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Novice chimpanzees cooperate successfully in the presence of experts, but may have limited understanding of the task

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Abstract
Despite many observations of cooperation in nature, laboratory studies often fail to find careful coordination between individuals who are solving a cooperative task. Further, individuals tested are often naïve to cooperative tasks and there has been little exploration of partnerships with mixed expertise. In the current study, we examined acquisition of a cooperative pulling task in a group with both expert ($N = 4$) and novice ($N = 11$) chimpanzees (*Pan troglodytes*). We used five measures of competence and understanding: (1) success at the task, (2) latency to succeed, (3) efficiency, (4) uncoordinated pulling, and (5) pulling when a partner was present versus absent. We found that novices showed evidence of trial and error learning and developed competence over time, whereas the behavior of experts did not change throughout the course of the study. In addition to looking at patterns over time, we compared the performance of novices in this *mixed-expertise* group to an earlier study of novices in a group of *all-novices*. Novices in the *mixed-expertise* group pulled the same overall amount but for shorter periods of time, leading to higher pulling rates than individuals in the *all-novice* group. Taken together, these results suggest that learning in the presence of experts led to rapid and frequent success, although not necessarily careful coordination.

Keywords Cooperation · Chimpanzee · Associative learning · *Pan troglodytes* · Coordination

Introduction

Cooperation has been observed and described in species spanning numerous taxa (Dugatkin 1997). In some cases, cooperation has been hypothesized to be highly complex. For example, in order to pull in a tray baited with food, one chimpanzee might recruit another to simultaneously pull on strings to move the tray closer, coordinating their behavior in time and space (Melis et al. 2006a). However, the cognitive abilities resulting in such behavior may not necessarily be as complex as they might seem (Bailey et al. 2013).

Research in the laboratory has sought to better understand the cognitive underpinnings of cooperative behavior. The key question examined is how carefully individuals are coordinating their behavior in space and time, which requires understanding not only that a partner is needed, but also the role the partner is playing in success. Many cooperative pulling studies look at the rate of behavior when a partner is present versus absent, with the expectation that individuals should pull less frequently when they are alone at the apparatus than when a partner is present (de Waal and Suchak 2010). This is observed in many species of primates (cotton-top tamarins: Cronin et al. 2005; capuchin monkeys: Visalberghi et al. 2000) but results in other taxonomic groups are more mixed (e.g., African gray parrots pull more when a partner is present: Péron et al. 2011; but rooks do not: Seed et al. 2008).

However, simply pulling more when a partner is present could be indicative of social facilitation, where individuals choose to interact with an apparatus because another individual is doing so, and even if they do understand that a partner

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needs to be there, pulling rates alone cannot identify carefully coordinated behavior. Indeed, in many studies individuals appear to be pulling frequently and rapidly, resulting in chance co-production (e.g., Chalmeau et al. 1997). Another measure such as efficiency, that is, how many or few extraneous actions the individuals are engaging in, is necessary, as individuals who coordinate more carefully should be more efficient (Drea and Carter 2009; Suchak et al. 2014). For example, one study of a novel pulling task in chimpanzees found that efficiency improved over time: In the beginning of the task, untrained chimpanzees were pulling on average around three times per chimpanzee per success, but by the end just 1.5 times (note that one pull per chimpanzee, or two pulls total, would be perfect efficiency, Suchak et al. 2014).

Another aspect of coordination is inhibiting behavior until a partner is ready to act. The "loose string" task is designed such that if one individual pulls their end of a rope before their partner, the rope releases and neither individual can pull in a tray baited with food. Chimpanzees succeed reliably at this task (Hirata and Fuwa 2007; Melis et al. 2006a, b, 2009). As an additional control, some studies have delayed the arrival of a partner to see if individuals are able to wait. Chimpanzees and elephants have succeeded at this type of task (chimpanzees: Melis et al. 2006a; elephants: Plotnik et al. 2011). Similarly, in a group-level study of chimpanzees in which all individuals in the group could approach and leave the apparatus freely, chimpanzees pulled more often after a partner had approached and was ready to pull than when there was no partner ready (Suchak et al. 2014). Further, Melis et al. (2009) gave chimpanzees a choice of two apparatuses, requiring the chimpanzees to coordinate their behavior in space and time. The chimpanzees were quite good at this, even when there was a conflict of interest between the partners over which apparatus was preferred. However, many other species fail to inhibit their actions during this and other tasks in which the partner's ability to participate is delayed (dogs: Ostojiu and Clayton 2014; rooks: Seed et al. 2008; parrots: Péron et al. 2011; crows: Jelbert et al. 2015), and it is possible that an individual who shows the appropriate waiting behavior is waiting to feel tension on the string, rather than waiting for the arrival of the partner.

Coordination in space and time can also be demonstrated in tasks where individuals serve complementary rather than parallel roles (Melis and Tomasello 2013; Fletcher et al. 2012). In one study where two chimpanzees performed complementary roles requiring different tools, the chimpanzees had to transfer the correct tool to their partner before obtaining rewards, demonstrating an understanding of not only the partner's role in success but also their needs (Melis and Tomasello 2013). Interestingly, although chimpanzees are quite good at coordinating complementary actions, unlike children, they do not seem to benefit from observing their partner in the other role (Fletcher et al. 2012). When roles were switched, children pick up on their new role faster, whereas the chimpanzees needed to learn the new roles from scratch.

There are other, more robust measures that also demonstrate an individual's understanding of the need for a partner and knowledge of a partner's role in success. For example, chimpanzees will sometimes recruit human or chimpