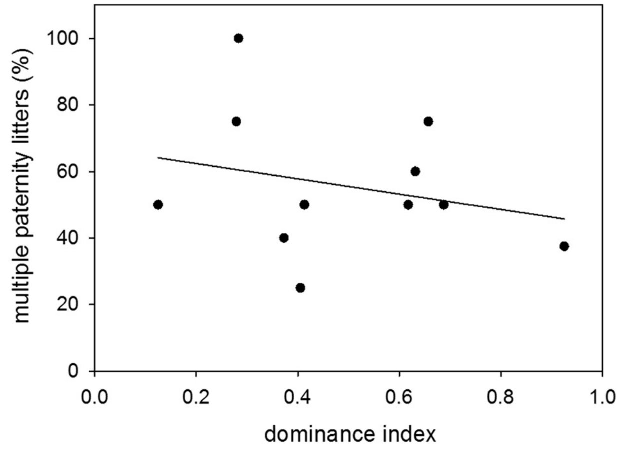

FIGURE 7 | Dominance and multiple paternities. Effect of dominance index on the proportion (%) of multiple paternity litters to sired litters. Data were based on observations of colony-housed males (60–359 days of age) over about 4 months. Statistics: $n = 11$; LM: $t = -0.78$, $p = 0.4563$.

Based on these findings, we would have expected significantly higher reproductive success in older than in younger colony-housed males. Surprisingly, there was substantial mating success in both age groups and no difference between the two. How can this finding be explained? The limited or incomplete control model of reproductive skew proposes that subordinates will reproduce when capacity of dominant individuals to monopolize reproduction is reduced (Clutton-Brock, 1998; Reeve et al., 1998). For example, increasing individual numbers in general and of male competitors in particular, can largely impede the control of reproduction by dominant males within a group (van Noordwijk and van Schaik, 2004; Spong et al., 2008). In the present study, with up to 28 individuals and a total of 12 males per colony, group sizes were probably also too large for an effective guarding of receptive females by the most dominant alpha males. Moreover, group composition and instability of the dominance hierarchy can further play a role in diminishing reproductive skew (Alberts et al., 2003; Spong et al., 2008). In our colonies, group composition was changed about every 6 weeks by removing old and adding young individuals, most likely also causing fluctuations in dominance relationships. Likewise, these factors might have decreased reproductive skew allowing for more mating opportunities in young subordinates.

But how exactly did young males realize reproductive success? High proportions of multiple paternities of about 55% in younger males suggest that stealing copulations was very common. In general, such sneaking is a male alternative reproductive tactic that can be found in many different species (Taborsky et al., 2008; Clutton-Brock, 2016) including other highly social rodents (Schradin et al., 2012). Therefore, it seems likely that younger males applied this tactic before reaching alpha positions. Interestingly, proportions of multiple paternity litters were neither dependent on age, as older males showed similar levels of about 50%, nor dependent on dominance status. Both findings further suggest a situation of "incomplete control" by alpha males. Besides sneaking, a second possible reproductive tactic of younger males was to fight and compete with other males and to achieve mating success via dominance. Indeed, although on average higher in older males, dominance indices of younger and older animals showed substantial overlap. Thus, it seems as if mating success appears to be frequent already during the process of attaining high ranking positions, and therefore before 7 months of age. A third tactic of younger males might have been to invest in relations with particular females. Under the complex conditions of the present study, the occurrence of female choice has been already described (Sachser, 1986). As females sometimes favor younger males that are directing high amounts of courtship behavior toward them (Sachser, 1986), this might have been another way to enhance reproductive opportunities.

Generally, the three proposed reproductive tactics are probably not fixed, but rather dynamically chosen options. As already shown in other species, life-histories can be diverse and flexible, and reproductive tactics may be switched more than once during a life time (Taborsky et al., 2008; Clutton-Brock, 2016); a phenomenon referred to as social flexibility (Schradin et al., 2012). Thus, the substantial mating success before reaching a high social status was probably due to tactics flexibly applied by males already with the onset of sexual maturity.

Irrespective of the applied reproductive tactics, males in colonies generally develop a low-aggressive phenotype over the course of adolescence to preclude costly agonistic encounters with older dominant males, as has been shown by a series of experiments (see section "Introduction"; Sachser et al., 2013, 2011). Consequently, younger males were on the one hand physiologically able to reproduce but on the other hand utilized a queuing tactic. Data of the present study show clearly that younger males reproduced irrespective of queuing. In addition, reproductive success achieved by males this way was far from just "making the best of a bad job" (Schradin et al., 2009). Taken together, socially queuing but still trying to mate whenever a female was in estrus seems the optimal way for maturing males to maximize fitness in this complex social situation.

One might argue that once an individual reaches sexual maturity that further behavioral adjustment to a more distant future would be superfluous. Our results, however, show that this need not be the case. Rather, the view that substantial behavioral plasticity exists well beyond sexual maturity (Fawcett and Frankenhuis, 2015; Sachser et al., 2018) is supported by the present findings. We hypothesize that this represents a general mechanism, not only to be found in guinea pigs but also in other social mammals. Thus, for males in complex social situations, the period from reaching sexual maturity until the establishment of a stable social role might be a time during which flexible reproductive tactics are employed more commonly than usually presumed.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

All procedures complied with the regulations covering animal experimentation within Germany (Animal Welfare Act) and the EU (European Community Council Directive 2010/63/EU) and were approved by the local authorities (Gesundheits- und Veterinäramt Münster, Nordrhein-Westfalen).

AUTHOR CONTRIBUTIONS

SK and NS conceived the study, designed the experiment, and supervised the work. AM, CR, and TZ collected the data. SK, AM, CR, SR, NS, and TZ analyzed and interpreted the data. SF and JK performed all statistical analyses. AM prepared the initial draft of the manuscript and created figures. All authors critically revised the manuscript and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2019.02810/full#supplementary-material

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Goats' Performance in Unsolvable Tasks Is Predicted by Their Reactivity Toward Humans, but Not Social Rank

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In order to clarify the ability of animals to communicate with humans, it is necessary to examine the behaviors of animals directed at humans, taking into account individual differences. This study investigated whether the behaviors of goats (*Capra hircus*) can be predicted when given an unsolvable task. Two experiments were performed in a paddock using 16 domesticated goats. In Experiment 1, behavioral tests were conducted to determine the goats' social rank and reactivity toward a stranger. In Experiment 2, the goats' behaviors in an unsolvable task and two control conditions in which either only a human or bucket was presented were examined. The behaviors of the goats were video-recorded and compared between the conditions. Then, we examined whether the behaviors of goats in the presence of both the human and unsolvable task can be predicted from the scores for social rank and reactivity toward humans. Compared with the control conditions, the goats increased physical contact with the human, but did not increase gazing. It is possible that differences in individual characteristics and long-term experiences with humans can lead to differences in human-directed behaviors of animals. Although the social rank order of the goats was clearly linear, there was no correlation between their behaviors in the unsolvable task and their social rank. The goats that tended to interact with the stranger in Experiment 1 were more likely to approach and establish contact with the human in the unsolvable task than goats that reacted more averse toward humans. There was no association between the level of reactivity toward the stranger and the goats' involvements in the unsolvable task. Therefore, it is possible that the goats which increased interactions with humans did not necessarily have low motivation to engage in unsolvable tasks, but relied on humans as a means of communication. In conclusion, the behavioral changes and its diversity as the responses toward short-term changes in the environment, such as the presence or absence of humans and unsolvable tasks, were related to differences in individual behavioral characteristics (i.e., reactivity toward humans).

Keywords: communication, goat, human–animal relationship, individual characteristic, social cognition

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INTRODUCTION

In order to improve human–animal relationships and animal welfare, increasing attention is being paid to the study of social cognitive abilities of domestic animals that are related to communicative behaviors toward humans. For example, in object choice tasks, dogs can use human gestures, such as pointing or gazing without training in order to select a container with food from two containers

(Miklósi et al., 1998). This ability is more advanced in dogs than human-raised wolves (Miklósi et al., 2003). This suggests that domestication has influenced this ability. Cats, experimentally domesticated foxes, and horses can also use social gestures of humans, such as pointing, in object choice tasks (cat: Miklósi et al., 2005; fox: Hare et al., 2005; horse: Maros et al., 2008; Proops et al., 2010). Thus, not only dogs, but other companion animals and livestock, have high levels of social cognitive abilities to respond to signs from humans.

So as to understand the abilities of animals to communicate with humans, it is necessary to examine not only their responses to social cues from humans, but also their communicative signals to humans. These signals include visual interactions, such as gaze alternations directed at humans and objects that animals want to access, and tactile interactions with humans (Krause et al., 2018). They contribute to attracting human attention (Marshall-Pescini et al., 2013; Alterisio et al., 2018). These behaviors can be examined using unsolvable tasks. During these tasks, we examine how animals interact with humans in the presence of food that they cannot access (Miklósi et al., 2000; Ringhofer and Yamamoto, 2016). Animal behaviors during these tasks have been studied in several species as shown below. Dogs can communicate the presence of food to humans by performing a “showing behavior,” such as gaze alternations and vocalizations (Miklósi et al., 2000). Horses can also gain the attention of humans in similar situations by performing gaze alternations (Malavasi and Huber, 2016), and they can change the way they communicate with humans depending on whether or not the humans know about the presence of food (Ringhofer and Yamamoto, 2016).

It has further been suggested that individual characteristics, particularly reactivity toward humans, may relate to the behaviors of animals directed at humans and to the problem-solving behaviors. For example, dogs with friendly relationships with humans tended to gaze at humans for a longer time when given an unsolvable task (Jakovcevic et al., 2012). In addition, both dogs and horses were similarly less likely to be involved in problem-solving tasks as their interest in humans increased. Dogs with good relationships with humans had lower problem-solving abilities (Topál et al., 1997). The problem-solving ability of horses is negatively correlated with their degree of interest in humans (Lesimple et al., 2012).

The present study focused on goats (*Capra hircus*). Goats have been domesticated since about 10,000 B.C. and have a long history of interaction with humans (Zeder and Hesse, 2000). Unlike dogs, which are companion animals, and horses, which have been used for transportation, goats have not been domesticated for the purpose of communicating with humans, but rather as food resources. However, goats have been shown to have a high level of social cognitive ability with respect to humans. For example, goats that were naïve to object-choice tasks can use pointing or touching as a signal (Kaminski et al., 2005), and goats can use the orientation of a human’s body to understand their attentional state (Nawroth and McElligott, 2017). In addition, goats, like dogs and horses, exhibit gaze alternations in accordance with the human’s attentional state during unsolvable tasks (Nawroth et al., 2016), indicating that they have high communication abilities toward humans. As far as the authors know, few studies have examined the differences in behaviors of goats during unsolvable tasks due to differences in individual characteristics. For example, Langbein et al. (2018) showed that short-term handling did not affect goats’ human-directed behaviors. However, it is predicted that the behaviors will vary for the following characteristics of goats. Goats have a clear social hierarchy, which affects their behaviors. Research has indicated that the choice of food for a low-ranking individual depends on whether it has been attacked by a high-ranking individual (Kaminski et al., 2006). Like goats, cattle have also been domesticated for food, and their coping strategies differ depending on rank, with high-ranked cattle entering a handling chute earlier than other cattle (Solano et al., 2004). Thus, we can say that the behaviors of low-ranked individuals depend on other individuals’ behaviors, while high-ranked individuals are more assertive than low-ranking individuals. In addition, it has been suggested that goats’ individual characteristics can be associated with their learning abilities; for example, goats with less sociability toward conspecifics perform better in visual discrimination tasks in which they select the correct cup of different color than with high sociability. Goats which are less exploratory perform better in non-associative cognitive tasks in which they track hidden objects than subjects with higher exploration behavior do (Nawroth et al., 2017). These findings suggest that individual characteristics may relate to goats’ behaviors not only among their own species, but also in their relationship with humans. Based on these knowledge and findings from previous research with dogs and horses (Jakovcevic et al., 2012; Lesimple et al., 2012), it is expected that individual characteristics, such as reactivity toward humans, are related to the behaviors of goats in unsolvable tasks. By comparing the behaviors of various animals during unsolvable tasks, we can determine whether they reflect differences in their relationships with humans during domestication. In addition, it can lead to the clarification of how individual characteristics are related to the flexibility of behaviors in a given environment in the process of domestication.

The purpose of this study was to investigate the behaviors of goats in an unsolvable task and determine whether their behaviors could be predicted from individual characteristics. In Experiment 1, goats’ social rank order and reactivity toward a stranger were examined. In Experiment 2, the goats’ behaviors in an unsolvable task and two control conditions in which either only human or bucket was presented (human-only condition, food-only condition, and human + food condition) were examined. Then, we compared the goats’ behaviors in these conditions and investigated whether their behaviors in the presence of the human and unsolvable task could be predicted from individual characteristics. We expected the goats to increase their engagement with the human and decrease their engagement with the bucket when both the human and food bucket were present, compared to when only the human was present, as well as horses (Ringhofer and Yamamoto, 2016). In addition, previous studies suggest that individuals with high rankings are likely to be more active in the task than with low ranking (Solano et al., 2004; Kaminski et al., 2006). We predicted that if this characteristic was reflected in individual observations, high-ranked individuals will be more actively involved in the unsolvable task than low-ranked individuals in the presence of the human and unsolvable task. Furthermore, we predicted that the more goats actively interact with the stranger, the more likely they are to rely on the human and the less likely they are to attempt the unsolvable task.

MATERIALS AND METHODS

Subjects and Housing

The experiments were conducted in the goat house at Tokyo University of Agriculture and Technology. Seventeen adult goats (15 females and 2 castrated males, 1–10 years old) were used. The goats were Japanese native breeds (*Shiba yagi* and *Tokara yagi*), which are easy to handle because of their small size (20–35 kg) and tameness. The goats lived in two groups of 7 and 10 animals. Students at the university fed and cleaned the house twice a day, in the morning and evening. All goats had no experience in training or participating in research other than for veterinary purposes, but all were used to human presence.

The experiment was carried out in the paddock of the goat house (3.0 m × 4.5 m; see **Figure 1**), which the goats were familiar with. Except for the food competition test, the goats participated in the experiments one by one. Goats not participating in the experimental session were kept indoor in the goat house. One goat exhibited "separation anxiety behavior" [abnormal increase in phonation in the direction of conspecifics, based on the definition from Lyons et al. (1993)] and the experiment was stopped; thus data from 16 animals were used for the final analysis. A human unfamiliar with the goats, who had no experience with the goats and did not know the purpose of the study, participated as the stranger in the tests of the goats' reactivity toward a human.

Procedure

The experimental scenarios are provided in **Figure 1**. In Experiment 1, the individual characteristics of the goats (social rank and reactivity toward a human) were tested. In Experiment 2, the behaviors of the goats when they faced an unsolvable-task were examined. The experiments were conducted from May to August 2018.

Experiment 1 (Individual Characteristic Test)

We conducted one test to determine the social rank of the goats and two tests to determine their reactivity toward a human.

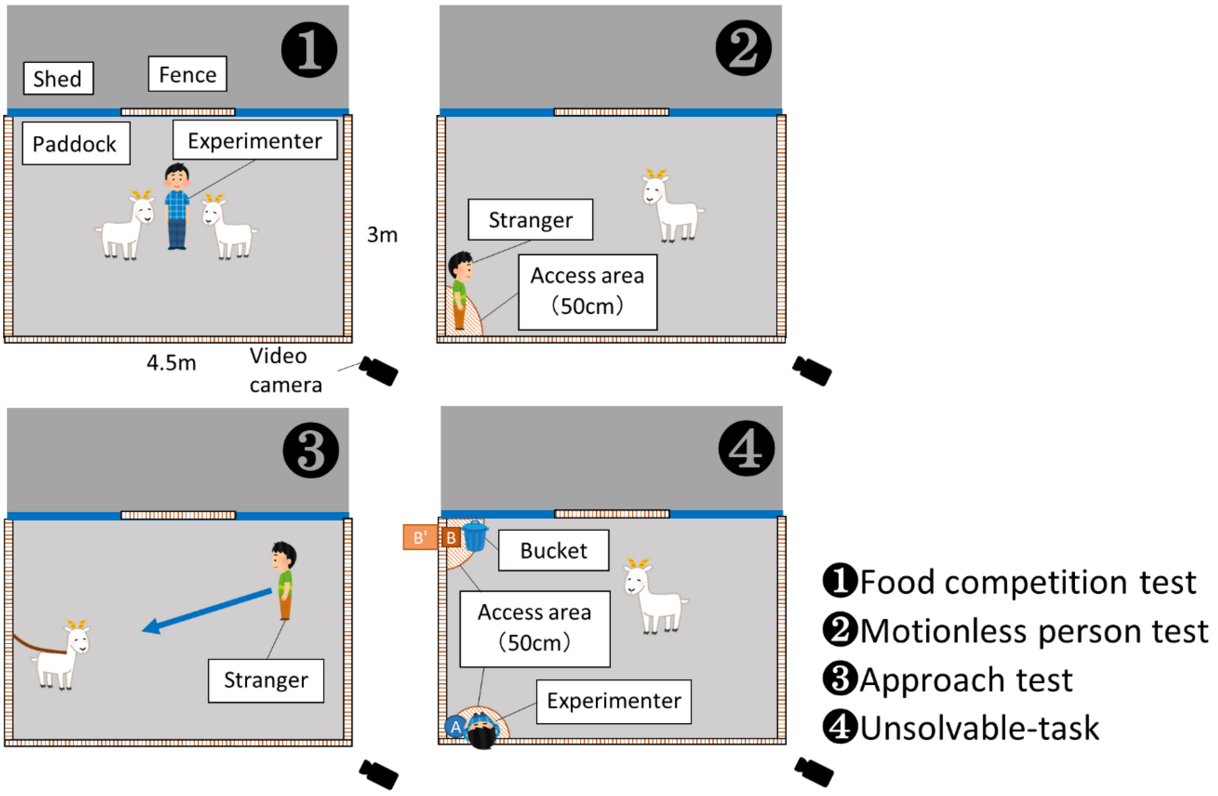

FIGURE 1 | Sketches of scenarios for Experiments 1 (panels ❶–❸) and 2 (panel ❹). The experiments were conducted in the same paddock (3 m × 4.5 m). The access area (50 cm) was established to record the duration of proximity by goats. In Experiment 2, the food bucket or experimenter or both were present in different conditions.

The social rank test and the tests for the reactivity toward a human were conducted in random order on different days on the basis that the individual characteristics were consistent.

Food competition test (social rank)

The procedure to examine the social rank of the goats was based on Kaminski et al. (2006). A pair of goats was led into the same compartment, and the experimenter stood between the two animals with a piece of food (a hay cube, which was daily food). When the two goats approached the experimenter and tried to smell the food, he placed it on the ground and allowed them to access it. The procedure was repeated three times. During the intervals between these trials, the animals were allowed more than 30 s to complete their swallowing and to settle down. All pair combinations in each group were tested. The test was conducted between 5 a.m. and 8 a.m., before the morning feeding, when the animals were considered to be the most willing to feed.

Reactivity toward human

In order to examine the reactivity toward a human, a motionless person test and an approach test (Seaman et al., 2002) were conducted. To reduce stress on the subjects, the approach test was conducted within 5 min after the motionless person test. These tests were conducted between 10 a.m. and 3 p.m., between the morning and evening feedings.

Motionless person test. The motionless person test (Seaman et al., 2002) was carried out in order to examine voluntary involvements with a human. The trial time was 5 min. The experiment began when the goat was released to the area where the stranger stood still, and then the experimenter left. During the trial, the stranger kept his eyes on the goat without moving his face or body. A fixed video camera was used for recording.

Approach test. The procedure of Søndergaard and Halekoh (2003) was used to examine the responses of leashed goats to an approaching stranger. The goat was leashed on the side of the paddock by a 1 m rope, and the test began about 30 s after the goat had settled down. The stranger approached obliquely at a pace of 1 step (50 cm) per second. If the goat remained stationary within 1.5 m, the stranger slowly brought his hand close to the face of the goat. If the goat did not escape and approached his/her nose to smell the hand, the stranger tried to touch the goat's neck.

Experiment 2 (Unsolvable Task)

Using Miklósi et al. (2000) and Ringhofer and Yamamoto (2016) as references, we examined the behaviors of goats toward a human and an unsolvable task. In this experiment, three conditions were tested, depending on the presence or absence of a human (the experimenter) and food: human-only, food-only, and human + food (2 min each). In the paddock, three points, A, B, and B′, were identified: Point A was the position where the human crouched down; Point B was the position where a colorless transparent bucket with a lid containing food (a hay cube) was placed; and Point B′ was a position on the opposite side of a fence (120 cm high) from Point B. The goats could see and touch the human and bucket, but they could not get the food until the experimenter opened the lid of the bucket at the end of each trial. During the trials, the experimenter turned his body toward B and crouched on A, ignoring the goats. The goats' behaviors were recorded with a fixed video camera. Experiment 2 was conducted between 5 a.m. and 8 a.m. before the morning feeding, when the goats were considered most willing because of food motivation. The human-only condition was conducted first and the food-only condition was conducted next. This is because if food was presented first, the goats may think it was time for feeding and their responses toward the human may change. In order to give the goats time to settle down, approximately 5 min interval elapsed between the human-only condition and the food-only condition. In order to eliminate the short-term learning effects of these conditions, the human + food condition was performed a few days later.

In the human-only condition, the behaviors of each goat toward the human were examined. The goat was released into the paddock, and the experimenter stood at B′ without the bucket and looked at the center of the paddock for 5 s. Then the experimenter entered the paddock and crouched down at A, beginning the recording. After 2 min, this condition was completed, and the experimenter left the paddock.

In the food-only condition, the behaviors of each goat toward the unsolvable task were examined. The experimenter held the food bucket at B′ and showed it to the goat for 5 s, and he then placed the bucket (with the lid on) at B. The experimenter then left the paddock and hid out of sight of the goat. After 2 min, the experimenter returned to the paddock and opened the lid of the bucket to feed the goat and maintain motivation for the bucket.

In the human + food condition, the behaviors of goats toward the human and the unsolvable task were examined. The experimenter placed the bucket with food at B′, as in the food-only condition. After the experimenter crouched down at A for 2 min, he opened the lid of the bucket and fed the goat, and the trial ended.

Behavioral Observation

Experiment 1 (Individual Characteristic Test)

In the food competition test, in which the social rank was examined, the frequency with which each individual obtained food was recorded for three trials (0–3 times), and goats who obtained food more than twice were regarded as dominants. Because the goats were reared in two paddocks, the ranks in each paddock were determined. In the motionless person test, which examined the reactivity toward the stationary stranger, the duration of the three behaviors shown in **Table 1** were recorded (0 to 300 s). In the motionless person test, the stranger

TABLE 1 | Behaviors in motionless person test and Experiment 2.

Behavior	Definition
Gazing	Turning head and ears in the direction of stimulus
Proximity	Approaching within 50 cm of stimulus
Contacting	Touching or smelling stimulus at a distance of 1 to 10 cm

Duration of gazing, proximity, and contacting to the stimulus were recorded (Motionless person test: 0 to 300 s, Experiment 2: 0 to 120 s).

TABLE 2 | Scores on the approach test and their definitions.

Score	Definition
1	Goat moved away from human before the human reached 1.5 m range
2	Goat stood still when human was within 1.5 m range
3	Goat sniffed human's hand
4	Human touched goat on the neck

TABLE 3 | Behaviors in Experiment 2.

	Condition		
Behavior	**Human-only**	**Food-only**	**Human + food**
Gazing at human	Latency, duration	N/A	Latency, duration
Proximity to human	Duration	N/A	Duration
Contacting with human	Latency, duration	N/A	Latency, duration
Gazing at bucket	N/A	Latency, duration	Latency, duration
Proximity to bucket	N/A	Duration	Duration
Contacting with bucket	N/A	Latency, duration	Latency, duration

Behaviors to human were recorded in the human-only condition and human + food condition, and behaviors with the bucket were recorded in the food-only condition and human + food condition. N/A indicates unrecorded items because there was no object to be compared.

recorded gazing as the time that the goats directed their heads toward him. In the approach test, the responses of the goats to the approaching stranger were scored as shown in **Table 2** (Søndergaard and Halekoh, 2003).

Experiment 2 (Unsolvable Task)

Duration and/or latency of the goats' behaviors to the human and/or bucket were recorded in the three conditions, as shown in **Table 3**. The definitions of the behaviors were the same as those of the motionless person test (**Table 1**).

Statistical Analysis

IBM SPSS Statistics version 19 was used for the statistical analysis.

Rank calculation and extraction of key parameters for reactivity toward human (Experiment 1)

Subjects were ranked by dominance according to Barroso et al. (2000) and Alvarez et al. (2003) as follows:

$$\begin{aligned} D(\text{Dominance}) = {} & \text{Number of goats displaced by the subject} \\ & /(\text{Number of goats displaced by the subject} \\ & +\text{Number of goats that displaced the subject}) \end{aligned}$$

We examined the relationship between the behavioral variables of the motionless person test (gazing, proximity and contacting) and the scores of the approach test using Spearman's rank correlation coefficient to extract the key parameters for the reactivity toward the stranger. The alpha level was adjusted by Bonferroni correction ($\alpha = 0.0083$). The primary parameter was determined to a variable or score that was significantly correlated with all other variables or scores related to the reactivity toward the stranger.

Comparison of behaviors between conditions in Experiment 2 and prediction by individual characteristics

Logarithmic transformation was carried out in order to ensure normality and homoscedasticity of the latency (gazing and contacting) and duration (gazing, proximity, and contacting) of the behaviors in the three conditions of Experiment 2 (human-only condition, food-only condition, human + food condition). Differences in these behavioral variables between the conditions (human-only condition vs. human + food condition, food-only condition vs. human + food condition) were then examined by multivariate analysis of variance (MANOVA) using a general linear model. We compared the human-directed behaviors (gazing, proximity, and contacting) between the human-only condition and human + food condition and the food bucket-directed behaviors (gazing, proximity, and contacting) between the food-only condition and human + food condition. The behavioral variables were set as the dependent variables, and the conditions were set as the independent variables. Also, a multivariate regression analysis was performed to examine whether the behaviors of goats in the presence of both the human and unsolvable task can be predicted from the scores for the social rank and reactivity toward the human. We used the logarithmic transformed latency and duration of the behaviors in the human + food condition as the dependent variable and the social rank score and the main scores for the reactivity toward the human as the independent variables. Stepwise method was used for the regression analysis to eliminate non-significant parameters and to select the best fit independent variables when predicting the dependent variables.

Coding reliability

The first observer performed all behavioral analyses. Since the judgments of the gazing were expected to be the most confusing behavior, a second independent observer who did not know the purpose of the experiment recorded the duration of the gaze behaviors toward the human and bucket (Experiment 2) for 13% of the total trials. Spearman's rank correlations confirmed that the recorded duration was highly correlated with that of the first observer ($r > 0.93$).

RESULTS

Scores of Social Rank and Reactivity Toward Human (Experiment 1)

The group structure was organized a linear hierarchy. There was no contradiction in the overall rank relationship among individuals (i.e., if D_1 is higher than D_2 and D_2 is higher than D_3, D_1 is necessarily higher than D_3). **Table 4** provides the Spearman's rank correlations between the three behavioral variables of the motionless person test and the scores on the approach test. The approach test score was significantly correlated with other scores for the reactivity toward the human (duration of gazing, proximity, and contacting toward a stranger in motionless person test). Thus, the score of the approach test was used as the primary parameter for the reactivity toward the human.

TABLE 4 | Spearman's Correlation Coefficient (and associated *p*-values) for the duration of the behaviors in the motionless person test and the scores in the approach test (*n* = 16).

	Motionless person test		
	Gazing	**Proximity**	**Contacting**
Motionless person test			
Proximity	0.355 (0.177)		
Contacting	0.527 (0.036)	*0.906 (0.000)*	
Approach test	*0.648 (0.007)*	*0.702 (0.002)*	*0.668 (0.005)*

α = 0.0083 (Bonferroni's correction), the significant combinations are shown in italics.

Comparison of Behaviors Between Conditions Concerning Unsolvable Task and Prediction by Individual Characteristics (Experiment 2)

Comparison of Behaviors in Three Conditions (Human-Only Condition, Food-Only Condition, and Human + Food Condition)

We compared the human-directed behaviors between the human-only condition and human + food condition and the food bucket-directed behaviors between the food-only condition and human + food condition (regarding the data before logarithmic transformation, see **Supplementary Appendix 1**). Significant differences were found in the following items.

Human − only condition vs. human + food condition

The latency of physical contact with the human was shorter in the human + food condition than in the human-only condition ($F_{1,30}$ = 4.23, p = 0.049, **Figure 2B**). In addition, the duration of physical contact with the human was longer in the human + food condition than in the human-only condition ($F_{1,30}$ = 4.623, p = 0.040, **Figure 2B**). There were no significant differences in the other behaviors (**Figures 2A,C**).

Food − only condition vs. human + food condition

The latency for gazing at bucket was longer in the human + food condition than in the food-only condition ($F_{1,30}$ = 4.328, p = 0.046, **Figure 2D**). The latency of contacting the bucket was longer in the human + food condition than in the food-only condition ($F_{1,30}$ = 4.943, p = 0.034, **Figure 2E**). There were no significant differences in the other behaviors (**Figure 2F**).

Predictions of Behaviors in Human + Food Condition Based on Individual Characteristics

The scores of the reactivity toward the human predicted the human-directed behaviors in the human + food condition. The longer the goats interacted with the stranger in Experiment 1, the more duration they spent for proximity and contacting with the human in the presence of the human and unsolvable task (proximity: p = 0.004, contacting: p = 0.009, **Table 5**). The social rank scores did not predict the behaviors in the human + food condition.

DISCUSSION

This study investigated the behaviors of the goats when given the unsolvable task and whether these behaviors can be predicted from the individual characteristics of the goats. Results indicated that in the presence of both the human and bucket, the goats touched the human sooner and longer than in the human only condition. In addition, it took less time to look at and touch the bucket when only the bucket was present than when both

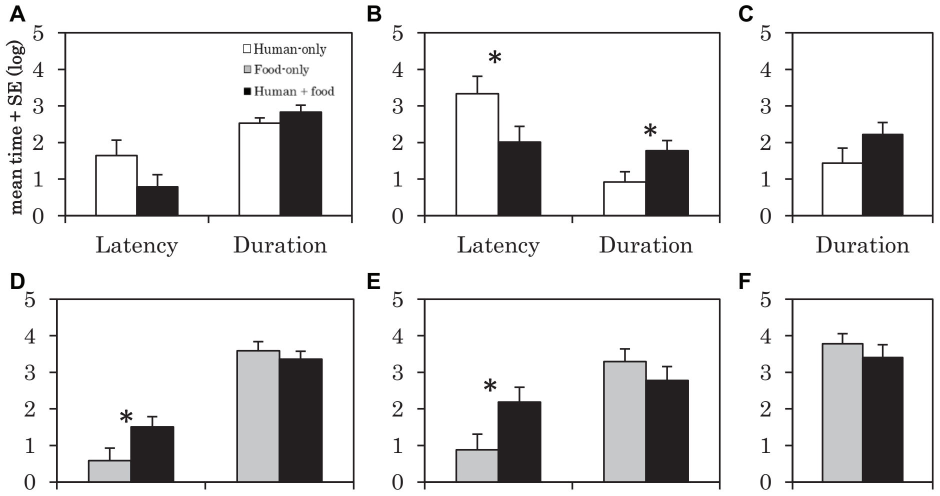

FIGURE 2 | Latency and duration of the behaviors in the human-only condition, food-only condition, and human + food condition in Experiment 2. Each graph shows the time of **(A)** gazing at human, **(B)** contacting with human, **(C)** proximity with human, **(D)** gazing at bucket, **(E)** contacting with bucket, **(F)** proximity with bucket. The vertical axis of the graph represents the logarithmically transformed mean + standard error of time for each behavior. α = 0.05, *p < 0.05.

TABLE 5 | Results of multivariate regression analysis.

Dependent variables	Independent variables	*r*	*B*	*R*	R^2	*F*
Proximity with human	Reactivity toward human	0.683	0.683**	0.683	0.466	12.215**
	Social rank	−0.112				
Contacting with human	Reactivity toward human	0.626	0.626**	0.626	0.392	9.018**
	Social rank	−0.177				

We used the behavioral variables in the human + food condition (latency and duration of gazing, proximity and contacting toward human and food) as the dependent variables. r: correlation coefficient, β: standard partial regression coefficient, R: multiple correlation coefficient, R^2*: coefficient of determination, and F: F-value.* $^{**}p < 0.01$.

the human and bucket were present. In other words, in the presence of the human and unsolvable task, the goats became more interested in the human and engaged more in contact with him, but were less interested in the task. We also examined whether the individual characteristics can predict the behaviors of the goats in the unsolvable task. The results showed that the goats which tended to interact with the stranger were more likely to approach and interact with the human during the unsolvable task. Conversely, it was not possible to predict the behaviors in the unsolvable task from the social rank. The results were generally in line with the expectations, except for the fact that the behaviors during the unsolvable task could not be predicted from the social rank.

Compared with the control conditions, the goats increased physical contact with the human, but did not increase gazing. The existence of gaze alternations could not be confirmed in this study because of the limitations of the condition setting. However, interestingly, when given an unsolvable task, goats performed gaze alternations to humans according to the human's attentional state (Nawroth et al., 2016). Goats used by Nawroth et al. (2016) have experienced a lot of positive interactions with humans and circumstances in which food is inaccessible. On the other hand, the goats used in this study experienced only basic interaction with humans such as routine feeding and caring. Langbein et al. (2018) found that differences in short-term handling did not affect the behaviors of goats toward humans. However, differences in the way the goats interact with humans over a long period of time in ontogeny may have affected how the goats communicate with humans. Besides, the reactivity toward humans was associated with the goats' behaviors during the unsolvable task. It is therefore quite possible that differences in individual characteristics, such as reactivity toward humans, and experiences with humans can lead to differences in human-directed behaviors of animals, such as gaze alternations. Previous studies showed that horses can also flexibly use the gaze alternations to convey their intentions to humans (Malavasi and Huber, 2016). Horses identify humans' intentions and expectations by looking at the human's visual attention status (Sankey et al., 2011). Thus, visual engagement is important not only within the species, but also in communication with humans. It is difficult to determine the essential meaning of behaviors from animals to humans, such as whether animals can acquire a human perspective and if theory of mind can be applied to animal behaviors. However, it is necessary to continue examining the degree of sophistication of human-directed signs of animals through intraspecific and interspecific comparisons.

The goats that tended to interact with the stranger were more likely to approach and contact with the human during the unsolvable task. In a previous study, dogs involved with humans for a longer time increased gazing at humans in an unsolvable task (Jakovcevic et al., 2012). Although there were differences in that the dogs used visual involvement and the goats used tactile involvements, the results indicate that the more animals react actively to humans, the more likely they were to engage with humans during unsolvable tasks. In previous studies using problem-solving situations, dogs with good relationships with humans had lower problem-solving abilities (Topál et al., 1997). In addition, the longer horses looked at a human in these situations, the longer it took to open a box with food (Lesimple et al., 2012). The unsolvable task used in our study was not comparable to results of these earlier studies using problem-solving situations, but they were consistent in that there were relationships between intensity of animals' interest in humans and the behaviors of them when they face difficulties in the presence of humans. However, in our study, the relationship between the levels of the reactivity toward the human and the behaviors toward the unsolvable task was not confirmed. Therefore, it is possible that goats which increased interactions with humans do not necessarily have low motivations to engage in unsolvable tasks, but rely on humans as a means of communication.

The behaviors in the unsolvable task could not be predicted from the social rank. This may be due to the fact that the social rank was not reflected in the context of individual behaviors or human interactions. In particular, a review by Hartmann et al. (2017) suggests that social relationships among horses do not affect human-horse relationships. However, in the daily feeding of goats, differences in the social rank are related to aggressiveness toward humans (Aschwanden et al., 2008; Miranda-de la Lama et al., 2013). Also, dominant cattle are willing to address the task of entering the handling chute, while subordinates adopt a passive strategy (Solano et al., 2004). During handling, subordinate goats approach closer to a handler than dominant goats (Miranda-de la Lama et al., 2013). This was the first study to examine the relationship between goats' social rank and behaviors during an unsolvable task. Based on previous studies, the way goats interact with humans may differ according to the social rank, and thus the way they attempt certain cognitive tasks may differ according to the social rank. Future studies should examine the relationship between the social rank and animal cognitive ability by examining how animals cope with cognitive tasks while in groups, as well as focusing on individual behaviors.

When the overall results of this study are interpreted in conjunction with previous studies and West-Eberhard (2005), the behavioral plasticity related to short-term changes in the environment, such as the presence or absence of humans and unsolvable tasks, was to some extent related to differences in the animals' experiences with humans. Conversely, all domestic animals have experienced human interaction in ontogeny and have repeated their learning over generations. Part of this learning came to be incorporated into genetic information in long-term relationships with humans in domestication, and it can be considered that it was strongly reflected in the differences in behaviors in daily feeding. In particular, in the case of the acquisition of food by domestic animals, optimal strategies have been adopted according to the levels of reactivity toward humans. For these reasons, some individual characteristics may be preferentially related to behavioral plasticity and its diversity in difficult situations related to food acquisition, even if species are different (Stamps and Biro, 2016). These individual differences in the behavioral plasticity and their factors need to be examined in the future. In order to clarify them, it is necessary to investigate other characteristics such as the exploration level toward the environment and some species-specific traits, with focusing on their interaction and the behavioral syndrome (Sih et al., 2004). In addition, only a small number of animals, mostly females, were used in this study. To generalize the results, we need to study more individuals, including differences between males and females. Furthermore, although the relationship between the diversity of animal cognitive abilities and behaviors has been investigated, the direction of the relationship varies. It is therefore necessary to further explore the factors that influence the direction of the association between cognition and individual characteristics (Dougherty and Guillette, 2018). It is possible to communicate effectively with animals by providing the knowledge obtained through these studies to daily relationships with animals. It will improve the welfare of animals and humans who interact with them.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

The procedure was in accordance with the Code of Ethics and Conduct of the Japanese Psychological Association. Since this study was a non-invasive experiment, it was not subject to review by the university's ethical committee for animal experiments.

AUTHOR CONTRIBUTIONS

NY designed the study, performed the experiments and data analysis, and drafted the manuscript. NK proposed the idea and revised the manuscript.

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SUPPLEMENTARY MATERIAL

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ORIGINAL RESEARCH
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Within-Family Environment and Cross-Fostering Stress Affect Behavior and Physiology in Wild Cavies (*Cavia aperea*)

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Stability of personality traits is well-documented for a wide variety of animals. However, previous results also suggest that behavioral phenotypes are plastic during early ontogeny and can be adaptively shaped to the social environment. In cavies (*Cavia aperea*), it has already been documented that the size at birth relative to siblings (size rank) greatly influences various behavioral and physiological traits that last at least until independence. The aim of the current study was (1) to investigate if behavioral and physiological differences between pups of the same litter persist until after independence and influence development long-lasting, (2) to determine the potential plasticity in response to changes in the early within-family environment by cross-fostering pups either to the same, a lower, or a higher size rank in a foster-family. We measured three behavioral traits (number of interactions with a novel object, distance moved in an open field, struggle docility) and two physiological traits (resting metabolic rate and basal cortisol levels). We predicted that cross-fostering into a litter where pups occupy the same size rank would not change the expression of traits. Cross-fostering to a different size rank should not influence the expression of traits if repeatability measures indicate low plasticity. Alternatively, if the traits are plastic, animals should adjust trait expression to fit with the size rank occupied in the foster litter. Initial differences in struggle docility, distance moved in an open field and in baseline cortisol concentration between pups of different size-ranks did not remain stable beyond independence. In addition, we found remarkable plasticity of the measured traits in response to cross-fostering to the same, a smaller or larger size-rank, suggesting that differences between pups are more the result of social constraints leading to adaptive shaping of individual phenotypes within a family. We also found a significant influence of the cross-fostering procedure itself. Cross-fostered individuals were less bold, grew slower and showed elevated resting metabolic rates. This finding suggests a cautious interpretation of previous cross-fostering studies and stresses the need for proper control groups to reliably separate the effect of cross-fostering *per se* from those induced by an experimental treatment.

Keywords: personality, early development, individual differences, family effects, cross-fostering, developmental plasticity, rank size

INTRODUCTION

Stability of personality traits is well-documented for a wide variety of animals ranging from spiders (Liedtke et al., 2015) to humans (Gosling, 2001; Putnam, 2011). However, it has also been documented that environmental and in particular social influences can modify the developmental trajectory of personality traits (Sachser et al., 2018; Trillmich et al., 2018). Studies revealed that the interaction between parents and offspring (quality/quantity of parental care) (e.g., Meaney, 2001) and factors like group size and composition (for example, sex and number of siblings) of a litter or a clutch affect personality traits potentially long-lasting (e.g., Benus and Henkelmann, 1998; Dimitsantos et al., 2007; Eccard and Rödel, 2011; Naguib et al., 2011).

Parental effects, i.e., non-genetic environmental effects transmitted from one or both parents to the offspring (Mousseau and Fox, 1998) have the potential to influence offspring development during the pre- and early postnatal phase. For instance, male mice (*Mus domesticus*) raised from day 4 on in a group containing males only have as adults a more active coping style (Benus and Henkelmann, 1998). Great tits (*Parus major*) from small broods show stronger stress responses than individuals from normal sized broods and individuals from female biased broods are faster explorers than those from male biased broods (Naguib et al., 2011). Such effects might arise due to constraints such as limited food supply, or may represent adaptive shaping of offspring to environmental and social conditions they are likely to encounter in the future (Gluckman et al., 2008; Nettle et al., 2013; Bateson et al., 2014).

In oviparous species, the earliest possibility of information transmission in development occurs even before fertilization. Mothers can change the composition of the egg, either by differentially allocating resources to the embryo (e.g., vitamins, nutrients) or by signals like hormones (e.g., Schwabl, 1996; Groothuis et al., 2005b; von Engelhardt and Groothuis, 2011; Groothuis and Taborsky, 2015). In mammals, there is a much greater opportunity for information exchange through the possibility for longer and reciprocal exchange of substances between mother and offspring during gestation (Del Giudice, 2012). Postnatally, parents can affect their offspring's development by differential food provisioning (Groothuis et al., 2005a). In mammals, mother's milk is an important pathway for nutrient transfer and hormone signaling that potentially influences offspring growth and personality (Peaker and Neville, 1991; Catalani et al., 2011; Hinde et al., 2015).

In addition to parental effects, the development of a certain behavioral and physiological type is known to be influenced by litter size and concomitant difference in competitive regime (Eccard and Rödel, 2011). Mammalian siblings might exert influences on each other and even the maternal state while still *in utero* (vom Saal, 1989). After birth, competition among siblings for limited resources is known to be an important mechanism shaping phenotypic development (Stockley and Parker, 2002). For example, differences among littermates are suggested to contribute to long-term individual differences in physiology and behavior. In rabbits (*Oryctolagus cuniculus*), individuals that occupy the periphery in the litter huddle are more proactive than their intermediate or central littermates (Reyes-Meza, 2011). Havier newborn rat pups are braver and more explorative (Rödel and Meyer, 2011). In humans, character displacement within the family is known to exert long-term effects and often carry-over until adulthood (Sulloway, 2010).

We have previously documented that relative size at birth in comparison to siblings exerts a major influence on various behavioral and physiological traits that last at least until independence in cavies (*Cavia aperea*; Guenther and Trillmich, 2015). Animals born as the largest pup in the litter were bolder, coped with stress more actively and had lower baseline blood cortisol concentrations than their siblings (Guenther and Trillmich, 2015). However, prior results also suggest that behavioral phenotypes remain plastic over a long period of time during early ontogeny and may be adaptively shaped during maturation (Guenther and Trillmich, 2013; Sachser et al., 2013; Guenther et al., 2018). Here, we raise two questions: (1) Do differences in behavioral and physiological phenotype among pups persist after independence and maturation when offspring have left the family environment? (2) Do pups express plastic responses and adapt to a change in social environment within the family, i.e., do they assume the behavioral and physiological characteristics of a novel size rank when cross-fostered?

Cross-fostering is a frequently used method to study treatment effects (e.g., Meek et al., 2001; Kessler et al., 2011), to test life history theory predictions (e.g., Rehling and Trillmich, 2007; Crino et al., 2020), to disentangle genetic from non-genetic effects (e.g., Francis et al., 2003; Groothuis et al., 2005a) or to disentangle pre- and postnatal effects (e.g., Horton, 1985; Wolf et al., 2011). Although cross-fostering experiments have proven to be an important tool to study the programing of neural, behavioral and physiological development in mammals (McCarty, 2017), recent studies show that cross-fostering itself might induce changes in the developmental trajectory (e.g., Bartolomucci et al., 2004). Therefore, the authors suggest to carefully interpret results from cross-fostering studies and include proper controls in the experimental design. Tests of effects due to cross-fostering have so far been limited to mice and rats – altricial species (Barbazanges et al., 1996; Bartolomucci et al., 2004; Hager et al., 2009; Matthews et al., 2011). There might, however, be differences between altricial and precocial species with respect to the influence of early experiences. In altricial species, the young are born after a short gestation and much of the development (neural, physiological) occurs after birth (Blumberg and Sokoloff, 1998; Sisk and Foster, 2004; Sisk and Zehr, 2005). The young require substantial maternal care, so the early postnatal period is an especially favorable time for early experiences to affect the development of young. By contrast, in precocial species, like guinea pigs (*Cavia aperea* f. *porcellus*) and their ancestors the wild cavies (*Cavia aperea*), the gestation period is long and pups are born highly developed and less dependent on milk intake than altricial young. Precocial young require less maternal care, and so the possibilities for maternal shaping of the behavior of the infant are relatively limited compared to altricial species. On the other hand, the long pregnancy offers great scope for prenatal influences on development (Rood and Weir, 1970; vom Saal, 1989; Sachser et al., 2013).

We therefore compare pups that are raised by their genetic mother, representing an undisturbed control group, and pups that are fostered to an unknown foster-family but occupy the same size rank in the foster-litter as in their natal-litter to test for effects of cross-fostering.

Given that we previously found a substantial repeatability of several traits correlated with size rank at birth, we predicted that cross-fostering into a litter where pups occupy the same size rank would not change the expression of traits. Cross-fostering into a different size rank (lower or higher than in their litter of origin) should also not influence the expression of the traits, if the repeatability measures indicate low plasticity of these traits. Alternatively, if the traits were highly plastic, animals should adjust trait expression to fit with the size rank occupied in the foster litter. As a control, we also observed a group of animals that remained in the litter of origin to test if the results of our previous study (Guenther and Trillmich, 2015) could be repeated.

MATERIALS AND METHODS

Animals and Housing

The animals used for this study originated from a captive breeding stock of wild cavies (*Cavia aperea*) kept and bred in Bielefeld since 1981. Wild-caught animals are crossed into the population every few generations to prevent potential effects of inbreeding or domestication. For breeding, females were transferred from outdoor enclosures under natural photoperiod and temperature to climate chambers located indoors. Females were housed singly in 0.8 m^2 enclosures equipped with a shelter, a rough stone, a feeding dispenser and a water bottle. Water, fresh hay and guinea pig pellets (Höveler, Germany) were available *ad libitum*. In addition, vitamin C (1 g/l) was added to the drinking water once a week and animals were supplemented with fresh greens such as carrots, bell pepper or apples, four times a week. Rooms were kept at 20 ± 2°C throughout the experiment. Initially, the photoperiod was set to 12:12 light:dark (L:D) for 4 weeks to reset information about the photoperiod in females. Thereafter, a male was introduced for 2 weeks and the light:dark cycle was set to 9.5 L:14.5 D. 15 min of light were added every 9 days to simulate the spring photoperiod. This was done because photoperiod is known to influence offspring development regarding life history, physiology, and behavior in cavies (Guenther et al., 2014; Rübensam et al., 2015; Finkemeier et al., 2016) and our experiments were run at different times of the year. Since pregnancy of cavies lasts for 60 days, offspring were born under 11:45 to 12 h light and experienced increasing photoperiod until the end of the experiments.

58 days after introducing males for breeding, we started to check enclosures 6 days a week for newborn pups. All pups were initially given a haircut for individual recognition. After weaning (24–30 days of age), pups were marked permanently with a subcutaneous pit tag (ID 100, TROVAN, passive transponder system, Euro ID, Weilerswist, Germany).

We conducted two experiments. *Experiment I* was run to test for reproducibility of size rank differences in non-cross-fostered pups as found in an earlier study (Guenther and Trillmich, 2015). Here, 22 females were bred, 19 of which gave birth (**Table 1**). In total, 45 offspring were tested for behavioral and physiological development. In *Experiment II,* 48 females were bred, of which 44 gave birth (**Table 1**). In this experiment, pups were cross-fostered shortly after birth (see experimental procedure). The aims of this experiment were (a) to test if cross-fostering to a higher or lower size rank would influence the early behavioral and physiological development long-lasting, i.e., if juveniles would adjust their phenotype to their new social niche, and (b) to test, if predictable size rank differences remain stable after cross-fostering, i.e., to control for any potential effects of the cross-fostering procedure on phenotypic development.

Experimental Procedures and Timeline

Pups were assigned a size rank in their litter of birth based on birth mass. Bigger pups are located closer to the cervix *in utero* and hence are also born before their smaller siblings (Schumann et al., 2014). In *Experiment II*, pups were cross-fostered within 3 days after birth depending on the availability of same-aged litters. Pups were distributed to new litters so that each foster-family consisted only of unfamiliar pups, i.e., all pups originated from different litters to ensure that all animals had equal starting conditions. Three days after pups had been introduced into their foster families, they were weighed again to estimate the effect of cross-fostering on body mass development. In *Experiment I*, pups were weighed a second time at 4 days of age.

A first round of behavioral and physiological testing was conducted around the time of weaning (i.e., at an age of 19–30 days) when pups were still kept together with their foster-family (*Experiment II)* or their family of birth (*Experiment I*). In total, each pup was tested in three behavioral (Open Field, Novel Object, Struggle) and two physiological tests (resting metabolic rate – RMR, baseline blood plasma cortisol concentration – CORT). Tests were conducted in random order and each pup was tested in only one test per day. After each test, the animal was given a minimum of 24 h rest to prevent any carry-over effects between tests. Animals completed all tests within 10–12 days. Behavioral tests were conducted between 9–12 am or 2–5 pm similar to previous studies where no time-of-day effect was found (Guenther and Trillmich, 2013; Guenther et al., 2014). CORT was taken at noon ± 10 min and RMR was measured between 9 am and 6:30 pm.

After the first test round had been completed for all pups in the litter, this litter was separated from its (foster) mother (at age 24–30 days). Pups were weighed to determine daily growth rate until weaning. Pups were thereafter kept in groups of two together with an unfamiliar and unrelated same-sex pup in identical enclosures until the end of the experiment.

Shortly after sexual maturation (∼50 days Guenther and Trillmich, 2013; Guenther et al., 2014), a second round of behavioral and physiological testing was conducted similar to the first round. Tests were conducted between 55 and 75 days of age for all animals to test for long-term effects of the early social niche. Males of this species often become aggressive when

TABLE 1 | Overview of the number of females used for breeding (N females breeding), the number of females that gave birth (N litters produced) and number of pups in brackets.

	N females breeding	N litters produced (# of pups)	N litters entering experiment	N pups entering experiment (male/female)	N pups cross-fostered
Experiment I	22	19 (50)	18	45 (23/22)	–
Experiment II	48	44 (89)	34	68 (34/34)	Same: 29 Up: 19 Down: 20

Litters were excluded, if they consisted of a single pup only, if two or more pups died before weaning or if there were no size- and age-dependent matches for cross-fostering of pups (Experiment II). Pups cross-fostered: "up" means cross-fostered into a litter so that its size rank was higher than in the birth litter; "same" means fostered to another litter but to the same size position as in the original litter; "down" cross-fostered so that it occupied a lower size rank in the new litter than in the original litter.

reaching sexual maturity. When this happened, we separated male pairs using wire-mesh so that animals still had visual and olfactory contact with each other but were prevented from interacting physically.

Physiology

CORT

Blood samples (~70 μl) were taken within 3 min after capturing the animal to avoid a rise of baseline concentrations due to handling stress (Romero and Reed, 2005). One experimenter held the animal on its lap while a second experimenter collected blood from the marginal ear vein into heparinised capillaries. Only one animal per enclosure was tested per day since capturing may stress the co-housed animals. Blood was centrifuged for 5 min at 10000 rpm and then stored at −20°C until further analyses.

Analysis was performed using a competitive enzyme immunoassay (RE52061 IBL, IBL International GmbH, Hamburg, Germany) using specific antibodies against cortisol (for further details see Kaiser et al., 2003). The antibody that we used cross-reacted with relevant steroids as follows: Prednisolone 29.8%, 11-desoxycortisol 8.48%, cortisone 4.49%, prednisone 2.12%, corticosterone 1.99%, 6b-hydroxycortisol 1.03%. Samples were evenly distributed across seven assays. The intra-assay% CV was 4.2% and the inter-assay% CV was 6.7%.

RMR

Two animals could be measured at the same time to assess resting metabolic rate. Each animal was placed into a metabolic chamber (transparent Plexiglas, 18 cm × 28.5 cm × 18 cm) located in a climatized cabinet (Rubarth Apparate, Laatzen, Germany). Measurements lasted for 3.5 h and were conducted under low light conditions and at 20 ± 1°C at the lower end of the thermoneutral zone. We used open flow respirometry with a continuous air flow of outside air of about 80 l/h (Mass Flow Meter FM 360, Tylan, Corp., Torrance, CA, United States). Oxygen consumption and CO_2 production were measured. Outside air was pumped through metabolic chambers under ambient pressure and thereafter continued into two successive coolers (M & C Cooler, Ratingen, Germany) for drying. Additional drying was achieved using scrubbers (Drierite, Fluka, Steinheim, Germany). For the measurement of O_2 and CO_2, a subsample of air flowed at 600 ml/min through an O_2 analyzer (Oxzilla FC, Sable Systems, Henderson, NV, United States) and a CO_2 analyzer respectively (Maihak AG, Hamburg, Germany). Chambers were measured alternately eight times for 10 min each per measurement. Between measurements of different chambers, we allowed 1 min to ensure that no air from the previous chamber was left and measured in the system. As resting metabolic rate, we used the 3-min period with the lowest stable O_2 consumption after an initial period of 30 min, which is the time animals usually need to calm down.

Behavior

Novel Object

Boldness was measured as number of interactions with an unknown object in the home enclosure. All other animals were gently removed from the home enclosure before testing. Then, a novel object was introduced approximately 20 cm from the shelter. The novel objects used for testing were a green egg cup in the first and a yellow rubber duck in the second test round. Interactions of the test animal with the object were video-recorded for 1 h.

Open Field

Fearlessness was measured as the distance moved (cm) when individuals were introduced into an open, unknown arena for 20 min. For the first 10 min, a semi-transparent shelter was present in the arena under which animals could hide. For the second 10 min, this shelter was removed from the arena. The arena was located in a silent room without any other animals present. The experimenter left the room at the beginning of the test.

Struggle Docility

To measure docility, an animal was gently captured and turned on its back in the hand of the observer for 30 s. We scored the time an animal actively struggled to escape this situation as a measure of stress-coping (Bonnot et al., 2018).

Ethics Statement

All experimental procedures were in accordance with German animal protection laws. Facilities were approved (2014) by the local government authority responsible for health, veterinary and food monitoring (Gesundheits-, Veterinär- und Lebensmittelüberwachungsamt Bielefeld). The experiments were performed under license 84-02.05.20.12.246 LANUV, Germany.

Statistical Analyses

For statistical analysis and graphing, R 3.2.3 and R 3.5.1 were used (R Development Core Team, 2008) with the package lme4 (Bates et al., 2015) for mixed models. Additionally, we used the packages ggplot2 (Wickham, 2009), effects (Fox, 2003; Fox and Weisberg, 2018), and emmeans (Lenth, 2019) to create the graphs. Residuals of the models were checked visually for distribution and variance homogeneity using Q–Q plots.

Separate models were run to analyze the first round of testing at weaning and the second round around sexual maturation. The only exceptions were the growth rates, because we had only one measurement. Furthermore, in all models of RMR, body mass at day 24 was included as additional fixed effect.

In order to calculate the effects of size rank on behavioral and physiological development in non-fostered litters, we used linear mixed models with a Gaussian distribution. Size rank (three level factor) and sex were fitted as fixed effects. Mother ID was included as a random effect, allowing random intercepts but not random slopes.

We employed linear mixed models with a Gaussian distribution in order to estimate the effect of cross-fostering to a similar size rank by including the size rank before and after cross-fostering in addition to sex. Mother ID and stepmother ID were included as random effects.

To analyze the effects of cross-fostering to the same, a higher or a lower size rank, linear mixed models contained the direction of fostering (three level factor: "same," "up," "down") and sex as fixed effects. Mother ID and stepmother ID were included as random effects and a Gaussian error distribution was used.

To test for temporal consistency, we estimated repeatability for all traits by using the R-package rptR (Stoffel et al., 2017). The same model structures as described before were used to estimate adjusted repeatabilities with 1000 bootstraps for estimating confidence intervals. As we wanted to assess individual consistency, we used individual identities as grouping factor in the model. Therefore, individual ID nested within mother ID were included as random effects. We used a likelihood ratio test (LRT) for significance testing of repeatabilities.

Finally, to assess the effect of the cross-fostering procedure, we log transformed the data for RMR and CORT and used a square root transformation for the data derived from the open field test to resemble a Gaussian distribution. While growth rate resembled a Gaussian distribution, data derived from the struggle docility test and the novel object test resembled a Poisson distribution. By combining the two control groups into one dataset, the distribution of the data changed. They became more left-skewed because many individuals from the non-fostered group did not struggle and had no interactions with the novel object at weaning. In addition, we found outliers in the data for the novel object test. Therefore, we compared model results from the full dataset and a dataset in which outliers were removed. The results with or without outliers were consistent with only one exception: the difference between first and second rank individuals became significant if we excluded the outliers. Diagnostic plots revealed a better fit of the model without outliers. To assess the effect of the cross-fostering procedure we employed linear mixed models with size rank of origin (three level factor), sex, treatment (two level factor: "foster," "non-foster") and time of testing (two level factor: "weaning," "maturation") as fixed effects, as well as the two-way interaction of treatment and time of testing. Mother ID was included as a random effect.

RESULTS

Effects of Size-Rank in Litter on Behavioral and Physiological Development in Natural Litters

First, we tested, if behavioral and physiological differences of the size rank within litter are reproducible (with respect to our earlier experiment, Guenther and Trillmich, 2015) with an independent set of animals and if such differences in size rank persist after maturation (*Experiment I).*

Size rank did not affect growth until weaning (**Supplementary Figure S1**) or RMR at weaning (**Supplementary Figure S2A**), but males grew on average half a gram more per day compared to females (males: 5.1 g; females: 4.6 g per day; $t = 2.07$, $p = 0.05$). CORT was significantly higher for animals occupying a lower size rank in the litter at weaning (rank 1 vs. rank 2: $t = -2.16$, $p = 0.04$; rank 1 vs. rank 3: $t = -3.51$, $p = 0.002$; rank 2 vs. rank 3: $t = -1.84$, $p = 0.08$) (**Figure 1A**). Animals of size rank two tended to interact less with a novel object ($t = -1.93$, $p = 0.07$), showing on average only half as many interactions as animals of size rank one (largest pup) (rank 1: 7.7 ± 2.4; rank 2: 3.2 ± 2.3 interactions, **Supplementary Figure S3A**). Significant size rank differences were found for the distance traveled in an open field (rank 1 vs. rank 2: $t = 3.11$, $p = 0.007$; rank 1 vs. rank 3: $t = 2.51$, $p = 0.02$; rank 2 vs. rank 3: $t = 0.10$, $p = 0.92$) (**Figure 1C**). Smaller siblings tended to struggle more than larger ones ($t = 1.91$, $p = 0.07$, **Supplementary Figure S4A**). Animals of size rank two struggled on average 67% and animals of size rank three 29% more than their siblings of size rank one. Except for growth rate (higher in males), no sex effects were found at weaning.

At maturation, when animals had been together with unfamiliar and unrelated same-sex individuals for about a month, effects of the size rank were reduced. The only remaining significant effect occurred in the distance traveled in an open field (rank 1 vs. rank 2: $t = 1.17$, $p = 0.26$; rank 1 vs. rank 3: $t = 2.95$, $p = 0.008$; rank 2 vs. rank 3: $t = 2.01$, $p = 0.058$) (**Figure 1D**). Neither CORT (**Figure 1B**), nor any other traits indicated earlier size rank differences (**Supplementary Figures S2B, S3B, S4B**). Sex differences were only found for CORT, with males having lower CORT concentrations than females (m: 294 ± 102 pg/ml, f: 646 ± 115 pg/ml, $t = -2.3$, $p = 0.03$).

To test for temporal consistency, we estimated repeatability for all traits (**Supplementary Table S1**). All traits showed high temporal flexibility as none of the traits was significantly repeatable.

Effects of Cross-Fostering and Size Rank in Litter After Cross-Fostering

We tested, if animals showed size rank differences when cross-fostered to same size ranks as in their natal litter. Comparable to

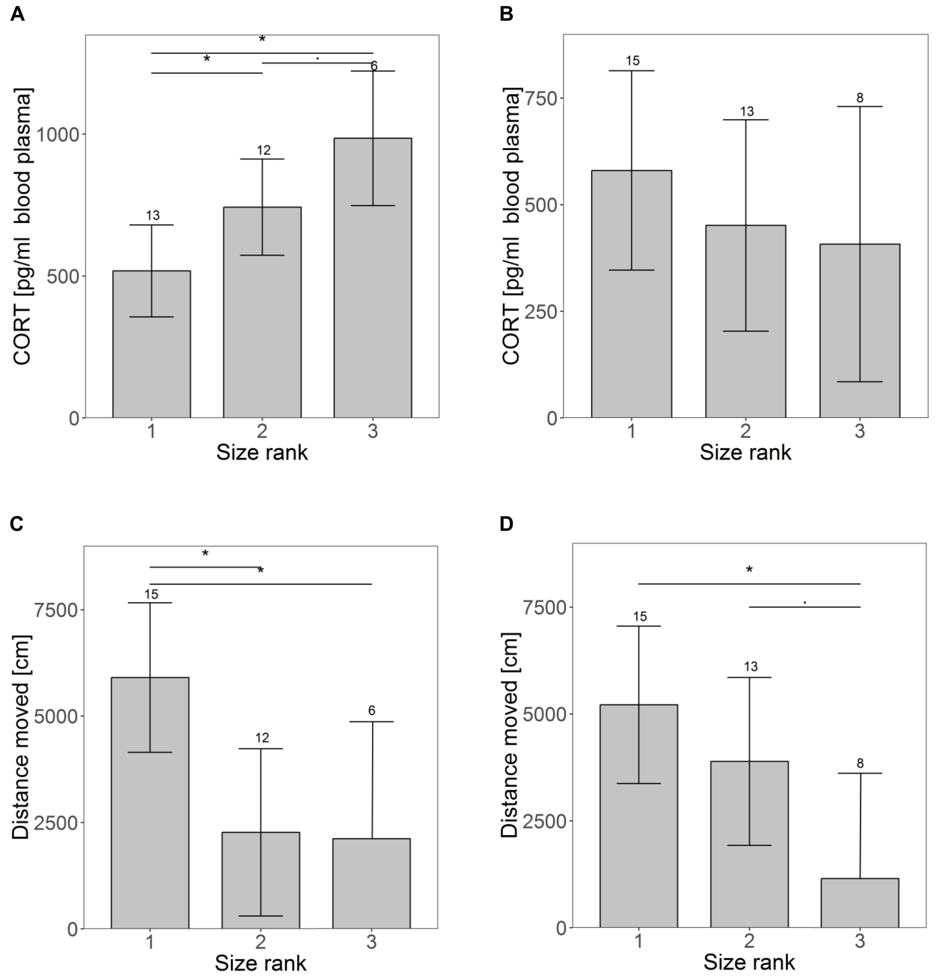

FIGURE 1 | Differences in personality and physiological traits over time for pups of different size ranks (1 indicates the largest pup). Panel A and B show differences in basal cortisol levels at the time of weaning **(A)** and maturation **(B)**. The images shows the distance moved in an open field at weaning **(C)** and maturation **(D)**. Shown are the estimated values derived from the mixed models on the behavioral traits ± confidence intervals (CI). Asterisks indicate significant differences among size ranks. Samples sizes are given above the CI.

non-cross-fostered animals, there were no size rank differences for growth rate, RMR, CORT or number of touches in the novel object test (**Table 2**). However, cross-fostering diminished the previously found size rank differences in distance traveled in open field and, opposite to the control group, we found a trend for smaller siblings to struggle less ($t = -1.96$, $p = 0.06$). At maturation, no effects of size rank were found for any trait. In addition, males and females only differed in RMR but no other trait, with males having on average a 58% higher RMR than females (m: 59.7 ± 7.54 kJ/kg*day^{-1}; f: 34.9 ± 6.33 kJ/kg*day^{-1}; $t = 2.4$, $p = 0.03$). Similar to the control animals, no trait showed a significant repeatability (**Supplementary Table S1**).

Effects of Cross-Fostering *per se*

Significant differences between the animals of *Experiment I* (control) and animals cross-fostered to the same size ranks (*Experiment II*) were found for growth rate and RMR (**Figures 2A,B**). Cross-fostered animals had lower growth rates ($t = -2.14$, $p = 0.04$) and elevated RMR ($t = -3.7$, $p = 0.001$). RMR generally increased with age ($t = 9.4$, $p < 0.001$). For cross-fostered animals, however, the increase was lower compared to non-cross-fostered animals ($t = -3.3$, $p = 0.001$). Neither CORT (**Figure 2D**, $t = -0.04$, $p = 0.96$), nor the distance traveled in open field ($t = -1.3$, $p = 0.19$), or struggle docility ($z = -0.38$, $p = 0.71$) differed between control and cross-fostered animals. Cross-fostered animals were less bold compared to control animals, on average touching a novel object only half as often as control animals (**Figure 2C**, $z = -2.8$, $p = 0.005$). In addition, the change of the number of touches between juveniles and mature animals was less strong in cross-fostered animals.

Effects of Cross-Fostering to a Different Size-Rank in Litter

Cross-fostering to a lower or higher size rank had only little influence on trait expression (**Table 2**). Neither weight development during the initial 3 days after cross-fostering

TABLE 2 | Mean estimates with their corresponding standard error of behavioral and physiological traits after cross-fostering.

Trait	Cross-fostered same		Cross-fostered up		Cross-fostered down	
	Weaning	Maturation	Weaning	Maturation	Weaning	Maturation
Growth rate [g/day]	4.5 ± 0.2	–	4.5 ± 0.2	–	4.4 ± 0.2	–
RMR [KJ/kg $*$ day^{-1}]	22.4 ± 1.3	47.4 ± 3.7	25.8 ± 1.6	42.2 ± 4.1	24.0 ± 1.5	49.2 ± 4.0
CORT [ng/ml]	627 ± 71.5	455 ± 68.1	761 ± 86.3	454 ± 80.9	597 ± 83.8	485 ± 78.5
# of touches	6.6 ± 1.0	6.0 ± 1.2	4.5 ± 1.2	4.9 ± 1.4	6.4 ± 1.2	4.9 ± 1.4
Distance moved [cm]	7526 ± 1189	7009 ± 1270	7134 ± 1436	6807 ± 1526	6464 ± 1397	7248 ± 1457
Struggle docility [s]	6.9 ± 1.1	5.8 ± 1.0	7.7 ± 1.4	2.7 ± 1.2	9.1 ± 1.4	4.2 ± 1.2

Shown are the three different foster groups: individuals that were fostered to the same size rank than in their litter of birth and individuals that were either fostered to a higher (up) or lower (down) size rank in litter. Weaning and maturation mark the two time points at which experiments were conducted.

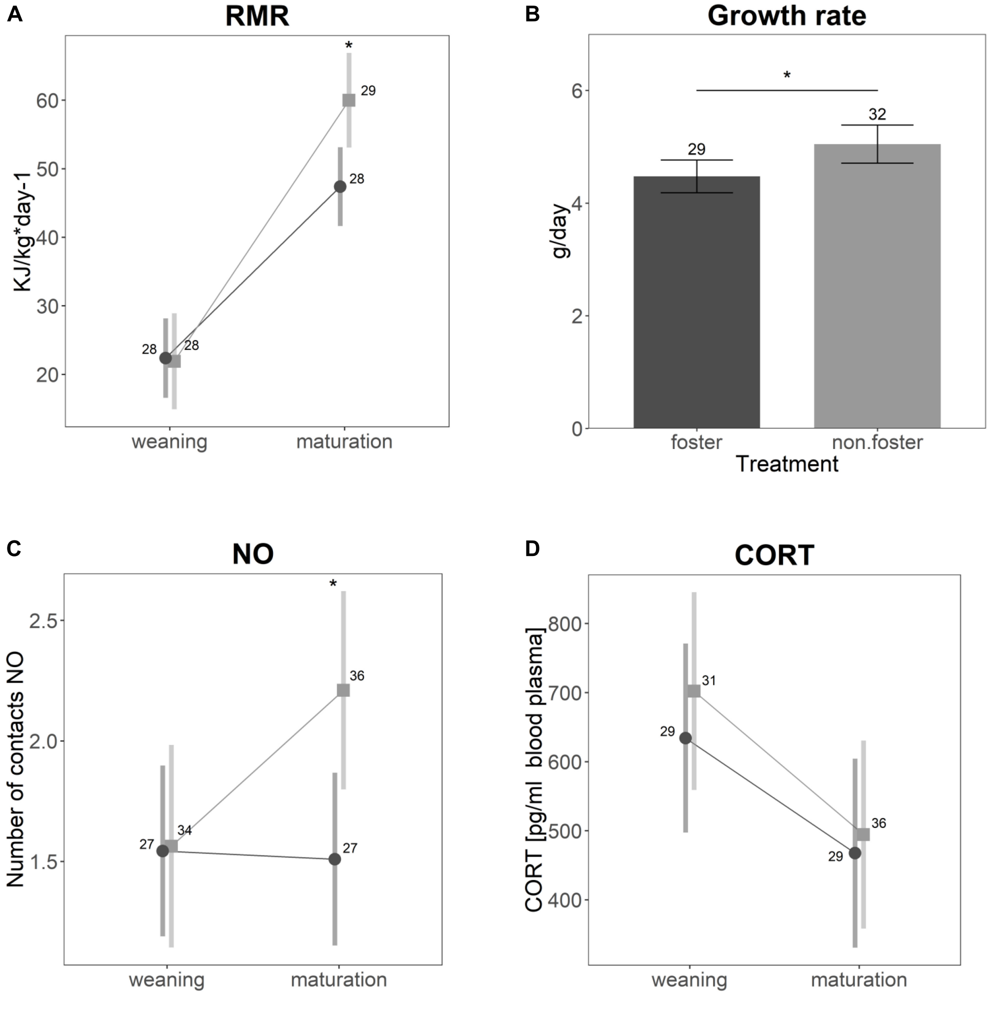

FIGURE 2 | Differences between the animals of *Experiment I* (non-fostered) in light gray and animals cross-fostered to the same size ranks (*Experiment II*) in dark gray for **(A)** specific resting metabolic rate, **(B)** growth rate, **(C)** number of contacts to a novel object, and **(D)** basal cortisol levels. Shown are the estimated values derived from the mixed models ± confidence intervals. Asterisks indicate significant differences. Samples sizes are given in the plot.

(same: + 0.77 ± 0.75 g; down: + 1.84 ± 0.87 g; up: 1.04 ± 0.89 g), nor growth rate until weaning differed between pups cross-fostered to the same, a lower or a higher size rank (**Figure 3A**). CORT also showed no difference between pups cross-fostered up or down (same: 595 ± 85 ng/ml; up: 729.5 ± 97.5 ng/ml; down: 565.1 ± 96.6 ng/ml). RMR however, tended to be elevated in pups that were cross-fostered to a higher size rank (same: 22.5 ± 1.6 kJ/kg*day^{-1}; up: 25.7 ± 1.9 kJ/kg*day^{-1}, t = 7.8, p = 0.08). This initial trend disappeared at maturation (t = −1.4, p = 0.17) (**Figures 3B,C**). Males had higher RMR than females,

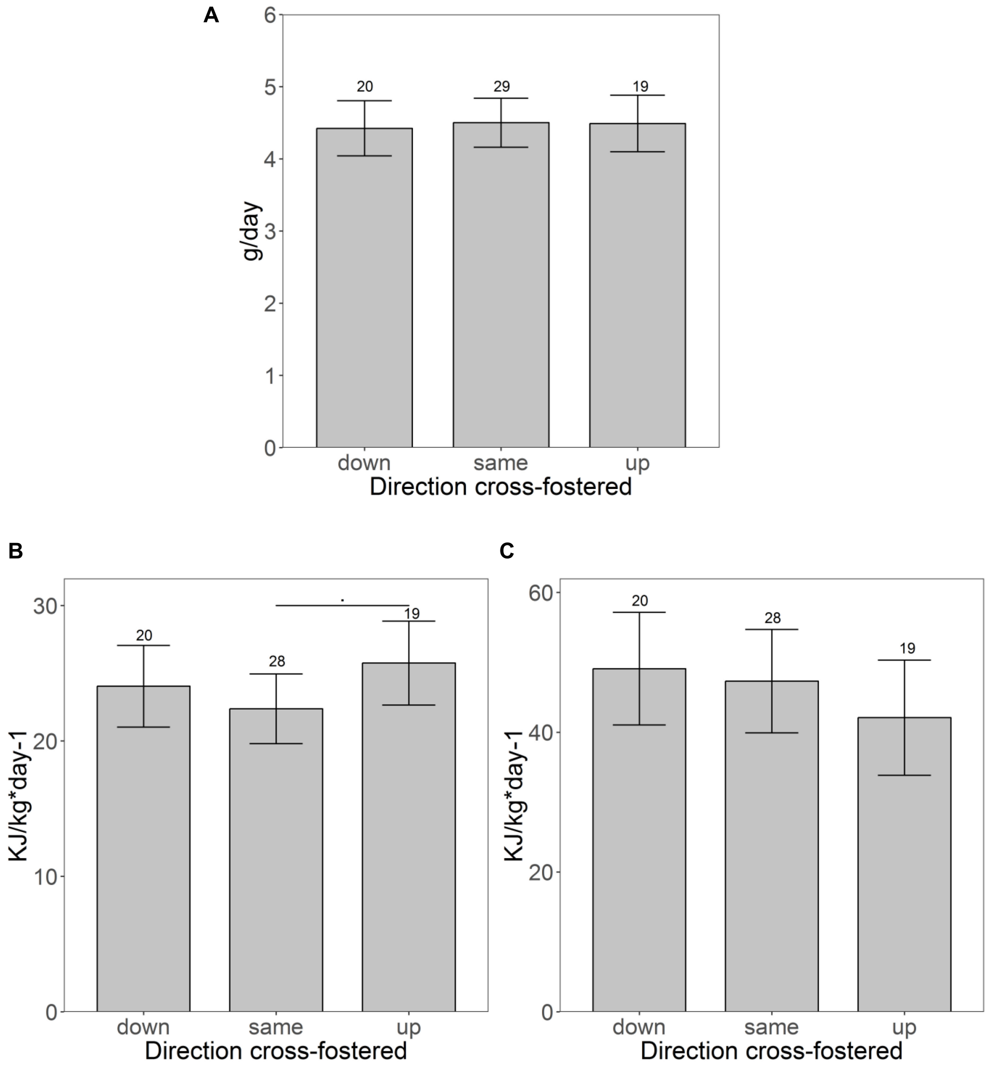

FIGURE 3 | Pups fostered to different size ranks. **(A)** Shows the growth rates and **(B,C)** show differences of the specific resting metabolic rate before **(B)** and after maturation **(C)** of pups fostered to different size ranks. Shown are the estimated values derived from the mixed models on traits ± confidence intervals. Samples sizes are given above the CI.

both, at weaning, and maturation (weaning: $t = 5.7$, $p < 0.001$, maturation: $t = 3.0$, $p = 0.004$). Neither the number of touches, nor the distance moved showed any differences between pups cross-fostered to the same or to other size ranks. For struggle docility, we also found no differences at weaning but pups that were cross-fostered to a higher size rank struggled significantly less than pups cross-fostered to a same size rank at maturation (same: 5.9 ± 1.2; up: 2.8 ± 1.5, $t = -2.0$, $p = 0.048$).

DISCUSSION

We aimed to investigate if behavioral and physiological differences between different-sized pups of the same litter persist until after independence and influence personality development long-lasting. Furthermore, we investigated the potential for plastic responses to changes in the early within-family environment by cross-fostering pups either to a same (i.e., remain in the same size rank), a lower (i.e., becoming the smallest pup), or a higher (i.e., becoming the largest pup) position in a foster-family. We found little evidence for long-term effects but remarkable plasticity in response to changes in the social environment. Moreover, we found a significant influence of the cross-fostering procedure itself on behavioral and physiological development (as further discussed below), something that has not been investigated in much detail despite the ubiquity of this procedure in the literature.

Plastic Responses to the Early Social Environment

As a first step, we verified that behavioral and physiological differences of the size rank within litter found in our previous study (Guenther and Trillmich, 2015) are reproducible with an independent set of animals. Pups born as the heaviest in the litter were the most fearless, bold and explorative and had the lowest plasma CORT levels around weaning. Although the effects we find in our sample were not all statistically significant (possibly due to a slightly lower sample size compared to the previous study by Guenther and Trillmich, 2015), they all point in the same direction as previously found. Comparable effects were shown in laboratory rats (*Rattus norvegicus*), where heavier pups were bolder and more explorative around weaning (Rödel and Meyer, 2011).

One possible explanation for differences in physiology and behavior in pups of different size ranks is that those may be a result of differential maternal provisioning. Studies showed that individuals receive different prenatal provisioning depending on their position *in utero* resulting in size differences between pups even several weeks before birth (Turner and Trudinger, 2000; Schumann et al., 2014). Previous findings implied a strong influence of prenatal maternal effects on personality differences of pups at an early age of 3 days (Guenther and Trillmich, 2015). Furthermore, prenatal maternal effects in guinea pigs and cavies have been shown to influence offspring behavior and physiology until adulthood (Sachser and Kaiser, 1996; Kaiser and Sachser, 1998, 2001). In domesticated guinea pigs, an unstable social environment during pregnancy causes masculinization of females and feminization of male offspring (Sachser and Kaiser, 1996; Kaiser and Sachser, 1998, 2001, 2005, 2009). Another example includes the adaptive programing to the season of birth. Animals born into autumn are less explorative, shyer and mature later, whereas animals born into spring conditions are more explorative, bolder and mature earlier (Guenther et al., 2014). As mentioned earlier (see section "Introduction"), in precocial species, the gestation period is relatively long, offering great scope for prenatal influences on development (Rood and Weir, 1970; vom Saal, 1989; Sachser et al., 2018). Mothers could adaptively program their offspring and follow a bet-hedging strategy. By diversifying the pups of a litter with different physiological and behavioral types, mothers could ensure that at least one of her offspring matches the future environmental conditions (Reddon, 2012).

Against our interpretation of an early long-term stable shaping of the phenotype, we find that these initial differences of the size rank disappear after maturation. Furthermore, none of the traits showed repeatability from the juvenile to the adolescent stage, suggesting high plasticity. This is in contrast with previous studies which demonstrated temporal consistency of the traits measured in the current study. However, in these previous studies, the phenotyping was conducted after juveniles had been separated from their mother and siblings, while in this study, the first round of testing was conducted when juveniles still lived in the family environment (Guenther and Trillmich, 2013; Guenther et al., 2014). This discrepancy suggests that differences between pups of different size within a litter largely represent the results of a size-related constraint arising from the competitive situation within the litter (Sulloway, 2010). If so, early behavioral differences among the pups may be achieved by adaptive shaping of individual phenotypes within the family. Rather than shaping an animal's phenotype long-term, however, these differences apparently only persist as long as the social context (i.e., the family) does not change.

When being cross-fostered, juveniles neither expressed a phenotype corresponding to their natal size rank, nor to their new size rank in the litter after cross-fostering. The fact that we find remarkably high plasticity of the offspring's phenotype implies that we only have a weak influence of prenatal maternal effects and that those effects are abolished postnatally by cross-fostering stress in the environment of a foster-mother and foster-siblings. Postnatal experiences and developmental plasticity, even later in life, offer an opportunity to readjust to the current environmental conditions. This might be necessary because informations provided by the mother earlier are not veridical, or the environmental conditions have indeed changed unpredictably, or because the offspring has emigrated to a new environment that is different from the previous one (reviewed in Sachser et al., 2011, 2013).

Effects of Cross-Fostering

We predicted that cross-fostering into a litter where pups occupy the same size rank would not change the expression of traits. Against our expectations, however, we did not find any size rank differences anymore, indicating that the process of fostering had a great impact on the behavioral and physiological development. A cross-fostering experiment in laboratory mice showed no difference in basal plasma CORT levels but found effects of cross-fostering on behavioral and physiological parameters, particularly in males. Cross-fostered males showed an increased exploration and smaller preputial glands – testosterone-dependent organs (Bartolomucci et al., 2004). In line with that, the lower RMR together with the lower growth rate and the more reactive behavior in the novel object test for the cross-fostered animals in this study indicate that cross-fostering is stressful and influences study results to a great extent.

As mentioned before (see section "Introduction"), cross-fostering is a frequently used method and mostly used in altricial species (Barbazanges et al., 1996; Bartolomucci et al., 2004; Hager et al., 2009; Matthews et al., 2011). However, only few studies have included appropriate controls to assess whether the process of fostering itself has an effect and reported the effects of fostering *per se* on various phenotypic measures in offspring (for review see, McCarty, 2017). Matthews et al. (2011) found that cross-fostering led to profound effects on cardiovascular and metabolic function in lab mice. Fostered mice showed increased appetite, body weight, abdominal fatness (in males only) and enhanced glucose tolerance. Furthermore, fostered male mice showed an increase in systolic blood pressure compared to mice reared by their genetic mother. Moreover, a study using a QTL approach showed that phenotypic plasticity does not only originate from additive genetic dominance effects but also from epigenetic effects such as genomic imprinting (Hager et al., 2009). The authors suggested that epigenetic effects of a locus on bodyweight and growth may vary as a result of changes particularly in the maternal environment through cross-fostering. Accordingly, our results also show differences in growth rates of fostered vs. non-fostered individuals. Overall, these results show that cross-fostering stress can have very different effects on different species and even strains (e.g., Barbazanges et al., 1996; Meek et al., 2001).

Postnatal manipulations, such as cross-fostering, at different times are shown to induce different effects on behavioral or endocrine traits (Barbazanges et al., 1996). The fact that different cross-fostering protocols are applied in different studies makes it difficult to compare the effects of cross-fostering between studies. Some studies use an all-litter foster design (e.g., Francis et al., 2003), others a one pup-foster design (e.g., McCarty and Lee, 1996) or a split-foster design (e.g., van Oers et al., 2015). Moreover, the choice of control groups varies in different studies. Some studies used in-fostered groups vs. cross-fostered groups, i.e., fostering pups to the same species/strain or to a different species/strain (e.g., Gomez-Serrano et al., 2001) while others compared fostered against non-fostered groups (e.g., Meek et al., 2001) or used a combination of both approaches (Cierpial et al., 1989). To our knowledge there is no published study investigating cross-fostering effects in non-altricial species.

In the current study, we show that cross-fostering effects also occur in a precocial species with similar effects to those found in altricial species. These findings have implications for both the interpretation of previous cross-fostering studies and the design of future studies using a cross-fostering approach in precocial species. We therefore stress the importance of well-designed control groups to reliably separate the effect of cross-fostering *per se* and other correlated experimental influences from the effects a specific experiment aims to measure.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available at https://doi.org/10.4119/unibi/2940638.

ETHICS STATEMENT

The animal study was reviewed and approved by Gesundheits-, Veterinär- und Lebensmittelüberwachungsamt Bielefeld.

AUTHOR CONTRIBUTIONS

AG and FT designed the experiment. AG collected the data. SK analyzed the data. SK and AG wrote the manuscript. All authors provided improvements to the manuscript and approved the final draft.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.00178/full#supplementary-material

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MINI REVIEW
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Regulation of Ant Foraging: A Review of the Role of Information Use and Personality

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Animals live in heterogeneous environments where food resources are transient and have to be exploited rapidly. Ants show a wide range of foraging strategies and this activity is tightly regulated irrespective of the mode of recruitment used. Individual foragers base their decision to forage on information received from nestmates (social information). Transmission of information can be in the form of direct physical interactions such as antennation or indirect exchange of information such as laying of pheromone trails. Foragers also rely on information from their internal states or experience (personal information). The interaction between these two sources of information gives rise to plasticity in foraging behavior. Recent studies have examined the role of personality (consistent inter-individual variation in behavioral traits) during ant foraging. Since colonies differ from each other in the distribution of personalities of their members, colonies may consistently differ in behavioral traits, giving rise to colony level personality. However, the interaction between information use and personality, especially at the individual level, remains unexplored. Here, we briefly summarize the literature on the effect of social and personal information on the regulation of ant foraging and the effect of personality on this behavior. We point out that a more focused examination of the interplay between personality and information use will help us understand how behavioral plasticity in the context of foraging is shaped at the colony and individual levels.

Keywords: behavioral plasticity, collective behavior, foraging, recruitment, social insects

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INTRODUCTION

Animals live in complex and heterogeneous environments with fluctuating resource availability. Effective decision making in different contexts is critical to their survival and fitness. In group-living species, including humans, collective decisions emerge from the actions of individual group members. The behavior of each individual is modulated by the behavior of others and affects the group as a whole (Conradt and List, 2009). Social insects such as ants live in colonies which consist of tens to millions of individuals and function as self-organized systems without central leadership (Jandt and Gordon, 2016). This is possible due to exchange of information among nest mates which allows individuals to coordinate their activities, thus maximizing colony efficiency (Duarte et al., 2011). Here, we first describe the different modes of foraging recruitment in ants. We then discuss how the use of different sources of information and consistent variation in behavioral traits among colonies and individuals contribute to bring about context-dependent plasticity in ant foraging behavior.

RECRUITMENT MECHANISMS IN ANTS

Of the more than 16,000 recorded species of ants (Bolton, 2020), foraging recruitment has been studied in detail in only a handful of species and they use different strategies to recruit nestmates to the food source (reviewed in Holldobler and Wilson, 1990).

(1) Tandem running: In this mode of recruitment, a recruiter who knows the location of the food source leads one nestmate at a time from the nest to the food source (reviewed in Franklin, 2014). Cohesion between the tandem pair is maintained by contiguous physical contact between the two ants and/or by short-range chemical signals emitted by the recruiter. The number of recruited foragers is largely proportional to the number of successful scouts as the recruits have to be actively guided by the recruiters on each trip.

(2) Mass recruitment using chemical trails: Here, ants that find a food source lay a pheromone trail while returning to the nest and this triggers the recruitment of nestmates (Wilson, 1962). The recruits, in turn, reinforce the trail while returning to the nest which leads to further recruitment (reviewed in Czaczkes et al., 2015). The number of ants joining the trail is a function of its strength. To prevent excessive mobilization of foragers, reinforcement of the trail is downregulated or an inhibitory signal may be produced.

(3) Group recruitment: In this case, one ant summons a few nestmates at a time from the nest and the recruited ants follow the leader ant closely to reach the food source. Although a trail may be laid by the leader, it is not enough to stimulate recruitment alone. Here, as in tandem running, the number of recruits will be determined by the number of successful scouts (Holldobler and Wilson, 1990).

(4) Group retrieving based on distant homing: This is another mode of recruitment that has been proposed where individual scouts appear to transmit information about a distant food source to groups of recruits through direct physical contact such as antennation. No other cues such as chemical trails or direct guiding is required for recruitment (Reznikova, 2008).

Independent of the recruitment strategy, the recruit receives information about the food source such as scent and type of food from the recruiter. This information helps the recruit in making its foraging decisions such as whether to initiate foraging, which food source to select and which path to follow.

USE OF SOCIAL AND PERSONAL INFORMATION IN REGULATION OF FORAGING

In social insect colonies, particularly in large ones, group members only have access to local information based on their position in the nest and the nestmates present in the vicinity (Mersch, 2016). Thus, foragers may not have direct access to information about food requirement of the colony. In addition, foragers have to choose from a range of alternatives such as type and location of food and path to the food source. Effective communication among workers is critical in regulating foraging activity. Individual foragers within a colony base their decisions to engage in foraging on social information received from their nestmates and their personal information. Social information may be obtained via direct interactions with nestmates and/or by indirect exchange of information. Foragers also rely on personal information based on their internal states, their interactions with the environment or their past experiences (reviewed in Dall et al., 2005). The majority of studies on information use during foraging have focused on trail laying species and there is little information available on species using other recruitment strategies.

Social Information

In trail laying species, the chemical trail, which usually contains multiple pheromones, transmits information about the food source to potential recruits. The number of ants laying trail pheromones as well as the intensity of pheromone deposition is related to the quality of food in several species such as the black garden ant *Lasius niger* (Mailleux et al., 2003; Detrain and Prieur, 2014), the pavement ant *Tetramorium caespitum* (Collignon and Detrain, 2010) and the Pharaoh's ant *Monomorium pharaonis* (Jackson and Châline, 2007). However, it has recently been suggested that pheromone trails may actually provide rather inaccurate information about food quality (Czaczkes et al., 2019). In addition to recruiting workers from the nest, the trail also stimulates scouts who are already outside to join the trail, as has been seen in the neotropical species *Pheidole oxyops* (Czaczkes and Ratnieks, 2012). Use of a combination of two pheromones – a long-lasting pheromone and a shorter lasting one – which allows colonies to track foraging resources more effectively while maintaining foraging cohesion has been documented in *M. pharaonis* (Jackson et al., 2006), the army ant *Leptogenys distinguenda* (Witte and Maschwitz, 2002) and the big headed ant *Pheidole megacephala* (Dussutour et al., 2009). In order to downregulate recruitment to a food source, *L. niger* foragers reduce pheromone deposition on trails that have already been heavily marked by trail pheromones (Czaczkes et al., 2013a) while a no-entry pheromone appears to repel foragers from unrewarding paths in *M. pharaonis* (Robinson et al., 2005).

Much information can be exchanged through direct physical contact between nestmates. High collision rates between foragers on a trail cause them to reduce pheromone deposition (Czaczkes et al., 2013b) or drive some ants to choose an alternate path in *L. niger* (Dussutour et al., 2004). Encounters between returning and outgoing foragers convey information about the partner's identity, the type of food being exploited and the richness of the food source. Leaf-cutter ants, *Atta cephalotes*, which collect leaves for the symbiotic fungus gardens inside their nests, use encounters on the trail to exchange information about the type of leaves being collected (Farji-Brener et al., 2010). Contact with food residues on a recruiter's body informs the recruits about the food type that is being exploited and this increases the success of finding the food patch in *L. niger* (Le Breton and Fourcassié, 2004). In tandem running species, continuous antennal contact between the recruiter and the recruit is essential for progression of the tandem run (Richardson et al., 2007). During each tandem run, the recruits get the opportunity to learn the path to the food source and they, in turn, recruit other nestmates (Franklin and Franks, 2012). Scouts of *Formica polyctena* appear to convey quantitative information about the location of food sources to recruits through antennal contact (Reznikova and Ryabko, 2011).

Cuticular hydrocarbons (CHCs) comprising of a blend of different hydrocarbons are present in a wax layer on the insect body (Blomquist and Bagneres, 2010). The CHC profile of individuals is related to their task repertoire and can inform the task decisions of nestmates. For example, it has been shown in the red harvester ant *Pogonomyrmex barbatus* that foragers have a higher ratio of saturated, linear hydrocarbons to linear alkenes and branched alkanes on the cuticle as compared to workers performing tasks inside the nest (Wagner et al., 2001). This forager-specific CHC profile not only helps in preventing water loss, which is critical as these ants forage in hot and dry conditions, but has also a communicative function by affecting task decisions of others (Greene and Gordon, 2003). Brief antennal contacts with a returning forager at the nest entrance allows inactive foragers to assess its CHC profile and whether it is carrying food. The combination of both odors is required to stimulate foraging in this species (Greene et al., 2013).

Personal Information

Personal information may be related to an individual's physiology with leaner individuals making extra foraging trips in response to an increased demand for foraging, as has been observed in *Temnothorax albipennis* (Robinson et al., 2009a). A forager's decision to initiate recruitment may be based on an internal response threshold such as ingestion of a desired volume of liquid food at a food source as shown in *L. niger* (Mailleux et al., 2000) and this threshold increases under conditions of starvation (Mailleux et al., 2006). Enhanced response to recruitment signals after a period of starvation has been observed in species such as *L. niger* (Mailleux et al., 2011), *Linepithema humile* and *Euprenolepis procera* (von Thienen et al., 2016). Personal information may also be based on prior experience. In *Ooceraea biroi*, foraging tendency among individuals of the same age is strongly correlated to successful foraging experiences in the past (Ravary et al., 2007). In two *Formica* species, individual foragers tend to return to sites where they have had positive experiences in the past (Tanner, 2009). Tandem running recruiters use visual landmarks to improve upon previously learnt routes (Pratt et al., 2001) and likelihood of becoming a recruiter increases with experience (Franklin et al., 2012).

Interplay Between Social and Personal Information

Individual ants extensively use both social and personal information to make foraging decisions but reliance on a particular source of information depends on its content relative to other sources. *L. niger* uses a combination of route memory and trail pheromones to maximize foraging efficiency (Czaczkes et al., 2011). In species that use visual cues to form route memory, low light conditions may lead to reliance on social signals rather than reliance on personal memories as has been reported in *L. niger* (Jones et al., 2019) and *Formica pratensis* (Beugnon and Fourcassié, 1988). In *T. albipennis*, contact with returning foragers at the nest entrance causes bouts of activity. In the absence of this social information, physiology of individual foragers predicts which ants will leave the nest as mentioned earlier (Robinson et al., 2009b). When there is a conflict between social and private information, individuals depend on personal information to make foraging decisions in many species such as *Acromyrmex subterraneus* (Almeida et al., 2018), *Formica lugubris* (Fourcassié and Beugnon, 1988), *L. niger* (Aron et al., 1993; Grüter et al., 2011), and *Paraponera clavata* (Harrison et al., 1989). The reverse, i.e., preference for social information over private information, has been observed in *L. humile* (Aron et al., 1993), *Atta cephalotes*, *Atta laevigata*, and *Acromyrmex octospinosus* (Vilela et al., 1987) while no clear preference for either is shown in *Iridomyrmex purpureus* (Middleton et al., 2018). It has been suggested that ants prioritize social or personal information based on the information content of each source and choose the source that provides more detailed, accurate and reliable information about the food source. Thus, a change in the accuracy and reliability of information from one of the sources may cause individuals to switch their choice of information source as has been demonstrated in *L. niger* (Czaczkes et al., 2019).

ROLE OF INDIVIDUAL AND COLLECTIVE PERSONALITY

The field of animal personality – defined as consistent inter-individual differences in behavioral traits across time and/or context – has seen rapid progress in the last two decades and personality traits have been documented in a wide range of taxa (Dingemanse et al., 2010). In social insects, in addition to individual differences in personality traits, groups differ consistently from each other in task performance and regulation of activity, giving rise to group level personality (Webster and Ward, 2011). For example, colonies may vary consistently in the baseline number of foragers that leave the nest to collect food. Group personality, or the particular configuration of behaviors expressed by the group, is likely to emerge from the differential aggregation of individual personalities comprising the colony or by external factors that vary consistently among colonies and affect colony behavior (Pinter-Wollman, 2012). Since the colony is the reproductive unit (Bourke, 2011), consistent behavioral variation among colonies may lead to fitness differences among them (Gordon, 2013). Certain behaviors such as boldness and aggression may be correlated at the population level and such suites of correlated behaviors are defined as behavioral syndromes (Sih et al., 2012). Within the behavioral syndrome expressed at the population level, each individual has a behavioral type; for instance, some individuals may be more bold and aggressive than others (Bell, 2007). Different behavioral types can coexist within a population (Wolf and Weissing, 2010).

Collective Personality

Several studies have looked at variations in behavioral traits at the level of the colony in different species of ants. In *P. barbatus*, colonies exhibit variation not only in the rate at which scouts leave the nest to search for food but also the ratio of outgoing foragers to returning foragers (Gordon et al., 2011). These differences in foraging activity among colonies persist from year to year (Gordon et al., 2013). Colonies of *Pogonomyrmex occidentalis* show consistent variation in the temporal pattern of foraging activity and also in the thermal range across which they forage (Cole et al., 2010). Colonies of *Temnothorax rugatulus* show consistency in their foraging effort and how they respond to different types of resources (Bengston and Dornhaus, 2014). Colonies of *Aphaenogaster senilis* that are more aggressive, readily explore novel environments and forage at higher temperatures (proactive colonies) are more successful than reactive colonies in retrieving food during intraspecific competition but suffer higher mortality rates (Blight et al., 2016). Colonies of *S. invicta* show persistent variation in foraging behaviors which is significantly related to colony growth (Bockoven et al., 2015). In *L. niger*, exploratory activity varies consistently among colonies and colonies with higher levels of exploratory activity discover and exploit food sources faster (Pasquier and Grüter, 2016). Colony personality is influenced by nest structure in *Messor andrei* and the foraging activity of colonies is consistent as long as they occupy the same nest sites (Pinter-Wollman et al., 2012). Behavioral syndromes have been identified at multiple levels in *Myrmica* ants where boldness is correlated with aggression at the caste level and with sociability at the colony level (Chapman et al., 2011).

Individual Personality

At the individual level, consistent variations in forager behavior has been observed in several species. In scouts of *L. niger*, intake of a desired volume of liquid is key to initiation of recruitment. This desired volume is specific to each individual, irrespective of its size, and remains constant over successive trips to a food source. There is also inter-individual difference in the persistence of trail-laying with some foragers never laying trails (Mailleux et al., 2005). Caste-based differences in personality traits have been identified in a few species. In *Myrmica rubra*, foragers are more active, exploratory, aggressive and attracted to light than workers who worked inside the nest (Pamminger et al., 2014). Foragers of *Camponotus aethiops* show better learning abilities and higher sucrose responsiveness than the nurses (Perez et al., 2013). However, it is not clear from these studies whether personality is related to the age of workers which determines which tasks they will perform. A few empirical studies have explicitly investigated the influence of personality of individual foragers on their foraging behavior. Learning performance was found to be correlated to exploration behavior in *C. aethiops* foragers with active explorers being slower to learn a task than less active ones (Udino et al., 2017).

FUTURE DIRECTIONS

Ant foraging behavior has been the focus of intensive studies for decades, yet much remains to be understood. We highlight a couple of avenues for further research that will give us a more comprehensive understanding of how individual and group level personality may affect the regulation of foraging in ants.

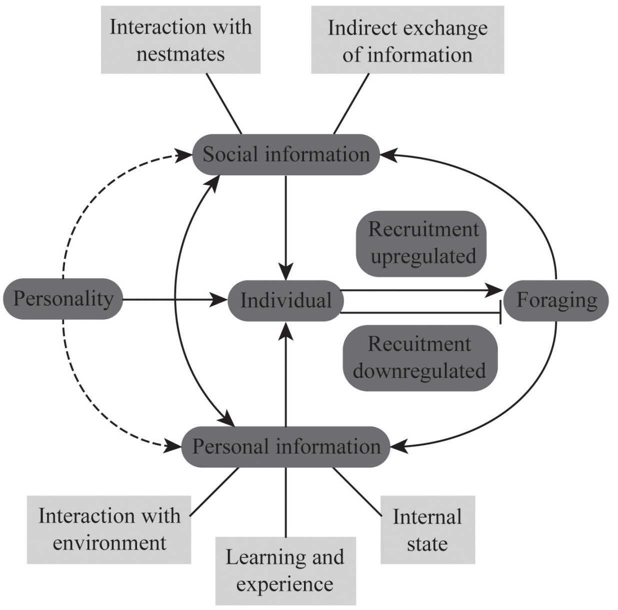

FIGURE 1 | The schematic represents the interplay between social and personal information and personality in regulating foraging behavior of individuals in ant colonies. The solid lines indicate known paths of interactions and the dotted lines indicate expected paths of interactions as discussed in the text. The arrowheads indicate the direction of the interaction. The different sources of information (social and personal) have been listed in the light gray boxes. The foraging decisions of individuals will determine collective foraging at the level of the colony.

(1) Numerous studies have separately investigated how the use of different sources of information and personality, largely at the colony level, influence foraging. However, the interaction between these two factors, particularly at the level of individual foragers, in giving rise to plasticity in foraging behavior (as shown in **Figure 1**) remains relatively unexplored. We predict that individuals with different personalities will vary in the manner in which they perceive and use information, prioritize personal and social information, and in their learning abilities (Carere and Locurto, 2011; Sih and del Giudice, 2012). As a result, they will differ in task specializations. For example, individuals who are bolder and show more exploratory activity may more readily become scouts who go out in the initial search for food. These individuals should also have more flexible learning abilities and rely more on personal information. Foragers who vary in their foraging strategies as in *Ectatomma ruidum* (McGlynn et al., 2015) or in their resource specialization as in *Formica aquilonia* (Iakovlev and Reznikova, 2019) should also vary in their personality traits and cognitive abilities. Since the task repertoire of individual ants changes with age, further studies are also required to understand whether personality traits of individuals remain constant across their lifetimes and how this affects their task choice and task performance at different stages of their life.

(2) In social insects, colony personality is determined by the distribution of individual personalities within the group and differences in the underlying personality distributions will affect collective behavior. Most studies on foraging regulation have been done at the colony level by essentially looking at the average behavior of the group as a whole. Variations in behavioral traits at the individual level are not adequately captured by such studies (for example, Pamir et al., 2011 in honeybees). Thus, exploration of the distribution of individual personality traits within colonies will shed further light on how collective foraging behavior is shaped. For example, a colony with a higher proportion of individuals who are bold and show high exploratory activity should be able to track changing food resources or detect new food sources more efficiently. Such studies can be done by manipulating group compositions as has been done with ants in other contexts (Carere et al., 2018; Neumann and Pinter-Wollman, 2019).

An integrated analysis of personality and information use at the individual and colony levels will give us a more comprehensive understanding of the emergence and maintenance of context-dependent plasticity in ant foraging behavior.

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Dynamics of Intersexual Dominance and Adult Sex- Ratio in Wild Vervet Monkeys

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Intersexual dominance relations are important for female mammals, because of their consequences for accessing food and for the degree of sexual control females experience from males. Female mammals are usually considered to rank below males in the dominance hierarchy, because of their typical physical inferiority. Yet, in some groups or species, females are nonetheless dominant over some males (partial female dominance). Intersexual dominance, therefore, also depends on traits other than sexual dimorphism, such as social support, social exchange, group adult sex-ratio, and the widespread self-reinforcing effects of winning and losing fights, the "winner-loser effect." The importance of sex-ratio and the winner-loser effect remains poorly understood. A theoretical model, DomWorld, predicts that in groups with a higher proportion of males, females are dominant over more males when aggression is fierce (not mild). The model is based on a small number of general processes in mammals, such as grouping, aggression, the winner-loser effect, the initially greater fighting capacity of males than females, and sex ratio. We expect its predictions to be general and suggest they be examined in a great number of species and taxa. Here, we test these predictions in four groups of wild vervet monkeys (*Chlorocebus pygerythrus*) in Mawana game reserve in Africa, using 7 years of data. We confirm that a higher proportion of males in the group is associated with greater dominance of females over males; a result that remains when combining these data with those of two other sites (Amboseli and Samara). We additionally confirm that in groups with a higher fraction of males there is a relatively higher (a) proportion of fights of males with other males, and (b) proportion of fights won by females against males from the fights of females with any adults. We reject alternative hypotheses that more dominance of females over males could be attributed to females receiving more coalitions from males, or females receiving lowered male aggression in exchange for sexual access (the docile male hypothesis). We conclude that female dominance relative to males is dynamic and that future empirical studies of inter-sexual dominance will benefit by considering the adult sex-ratio of groups.

Keywords: the winner-loser effect, dominance hierarchy, fierceness of aggression, female dominance over males, adult sex-ratio, vervet monkeys

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INTRODUCTION

In many group-living animals there is a dominance hierarchy and dominant individuals usually have priority of access to resources (Drews, 1993). In terms of dominance between the sexes, females may benefit from dominating males for several reasons, for instance by:

(A) suffering less sexual coercion (Smuts and Smuts, 1993; Muller and Wrangham, 2009; Surbeck and Hohmann, 2013; Palombit, 2014),
(B) having more freedom in choosing mates (Soltis, 1999; Muller and Wrangham, 2009; but see Rosenblum and Nadler, 1971),
(C) being able to protect their infants better against harassment by males (Smuts and Smuts, 1993; Muller and Wrangham, 2009).
(D) having more opportunity to lead group movement, which may result in feeding priority (Waeber and Hemelrijk, 2003; Overdorff et al., 2005; Van Belle et al., 2013).

However, only in rare cases females are dominant over males. This happens in primates in lemurs where the sexes have approximately equal body size and in spotted hyenas where females are slightly larger than males. In most mammals, however, males are larger and more dangerous in their weaponry (e.g., they have larger canines) than females (Clutton-Brock, 2016) and therefore, are usually considered to be dominant over females. If body size and weaponry (so-called prior attributes) alone contributed to an individual's position in the hierarchy, then in those species where each adult male is larger than each adult female in the group (as in many mammalian species), all males should always be dominant over all females (the so-called prior attribute hypothesis, Chase et al., 2002). However, this is not always the case and smaller females are sometimes observed to beat larger males, so-called partial female dominance (Smuts, 1987). This is usually explained as a consequence of coalitions among females against males (Smuts, 1987; Smuts and Smuts, 1993; Parish, 1994; Setchell et al., 2006; White and Wood, 2007), but could also be a consequence of males reducing aggression to females for getting sexual access to them, referred to as the docile male hypothesis (Surbeck and Hohmann, 2013). Most interestingly for the present paper, a computational model, called DomWorld, showed that competitive interactions may make females dominant over some males through the self-reinforcing effects of winning and losing fights; the winner-loser effect (Hemelrijk et al., 2008). These self-reinforcing effects imply that, after losing a fight, the loser is more likely to lose again and, after winning, it is more likely to be victorious (Chase, 1974; Hsu et al., 2006; Franz et al., 2015). The build-up of a dominance hierarchy via the winner-loser effect is referred to as the "self-organization hypothesis" (Hogeweg and Hesper, 1983; Dugatkin, 1997; Hemelrijk, 2000). The model DomWorld comprises individuals that group, compete and experience the self-reinforcing effects of conflict outcomes. In it, males and females are identical in all respects except in two aspects of their fighting ability (reflecting prior attributes). Firstly, males start with a higher initial fighting power (dominance) than females, though fighting ability subsequently changes over time via the winner-loser effect. Secondly, the aggression of males is more intense, and thus has more impact, than that of females. For instance, being hit or trampled by a male involves more physical damage to the victim than by a female. The model shows that despite these favorable prior-attributes for males, the winner-loser effect may result in females becoming dominant over a few males in species where aggression is fierce. Intense or fierce aggression involves behavior, such as chasing, hitting and biting, as shown, for instance, by both sexes in rhesus monkeys, *Macaca mulatta* (Cheney and Seyfarth, 1990; Hemelrijk et al., 2008; Thierry et al., 2008). Female dominance over males happens in the model because the large impact of the winner-loser effect causes some males and females to lose much of their fighting ability and others to gain a lot. Thus males may drop in their fighting ability below certain females, without necessarily having had a direct conflict with these females. When aggression is mild, female dominance is less likely to emerge because the impact of winning and losing fights is minor and therefore the individuals neither rise, nor sink much in their fighting ability and thus, their rank. Therefore, when aggression is mild and females start with a lower fighting capacity than males, the females remain subordinate. Tonkean macaques (*M. tonkeana*) are an example of a primate species which exhibit mild aggression during conflicts (such as staring), and therefore the outcomes of their fights have only a small impact (Thierry et al., 2008).

For a species with high intensity of aggression, the model DomWorld has three predictions. First, the higher the proportion of males in the group, the more dominant females become over males. This happens only when the intensity of aggression of males is higher than that of females, as is usual in primates with male-biased sexual dimorphism (Albers and de Vries, 2001; Clutton-Brock and Huchard, 2013). Second, in groups with more males greater dominance of females over males through greater subordinance of males in the model is due to the greater relative frequency of male-male fights (which have high impact compared to fights with females). Third, in groups with a greater proportion of males, females are expected to win fights against males more often as proportion of their fights with all adults. Thus, the first prediction concerns a general pattern and the second and third one are associated processes. The relationship between the proportion of males in the group and female dominance over males has subsequently been tested and confirmed in a few groups of rhesus monkeys, and in a small dataset combining groups of several species of despotic macaques with intense aggression (Hemelrijk et al., 2008). Yet, when combining data from several species, the correlation is confounded by the effects of species-specific differences in sexual dimorphism. Thus the correlation is best studied among groups of a single species. Additionally, there is an indication for a similar process in humans. Here, "female influence" on a collective decision was taken as a proxy for female dominance and it was shown that this increases with proportion of men in the group (Stroebe et al., 2016).

These positive associations between proportion of males on the one hand, and on the other hand, female dominance, proportion of fights among males and proportion of victories of females over males, may well be a general phenomenon among groups within species, because the model DomWorld involves only four phenomena (processes and traits) and these are probably present in many mammals: First, the self-reinforcing effects of winning and losing fights (Hsu et al., 2006); second, strong intensity of aggression (with clear impact of an outcome of a fight on dominance); third, stronger intensity of aggression in males than females (note that most mammals have male-biased sexual dimorphism (Clutton-Brock, 2016) and therefore probably stronger aggression intensity in males); and fourth, a range of different sex ratios of groups (so that we can study a sufficiently large range of adult sex ratios).

To investigate the generality of these dynamics in dominance between the sexes, in the present study we investigate them in the vervet monkey (*Chlorocebus pygerythrus*). We chose vervet monkeys as this species shows fierce aggression (Cheney and Seyfarth, 1990) and some degree of female dominance over males (Struhsaker, 1967; Smuts, 1987; Hemelrijk et al., 2008; Young et al., 2017). Although the self-reinforcing effects of winning and losing fights have not yet been studied empirically in vervet monkeys, it is likely that they operate in this species, because the winner-loser effect has been shown in many taxa (Hsu et al., 2006) including primates, namely rhesus monkeys (*M. mulatta*; Mendoza and Barchas, 1983; Neumann et al., 2011; Snyder-Mackler et al., 2016), crested macaques (*Macaca nigra*), yellow baboons (*Papio cynocephalus*), anubis baboons (*Papio anubis*; Franz et al., 2015), and chimpanzees (*Pan troglodytes*; Newton-Fisher, 2017). Moreover, in vervet monkeys it is likely that males are more intense in their aggression than females because of their sexual dimorphism. Further, we have long-term data on conflicts collected from 2011 until and including 2017 in four groups of vervet monkeys living under natural conditions at the Inkawu Vervet Project (IVP), in Mawana Game Reserve, KwaZulu Natal, South Africa.

In line with the self-organization hypothesis, we predict that processes of self-organization in groups of vervet monkeys imply that a higher proportion of males in a group will result in an increase of (a) female dominance over males, (b) proportion of male-male fights, and (c) proportion of victories of females over males.

In case greater female dominance in groups with a higher proportion of males is found, we also examine two alternative hypotheses for the self-organization hypothesis namely whether this pattern may result from (1) higher frequencies of support received by females from either sex in fights against males, the social support hypothesis (Smuts, 1987) and from (2) lowered aggression of males to females as a kind of sexual exchange, when competing with more males (sometimes labeled the docile male hypothesis; Surbeck and Hohmann, 2013).

Besides, we test the relationship between female dominance over males and proportion of males in the group not only with data in Mawana but also with data from the literature on two other sites, Masai-Amboseli Game reserve, south-central Kenya, East Africa (Struhsaker, 1967) and the Samara Private Game Reserve, South Africa (32°22’S, 24°52’E; Young et al., 2017).

MATERIALS AND METHODS

Species

In vervet monkeys, females are philopatric and males usually migrate at around 4–5 years of age. Female rank is influenced by kinship (the youngest daughter will usually attain the rank just below her mother), whereas an adult male’s rank depends on his own ability to win conflicts against other adult males (Cheney and Seyfarth, 1990) and may also be strengthened by social positive relations with females (as reflected in grooming and proximity; Young et al., 2017).

As to sexual dimorphism, body weight of males is on average 1.4 times that of females in the wild (males weigh on average 5.7 ± 0.07 kg and females 4.1 ± 0.05 kg; Turner et al., 2018), males are significantly more muscular than females and adult canine lengths of males is about 1.3 times that of females (Bolter and Zihlman, 2003).

Data Collection in Mawana Game Reserve

Behavioral data were collected as part of the IVP in Mawana Game Reserve, KwaZulu Natal, South Africa between January 2011 and December 2017 in four neighboring groups of wild vervet monkeys, named Ankhase, Baie Dankie, Kubu, and Noha. The home ranges of all groups differ in their spread of vegetation and within each home range there are areas of cluttered vegetation, for instance close to the river, and areas of more spread out vegetation, for instance large areas of acacia.

Group size included typically about 30 individuals in total with on average 13.8 adults and ranged between 7 to 24 adults. We confined our analyses to adults; a female was considered to be adult after she had given birth, and a male after his first dispersal to another group.

The monkeys were habituated to human presence from 2010 onward. Data collection on a group started after human observers could approach each monkey within 10 meters. Data were collected during several days a week continuously throughout the year. Per group we collected data for the following hours and days, in group Ankhase 9763 h during 1553 days, in Baie Dankie 12,044 h during 1,707 days, in Noha 12,141 h in 1,729 days, and in group Kubu 5,367 h in 937 days. Observers moved throughout the group in order to collect scan and focal data on all group members and to reduce bias toward particular individuals.

Data on conflicts were recorded with *ad libitum* sampling while observers were collecting scan and focal sampling data, while habituating groups, or conducting field experiments. Conflicts were defined by the occurrence of one or more of the following elements in a social interaction: “hit,” “bite,” “grab,” “stare,” “attack,” “chase,” “displacement,” “steal food,” “hand on head,” and “aggressive call.” For each conflict, the following was recorded: the time of the event, the identity of the opponents, the winner and the identity of the group. To determine the dominance position of an individual in the group, we used only dyadic conflicts ignoring polyadic conflicts that involved more members. An individual was considered to have won a conflict, if its last behavior in the conflict was aggressive (as defined above) *and* the last behavior of its opponent was submissive ("avoid," "jump aside," "crawl," "leave," "retreat," "flee," and "scream"). If either opponent's last behavior was ambiguous (e.g., "undetermined vocalization"), its directly preceding behavior was used instead to determine the outcome of the conflict. Still, the behavior of one opponent had to be clearly aggressive, *and* that of the other clearly submissive, for the conflict to be included. In the case of an ambiguous outcome, conflicts were discarded for determining dominance. The intensity of each conflict was recorded as either severe (hit, bite, chase, grab, or steal food) or mild (stare, displace, and aggressive call). In our analysis of the social support hypothesis, we defined support in a conflict, as the case in which a third individual joined in a fight between two others by attacking one of the opponents. All researchers were trained and tested to reliably identify all individual monkeys.

Data and Analysis of Mawana Game Reserve

We put conflicts in matrices per group per year, with the identity of winners listed in rows and of losers listed in columns. We confined our analyses to dyadic interactions among adults and studied in total 159 adults during 37,083 observation hours. Data on adults were included only if they had been present in the group for at least half a year. Thus, in the case of females, because they are adult after giving birth, females were included only if they had given birth to their first offspring more than 6 months ago or longer and immigrant males were included after they had been in the group for 6 months or longer. Conflict matrices (referred to as group-year points) were used in our analysis only when (1) at least 50 conflicts were recorded in a given year, and (2) the conflicts had been collected throughout an entire year (excluding data collected during a shorter period). We chose a period of a full year rather than half a year, in order to reduce the effect of the short period of hierarchical instability that happened after the single migratory period that took place each year. In total we recorded 3123 conflicts over 16 group-year points collected for four groups during 7 years. On average individuals were recorded to participate in 28 conflicts per year (range: 7 to 153).

We used the total number of dyadic, agonistic interactions among all adults per group and year (excluding cases of support in conflicts) to determine the linear dominance hierarchy. We ranked individual adults in a group according to their fraction of winning fights of all fights with each partner averaged over all interaction partners with whom they had been in conflict (discarding group members with whom they had no interactions), the so-called average dominance index, ADI (Hemelrijk et al., 2005). Thus, this index controls for some dyads having more interactions than others. A higher value implies greater dominance of an individual. We choose this method because of its robustness, as compared to other measures such as IS&I and Netto (Hemelrijk et al., 2005). Its outcome and robustness are the same as that of David Score, provided that missing values are taken care of properly when calculating the David Score.

We quantified relative female dominance in a group (the female dominance index, FDI) as the proportion of males over which the females were dominant on average (Hemelrijk et al., 2008). Using the dominance hierarchy of both sexes based on the average dominance index, ADI we summed over all females the number of males that were ranking below each female (and in the case of a tie, males were counted as half) and divided this by the maximum number of males that could have ranked below all females (which equals the number of females multiplied by the number of males; Hemelrijk et al., 2003). This FDI over males ranges from 0 (all females are subordinate to all males) to 1 (all females are dominant over all males; Hemelrijk, 1999; Hemelrijk et al., 2008). We investigated whether the proportion of adult males of the total number of adults in the group was related to (a) the female dominance index, FDI, (b) the proportion of fights of males with other males of all their fights with adults, and (c) proportion of fights won by females of all their fights with adults ($n = 16$ group-year points, **Table 1**).

Further, to investigate the social support hypothesis, by testing for a relationship between proportion of males in a group and how often females received support from males in dyadic conflicts against other males, we calculated for each group-year, the average proportion of male-female dyadic conflicts in which females were supported by another male. We studied the relation between these averages and the proportion of males in the group. We removed two groups with only one male (Noha in 2011 and Kubu in 2017, **Table 1**) as male support against males was here impossible) leaving 14 group-year points. We similarly investigated support received from females by females in their fights against males.

To test the docile male hypothesis, we examined whether the intensity and frequency of aggression from males toward females was reduced in periods of stronger competition for access to females. We compared intensity and frequency of aggression of males to females during the mating season (from April until and including July, 4 months) to the rest of the year (8 months).

Data and Analysis From Studies in Amboseli and Samara Private Game Reserve

We determined the dominance hierarchy and female dominance index, FDI in two groups in Amboseli using the same analyses as in Mawana. Data in Amboseli were collected in a study of one year shown in Tables 6 and 7 in Struhsaker (1967). We also determined the FDI in Samara private game reserve using data of three groups collected during a study of 3.5 years on three groups and shown in **Figure 1** of the article by Young and colleagues (Young et al., 2017; **Table 1**).

Statistics

Self-Organisation Hypothesis

To test whether he female dominance index, FDI could be predicted by proportion of males in Mawana, we used a Generalized Linear Mixed Model (GLMM), assuming a beta-binomial distribution for the total number of cases that individual males were subordinate to each of the females, summing

TABLE 1 | Information on the reserve, the group-name, number of adults of each sex, male proportion, female dominance, and individual rankings of both sexes per group per year. * means the adjacent individuals have the same average dominance index, ADI.

Reserve	Group	Year/ Period	Male#	Female #	Male Pro-portion	Female dominance	Ranking from high to low (*means the adjacent individuals have the same ADI)
Mawana	Ankhase	2011	2	5	0.29	0	M, M, F, F, F, F, F
Mawana	Ankhase	2012	6	6	0.5	0.58	M, F, F, M, F, F, M, M, F, F*, M*, M*
Mawana	Ankhase	2013	4	9	0.31	0.51	F, M, F, F, M*, F*, F, F, M, F, F, M, F
Mawana	Baie Dankie	2011	4	8	0.33	0.25	M, M, F, F, F, M, F, F, M, F*, F*, F*
Mawana	Baie Dankie	2012	4	12	0.25	0.46	F, M, F, M, F, F, F, F, F*, F*, F, M, F, M, F, F,
Mawana	Baie Dankie	2013	4	11	0.27	0.43	M, F, F, F, F*, M*, F*, F, F, M*, F*, M*, F, F*, F*
Mawana	Baie Dankie	2014	8	7	0.53	0.42	F, M, M, M*, M*, F, F, M*, F*, M, F, M*, F*, F*, M*
Mawana	Baie Dankie	2015	6	11	0.35	0.38	F, M, F, M*, M*, M, F, F, F, F, F*, F*, M, F, F*, F*, M*
Mawana	Baie Dankie	2016	6	11	0.35	0.27	M, M, M, F, F, F, M* F*, F*, F, F, M, M, F, F, F*, F*
Mawana	Baie Dankie	2017	12	12	0.5	0.40	F, F, M, M, M, M, F, M, M*, F*, M, M, F, F, M, F, F, M, F, M, F, F, F, M
Mawana	Kubu	2017	1	5	0.17	0	M, F, F, F, F, F
Mawana	Noha	2011	1	9	0.1	0	M,F, F, F, F, F, F, F, F, F
Mawana	Noha	2012	5	10	0.33	0.52	F, F, M, F, F, M, M, F, F, M, F, F, F, F, M
Mawana	Noha	2013	5	11	0.31	0.45	F, F, M, F, M, M, F*, F*, F, F, M, F, F, F, M, F
Mawana	Noha	2014	7	11	0.39	0.27	F*, M*, F, M, M, F*, M*, M*, F, F*, F*, M*, M+, F+, F, F*, F*, F*
Mawana	Noha	2016	2	6	0.25	0.08	M, F, M, F, F, F, F, F
Samara	PT	1	10	9	0.53	0.28	M, M, M, F, M, M, F, M, M, F, F, F, M, F, F, M, M, F, F
Samara	PT	2	10	9	0.53	0.32	M, M, F, M, M, F, F, M, M, M, F, M, F, F, F, M, M, F, F
Samara	PT	3	7	12	0.37	0.44	F, M, F, F, M, M, F, F, F, M, F, M, M, F, F, F, M, F, F
Samara	PT	4	6	11	0.35	0.52	F, F, F, F, M, F, M, F, M, M, M, F, M, F, F, F, F
Samara	PT	5	6	10	0.38	0.47	F, F, M, F, M, M, F, M, F, F, M, F, F, F, F, M
Samara	PT	6	4	10	0.29	0.18	M, F, F, M, M, F, M, F, F, F, F, F, F, F
Samara	RBM	1	13	12	0.52	0.26	F, F, M, F, M, M, M, M, M, M, M, M, M, M, M, F, F, M, F, F, F, F, F, F, F
Samara	RBM	2	19	13	0.59	0.26	M, M, M, F, F, M, F, M, M, M, M, M, M, M, M, M, F, M, M, M, F, F, M, F, F, M, F, M, F, F, F, F
Samara	RBM	3	15	13	0.54	0.53	F, F, F, M, F, F, F, F, M, M, M, M, M, M, M, M, M, M, M, M, F, M, M, F, F, F, F, F
Samara	RBM	4	19	13	0.59	0.68	M, M, F, F, F, F, M, M, M, F, F, M, F, M, F, F, F, M, F, M, F, M, M, M, M, M, M, M, M, F, M, M
Samara	RBM	5	16	13	0.55	0.51	F, F, M, F, F, M, M, F, M, F, M, M, M, M, M, F, M, M, F, F, M, M, M, M, F, F, M, F, F
Samara	RBM	6	13	13	0.5	0.5	F, F, M, M, M, M, F, M, M, F, M, F, F, M, F, F, F, M, F, F, F, M, F, M, M, M
Samara	RST	1	15	21	0.42	0.41	F, F, M, M, F, F, M, F, F, M, M, F, M, M, M, M, M, M, F, F, F, F, M, F, F, F, F, F, M, F, F, F, M, F, M, F
Samara	RST	2	12	15	0.44	0.47	F, F, M, M, M, F, F, F, M, F, F, M, M, F, M, M, F, F, M, M, M, F, F, F, M, F, F
Samara	RST	3	10	15	0.4	0.23	F, M, M, F, M, M, F, M, F, M, M, F, M, F, M, F, M, F, F, F, F, F, F, F, F
Samara	RST	4	13	17	0.43	0.53	M, M, F, F, M, F, F, F, F, F, F, F, M, F, M, M, M, F, M, M, F, M, F, F, M, M, F, M, F, F
Samara	RST	5	13	16	0.45	0.45	F, F, F, M, F, F, M, M, M, M, M, F, M, F, F, F, M, M, M, F, M, F, M, F, M, F, F, F, F
Samara	RST	6	14	16	0.47	0.43	F, M, M, F, F, F, M, F, M, F, M, M, F, M, M, M, F, F, M, M, F, F, M, M, F, M, F, F, F, F
Amboseli	1530		2	3	0.4	0.17	M, F, M, F, F
Amboseli	P		3	4	0.43	0.38	M, F*, F*, M*, F, F*, M*

^*Although there were six females resident in Kubu in 2017, one did not participate in any conflict was therefore excluded from further analysis.*

**These individuals had tied values for their dominance index (ADI) with one or more of the adjacent individuals also marked with a *.*

them over all females of a group (using $N = 16$ group-year combinations). The choice for this model is motivated by the fact that the female dominance index in a group (FDI) is the sum of the total number of males dominated by each of the females (thus the same male may be counted several times if it is dominated by several females) divided by the total number of males that could have been dominated by each female, summed over all females. Note that this equals the average of the fraction of

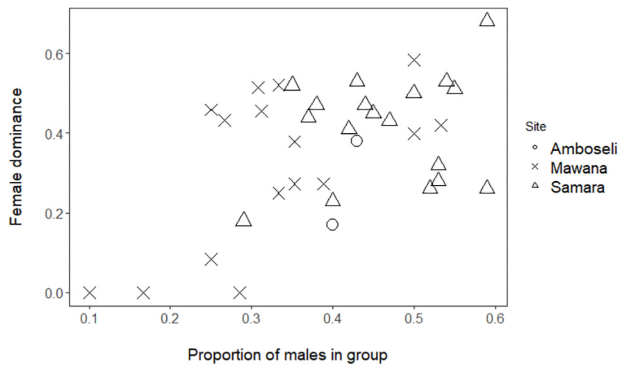

FIGURE 1 | Female dominance, FDI, versus proportion of males (only adults are concerned) in Mawana game reserve (symbol: cross), Amboseli (symbol: circle; Struhsaker, 1967), and Samara Private game reserve (symbol: triangle; Young et al., 2017).

males subordinate to each female. The beta-binomial distribution (instead of the ordinary binomial distribution) is used to handle possible overdispersion, as there is no reason to believe that the variation of the fractions will be of binomial origin only. In the GLMM we related the female dominance index, FDI in a group to the proportion males, using a logit link function, as is common for binary data. We introduced crossed random group effects for groups and years into the model to handle repeated observations of the same group over different years and to account for differences between years (possibly reflecting climatological effects).

Using the extended dataset of three sites (Mawana, Samara, and Amboseli), we analyzed the relationship between the female dominance index as the response variable (FDI) and explanatory variables proportion of males in the group and sites (together forming the fixed part of the model) and crossed random effects of groups and years, using a betabinomial GLMM (**Table 1**, $N = 36$ group-year combinations).

We tested the associated processes related to the proportion of fights among males and the proportion of victories of females over males only in Mawana: The response variables, proportion of fights among males of all of fights by males and the proportion of fights won by females over males, were related to the proportion of males in a group again using betabinomial GLMMs ($N = 16$ group-year points). The random part of the GLMMs consisted of crossed random effects of years and groups.

Alternative Hypotheses

We tested the following alternative hypotheses only in Mawana.

In case of the social support hypothesis, the response variables proportion of support of fights with males received from males by females ($N = 16$ group-year points) and the support proportion received from females by females ($N = 16$ group-year points) were analyzed with GLMMs, as described for female dominance.

To test the docile male hypothesis, we analyzed the number of conflicts of males with females per male aggressor per month in three ways, (1) in total ($N = 221$ male-month combinations, 39 males), (2) the mild conflicts ($N = 194$ male-month combinations, 38 males), and (3) severe conflicts ($N = 80$ male-month combination, 28 males) separately. We used GLMMs with a truncated negative binomial distribution, fixed effect for mating season (Y/N) and crossed random effects for group and year and individual aggressor nested within group and year. Because only males with at least one fight were considered, the truncated negative binomial distribution, which assumes that counts ≥ 1, was used as probability distribution for the numbers of conflicts.

General Information on Statistics

All GLMM models were fitted using the glmmTMB package (Brooks et al., 2017) of *R* (version3.6.1, R Core Team, 2019). In the **Supplementary Material** we give statistics on model diagnostics [goodness of fit statistics based on simulated residuals as described in the R-package DHARMa (Hartig, 2019)] and model performance [omnibus likelihood ratio tests comparing the fitted model with the null model, and pseudo R^2 based on likelihoods using R-package MuMIn (Barton, 2019)].

Since the conceptual details of GLMMs are not as clear as those of correlations and to indicate the robustness of our results, we mention that we also have tested these patterns with the more old-fashioned methods of correlations (Pearson and Kendall, where suited) and Bonferroni Holm methods, ignoring the repeated observations on some individuals that returned in different group-year points. This has led qualitatively to the same results, see **Supplementary Material**.

RESULTS

The Self-Organisation Hypothesis

Female dominance index over males, FDI, in wild vervet monkeys in Mawana Game reserve had an average value of 0.31 (standard deviation = 0.20, min = 0, and max = 0.58) which resembles the values for the Samara private game reserve with an average value of 0.42 (standard deviation = 0.13, min = 0.18, and max = 0.68). Female dominance, FDI, in both reserves is higher than the average value of 0.27 found for the two groups in Amboseli (groups 1530 and Struhsaker, 1967; Hemelrijk et al., 2008; for group size, composition, and ranks, see **Table 1**).

We showed that female dominance over males, FDI, is significantly positively associated with the proportion of males in the group in Mawana (GLMM, 4 groups, 16 group-year-points, regression coefficient $\beta = 3.6$, SE 1.2, z-value 3.0, and $P = 0.002$; **Figure 1**). Although in the data of private game reserve Samara separately, the same association was positive, but non-significant (GLMM, 3 groups, $n = 18$ group by half year records, $\beta = 1.23$, SE = 1.49, z-value = 0.83, and $P = 0.41$), when we combined the data of the three sites, Mawana, Amboseli and Samara, the FDI and proportion of males were significantly associated [GLMM, 9 groups (4 in Mawana, 3 in Samara, 2 in Amboseli), 36 group-year points, $\beta = 2.6$, SE = 0.95, z-value = 2.21, and $P = 0.0064$, **Figure 1**]. No significant differences in female dominance, FDI, corrected for proportion of males were found between sites (same data set, $N = 36$, likelihood ratio test $X^2 = 0.14$, and $P = 0.93$).

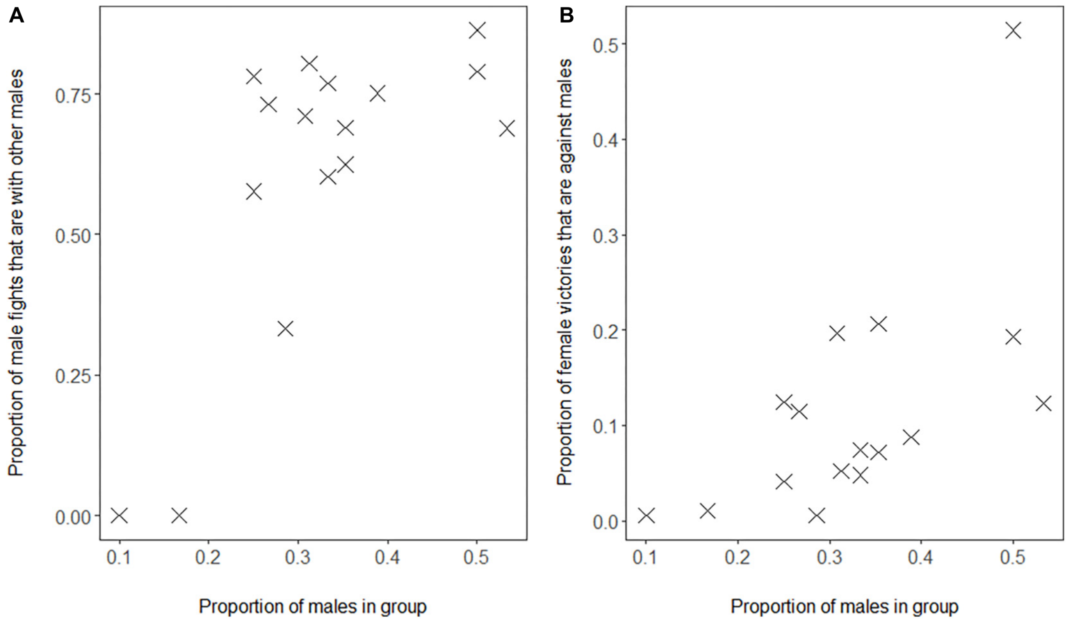

FIGURE 2 | Proportion of males in Mawana versus **(A)** proportion of fights of males with other males out of all fights of males with adults, **(B)** proportion of fights won by females against males out of all fights of females with adults. Note that also after removing the outlier in **B**, our result is significant (slope = 5.1, *z*-value = 3.49, and *P* = 0.0005).

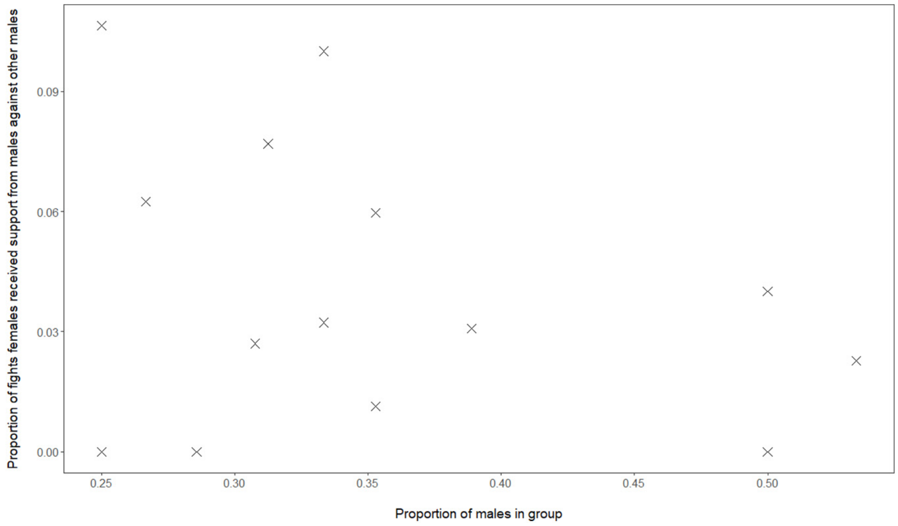

FIGURE 3 | Data from vervets in Mawana regarding the proportion of males versus the proportion of fights of females against males in which females receive support from males.

We confirmed the associated processes based on the self-organization hypothesis, namely that in groups with a higher proportion of males, (a) males fight relatively more with other males as proportion of their interaction with both sexes (**Figure 2A**, GLMM, 4 groups, 16 group-year points, regression coefficient β = 9.27, SE 2.27, *z*-value 4.08, and *P* = 0.00005) and (b) females win conflicts with males more often as a proportion of their winning conflicts with either sex (**Figure 2B**, GLMM, 4 groups, 16 group-year points, 126 females, regression coefficient β = 6.96, SE 1.66, *z*-value 4.20, and *P* = 0.00003).

Alternative Hypotheses

The Social Support Hypothesis

Although, in our data of Mawana, we have calculated the dominance indices using only dyadic interactions, the social support hypothesis cannot be excluded, namely that in groups

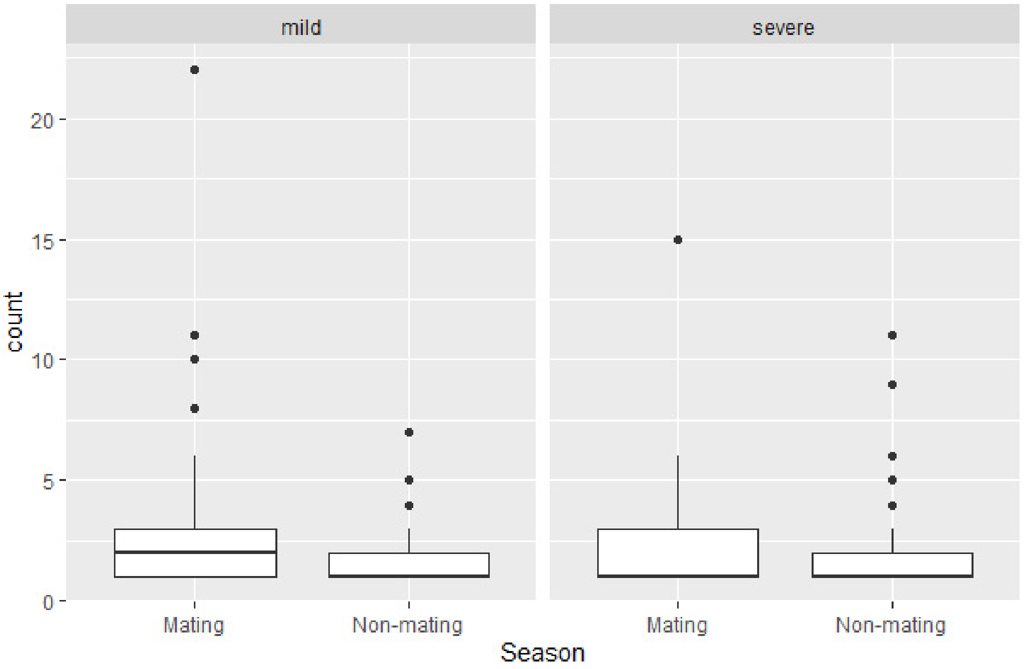

FIGURE 4 | Boxplots of number of severe and mild conflicts initiated from males to females per month per male in the mating season (from April till and including July) and in the rest of the year.

with a greater proportion of males, female dominance over males, FDI, may be higher due to females receiving more support from either sex, when females are in conflict with a male. When studying support in fights received by females, we do not find a correlation between proportion of males in the group and proportion of female-male conflicts in which the female was supported by another male (GLMM, 4 groups, 16 group-year points, regression coefficient β = 1.86, SE 2.30, *z*-value 0.81, and *P* = 0.42, see **Figure 3**). However, when the proportion males in the group was higher this was positively associated with a greater proportion of female-male conflicts in which the female was being supported by another female (GLMM, 4 groups, 16 group-year points, regression coefficient β = 56, SE 1.61, *z*-value 2.83, and *P* = 0.005).

Docile Male Hypothesis

The docile male hypothesis was not supported by our data, neither when analyzing data on all conflicts, nor when analyzing mild and severe conflicts, separately. Note that in our 16 group-year sample, 3675 conflicts recorded were coded as mild, and 726 as severe. Based on the GLMMs, the total aggression of males to females per month was even lower (though not-significantly so) during the non-mating season when considering all conflicts (regression coefficient for non-mating season β = −0.18, SE = 0.23, *z*-value = −0.81, and *P* = 0.42), the number of mild conflicts (β = −0.47, SE = 0.29, *z*-value = −1.62, and *P* = 0.10) and the number of severe conflicts (β = −0. 35, SE = 0.36, *z*-value = −0.97, and *P* = 0.33, **Figure 4**).

DISCUSSION

We confirmed in wild vervet monkeys the theoretical prediction (Hemelrijk et al., 2008), that higher female dominance over males is associated with a higher proportion of males in the group (in Mawana, and in the combination of three sites in Africa, namely Mawana, Samara, and Amboseli). We additionally confirmed that the higher the proportion of males in the group, the more often males interacted agonistically with other males relative to interacting with all adults and the more often females won fights against males versus against all adults. This confirms the three predictions of the model DomWorld and indicates that self-reinforcing effects of winning and losing fights may underlie dynamics of dominance between the sexes in vervet monkeys.

Further, we found neither an indication that, in groups with a higher proportion of males, females become higher in rank by receiving more support from males in fights with other males, the social support hypothesis (Smuts, 1987; Smuts and Smuts, 1993; Parish, 1994; Setchell et al., 2006; White and Wood, 2007), nor that females increase rank, because males are reducing aggression to females for getting access to them, as suggested in the docile male hypothesis (Surbeck and Hohmann, 2013). Whereas males experience the strongest competition for access to females in the mating season, in this season they do not reduce aggression toward females compared to outside this season. We find, however, that in groups with a higher proportion of males, females are receiving more support from females. This does not necessarily mean that females become higher in rank due to the support they received from other females. Instead, they may already be higher in rank than males they support against. Their high rank relative to males may have arisen by the self-reinforcing effects of winning and losing fights. In such a case, female support itself may be a side effect of females being already higher in rank relative to males and thus, experiencing less risk in joining other females against males in groups with more males. We gave a similar argument for the higher frequency of support among females in bonobos versus chimpanzees (Hemelrijk, 2002); since, compared to female chimpanzees, female bonobos are already higher in rank than their male group members, they experience less risk to join in fights of other females against males.

Two further alternative explanations for finding the positive association between female dominance over males and proportion of males in the group are:

First, rather than being a consequence of group composition, female dominance over males causes the composition of the group, meaning that in some groups, females of high dominance permit more males to enter the group, because males are not aggressive toward anyone. However, this can be excluded in Mawana, because males are on average more aggressive than females in 15 out of our 16 group-year points (Wilcoxon signed-rank test, $N = 16$, $V = 4$, and p-value = 0.0002).

Second, in groups with more males, males may compete more for sexual access to females. As females may here be a limiting resource, this may increase the female's value and thus, dominance relative to males (Goodall, 1986). In line with our self-organization hypothesis, this would imply that the total frequency of male-male aggression is higher in groups with more males, which we confirm in Mawana and so we are unable to exclude this hypothesis.

Although female primates have usually been considered to rank below males because of the smaller size of their body and canines, some dominance by females over males has already been found in vervet monkeys in Amboseli and in Samara (Struhsaker, 1967; Hemelrijk et al., 2008; Young et al., 2017). We have confirmed this in a new site, Mawana. We show that, combining data of the three sites, the degree of female dominance over males, FDI, in wild vervet monkeys is on average 0.36 (SE = 0.03), thus, below co-dominance of 0.5. In all three sites combined, the relation between proportion of males and the index of female dominance over males, FDI, was positive and significant. The non-significant but positive trend in the data of private game reserve Samara separately may be related to the smaller range of sex ratios over which this correlation was studied in Samara (0.1 to 0.5 in Mawana and 0.3 to 0.6 in Samara).

In future work it would be interesting to quantitatively study the degree of female dominance over males in many species of mammals with male-biased sexual dimorphism (including and beyond primates) living in multi-male groups with different proportions of males and study how these species differ in the relation between proportion of males and degrees of female dominance over some males. We particularly expect the association to be found for species for which some female dominance over males has been reported despite male-biased sexual dimorphism. In primates, for instance, these are bonobos (Vervaecke et al., 2000), capuchin monkeys (Izawa, 1980), several species of macaques (Rhine et al., 1989; Hemelrijk et al., 2008), common chimpanzee (Hemelrijk and Ek, 1991), common squirrel monkey (Masataka and Biben, 1987), and the gray langur (Sommer et al., 2002). It would also be interesting to see whether the adult sex ratio depends on certain environmental conditions. As to the winner-loser effect, it should be specifically tested in vervet monkeys, like it has been in baboons (Franz et al., 2015) and other species.

We explicitly note that, our theory based on DomWorld, was not developed for species (almost) lacking sexual dimorphism in body size and aggression intensity, such as hyenas and lemurs, and having special adaptations related to female dominance such as masculinized genitals or high levels of testosterone (von Engelhard et al., 2002; Wagner et al., 2007).

According to the theoretical study, DomWorld, the positive relation between proportion of males and female dominance over males should be absent (or weaker) in species with aggression that is mild, for example, in tonkean macaques and in crested macaques (Hemelrijk et al., 2008). What precise phases of different degrees of female and male dominance pass through, when sex ratio changes in groups, should be studied experimentally in detail similarly to the transitivity analyses of Lindquist and Chase (2009) and be related to the winner loser effect and to spatial structure (Hemelrijk et al., 2017).

Note that our explanation for different degrees of female dominance over males is integrative in the sense of considering a combination of traits (the winner-loser effect, species-specific intensity of aggression, higher intensity of aggression by males than females and a range of sex ratios of a group), and their consequences. This integrative aspect is typical for explanations based on self-organization.

Along the lines of studies testing the effects of self-organization in complex systems, we conclude that inter-sexual dominance in vervet monkeys probably depends on the winner-loser effect, because it depends on the adult sex ratio of a group. In order to establish the winner-loser effect convincingly, however, is beyond the scope of this paper. For this further studies are needed examining time-series in aggressive interactions in empirical data (as done, for instance, by Franz et al., 2015). In general, based on our results in vervet monkeys, we urge future empirical studies of intersexual dominance to also take sex-ratio and fierceness of aggression into account.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The study was approved by the relevant authority (Ezemvelo KZN Wildlife, SouthAfrica) and by the funders. The study conforms with the ASAB/ABSguidelines for the care and use of animals. We used non-invasive observational methods of data collection on animals in their natural habitats, and all individuals were habituated to human observers.

AUTHOR CONTRIBUTIONS

CH conceived the idea of this manuscript and wrote the main part of the manuscript, and contributed to the statistical analysis, figures and tables. EW designed the data collection and trained the team to it; coordinated the field site; funded most of the data collection; contributed to the data analyses; and wrote part of the manuscript and commented on it. MW extracted the data, conducted the statistical analyses, contributed to the writing of parts of the materials and methods and results. JB collected some of the data, contributed to the data analyses, and contributed to the writing of part of the materials and methods and results. GG contributed to the data analyses and their description in the materials and methods and results.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.00839/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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CORRECTION
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Corrigendum: Dynamics of Intersexual Dominance and Adult Sex- Ratio in Wild Vervet Monkeys

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Keywords: the winner-loser effect, dominance hierarchy, fierceness of aggression, female dominance over males, adult sex-ratio, vervet monkeys

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A Corrigendum on

Dynamics of Intersexual Dominance and Adult Sex- Ratio in Wild Vervet Monkeys
by Hemelrijk, C. K., Wubs, M., Gort, G., Botting, J., and van de Waal, E. (2020). Front. Psychol. 11:839. doi: 10.3389/fpsyg.2020.00839

In the original article, there was a mistake in **Table 1** as published. The values for the female dominance (index) and dominance ranking from high to low of adults for all group-year points in Mawana were incorrect, apart from in Baie Dankie 2013 where only the ranking of adults was incorrect and in Noha 2011 where all information was correct. The number of females was incorrect in Kubu 2017 and so was the proportion of males; in Noha 2012 the number of males was incorrect and therefore the proportion of males was incorrect. Data on Baie Dankie 2014 were added. Data on Noha 2015 are omitted. The corrected **Table 1** appears below.

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

TABLE 1 | Information on the reserve, the group-name, number of adults of each sex, male proportion, female dominance, and individual rankings of both sexes per group per year. * means the adjacent individuals have the same average dominance index, ADI.

Reserve	Group	Year/ Period	Male#	Female #	Male Pro-portion	Female dominance	Ranking from high to low (*means the adjacent individuals have the same ADI)
Mawana	Ankhase	2011	2	5	0.29	0	M, M, F, F, F, F, F
Mawana	Ankhase	2012	6	6	0.5	0.58	M, F, F, M, F, F, M, M, F, F*, M*, M*
Mawana	Ankhase	2013	4	9	0.31	0.51	F, M, F, F, M*, F*, F, F, M, F, F, M, F
Mawana	Baie Dankie	2011	4	8	0.33	0.25	M, M, F, F, F, M, F, F, M, F*, F*, F*
Mawana	Baie Dankie	2012	4	12	0.25	0.46	F, M, F, M, F, F, F, F, F*, F*, F, M, F, M, F, F,
Mawana	Baie Dankie	2013	4	11	0.27	0.43	M, F, F, F, F*, M*, F*, F, F, M*, F*, M*, F, F*, F*
Mawana	Baie Dankie	2014	8	7	0.53	0.42	F, M, M, M*, M*, F, F, M*, F*, M, F, M*, F*, F*, M*
Mawana	Baie Dankie	2015	6	11	0.35	0.38	F, M, F, M*, M*, M, F, F, F, F, F*, F*, M, F, F*, F*, M*
Mawana	Baie Dankie	2016	6	11	0.35	0.27	M, M, M, F, F, F, M* F*, F*, F, F, M, M, F, F, F*, F*
Mawana	Baie Dankie	2017	12	12	0.5	0.40	F, F, M, M, M, M, F, M, M*, F*, M, M, F, F, M, F, F, M, F, M, F, F, F, M
Mawana	Kubu	2017	1	5	0.17	0	M, F, F, F, F, F
Mawana	Noha	2011	1	9	0.1	0	M,F, F, F, F, F, F, F, F, F
Mawana	Noha	2012	5	10	0.33	0.52	F, F, M, F, F, M, M, F, F, M, F, F, F, F, M
Mawana	Noha	2013	5	11	0.31	0.45	F, F, M, F, M, M, F*, F*, F, F, M, F, F, F, M, F
Mawana	Noha	2014	7	11	0.39	0.27	F*, M*, F, M, M, F*, M*, M*, F, F*, F*, M*, M+, F+, F, F*, F*, F*
Mawana	Noha	2016	2	6	0.25	0.08	M, F, M, F, F, F, F, F
Samara	PT	1	10	9	0.53	0.28	M, M, M, F, M, M, F, M, M, F, F, F, M, F, F, M, M, F, F
Samara	PT	2	10	9	0.53	0.32	M, M, F, M, M, F, F, M, M, M, F, M, F, F, F, M, M, F, F
Samara	PT	3	7	12	0.37	0.44	F, M, F, F, M, M, F, F, F, M, F, M, M, F, F, F, M, F, F
Samara	PT	4	6	11	0.35	0.52	F, F, F, F, M, F, M, F, M, M, M, F, M, F, F, F, F
Samara	PT	5	6	10	0.38	0.47	F, F, M, F, M, M, F, M, F, F, M, F, F, F, F, M
Samara	PT	6	4	10	0.29	0.18	M, F, F, M, M, F, M, F, F, F, F, F, F, F
Samara	RBM	1	13	12	0.52	0.26	F, F, M, F, M, M, M, M, M, M, M, M, M, M, M, F, F, M, F, F, F, F, F, F, F
Samara	RBM	2	19	13	0.59	0.26	M, M, M, F, F, M, F, M, M, M, M, M, M, M, M, M, F, M, M, M, F, F, M, F, F, M, F, M, F, F, F, F
Samara	RBM	3	15	13	0.54	0.53	F, F, F, M, F, F, F, F, M, M, M, M, M, M, M, M, M, M, M, M, F, M, M, F, F, F, F, F
Samara	RBM	4	19	13	0.59	0.68	M, M, F, F, F, F, M, M, M, F, F, M, F, M, F, F, F, M, F, M, F, M, M, M, M, M, M, M, M, F, M, M
Samara	RBM	5	16	13	0.55	0.51	F, F, M, F, F, M, M, F, M, F, M, M, M, M, M, F, M, M, F, F, M, M, M, M, F, F, M, F, F
Samara	RBM	6	13	13	0.5	0.5	F, F, M, M, M, M, F, M, M, F, M, F, F, M, F, F, F, M, F, F, F, M, F, M, M, M
Samara	RST	1	15	21	0.42	0.41	F, F, M, M, F, F, M, F, F, M, M, F, M, M, M, M, M, M, F, F, F, F, M, F, F, F, F, F, M, F, F, F, M, F, M, F
Samara	RST	2	12	15	0.44	0.47	F, F, M, M, M, F, F, F, M, F, F, M, M, F, M, M, F, F, M, M, M, F, F, F, M, F, F
Samara	RST	3	10	15	0.4	0.23	F, M, M, F, M, M, F, M, F, M, M, F, M, F, M, F, M, F, F, F, F, F, F, F, F
Samara	RST	4	13	17	0.43	0.53	M, M, F, F, M, F, F, F, F, F, F, F, M, F, M, M, M, F, M, M, F, M, F, F, M, M, F, M, F, F
Samara	RST	5	13	16	0.45	0.45	F, F, F, M, F, F, M, M, M, M, M, F, M, F, F, F, M, M, M, F, M, F, M, F, M, F, F, F, F
Samara	RST	6	14	16	0.47	0.43	F, M, M, F, F, F, M, F, M, F, M, M, F, M, M, M, F, F, M, M, F, F, M, M, F, M, F, F, F, F
Amboseli	1530		2	3	0.4	0.17	M, F, M, F, F
Amboseli	P		3	4	0.43	0.38	M, F*, F*, M*, F, F*, M*

^Although there were six females resident in Kubu in 2017, one did not participate in any conflict was therefore excluded from further analysis.

**These individuals had tied values for their dominance index (ADI) with one or more of the adjacent individuals also marked with a *.*

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Trail Pheromone Does Not Modulate Subjective Reward Evaluation in *Lasius niger* Ants

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Comparing the value of options is at the heart of economic decision-making. While an option may have an absolute quality (e.g. a food source has a fixed energy content), the perceived value of the option may be malleable. The factors affecting the perceived value of an option may thus strongly influence which option is ultimately chosen. Expectations have been shown to be a strong driver of perceived value in both humans and social insects, causing an undervaluation of a given option if a better option was expected, and an overvaluation if a poorer one was expected. In humans, perceived value can be strongly affected by social information. Value perception in some insects has also been shown to be affected by social information, showing conformism as in humans and other animals. Here, over a series of experiments, we tested whether pheromone trail presence, a social information source, influenced the perceived value of a food source in the ant *Lasius niger*. We found that the presence of pheromone trails leading to a sucrose solution does not influence food acceptance, pheromone deposition when returning from a food source, drinking time, or frequency of U-turns on return from the food. Two further assays for measuring changes in food acceptance, designed to increase sensitivity by avoiding ceiling effects, also showed no effect of pheromone presence on food acceptance. In a separate study, *L. niger* have also been found to show no preference for, or avoidance of, odors associated with foods found in the presence of pheromone. We are thus confident that trail pheromone presence does not affect the perceived value of a food source in these ants.

Keywords: social information, value perception, preference, conformity, recruitment, pheromone trails

INTRODUCTION

Understanding the mechanisms behind decision-making is key to understanding animal behavior. Decision-making systems lie on a trade-off continuum between cheap (in terms of processing power or time) but inaccurate systems and costly but more reliable ones. Perhaps the cheapest but least accurate is random choice. Somewhat costlier, but much more effective, is the use of heuristics ('rules of thumb'), such as "do what I did last time," "do what is easiest," or "do what others are doing." Finally, the value of each decision outcome can be estimated and compared to other available options, often resulting in a choice for the option reaping the largest total reward. This type of decision-making is the basis of the majority of human economic decision-making models, such as the Expected Utility Theory (Mankiw, 2011), as well as of classical optimality-based models of animal behavior (Krebs et al., 1978; Stephens and Krebs, 1986). In order to compare the value of options, however, one must first assign a value to each option. Value perception thus has a large influence on decision-making.

The perceived value of options can be influenced by various things such as aspects of the option itself, or attributes of the decision maker. Moreover, the influences on perceived value may be absolutely rational, boundedly or ecologically rational, or completely irrational. Examples of completely rational influences on perceived value include time discounting (Frederick et al., 2002; Craft, 2016; Hayden, 2016), although often such time-discounting is too strong to be considered fully rational (Hillemann et al., 2014; Hayden, 2016).

However, perceived value can be influenced irrationally as well. For example, it has been argued that risk aversion when risking gains, and risk-seeking when risking losses, can emerge directly from the non-linear nature of perception and learning (Kacelnik and El Mouden, 2013), resulting in irrational behavior (but see Lim et al., 2015). Similar mechanisms can also result in a preference for rewards experienced when in a low state (e.g. hungry or stressed) over otherwise identical rewards experienced when in a high state (Schuck-Paim et al., 2004; Pompilio et al., 2006; Aw et al., 2011), or a preference for rewards associated with harder work over easier-to-access rewards (Kacelnik and Marsh, 2002; Czaczkes et al., 2018).

Finally, value attribution can itself be carried out by following heuristics, which allow more rapid valuation at the risk of making errors. This is often termed 'bounded rationality' (Simon, 1990) or 'ecological rationality' (Todd and Gigerenzer, 2012), as they often result in optimal behavior given the resource and information limits humans and animals find themselves under. For example, valuation can be performed in a relative manner: rather than assign independent valuations to each option, options can be compared and ranked along one or a few criteria. This can cause the perceived value of an option to rise or fall, depending on the reference point (Kahneman and Tversky, 1979; Flaherty, 1996). Such relative value perception is common in humans (Camerer, 2004), and has been described in animals, including rats, honeybees, and ants (Bitterman, 1976; Flaherty, 1996; Wendt et al., 2019). Relative valuation can result in irrational behavior such as taking into account irrelevant alternatives, resulting in decoy effects which have been reported in humans, other vertebrates, insects, and even slime-molds (Huber et al., 1982; Shafir et al., 2002; Latty and Beekman, 2011; Sasaki and Pratt, 2011). Another important influence on perceived value, which can be boundedly rational, is social information: how others evaluate the option may affect one's own evaluation.

Social information has a very large impact on many aspects of decision-making. Strategic information use – whether to rely on privately acquired information or social information – has received extensive attention by researchers (Coolen et al., 2003; Dall et al., 2005; Kendal et al., 2005, 2009; Leadbeater and Chittka, 2007). Social information use allows the costs of information collection to be avoided (Valone and Templeton, 2002). However, social information may be less nuanced than privately collected information, for example lacking the full suite of sensory dimensions offered by privately acquired information (Czaczkes et al., 2019). Social information is also open to dishonest signaling from competitors (Bugnyar and Heinrich, 2006), and carries its own costs, such as time invested in acquiring and providing social information (Dechaume-Moncharmont et al., 2005; Grüter and Leadbeater, 2014). Nonetheless, social information use, and the copying of others, is extremely common in both humans and non-human animals (Rendell et al., 2010). In humans, conformity can result in people changing their evaluation of item quality depending on the evaluation of others (Pincus and Waters, 1977; Bone, 1995; Jayles et al., 2017). By analogy, animals may also change their evaluation of a resource according to the revealed evaluation of others. Indeed, inadvertent social information – the observation of the behavior of others – has been shown to strongly influence preference, for example during food selection in rats (Jolles et al., 2011) and bees (Avarguès-Weber et al., 2018) or mate selection in fruit-flies (Mery et al., 2009; Danchin et al., 2018). For social insects, social information is relied on to make collective decisions, as usually a collective decision must be reached without all individuals having direct experience of all the options, or even more than one option (Robinson et al., 2009). Pheromone trails are an important source of social information for many ants. They not only signal resource location, but correlate (albeit very roughly) with resource quality (Beckers et al., 1992; Detrain and Prieur, 2014; Wendt et al., 2019), and act as an important source of reassurance to experienced foragers, allowing them to run faster and straighter (Czaczkes et al., 2011). Pheromone deposition, in turn, can reflect the certainty of an ant's memory, and whether its environment has changed (Czaczkes and Heinze, 2015).

Several studies have shown an effect of intentional social information (signals) on subjective evaluation in insects. A study on the stingless bee *Melipona quadrifasciata*, showed that thoracic vibrations from the donor during trophallaxis increase with increasing food quality, and result in improved associative learning in the receiver (Mc Cabe et al., 2015). This effect may also work via modulating perceived value, but may alternatively function via other supports to learning, such as increasing the receiver's attention. More conclusively, Baracchi et al. (2017) demonstrated that aversive pheromones can reduce the appetitive response in honeybees to sucrose, while attractive pheromones, usually used to signal the nest entrance, can increase appetitive responses. Rossi et al. (2018) demonstrated the converse pattern for aversive stimuli, which were enhanced by aversive pheromones and reduced by attractive ones. Even sex pheromones appear to positively modulate the response to food rewards in moths and honeybees (Hostachy et al., 2019; Baracchi et al., 2020). Finally, and very relevant for the current study, Rossi et al. (2020) conducted a study in parallel to ours, and asking an identical question to that investigated here. They found a positive effect of pheromone trails on resource evaluation in the Argentine ant, *Linepithema humile*.

The ant, *Lasius niger*, is an emerging insect model in the study of value perception and social information use (Grüter et al., 2011; Czaczkes et al., 2019; Wendt et al., 2019). Here, we set out to test whether *L. niger* ants are influenced by social signals when evaluating food quality. Resource evaluation by

L. niger is distorted by a range of non-social effects, such as by comparison against other resources (Wendt et al., 2019), by shared associations with previously evaluated food (Wendt and Czaczkes, 2020), and by the effort invested in obtaining a reward (Czaczkes et al., 2018). Inadvertent social information also affects resource evaluation, with ants undervaluing resources consumed in the presence of other ants, and preferring odors associated with solitary feeding over those associated with group feeding in a binary choice assay (Wendt et al., 2020). As in many other ants, *L. niger* deposit pheromone trails to food sources, and deposit more pheromone to resources they perceive as being of higher quality (Beckers et al., 1992; Detrain and Prieur, 2014; Frizzi et al., 2018; Wendt et al., 2019). Pheromone deposition is also depressed by repeatedly encountering nestmates on the trail or while feeding (Czaczkes et al., 2013b; Wendt et al., 2020) or by trail pheromone already being present on the substrate (Czaczkes et al., 2013a). In a series of experiments, we test whether the presence of a strong pheromone trail, implying positive evaluation by nestmates, drives preference or distorts perceived value in *L. niger* foragers.

MATERIALS AND METHODS

Animals

All experiments were conducted on queenless *Lasius niger* colony fragments consisting of ca. 2,000 workers and small amounts of male brood, which were kept in plastic foraging boxes with a layer of plaster of Paris on the bottom and a circular plaster nest (14 cm diameter, 2 cm high). The colonies were provided with 1M sucrose syrup and water *ad libitum* and were starved 4 days prior to testing. The number of ants and colonies tested in each experiment is provided in **Table 1**.

Pheromone Extraction

A pheromone extract was created following a procedure modified from von Thienen et al. (2014). *L. niger* workers were killed by keeping them in a freezer for 45 min. Afterwards, pheromone was obtained by dissecting the gaster to isolate the hindgut and rupturing it in a vial containing dichloromethane (DCM) as solvent. This way, solutions of three different strengths were created: (i) strong – 8 glands per ml DCM, (ii) medium – 4 glands/ml or (iii) weak – 2 glands/ml DCM, henceforth referred to as 2, 4, and 8 gl/ml. Trails created using 10 μl of the 4-gland solution over 10 cm are the equivalent of a strong naturally formed trail (von Thienen et al., 2014). A DCM-only solution was used as control. All solutions were stored at −20°C and kept on ice during experiments. To reduce for evaporation, the vials were immediately closed after solution was taken out and the solutions were replaced after three sessions at most. The content of the solutions was unknown to the experimenter and also during video analysis (see below).

TABLE 1 | Number of ants and colonies tested in each experiment – colonies are in brackets.

Solution	Trail attraction	Experiment 1	Experiment 2	Experiment 3
2 gl/ml	366 (2)	22 (6)	16 (4)	–
4 gl/ml	178 (3)	22 (6)	–	233 (11)
8 gl/ml	254 (4)	23 (6)	16 (4)	–
DCM	198 (3)	24 (6)	14 (4)	237 (11)

Statistical Analysis Tools

All analyses were conducted in R version 3.6.3. Data handling and visualization were performed using the xlsx, dplyr, and ggplot2 packages (Dragulescu and Arendt, 2020; Wickham et al., 2020a,b). For statistical analyses, (generalized) linear mixed models were run using the glmmTMB package (Magnusson et al., 2020). All models were tested for fit using the DHARMa package (Hartig, 2020). Main effects were tested using the Anova command from the car package (Fox et al., 2020). To test performance against chance level of 50% and to conduct pairwise comparisons, we used the emmeans package (Lenth et al., 2020). For those comparisons, we provide the 95% confidence interval for the pairwise difference between levels for linear mixed models (where 0 corresponds to no difference), or the 95% confidence interval ratio for generalized linear mixed models (where 1 corresponds to no difference). In cases of simultaneous inference, *p*-value adjustments for multiple comparisons were conducted using the mvtnorm package (Genz et al., 2020). Please see the Electronic **Supplementary Material** (ESM) 1 for an analysis protocol covering all analysis steps with limited commentary and for a comprehensive list of package versions. All raw data used for analysis can be found in Electronic **Supplementary Material 2**.

Concentration-Dependent Pheromone Trail Attraction

We first assessed whether the pheromone solutions were perceived by ants, i.e., evoked following behavior. To this end, we measured the attraction of three different pheromone concentrations (2, 4, or 8 gl/ml, see above) against a solvent-only (DCM) solution, as well as DCM against itself.

Procedure

Ants were allowed onto a Y-maze (following Czaczkes, 2018, **Figure 1A**) via a drawbridge. One of the 10 cm long arms presented a disposable paper overlay with a trail of DCM created by applying 3 μl × 2μl of DCM with a glass microcapillary (Servoprax GmbH, Germany). On the other arm, the same amount of one of the 3 pheromone solutions was also applied on disposable paper. As control for potential biases of the setup, we also presented DCM on both arms of the Y-maze. The maze stem was covered with untreated paper. We then counted and removed all ants which crossed a line 9 cm inwards of either arm for 10 min. After the test, the ants were put back into the colony. Each solution was tested separately on both sides to control for side biases.

Analysis

To test whether applied pheromone extracts significantly affect ants' decisions in a Y-maze, we calculated a ratio of ants moving toward the arm with applied pheromone ($\frac{N \text{ ants chose pheromone}}{N \text{ total}}$). In the DCM only control, one DCM side was picked for the

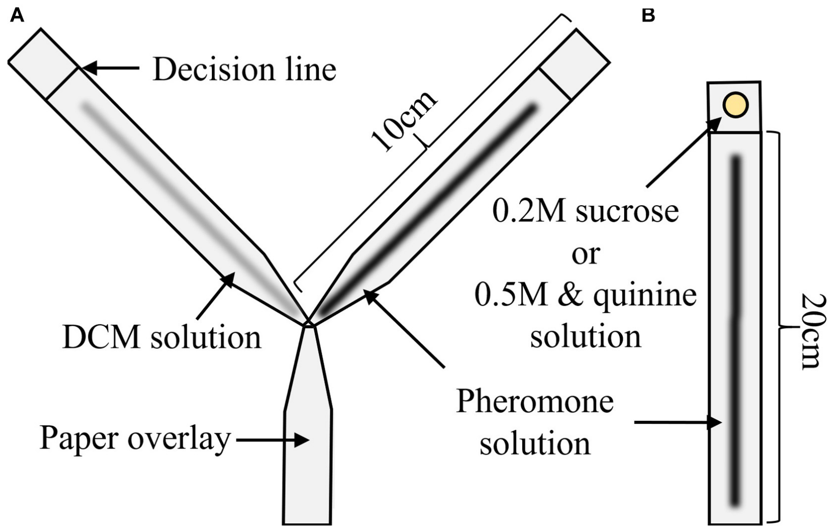

FIGURE 1 | Setups used during the experiments. **(A)** To assess pheromone attraction, ants had to decide between a 10 cm × 1 cm arm treated with DCM (here left, gray) or pheromone (here right, black). When ants reached the decision line, their decision was scored and they were there removed from the maze. **(B)** In experiments 1 and 2, ants crossed a runway treated either with pheromone (shown in black) or DCM (not shown) to reach a sucrose syrup drop at the end of a 20 cm × 1 cm long runway. In experiment 3, the setup was identical, but instead of a 0.2 M sucrose syrup, 0.5 M sucrose containing either 58.6 or 78.1 μM quinine was presented. Please note that the applied pheromone solutions were invisible once applied and are colored here for illustration purposes.

enumerator. We then ran a linear mixed model (LMM) with solution, side of pheromone application, and their interaction as independent variables. To account for colony variability, we also added colony as random intercept. The model formula was:

$$Ratio_{(Antschosepheromone)} \sim Solution_{(DCM,2,4,\ or\ 8\ gl/ml)} * Side\ of\ pheromone_{(left/right)} + random\ intercept_{(Colony)}.$$

Experiment 1 – Food Acceptance After 4 Days of Food Deprivation

Overview: in this experiment, ants had to cross a runway treated with either pheromone-DCM or DCM-only solutions established as above. At the end of the runway, a 0.2 M sucrose syrup droplet was presented (see **Figure 1B**). 0.2 M sucrose was used as it was shown to lead to lower overall food acceptance by ants (Wendt et al., 2019), which should be strengthened by the fact that colonies were fed with 1 M sucrose before starvation. Lower food acceptances should reduce overall acceptance levels, allowing us to identify any positive effects of pheromone on food acceptance.

Procedure

The setup consisted of a 20 cm long runway which was covered by a paper overlay marked with one of the 4 solutions containing different amounts of pheromone (see **Table 2**). A solution was applied on the 20 cm long paper overlays by drawing a line of 6 μl × 2 μl of solution over the whole 20 cm (see above for details).

One ant at a time was allowed onto the setup using a bridge to cross the runway and drink at the 0.2 M sucrose syrup while being recorded from above with a Panasonic DMC-FZ1000 camera. While the ant was drinking at the feeder platform, the paper overlay of the runway was carefully replaced with a fresh one without interrupting the ant. This was done to prevent the presence of pheromone solution from affecting the pheromone deposition of the ant on its way back. Pheromone depositions were counted on the 20 cm long runway to the nest. Pheromone deposition in *L. niger* is a stereotyped behavior and deposition events can be counted by eye (Beckers et al., 1993). After each experimental run, the investigated ants were freeze killed in order to prevent pseudo-replication. The setup was cleaned using ethanol after each experimental run. All data used for analysis, except for pheromone depositions, was extracted from the recorded videos using the free video analysis software Solomon Coder (Péter, 2018). The extracted variables are described in **Table 3**.

Analysis

All statistical models followed the same structure:

$$Dependent\ variable \sim Independent\ variable + random\ intercept_{(Colony)}.$$

All durations were log transformed to account for right-skewed distributions and analyzed using a Gaussian

TABLE 2 | Number of ants choosing a pheromone treated or DCM (control) treated arm of a Y-maze over 10 min.

Solution	Ants at pheromone	Ants at DCM	Ratio	Pheromone on left/total trials
DCM only	100	98	0.51	3/6
2 gl/ml	249	117	0.73	3/6
4 gl/ml	155	23	0.85	3/6
8 gl/ml	231	23	0.94	4/7

Note that in the DCM only treatment, DCM without pheromone was present on both sides, one of which is shown in the 'Ants at pheromone' column.

TABLE 3 | Overview of variables obtained from video analysis in experiments 1 and 2, with references supporting their link to perceived value.

Variable	Description	Support
Food acceptance	Scored 1 if ant touched sucrose drop and did not move for 3 s, otherwise scored 0	Detrain and Prieur, 2014; Oberhauser and Czaczkes, 2018; Wendt et al., 2019; Rossi et al., 2020
Duration of first drinking	Seconds spent until first drinking interruption	(Wendt and Czaczkes, 2020), also *a priori* due to its relationship with food acceptance.
Total drinking time	Seconds ant spent drinking overall	Josens et al., 1998; Detrain and Prieur, 2014; Wendt and Czaczkes, 2020
Drinking interruptions	Total number of drinking interruptions. Counted once the ant touched the sucrose drop again	Informal observations of more drinking interruptions for less-preferred food
U-turns to food, U-turns to nest	Number of U-turns followed by at least 2 cm walking in opposite direction. Turning back to the initial direction was not counted.	Informal observations of more U-turns when returning from less-preferred food
Duration to food	Seconds needed to traverse the 20 cm runway to the food	Ants run faster on pheromone-laden trails; an internal control for pheromone trail efficacy (Czaczkes et al., 2011).
Total time on setup	Seconds the ant spent on the setup (excluding bridge)	Informal observations of more time spent on setup for less-preferred food

(normal) error distribution, while count data (drinking interruptions, U-turns, and pheromone depositions) used a Poisson distribution or, if the model fit was poor, a negative binomial distribution (see Electronic **Supplementary Material 1** for details).

Video analysis provided us with multiple variables of potential interest, some of which might co-vary. We thus picked one variable – duration of first drinking event – *a priori* as the main focus of our analysis. In addition, we tested all relevant other variables separately in an explorative analysis. Picking one variable *a priori* as our focus was important to avoid multiple hypothesis testing. We picked duration the first of drinking event, as this is analogous to the well-established food acceptance score (Oberhauser and Czaczkes, 2018; Wendt et al., 2019), but due to being a continuous variable, should be more sensitive.

Experiment 2 – Food Acceptance After 2 Days of Food Deprivation

Due to the high food acceptance in experiment 1, we repeated the experiment after only 2 days of starvation. This was expected to lower the observed food acceptance (Oberhauser et al., 2018). Furthermore, only 3 solutions were used which covered the whole range used in this study: 2 gl/ml, 8 gl/ml, and DCM-only.

Procedure and Analysis

The procedure was the same as in experiment 1, except that the treated paper overlay was not exchanged while the ant was drinking, as pheromone depositions were not scored in experiment 2. The analysis was the same as in experiment 1.

Experiment 3 – Food Acceptance of Sucrose-Quinine Solution

Perceived food value in experiments 1 and 2 may have been so high as to be close to maximum. This may have resulted in a ceiling effect, preventing additional increases in perceived value due to pheromone trails. To counter this, we reduced food acceptability here by adding small amounts of quinine. We used the same setup and procedure as in experiments 1 and 2. However, instead of presenting a 0.2 M sucrose syrup, we instead used 0.5 M sucrose and decreased its attractiveness by adding quinine (Merck KGaA, Darmstadt, Germany). We piloted the ants' food acceptance on a serial dilution starting with a 10 mM quinine in 0.5 M sucrose solution and halving the quinine content in each step until we reached a food acceptance of around 50%, meaning that half of the ants interrupted drinking within the first 3 seconds. 50% acceptance was reached in step 8, which corresponded to a 78.1 μM quinine solution. Furthermore, we also added an 8.5 dilution to get closer to a food acceptance of ∼50%, which corresponded to a 58.6 μM quinine solution. We only tested ants on DCM-only and 4 gl/ml pheromone solutions.

Analysis

For the analysis, we included pheromone solution and quinine dilution as predictors as well as their interaction. As the response variable was binary (1/0), we used a binomial error distribution. The model was as follows:

$$Food\ acceptance_{(1or0)} \sim Solution_{(4\ gl/mlorDCM)} * Quinine\ dilution_{(58.6\ \mu Mor78.1\ \mu M)} + random\ intercept_{(Colony)}.$$

As there was no evidence of a pheromone solution effect (see section "Results"), we chose to forego the extensive video analysis necessary to extract the data needed for the other analyses performed in experiments 1 and 2.

RESULTS

Concentration-Dependent Pheromone Trail Attraction

An overview of the overall results can be found in **Table 2**. Pheromone was present on the left for 50% of trials (3 of 6) except for the 8 glands/ml condition (4 of 7) (see **Table 2** and Electronic **Supplementary Material 1**). The four solutions differed significantly in their attraction to ants ($\chi^2 = 75.79$, $p < 0.0001$). Neither the side of pheromone presence nor the interaction between concentration and side had a significant effect ($\chi^2 = 1.11$, $p = 0.29$; $\chi^2 = 3.76$, $p = 0.29$, respectively). All pheromone concentrations were chosen significantly more often than by chance alone (8 gl/ml: 94.4%, $p < 0.0001$, 4 gl/ml: 85.1%, $p < 0.0001$, 2 gl/ml: 73.4%, $p = 0.0001$), while ants chose randomly when only DCM was present (51.2%, $p = 0.99$).

Pairwise comparisons showed that all concentrations attracted significantly more ants than DCM [DCM vs. 2 gl/ml, 95% confidence interval of pairwise contrast difference (CI_{diff}) = 0.07–0.37, $p = 0.0042$; DCM vs. 4 gl/ml, (CI_{diff}) = 0.18–0.49, $p = 0.0001$; DCM vs. 8 gl/ml, CI_{diff} = 0.28–0.58, $p < 0.0001$, see Electronic **Supplementary Material 1**], while only the strongest and weakest pheromone concentrations differed significantly in their attraction (8 gl/ml vs. 2 gl/ml, CI_{diff} = 0.06–0.36, $p = 0.005$).

Experiment 1 – Food Acceptance After 4 Days of Food Deprivation

In total, 91 ants from 6 colonies were tested. *Duration to food* was significantly different between solutions ($\chi^2 = 32.34$, $p < 0.0001$), with all pheromone solutions leading to significantly shorter time spent on the runway than the control DCM-only solution [DCM vs. 2 gl/ml, 95% confidence interval of pairwise contrast ratio (CI_{ratio}) = 0.55–0.83, $p < 0.0001$; DCM vs. 4 gl/ml, CI_{ratio} = 0.58–0.88, $p = 0.0006$; DCM vs. 8 gl/ml, CI_{ratio} = 0.54–0.81]. The number of *U-turns on the way to the food* did not differ between treatments ($\chi^2 = 4.18$, $p = 0.24$). These measures are taken before the food is encountered, and so do not reflect perceived value of the food source.

Ants had a very high food acceptance, with only one ant interrupting drinking within the first 3 s. However, pheromone deposition was very low, with only 10 ants depositing pheromone on the way back. Thus, those two variables were not used for analysis.

The *duration of the first drinking event* did not reveal any significant effect of pheromone ($\chi^2 = 0.39$, $p = 0.94$, see **Figure 2A**). Similarly, *total drinking time* and *total time on setup* also did not differ significantly among solutions ($\chi^2 = 3.08$, $p = 0.38$; $\chi^2 = 5.23$, $p = 0.15$, respectively, **Figures 2B,E**).

Furthermore, the *number of interruptions* differed significantly between the solutions ($\chi^2 = 14.73$, $p = 0.0021$, **Figure 2C**). Pairwise analysis revealed significantly more interruptions in the highest pheromone concentration (8 gl/ml) than the DCM-only control (CI_{ratio} = 1.04–1.82, $p = 0.0186$), while the other two pheromone solutions did not differ significantly from DCM (2 gl/ml vs. DCM, CI_{ratio} = 0.65–1.22, $p = 0.73$; 4 gl/ml vs. DCM, CI_{ratio} = 0.86–1.55, $p = 0.48$). The number of U-turns on the way back to the nest did not differ significantly from DCM ($\chi^2 = 4.51$, $p = 0.21$, **Figure 2D**).

Experiment 2 – Food Acceptance After 2 Days of Food Deprivation

In total, 46 ants from 6 colonies were tested. Surprisingly, the *duration to food* showed no difference between solutions ($\chi^2 = 2.56$, $p = 0.28$). The number of U-turns to the food differed significantly ($\chi^2 = 6.69$, $p = 0.0352$). This difference was caused by significantly more U-turns in the presence of the highest pheromone concentration compared to DCM (8 gl/ml vs. DCM, CI_{ratio} = 1.04–5.15, $p = 0.0381$; 2 gl/ml vs. DCM, CI_{ratio} = 0.58–3.31, $p = 0.57$).

Ants again had a very high food acceptance, with only three ants not accepting the food. As in experiment 1, the *duration of the first drinking event* did not reveal any significant effect of pheromone ($\chi^2 = 1.22$, $p = 0.54$). This was also the case for the *total drinking time* ($\chi^2 = 4.22$, $p = 0.12$) and *total time spent at setup* ($\chi^2 = 0.52$, $p = 0.77$). Unlike in experiment 1, the number of interruptions did not differ significantly between the solutions ($\chi^2 = 1.79$, $p = 0.41$). The number of *U-turns* to the nest also showed no difference between solutions ($\chi^2 = 3.1$, $p = 0.21$).

Experiment 3 – Food Acceptance of Sucrose-Quinine Solution

In total, 470 ants from 11 colonies were tested. No difference in food acceptance was found between the 4 gl/ml and DCM-only solutions ($\chi^2 = 0.3$, $p = 0.59$, see **Figure 3**). The lower quinine concentration (58.6 μM), unsurprisingly, had significantly higher acceptance ($\chi^2 = 9.81$, $p = 0.0017$).

DISCUSSION

Over a series of experiments we tested whether the presence of social information, in the form of pheromone trails advertising high-value food, influences perceived value in an ant. However, although there was a good reason to expect such an effect (see section "Introduction"), we found no evidence for such a value-distortion effect and conclude that pheromone trail presence does not distort value perception in *L. niger*. We base this conclusion primarily on two lines of evidence which we defined *a priori* as our main variables of interest: Lack of increase in first drinking event length (experiments 1 and 2, **Figure 2A**), and lack of change in acceptance rates (experiment 3, **Figure 3**), both variables which correlate with perceived value (see **Table 3**). However, other factors which are expected to correlate with perceived value, but were analyzed only in an explorative manner, also showed no effect. These include duration of time spent feeding (**Figure 2B**) and total time spent on the setup (**Figure 2E**). However, the pheromone trails we created were clearly biologically active: ants followed them in a dose-dependent manner and showed some evidence of running faster on pheromone trails in experiment 1, but not in experiment 2. While the artificial trails used lacks some aspects of a naturally laid trail (the dotted two-dimensional structure, concurrent cuticular hydrocarbons), we believe that it mimics real trails well enough for us to make strong conclusions.

Nonetheless, one comparison returned significant effects: in experiment 1 (but not experiment 2), we found significantly more feeding interruptions in the 8 gland/ml treatment as compared to DCM-only controls. Taken at face value, this result would suggest that extremely high levels of trail pheromone may be aversive. However, the lack of concurrence between the almost identical experiments 1 and 2, the small difference, and the broad confidence intervals of the estimates, leads us to place little weight on this finding – especially given that these effects are only present at the highest pheromone trail strength. More critically, the vast majority of the evidence implies no effect. This includes the very highly powered experiment 3 ($n = 470$), which showed

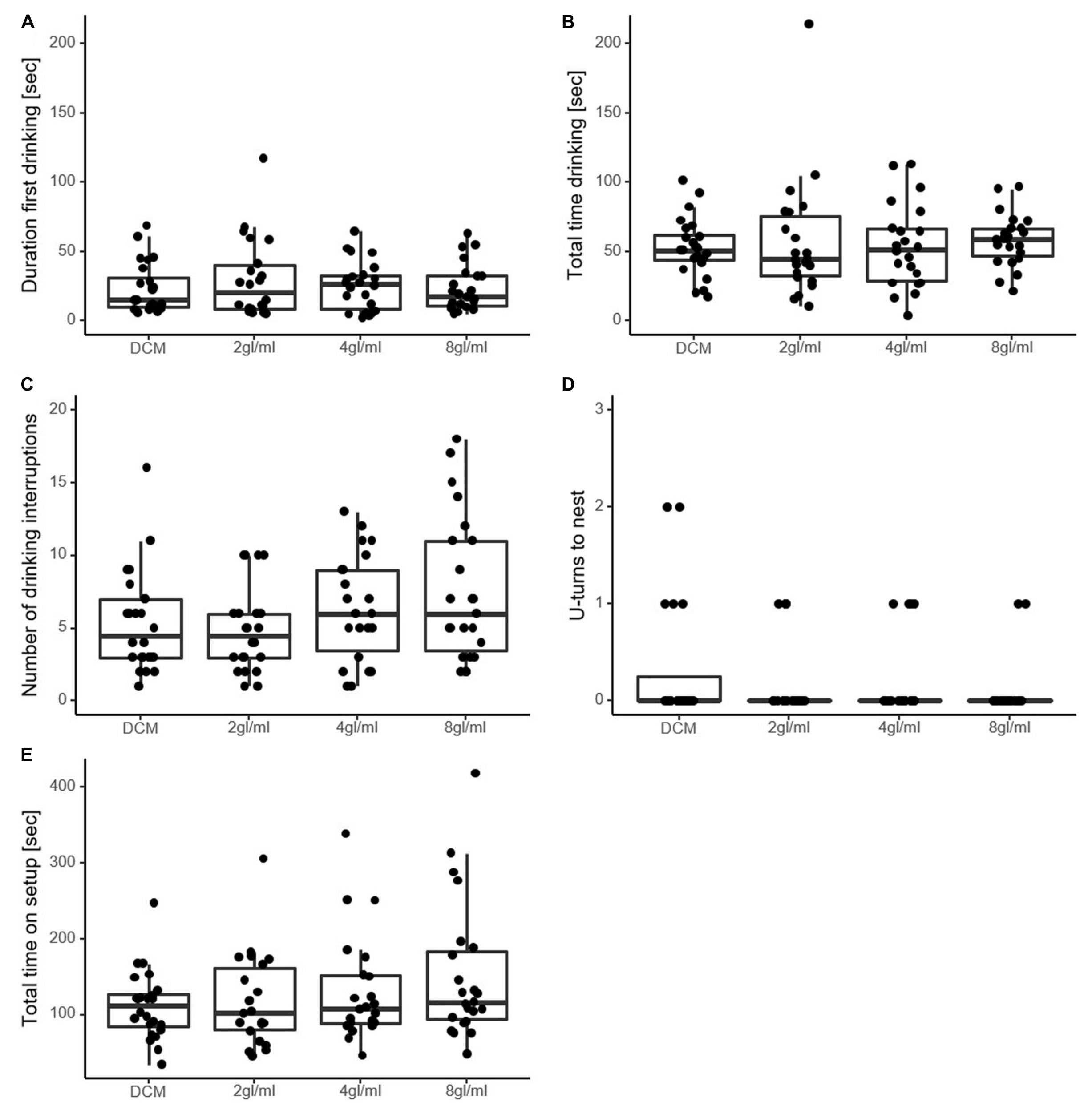

FIGURE 2 | Measures of perceived food value in experiment 1. **(A)** Seconds ants spent drinking until they first moved away from the sucrose drop. **(B)** Seconds spent drinking in total. **(C)** Number of drinking interruptions over the course of the trial. **(D)** Number of U-turns made by the ant on the way back to the nest. Was only counted when ants moved at least 2 cm in an opposite direction. The majority of ants did not perform U-turns. **(E)** Seconds the ants spent on the setup in total. Note that none of the variables differed significantly between the solutions, except in **(C)**, where 8 gl/ml is significantly higher than DCM. DCM, dichloromethane solvent; Xgl/ml, x pheromone glands per milliliter DCM.

very good sensitivity to small changes in aversive substance, but no evidence of value distortion due to pheromone presence. In addition, a separate study (Oberhauser et al., in preparation) also showed no value distortion effects of pheromone, using identical associative learning methods to those that have been used successfully to detect many such effects in the same species (Czaczkes et al., 2018; De Agrò et al., 2019, 2020; Wendt et al., 2019, 2020; Wendt and Czaczkes, 2020). Thus, while completely proving a lack of effect is not possible, we are nonetheless quite confident that pheromone trail presence does not influence perceived value in *L. niger*.

In drawing this conclusion, we are making the assumption that any value-distorting effect would be linear, in that we only tested trails equivalent to a well-established trail (4 glands per ml), half that strength, and double that strength (von Thienen et al., 2014). We chose strong trails in order to detect even very weak effects, if they exist. However, it is theoretically possible that such value distortion effects would exist for very weak pheromone trails, but

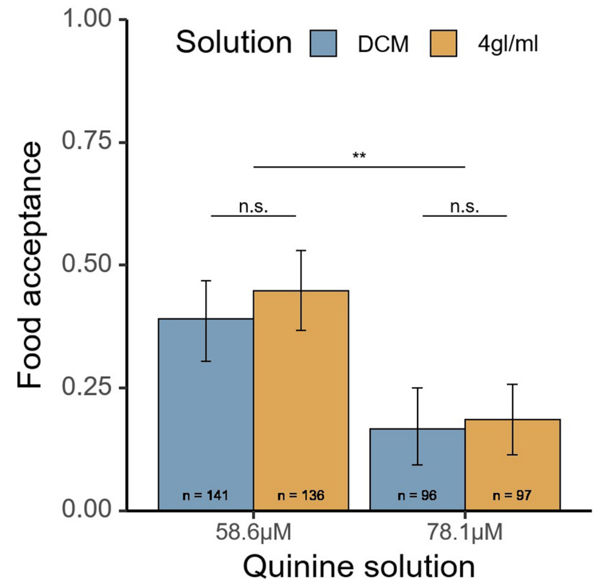

FIGURE 3 | Food acceptance of the quinine solution in experiment 3 after passing a runway treated with pheromone (4 gl/ml) or DCM solvent (DCM). Food acceptance of 1 would correspond to uninterrupted drinking in the first 3 s. Quinine solution corresponds to XμM of quinine in 0.5 M sucrose syrup. 4 gl/ml, 4 pheromone glands per milliliter DCM. $^{**}p < 0.01$; n.s., not significant.

disappear again at strong but natural levels. We can conceive of no convincing biological explanation for why this should be the case, and so remain confident about the lack of effect we describe.

We originally hypothesized that conformism would be seen in ants, whereby social information suggesting a high-value resource (a strong pheromone trail) would increase the perceived value of this resource, since such effects are strong in humans (Cohen and Golden, 1972; Bone, 1995; Shi et al., 2016; Jayles et al., 2017), as long as the difference between the social ratings and the absolute value of the product is small. Recent research has found many parallels between value perception in humans and insects (Shafir et al., 2002; Sasaki and Pratt, 2011; Tan et al., 2015; Czaczkes et al., 2018; Oberhauser and Czaczkes, 2018; Wendt et al., 2019), even resulting in irrational behavior, suggesting that a further parallel was likely. Reliance on social information to make valuation decisions is common in animals (Kendal et al., 2004; Danchin et al., 2018; Otake and Dobata, 2018), especially when no other useful information sources are available. Studies on honeybees report that alarm and Nasanov (attractive) pheromones can modulate the response to positive and aversive stimuli (Baracchi et al., 2017, 2020; Rossi et al., 2018).

Importantly, a study conducted in parallel to our own (Rossi et al., 2020) found just such an effect when studying the Argentine ant *Linepithema humile*. This study found that Argentine ants pre-exposed to artificial pheromone trails showed higher food acceptance for a range of sucrose solution concentrations, although they found no effect on feeding duration. While the methodologies differed (pre-exposure was away from the feeding context, and artificial pheromone trails were used which may be much stronger than naturally formed trails), we believe the reason for the different findings is the species used. The contrast between our results and those reported by Rossi et al. (2020) mirrors a similar contrast between the two species in pheromone use: when making navigational decision, *L. niger* relies much more strongly on private information (route memory) than pheromone trail information, when the two conflict (Aron et al., 1993; Grüter et al., 2011; von Thienen et al., 2016). By contrast, *Li. humile* relies more strongly on pheromone information, and follows that preferentially when it conflicts with route memory (von Thienen et al., 2016). It is interesting that this differential reliance on social information extends beyond navigation into subjective resource evaluation. However, honeybees tend, like *L. niger*, to ignore social information if it conflicts with private information (Grüter et al., 2008), and yet show robust modulation of subjective reward or punishment evaluation due to social information (Baracchi et al., 2017, 2020; Rossi et al., 2018).

Most demonstrations of parallels between human and animal behavior have generally been in the context of individual decision-making. *L. niger* make coordinated collective decisions, based on the evaluations of individuals. Conformism in resource evaluation during collective decision-making would likely be detrimental, as it reduces the number of independent evaluations available, and thus the accuracy of collective decisions (Pratt and Sasaki, 2018). Indeed, it is precisely independent evaluation of resources which allows collective decision-making by insects to side-step individual-level cognitive biases, and enables rational collective decision-making to emerge from decisions by individuals that fall prey to cognitive fallacies (Sasaki and Pratt, 2011; Sasaki et al., 2018, 2020). One exception may be in the formation of quorums during collective decision-making, where evaluation conformism would result in positive feedback, and potentially speed up quorum formation for suitable options (Bose et al., 2017; Marshall et al., 2019). From the results of Rossi et al. (2020), we predict that more conformist Argentine ants will be more likely to make irrational collective decisions than *L. niger*, which in turn will be more likely to make irrational collective decisions than the *Temnothorax* ants studied by Sasaki and Pratt (2011) and Sasaki et al. (2020).

More broadly, during resource evaluation where the attributes of the resource are clear, there is little benefit to using social information. Social information becomes valuable when gaining high-quality personal information is costly, or when it is not available (Danchin et al., 2004; Kendal et al., 2005, 2009). As the ant has already paid any costs associated with gaining personal information, there would seem to be no additional reason to attend to social information which give less reliable readings of the same resource attributes. It is possible that Argentine ants respond positively to such social information in order to build in an addition positive feedback loop, accelerating collective decision-making as the cost of increased inflexibility. Alternatively, modulating subjective evaluation due to (potentially irrelevant) social information may be a pleiotropic effect which is not repressed in some species.

Evaluation seems to be unaffected by social information signaling resource value. However, pheromone deposition is: *L. niger* ants deposit less pheromone when encountering nestmates on trails (Czaczkes et al., 2013b), at food sources (Wendt et al., 2020), and on pheromone-marked paths (Czaczkes et al., 2013a, 2016). This implies that ants can disentangle their evaluation of a resource from their recruitment to it: ants can lower pheromone deposition when encountering many other foragers, or on paths with pheromone trails, without changing their evaluation of the food they are returning to. This may allow them to make more accurate foraging decisions in the future. For example, ants modify their perceived value of a food source after being offered substantially better (or worse) food from nestmates (Wendt et al., 2019), and may use this information to decide whether to continue exploiting a known food location or try a new one (Czaczkes et al., 2019).

While pheromone trails (social signals) do not influence the perceived value of a food source for *L. niger*, nestmate presence at the food source, a social cue, does seem to have such an effect: Ants prefer to forage on otherwise identical food sources which are not accompanied by nestmate presence (Wendt et al., 2020). These results seem inconsistent. We interpret these differences as arising from the very different temporal nature of the information. Pheromone trails are long lasting – a strong *L. niger* trail is detectable by ants after at least 8 h (Evison et al., 2008). They thus can become outdated, providing false exploitation-level information if exploitation level changes – for example due to a brief spell of inclement weather. Ant colonies can become 'trapped' by outdated pheromone trail information (Beckers et al., 1990; Latty and Beekman, 2013). By contrast, nestmate encounters provide an instantaneous reading of exploitation level. Ants may thus do well to attend to the instantaneous information when making foraging choices, but may ignore the possibly outdated pheromone information. This is especially likely as, in the current experiment, the ants were tested alone, so had first-hand information that the resource was underexploited, and that the pheromone information did not match current foraging conditions.

In conclusion, we found no effect of pheromone trail presence on the perceived value of a food source. This is in contrast to results reported in other ant species (Rossi et al., 2020), honeybees (Baracchi et al., 2017, 2020; Rossi et al., 2018), and even a moth (Hostachy et al., 2019). Why some animals in some situations are influenced by social information, when other animals in the same situation or the same animal in a different situation are not, is a major question which remains to be tackled.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

FO, SW, and TC conceived the experiments. FO conducted the experiments and analyzed and visualized the data. All authors wrote the first draft, revised and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.555576/full#supplementary-material

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CONCEPTUAL ANALYSIS
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Minimal Organizational Requirements for the Ascription of Animal Personality to Social Groups

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Recently, psychological phenomena have been expanded to new domains, crisscrossing boundaries of organizational levels, with the emergence of areas such as social personality and ecosystem learning. In this contribution, we analyze the ascription of an individual-based concept (personality) to the social level. Although justified boundary crossings can boost new approaches and applications, the indiscriminate misuse of concepts refrains the growth of scientific areas. The concept of social personality is based mainly on the detection of repeated group differences across a population, in a direct transposition of personality concepts from the individual to the social level. We show that this direct transposition is problematic for avowing the nonsensical ascription of personality even to simple electronic devices. To go beyond a metaphoric use of social personality, we apply the organizational approach to a review of social insect communication networks. Our conceptual analysis shows that socially self-organized systems, such as isolated ant trails and bee's recruitment groups, are too simple to have social personality. The situation is more nuanced when measuring the collective choice between nest sites or foraging patches: some species show positive and negative feedbacks between two or more self-organized social structures so that these co-dependent structures are inter-related by second-order, social information systems, complying with a formal requirement for having social personality: the social closure of constraints. Other requirements include the decoupling between individual and social dynamics, and the self-regulation of collective decision processes. Social personality results to be sometimes a metaphorical transposition of a psychological concept to a social phenomenon. The application of this organizational approach to cases of learning ecosystems, or evolutionary learning, could help to ground theoretically the ascription of psychological properties to levels of analysis beyond the individual, up to meta-populations or ecological communities.

Keywords: personality, organizational approach, social insects, group behavior, information, social minds

INTRODUCTION

Do social animals constitute a new entity, a superorganism? If they do, this potentially independent new layer of organization could have a psychology of its own. This new social layer could then implement new social learning algorithms, potentially apart from the learning capacity of single bees or ants or any other social animal (Sasaki and Pratt, 2011). If this putative social psychology proves to be an emergent property in the hard sense, this new organizational level could have a personality of its own, even one that is different from the personality of the constituent individuals. Indeed, recent studies have evaluated at these upper organizational levels, from colonies to ecosystems, the onset of psychological phenomena that were originally described at the level of the individual, such as personality (Planas-Sitja et al., 2015), or learning (Power et al., 2015).

Before discussing the existence of these upper level, socio-psychological phenomena, such as social personality, one should be clear about what is precisely the lower-level phenomena, in this case, individual personality. Animal personality is defined as inter-individual differences in behavior that remain similarly different throughout repeated measurements performed in the same population (Carter et al., 2013). On the basis of this operational definition, personality has been attributed to highly unusual organisms such as anemones (Briffa and Greenaway, 2011) or even bacteria (Davidson and Surette, 2008). But operational definitions only specify, partially and temporarily, which kinds of operations count as empirical indicators for the referents of their concepts; they are temporarily in place of a concept that is the actual objective of the investigation, and they presuppose an underlying common cause for the measurements, without investigating the specific nature of the phenomena at stake (Feest, 2005), a situation that can potentially lead to puzzling outcomes, particularly when if this presupposition is violated. To evaluate more closely why the uncritical use of this simple operational definition of personality can be misleading, we propose a thought experiment.

Take the Homeostat, a simple electronic artifact basically constituted of four coupled control units (akin to batteries), a system that stabilizes the effects of any external disturbances introduced into it (Ashby, 1960). While a range of disturbances (inputs) to the Homeostat would result in the system returning to its stable configuration at a certain pace, Homeostats with slightly different initial configurations would return to stability at different paces, and this "inter-individual" difference in the pace to recovery would be stable and repeatable (Ashby, 1960). Stable and repeatable differences in the output (behavior) of individuals is the very operational definition of personality. Thus our thought experiment resulted in a puzzling outcome, i.e., the ascription of personality to a simple electronic artifact built in the 1960s. This rather absurd result emphasizes the difficulties that arise from the uncritical use of operational definitions.

While the use of simple operational definitions is certainly valuable when there is an agreement that the systems under analysis share basic organizational principles, like individual ants, bees, or spiders, the same should not necessarily hold when analyzing simultaneously systems at upper other levels of organization. Social organization does not need to mimic, and is not implied by, individual organization, and thus from the fact that a biological individual has personality (a lower level, intraindividual organization) it does not follow that a society or group of such individuals also should have a personality (at an upper level, social personality organization) of its own. Upper and lower levels of organization could adhere to distinct organizing principles, and if that is the case, operational definitions will not suffice. Thus, if we are investigating the presence of personality (or any other psychological phenomena) in upper-level biological systems, such as colonies, populations or ecosystems, the use of operational definitions could lead to unreliable outcomes, such as the one obtained above, in our Homeostat thought experiment.

A complete ontology of personality as a phenomenon is out of the scope of the present contribution, but it remains clear that personality is connected to basic defensive and approach information systems, in a general model of behavioral regulation (Corr, 2008, 2010). The regulation of behavioral action over the environment is a requirement for minimal autonomous agency (Moreno, 2018), and personality would be a particular and individualized way of regulating behavioral expression. Thus, a minimal definition of personality would consider it as a particular, individualized way of sensing and processing information, while stable behavioral outputs, repeatable across contexts, would be the outcome of personalities. This simple step allows a closer circumscription of the phenomena. If personality is a particular, individualized way to sense and process information, one could measure the information processing organization not only indirectly (through behavior), but also directly, evaluating the functioning of the circuitry underlying individualized behavioral control (Neubauer and Fink, 2010). This small definitional step in the direction of an ontology of personality suffices for our needs in the present study because, if personality is a particular and stable way to sense and process information, then social personality would also require a particular, underlying, stable organization, now at the social level, devoted for social information sensing and processing.

This definitional step leads to the discussion of the minimal requirements for autonomy in an organization devoted to information processing, and here we take advantage of the organizational approach in philosophy of biology to formalize these minimal requirements. For example, the organizational approach establishes the requirement of a regulatory feedback system that computes over the various subsystems, performing second-order closure of constraints (e.g., Moreno and Mossio, 2015).

Therefore, in this paper, we aim to analyze the adequacy of the application of social psychology terms to colonies, with the aid of Moreno and Mossio (2015) organizational approach to minimal autonomous agency, and using social insects as a case study. We will focus particularly on specific, well studied case systems of social insect behavior, case systems which provide enough detail for us to perform this organizational analysis. As a consequence, our analysis will apply to social insects in general only insofar as the behaviors (for example, foraging recruitment, house hunting) herein developed share general features across taxa systems. Throughout the paper we use the concept of social cognition as an emergent phenomena not reducible to individual cognition, one that is fundamentally based on the interactions between individuals, on participatory capabilities (De Jaegher et al., 2010).

To perform our analysis, we will start presenting an overview of the uses of social personality concepts in the literature. We will highlight the generalized ample use of an operational definition of animal social personality, and point to the need for a better understanding of its ontology, so as to adequately apply the concept of individual personality to a new, social level of organization. We will then summarize the use of social information networks in exemplar cases of social insects, searching for this new autonomous level of social organization. From that, we will present Moreno and Mossio (2015)'s organizational approach and the minimal requirements for the realization of cognition in autonomous systems. We shall move on then to the application of this organizational approach to examples of social insect colonies, analyzing the occurrence of social cognition on those systems. We end up concluding that socially self-organized systems, such as ant trails, or bee's recruitment groups, are too simple to have social personality. We briefly extend our conclusions to discuss other similar cases, such as ascriptions of learning for whole ecosystems.

INDIVIDUAL AND SOCIAL PERSONALITY

Until a couple of decades ago, most of the behavioral differences among individuals of the same species were considered only slight variations due to plasticity or noise that could be dismissed in behavioral studies (Japyassú and Malange, 2014). Exceptions were the behavioral variation in different castes in social insects (e.g., Wilson, 1971) and the discrete alternative behavioral strategies in a few species (Gross, 1996; Widemo, 1998). The identification of consistent behavioral differences between individuals across contexts and/or time in a number of species resulted in the field of animal personality. In this field, inter-individual variation is recognized as a different source of behavioral variation that not only can be selected for, it can also persist and be transmitted through generations (Dingemanse and Réale, 2013).

Animal personality has been studied in invertebrates and vertebrates, in wild and domestic animals, with important ecological and evolutionary implications. An example of significant evolutionary implications of personalities is the effect of correlated behaviors in the evolution of a phenotypic trait (Sih et al., 2004). Considering that different behaviors are connected through the same personality type, they evolve as a package even when under contrasting selective pressures. Personality acts as a constraint for selection (Lynch and Walsh, 1998) and can result in apparently suboptimal characters (Dingemanse and Réale, 2013).

There are many factors thought to affect the evolution and maintenance of animal personality. They include genetic differences between individuals (e.g., van Oers et al., 2005), as well as physiological constraints that can change during the lifetime of an individual. Also, individuals' experiences and environmental factors are extremely important. Specifically, social behavior seems to play an important part in the development of animal personality. The frequent interactions between individuals facilitate behavioral consistency and personality diversification in the colony, reducing the conflicts amongst its members (Bergmüller and Taborsky, 2010).

More recently, this concept is being applied to groups. From studies that identify consistent collective behavior in some species, colonies as a whole are considered to have personalities (for a recent review, see Wright et al., 2019). This is a result of the understanding that a colony is a reproductive unit and will be selected as a different level of organization (Jandt et al., 2014), developing their own behavioral characteristics. The definition of group personality is the same as the definition of individual personality (consistent behavioral differences across contexts and/or time), only that measured using characteristics of the collective, and not individual behavior (Wray et al., 2011; Scharf et al., 2012; Bengston and Dornhaus, 2014; Bengston and Jandt, 2014; Jandt et al., 2014; Blight et al., 2016; Jandt and Gordon, 2016; Pasquier and Grüter, 2016; Marting et al., 2018; Wright et al., 2019).

Similar to individual personality, group personality seems to be affected by factors such as genetics, physiology, and environment, but in the case of group personality, these factors are measured at the group level (Wright et al., 2019). This application is also possible because cohesive social groups can be taken as individuals, as in the case of social insects' super organisms (Holldobler and Wilson, 2009).

Since collective personality requires collective behavior, it is important to understand how authors differentiate collective behavior from individual behavior. Collective behavior is considered to be an emergent property of the behavior of individual workers (Camazine et al., 2001; O'Donnell and Bulova, 2007; Sumpter, 2010). However, most collective personality studies do not explain the mechanisms involved in the behavior being tested, so that the ascription of collectivity is given by the nature of the test. If the test measures a collective outcome, such as colony defensive behavior, nest repair (Wray et al., 2011) or exploratory activity (Blight et al., 2016), the behavior would be considered collective. Here, one possible problem with these approaches it that collective behavior or decision can sometimes derive basically from individual behavior or decision (Huebner, 2013; Feinerman and Korman, 2017), and in these cases we would expect individual personalities to determine collective personality. When that is the case, the collective outcome could be explained merely by individual behavior; moreover, there would be no autonomous organization (in the sense of Mossio and Moreno, 2010; Moreno and Mossio, 2015) at the social level. In the absence of social autonomy there would be no reason to measure personality at both the lower (individual) and the upper (social) level, since one level predicts the other. One interesting example is the work of Jolles et al. (2017), that explains fish collective behavior through variations of two axes of individual personality (sociability and exploration).

Their mechanistic model, based on individual personality traits, predicts the structure of the group, leadership and group foraging behavior.

Our review agrees with previous reviews (Jandt et al., 2014; Wright et al., 2019) showing the prevalence of a pragmatic, essentially operational definition of social personality, one that is based on the repeatability of (group) behavioral scores across contexts and time. Operational definitions describe how to identify the phenomena in the object of study, instead of defining exactly what personality really is. In other words, they tend to be much more descriptive (pointing to what there is), instead of proposing a concept or a theory, from a more prescriptive point of view. This is the reason why it is possible to apply an (operational) definition of personality to objects to which we would not intuitively ascribe personality, such as the Homeostat electronic artifact (Ashby, 1960, see section "Introduction"). This is another possible problem of directly upgrading to the social level operational definitions of personality that were conceived at the individual level: the scope of validity of the concept (for instance, evaluating the consequences of applying it to limiting cases) should be critically examined before the upgrading. This is definitely something that needs further investigation and clarification, a work appropriate for a conceptual—both scientific and philosophical—analysis.

In human studies, personality requires a coordinated and consistent response to environmental challenges. Accordingly, we would expect a minimum form of integration in the animal groups to be able to apply this concept at the social level of organization. Unfortunately, it is not clear, in most personality studies, if there is any mechanism that would be responsible for this integration, such as information sharing, or if the same results would obtain if each individual was acting independently, without social coordination.

In this paper, we aim to highlight one important characteristic that justifies the application of this concept to a group: there is a new level of organization and because of that, a new selective pressure. One way to identify this organization is through the flow of information within the system resulting in an autonomous social entity. In the next section, we summarize the use of social information networks in exemplar cases of social insects. Then, we will present an organizational approach to autonomous agency that can help us analyze the use of the concept of individual personality at the colony level.

INFORMATION NETWORKS WITHIN SOCIAL INSECTS

Social insects are model animals in the study of social behavior, and communication pervades the organization of the colony, regulating relevant social tasks, from the recruitment of foragers (Dornhaus et al., 2003; Thom et al., 2007), to the selection of novel nest sites, or the organization of internal tasks within the colony (Seeley et al., 2012). It seems clear that there are information flows within the colony (Alem et al., 2016; Reznikova, 2017), and communication seems to be so central to social insect organization that the experimental disruption of relevant communication channels can even revert a social species to a solitary way of life (Yan et al., 2017).

Information flow can rely on diverse communication mechanisms such as physical interaction, pheromone use, auditory calling, vibrational signals, and trophallaxis. While some signals are unconditionally amplified by all receivers (i.e., signal transmission without social modulation), resulting in strong and almost instantaneous responses at the level of the colony, such as scent alarm triggering escape responses in ants (Jeanson and Deneubourg, 2009), most colony tasks are socially modulated at various degrees. As one example, an ant from a group that is collectively transporting a large food item may lose contact with the scent trail during the task; to avoid losing the correct direction, the group decides based on the transient amplification of individual-based knowledge: individuals who do not know where to push the load, follow the others, while those who know push in the right direction (Gelblum et al., 2015). There are various ways for social interactions to result in collective decisions, some relying heavily on individual decisions, with no social modulation, and others with varying levels of social modulation, up to the point that some decisions are only available at the group level, including emergent collective cognition, for example, during nest construction (Feinerman and Korman, 2017).

Here we will summarize a few of the best-studied signaling systems in social insects, focusing on two exemplar case systems: the collective choice of new nest sites (house hunting) and the collective choice of new foraging patches. Considering the huge diversity of social systems within either ants (Heinze et al., 2017; Reznikova, 2020) or bees (Wcislo and Fewell, 2017), our narrow focus here is to be taken as a first exploration in the application of organizational principles to the nascent field of animal social personality. Thus, our conclusions will generalize to social insects only insofar as the systems herein developed share relevant properties across social insects' organizations, such as the reliance on social signaling and the formation of self-organized social structures.

Collective House Hunting

House hunting has been well studied in ants of the genus *Temnothorax* and in the honeybee *Apis mellifera* (Marshall et al., 2009; Sasaki and Pratt, 2018). Ant scouts recruit others to a new nest by tandem running, slowly guiding the novice to the new site (Franks and Richardson, 2006), and the poorer is the new nest site, the longer they pause before recruiting new novices, resulting in lower rates of recruitment for the poorest sites (Mallon et al., 2001). Ants do not usually rely on scouts that have visited multiple candidate sites; instead, they rely on the competition between alternative recruitment groups. Colonies show a preference for adequately sized cavities with small entrances and low interior light levels, choosing in a few hours the best option available (Franks et al., 2003). When the number of scouts tandem running for one site reaches a threshold they switch to a faster recruitment strategy, transporting directly novice scouts instead of slowly guiding them to the new site (Franks et al., 2002). This new recruitment strategy boosts the favored option, that soon becomes the dominant option.

For honeybee swarms, the process is partially similar to the ant's house searching algorithm, but the algorithm is implemented with different mechanisms. Instead of tandem runs, bees recruit novices with a waggle dance indicating quality, direction, and distance of the candidate nest site. Some scouts cease dancing, while others switch their allegiance to other candidate nest sites (Camazine et al., 1999; Seeley and Buhrman, 1999, 2001; Visscher and Camazine, 1999). Finally, and contrasting to the ant procedure, bees include not only positive, but also negative feedback loops in the search algorithm, performing stop signals against rival nest sites, and thus increasing the reliability of the decision process (Seeley et al., 2012). The colony-level decision results mainly from scouts spontaneously stopping to dance for less favorable sites, and from stop signals against competing sites, resulting in more new scouts being recruited to the best site. Eventually, a consensus is reached, with all recruits dancing to one single option, and leading the swarm to take off to the new site.

Collective Choice of Foraging Patches

One of the largely studied social decision mechanisms in ants is mass recruitment (Kolay et al., 2020; Reznikova, 2020). The decision between alternative foraging patches in mass recruitment results from the conditional amplification of individual scent signals during mass recruitment: the first finder marks the trail with pheromone in her way back to the nest, thus recruiting others to the foraging patch, but in many species, the recruited foragers also strengthen the first trail markings only in their way back to the nest, i.e., after evaluating by themselves the foraging patch (Beckers et al., 1992a; Mailleux et al., 2003). When there are alternative simultaneous trails, the differential amplification of one of the alternatives eventually leads to one single lasting trail. This differential amplification can occur either by the recruitment of a larger number of scent marking scouts, as a result of strongly marked trails eliciting disproportionately stronger responses than weakly marked trails (Sumpter and Beekman, 2003), or by each scout marking the preferred route with higher pheromone concentrations (Jaffe and Howse, 1979; Beckers et al., 1992b). Direct contact between recruiters informs about the food type (Le Breton and Fourcassié, 2004) and appear to convey information about the location of food sources (Reznikova and Ryabko, 2011), thus potentially informing the choice among trails. Down regulation of a trail occurs when recruits reduce pheromone deposition (Czaczkes et al., 2013) or use a no-entry pheromone over a trail (Robinson et al., 2005). Now for *Apis mellifera*, the distance from the food source to the hive is an important parameter in the dance signaling system: round dances inform about nearby, while the waggle dances inform about more distant resources. In any case, bees only dance after returning from highly profitable resources, and the nature and quality of these resources are informed directly through the floral scents stuck in the recruiter's body and through regurgitating resources at the dance floor. The cognitive feats of an individual dancer include, among others, measuring the hive-resource distance through the optic flow in the journey back to the hive, evaluating (from the hive) the angle from the resource to the sun through polarized light, changing the coordinate system of this celestial angle to the vertical plane of the hive comb, and transducing the optical flow distance to the duration of the waggle run (Holldobler and Wilson, 2009). The success of the recruitment for a foraging patch increases with the dance floor vibration intensity (Sandeman et al., 1996), and with the frequency of the shaking signal: the worker climbs and shakes successive nestmates, thus bringing new workers to the dance floor (Seeley, 1995). Recruitment decreases with the frequency of multi-functional stop signals (Kirchner, 1993). Stop signals also promote cross-inhibition between competing foraging patches (Seeley et al., 2012) and increase the number of bees retrieving the food resources from the dance floor to the interior of the colony (Thom et al., 2003). Retrieving food from the dance floor to the interior of the colony can also be increased by the tremble dance signal (Seeley, 1995), whereby the signaler wanders irregularly about the combs shaking their bodies with their front legs held overhead, recruiting passing bees to nectar processing.

The Organizational Approach to Autonomous Behavior

Since we are assuming the organizational approach in philosophy of biology as a theoretical landmark to interpret the ascription of personality and cognitive functions to social colonies, we will describe this approach in this section.

Organizational approaches have emerged in philosophy of biology in the 1990s and are becoming prominent along the last decades (e.g., Schlosser, 1998; Collier, 2006; Christensen and Bickhard, 2002; Delancey, 2006; Mossio et al., 2009). Biological systems, organized in a closure of constraints, are not only more complex, but also enable the potential increase of functional complexity, when compared to the simpler and qualitatively distinct self-organized systems (Moreno and Mossio, 2015, p. 18). One of the reasons for the prominence of organizational approaches is its philosophically coherent and integrative, as well as heuristically fruitful grounding of the teleological aspect of the functional ascriptions in biology (which we will explain below).

In order to present the organizational approach by Moreno and Mossio, let's consider the functional relationship between a trait and the organism of which it is a part. More formally, according to this perspective, a trait T has a function in the organization O of a system S if and only if the following conditions, Cn, are satisfied:

C_1: T exerts a constraint that contributes to the maintenance of the organization O.
C_2: T is maintained under some constraints of O.
C_3: O realizes closure (Moreno and Mossio, 2015, p. 73).

This definition can be illustrated with an example. On the one hand, the bee's gut (T) exerts a constraining action on the physicochemical flow (represented by the ingested food) through all the bee body (the system S), and in this way contributes to the maintenance of the organization O of S. This corresponds to C_1 in the formalization above, which represents a bottom-up influence (from the part to the whole system). On the other hand, according to C_2, the gut (T) is maintained under constraints of the organization O of S. That is to say, the gut depends on other structures (such as the eyes, the wings, etc.) which constitute the very organization of the system S, since the gut needs, for instance, to receive nutrients (instead of toxic substances) that come from other organs, in order to maintain itself. This is a top-down relationship (from the organization as a whole to the part). Finally, according to C_3 the organization O of S realizes closure, because of the very nature of the relationships described at C_1 and C_2. Closure, in general, means that a sequence of natural processes realizes a causal loop (see Nunes-Neto et al., 2014; Moreno and Mossio, 2015). For a schematic representation (see **Figure 1**).

There are two kinds of closure: closure of processes and closure of constraints. Closure of processes happens when, for instance, a process A causes a process B, which causes C, which, in turn, causes A. Some purely physical or chemical systems are characterized by a closure of processes. A closed glass bottle half full of water, receiving solar radiation is a good example. The solar radiation traverses the walls of the bottle and heats the water, which reaching one given temperature, evaporates. The water vapor rises and condensates in the top of the bottle, thus, falling as liquid water, which is now again subject to evaporation. The cycling of water molecules inside the bottle is a physicochemical circular flow, constrained only by external entities, in this case the glass and the solar radiation. The glass and the sun act, then, as external constraints, which are not regenerated by the cyclic thermodynamic flow of water.

By its turn, closure of constraints is a result of a complex organization, for which biological organisms are paradigmatic. A constraint happens when not only a flow of matter and energy (processes) forms a causal loop, but also biological structures (such as the bee organs) affect each other in mutual dependence relationships, and also determine a reduction in the degree of freedom of the flow of matter and energy, in other words, constrain the flow of matter and energy. Here, the idea of mutual dependence between constraints is crucial. Formally, a set of constraints C performs closure when, for each constraint C_p, belonging to C, (i) C_p depends directly on at least one other constraint in C (i.e., C_p is *dependent*) and (ii) there is at least one other constraint C_q, also belonging to C, which depends on C_p (i.e., C_p is an *enabling condition*). This mutual dependence generates the capacity of self-maintenance, which is specific to the way autonomous systems realize closure (for more details, see Moreno and Mossio, 2015).

In sum, going back to our example, we could say that the gut produces an effect (its function, to digest and absorb nutrients) which contributes to the maintenance of other organs (say, the

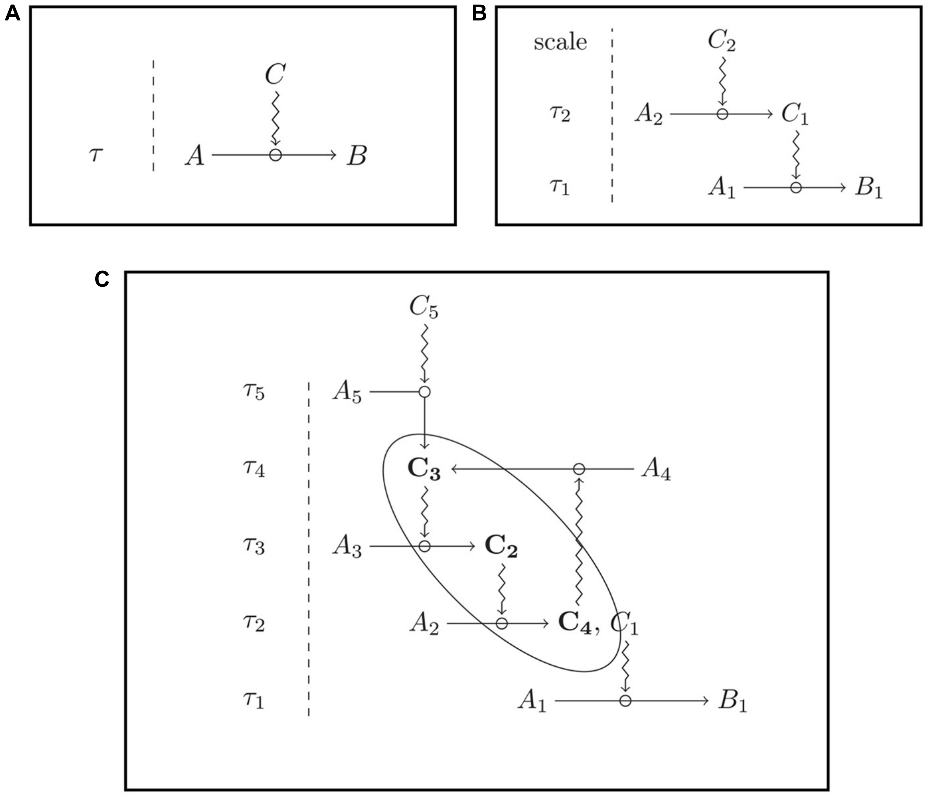

FIGURE 1 | Constraints act upon processes and remain stable at the scale of these processual changes. **(A)** The constraint C acts over a process A > B; **(B)** dependence between constraints: the constraint C1 is dependent on the presence of another constraint, C2; **(C)** closure of constraints: the constraints C3, C2, and C4 are mutually dependent upon one another. Ai, Bi, and Ci are entities within a system; τi, specific time scales; the simple arrows indicate processes; the zig-zag arrow indicate constraining actions (from Moreno and Mossio, 2015, figures elaborated by Maël Montévil).

wings), as it makes it possible that nutrients are delivered to them. The wings allow flying, which is a condition of possibility for finding new food, raw material for the gut performing its function, which closes the cycle.

As Mossio et al. referring to organizational closure, put it:

organizational closure justifies explaining the existence of a process by referring to its effects: a process is subject to closure in a self-maintaining system when it contributes to the maintenance of some of the conditions required for its own existence. In this sense, organizational closure provides a naturalized grounding for a teleological dimension: to the question 'Why does X exist in that class of systems?', it is legitimate to answer 'Because it does Y' (Mossio et al., 2009, p. 825).

The organizational approach was originally applied to individual organisms and their traits as the functional units. However, we could conceive also the individual organisms, or the sets composed by them (such as colonies, populations, or communities), as the functional units themselves, thus applying the organizational approach to other levels within the ecological systems (Nunes-Neto et al., 2014, p. 131). More recently the scope of the functional units was broadened, in order to include abiotic items, once they can also play the role of constraints on the flow of matter and energy (El-Hani and Nunes-Neto, 2020). Thus the organizational approach can be applied to a broad range of levels in the biological hierarchy and, accordingly, we will use it to evaluate if one same psychological predicate can be found not only at the individual but also at the social level.

APPLICATION OF THE ORGANIZATIONAL APPROACH TO SOCIALITY

The organizational approach depicted above has a long history (see Gilbert and Sarkar, 2000; Wolfe, 2010), and allows for a principled ascription of functions within the biological hierarchy (Mossio et al., 2016), sanctioning functional ascriptions to both biological organisms (Mossio et al., 2009) and ecological systems (Nunes-Neto et al., 2014), a quality that is relevant for our purposes, since we are trying to specify the putative existence of a socio-psychological (a social mind) level on top of psychological individuals.

For example, the application of organizational principles to individuals has shown that to perform adaptively complex behavior, the cognitive system, as exemplified by the nervous system of individuals, should present some properties (Moreno and Mossio, 2015, pp. 167–193). First, as responsible for the mediation between internal (bodily) and external (environmental) sensorimotor coordinations, the cognitive system should not follow strictly the dynamics of either the internal or the external stimuli, that is, the cognitive system must show dynamic decoupling from the dynamics of both its internal (metabolic, physiologic) and external (ecologic) drivers. Second, the cognitive system should show second-order closure of constraints (see the section above), meaning that information should flow through a net of co-dependent constraints that are themselves generated within the very cognitive system. Third, for the possibility of adaptive adjustment in behavior, the cognitive system should be able to regulate its own functioning, meaning that there should be some internal constraints that only become active when the whole cognitive system is risking to fall out of bounds. The activation of these regulatory, constitutive constraints, could turn cognitive functioning back to normality either by maintaining the actual organization of constraints through calibrations on the flux of information, or by changing the actual organization of co-dependence between the constraints (i.e., the cognitive system enters into a novel organizational state). Together, these three requirements imply the autonomy of the cognitive system, meaning that the cognitive system is not merely responsive to either the internal (metabolic-physiologic) or the external (ecologic) drivers, but instead that it is an active system with its own structure and normative rules, built upon a history of interactions with these very drivers.

So, what happens when we jump from the cognition of an individual to the cognition of a social, or collective system? Social cognition in insects has sometimes been labeled as the product of a liquid brain (Solé et al., 2019), i.e., the product of a system where the "neurones" are not static (as in usual, solid brains) but instead are mobile agents (ants, bees, termites) that exchange, store and process information to obtain a collective decision. In this parlance, our question would thus be: do liquid brains have personality? To answer this question, we develop bellow a conceptual analysis, evaluating three requirements for autonomy of personality at a social level (**Table 1** summarizes our main findings).

Closure of Constraints at the Social Level

Information flow within the social system occurs through communication between individuals, and following our review of social insect communication, we find that these requirements for social cognition sometimes do not hold at the social level.

For example, the recruitment processes for the choice of a foraging patch, or of a new nest site, are paradigmatic examples of self-organized systems that constrain the flow of information to, and within the colony. But self-organization by itself does not imply the existence of a closure of constraints, because self-organized systems have one single, macro-level constraint, and therefore they are not able to instantiate any co-dependence between constraints (Mossio et al., 2009). In our exemplar case, although one single mass recruitment trail certainly constrains the flux of information to individual ants, feeding back the recruitment of new foragers to the trail, and thus contributing to its own self-maintenance (i.e., it is a self-organized system), it is constituted by one single constraint (the trail itself), and thus cannot by itself realize a closure of constraints. The trail is, in this organizational analysis, comparable to physicochemical dissipative structures, self-organized systems such as the flame of a candle, or Bénard cells (the bubbles that appear spontaneously when heating water), but it could not by itself be considered, at the collective level, a cognitive system.

But there is more to insect societies than isolated self-organized social structures (SOSSs). The collective choice

TABLE 1 | Fulfillment of the organizational requirements for the ascription of social personality in particular cases of self-organized social processes.

Self-organized social structures	Social closure of constraints	Decoupling between individual and social dynamics	Regulation of collective decision processes	References
House hunting in Temnothorax	No	No	No	Mallon et al., 2001; Franks et al., 2002, 2003; Franks and Richardson, 2006
House hunting in *Apis mellifera*	Yes	No	No	Camazine et al., 1999; Seeley and Buhrman, 1999, 2001; Visscher and Camazine, 1999; Seeley et al., 2012
Recruitment for foraging in *Lasius niger*	No	Yes	No	Beckers et al., 1992a,b; Mailleux et al., 2003; Czaczkes et al., 2013
Decision between competing foraging recruitment trails in *Monomorium pharaonis*	Yes	Yes	No	Sumpter and Beekman, 2003; Robinson et al., 2005
Mass recruitment in *Atta cephalotes*	No	Yes	No	Jaffe and Howse, 1979
Decision between competing foraging recruitment vortices in *Apis mellifera*	Yes	No	No	Kirchner, 1993; Seeley, 1995; Holldobler and Wilson, 2009; Seeley et al., 2012
Integration between distinct tasks in *Apis mellifera*	Yes	No	No	Seeley, 1995; Thom et al., 2003

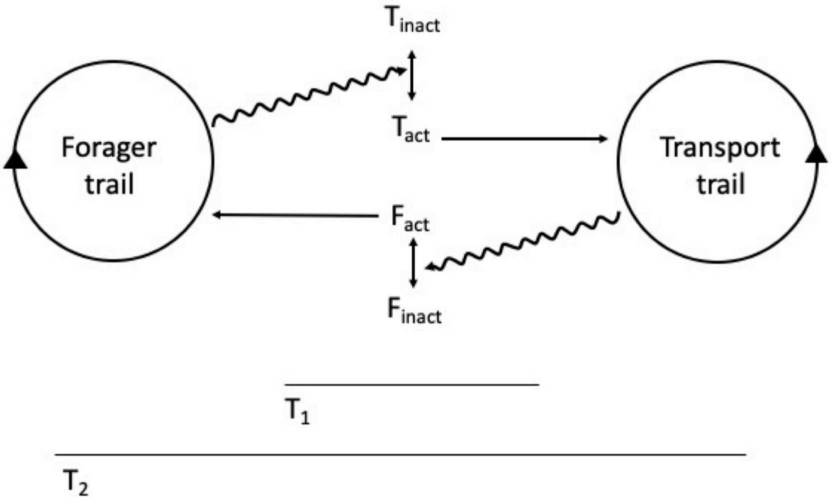

FIGURE 2 | Forager and transporter trails (socially self-organized systems—SSSs) constrain information flow, thus causing individuals to change their internal state, between inactivity (inact) and activity (act). As a result, both SSSs act indirectly upon each other through recruitment processes. Both transporters (T) and foragers (F) are depicted; T1 and T2 are different time scales.

between competing foraging patches (or competing nest sites) relies basically on the differential recruitment of new individuals to one of the competing options, through the positive feedback within each option, and also through the addition of negative feedback across competing options. Thus, when there are two alternative vortices of recruitment at the same time, we do have two collective structures constraining the flow of information through the individuals, so that there is the possibility of a co-dependence between constraints, and thus a possibility of fulfilling one of the requirements for cognition at the social level.

When the choice between competing recruitment options depends overly on the differential amplification of distinct trails, there is scant need for interactions between the two competing trails. When this is the case, the two trails are each one a constraint to information flow within the colony, but the constraints do not interact significantly with one another, there is no clear flow of information between the trails, meaning, again, that there is no closure of constraints. Thus, when there is no significant interaction between the constraints (no closure of constraints), the resulting phenomenon, the collective choice of one of the available resource patches, is fundamentally a result of individual cognition guided by self-organized processes. While this is certainly a social decision process, it does not reach the complexity required for a closure of constraints, and thus it does not attain autonomy at the social level. The competing trails would, in cases like this, be akin to distinct bubbles of water (Bénard cells) differentially growing through the "recruitment" of nearby water molecules during the heating of water, a recruitment that feeds back the competing self-organized processes.

The situation seems different for *Apis mellifera* or *M. faraonis*, which show a significant interaction between distinct recruitment groups through stop signals that promote cross-inhibition between competing options (Robinson et al., 2005; Seeley et al., 2012). These species seem thus to rely on more than self-organization to choose the best option: there is signal processing between the competing vortices of recruitment, and thus the final choice involves a second order, across sites information processing system. This second-order information processing system could qualify as cognition at the social level, that is, on top of individual cognition because, from an organizational standpoint, when there is significant interaction between the constraints (recruitment vortices), there is the possibility of appearing a closure of constraints (see Mossio et al., 2009 and the section above). Interaction between SOSSs (the recruitment vortices in the example above) can also occur between distinct, spatially contiguous tasks in a colony (**Figure 2**). For example, while an external ant trail focus on bringing pieces of leaves into the nest, another trail focus on transporting these pieces to inner parts of the colony, or while a group of external forager bees focuses on bringing nectar to the comb, another group focuses on further nectar processing, within the colony. In these cases we also can have interactions between two self-organized activities: external forager bees make the tremble dance signal, whereby the signaler recruits passing bees to the internal nectar processing task (Seeley, 1995). There can also be indirect interaction between contiguous tasks: the continuous action of external ant foragers generates a pile of resources, which then stimulates workers within the colony to further process the pile, a process denominated stigmergy (Theraulaz and Bonabeau, 1999). Through either direct or indirect interaction, the complementary tasks (i.e., the distinct transport SOSSs) constrain the flow of information, and thus the decision process of individuals, in a way that instantiates a co-dependence between these very constraints (**Figure 1**).

The argument above could be more general, including not only two, but all the task forces in a colony, in species where there is heterogeneity of tasks. In general, considering the whole colony, heterogeneous interaction profiles across individuals emerge with colony size increase and, with that, information flow becomes modularized (Naug, 2009). The evolution of task specialization with colony size increase would thus create informational compartments within the colony, with highly connected individuals at the edge of these compartments (O'Donnell and Bulova, 2007). If direct or indirect connectivity between contiguous tasks imply closure of constraints, as discussed above, then the colony could be considered to have a second order, social information processing system.

Decoupling Between Social and Individual Dynamics

Closure of constraints at the social level is but one of the requisites for autonomous social cognition. There must also exist a decoupling between the dynamics of the cognitive system and the dynamics of both its internal and external drivers, that is, in the case of individual cognitive agents, internal metabolic signaling (physiology) and external environmental stimuli. At the social levels, the equivalent to internal metabolism would be the social physiology, the decentralized interactions between colony members. But these interactions are not easily distinguishable from the information flow (between and within its SOSSs). This is because, differently from what happens within the nervous system, where the rapid dynamics of information flow surpasses the slower dynamics of body metabolism, thus allowing for an effective integration across distant body parts, at the social level, the information flow, both between and within SOSS, is obtained by these very interactions: information flow and interactions are one same thing. The second-order, social information processing system seems stuck in the same dynamics of the interactions between individuals (it is constituted by these very interactions), i.e., it is stuck in the dynamics of social physiology. This could explain why frequently the dynamics of collective behaviors mimics the dynamics of ecological drivers (Gordon, 2019): there is no autonomous level of social information processing, resulting in a social system that is by default coupled to its external drivers.

In some circumstances, however, the dynamics of social information could be decoupled from social interactions. This could occur when there is indirect interaction, through contact pheromones, or in the case of stigmergy. This is because indirect interaction relies on social assets (a collective mass of pheromones in a trail, a pile of resources), which have a dynamics that is slower than the dynamics of direct, inter-individual interactions. But while the second-order, nervous system based individual cognition is able to integrate distant parts of the organism because of its fast dynamics, social insects could sometimes have a second-order, social information processing system that is, on the contrary, slower than the direct interactions themselves. Slower processes cannot integrate a bunch of faster processes, and thus are unable to produce real-time, concerted social responses that attend simultaneously to various colony demands.

Regulation of Collective Decision Processes

The last formal requirement for autonomy at the social level is the possibility of self-regulation of the social decision processes. This would require one or a few SOSSs that would enter into action when the system is out of bounds, interfering with information flow or with the very organization of constraints (Moreno and Mossio, 2015).

Although the existence of these regulatory constraints is possible, the very decentralized nature of colony organization, relying heavily on anonymous agents using local information and indirect interactions (Feinerman and Korman, 2017), seems to reduce the possibility of regulation through supplementary social structures. There is certainly regulation of interactions by individuals (Kolay et al., 2020). For example, *Monomorium* ants produce a volatile pheromone that repels workers from unprofitable resources (Robinson et al., 2005), thus contributing, for example, to the decline of an established trail. But, as we have discussed above, the whole trail (from its creation to its extinction) is a SOSS and, as such, it is a very intricate process from the point of view of the individuals that create it, but from the point of view of the social organization, it is way too simple. Any SOSS is constituted by one single constraint (see above "Closure of constraints at the social level"), and to allow for regulation one needs at least three constitutive constraints (SOSSs): a regulator constraint that enters into action only when needed (when the system is out of bounds), so as to modify the interaction between the two remaining, co-dependent constraints. We should be careful not to mix levels of analysis: regulation of individual interactions is paramount for an analysis at the level of the individuals, but we are here working at the social level, searching for SOSSs that regulate the interactions between other SOSSs.

DISCUSSION

Although we concur that the ascription of psychological predicates to individual ants, bees, or any other social animal, is itself literally correct (Figdor, 2018), the same may not hold true for the ascription of psychological predicates to upper, social level entities. Considering personality as connected to a very general view of cognition as information processing (Shettleworth, 2010), framing this general view within an organizational approach, a very effective theoretical development for studying functions across levels of biological organization (Mossio et al., 2016), we found conflicting results concerning the ascription of personality to social entities.

A general result of the conceptual analysis is that one cannot uncritically ascribe psychological predicates to self-organized social structures (SOSSs), such as termite or ant trails, or bee scouts recruiting for a single resource patch, because these social entities constitute themselves in a single constraint (to information flux). In this case, there is no upper individual, social level of cognition, no two self-organized social structures that generate one another and perpetuate themselves, by driving information flow through the colony.

To be clear, this is not to say that there is no emergent cognition. Self-organized processes are paradigmatic models for emergent phenomena, and cognition is no exception at it, for collective behaviors, such as collective motion patterns or collective predator avoidance patterns, do emerge from individual interactions (Ioannou et al., 2011). Individuals do communicate or interact with one another in these self-organized, social processes, but the collective, sometimes emergent outcome relies mostly on individual cognitions trapped in non-linear feedback loops that are characteristic of selforganized processes. The social structure that emerges in these cases is, from a modeling perspective, akin to a physicochemical dissipative structure, and in this way, it is too simple as a social structure, one that is unable to fit even in the simplest models of closure of constraints (**Figure 1C**). There is emergent cognition, but not one complex enough to be sustainable, autonomous at the social level: there is no social cognition.

This first conclusion has many practical consequences for research in social personality. For example, the finding of stable, across-colonies differences in a collective trail property, such as the timing to form mass recruitment trails, or the timing to recover from an experimental perturbation performed on such an isolated trail, the stability on any of these measurements should not be taken as an index of the existence of social personality, because they simply reflect a combination, albeit a non-linear and sometimes complicated one, of the individual personalities already present in that trail. No further psychological, autonomous social system of information processing is required to explain the observed pattern.

When the measurement of social personality involves not one, but two or more interacting trails, recruitment processes, or more generally, SOSSs, then our conceptual analysis portrays a more nuanced outcome. If there are negative and positive feedbacks occurring between the SOSSs (**Figure 2**, **Table 1**) the social system is complex enough to show closure of constraints, presenting a second-order, social information processing system on top of the first-order, individual information processing system. At a lower level of analysis, at the level of individual cognition, a second-order processing could be implied in the cross inhibition between integrating populations of neurons, and it would be crucial for effective behavioral choice in individual decision-making tasks (Bogacz et al., 2006; Bogacz, 2007).

But not all collective SOSSs choices (between food patches, nest sites, routes) possess a second-order, social information processing system: some choices, as the above discussed case of the Pharaoh's ant, are better characterized as effected through a population of independent, barely interacting socially self-organized structures (trails). In these cases, the observation of any stable, cross-colonies differences in any of the collective choice's attributes should not be taken as an index of social personality.

There are plenty of differences across social species in the dynamics of their collective behavior (Gordon, 2019), and thus each different organizational profile requires close inspection. For example, there are ant species with specialization of tasks within one single fixed foraging team, with one single nest comprising thousands of foraging teams, sometimes organized in interconnected, multi-domus nests (Reznikova, 2020). Notwithstanding the variability in social insect organization and dynamics, a rule of the thumb would be that, considering that heterogeneity of connectivity (of the network of interactions across individuals) increases with colony size (Naug, 2009), with larger colonies showing a more modularized structure (larger number of information comportments), then the larger the colony the higher should be the probability of interactions to occur between contiguous informational compartments. If, as we have shown above, the existence of reciprocal interactions (with positive and negative feedbacks) between SOSSs complies with the formal requirements for closure of constraints, the larger the colony, the more there are opportunities for the emergence of social cognition. Coupling between the dynamics of the environment and that of socially self-organized structures is not rare at all among social insect societies (Gordon, 2019), but this coupling is a sign of heteronomy. If one is interested in social, instead of individual cognition, then one is searching for autonomy, and accordingly the phenomena of interest are those that reflect the uncoupling between the flow of social information and the flow of information regarding both the external environment and the internal, social physiology.

Although none of the studied systems complies with all the formal requirements for social cognition, particularly regarding the requirement of a social self-regulation of the interactions between SOSSs, the application of the organizational approach to social systems seems to provide a more nuanced take on the issue of social personality. Some collective decisions (the ones that require the interaction between several SOSSs), performed by some species (those with positive and negative feedback systems), when measured at groups of certain (large) sizes, have the potential to be connected to a social level of personality, one that would be autonomous in relation to lower, individual levels of personality. Thus, a conceptual analysis based on a fair amount of knowledge regarding the communication structure, across and within several tasks, is required before studying social personality in any particular case.

We hope that the organizational approach herein developed helps to ground theoretically the emerging area of social personality, inspiring its application to further, related areas. For example, there have been proposals conceiving ecological communities as learning structures, with the ecological relations between species as analogs to synapses in the nervous system, and thus with individual learning, through changes in nervous system topology, as being functionally equivalent to ecosystem learning, implemented as changes in the topology of the ecological relations (Power et al., 2015). A similar proposal seems to somewhat entangle evolutionary and learning processes (Watson and Szathmáry, 2016). The application of the organizational approach would help to clarify conceptually these broad analogies. In general, while researchers in ecology are mostly interested on the biological constraints to the flux of matter and energy, our approach would instead force a focus on the cognitive constraints to the flow of information, on the psychological constraints that guide the ecological relations, helping thus to bias evolutionary processes.

AUTHOR CONTRIBUTIONS

All authors have written collaboratively the first version of the text. LN contributed to the review of social personality uses. NN-N contributed presenting the organizational approach. HJ contributed with the introduction, the review of social insect communication, the application of the organizational approach to social insects, and the discussion. All authors have reviewed and contributed to the final version of the text. HJ and LN contributed with the original idea, and all authors contributed to the development of the general logic of the main argument.

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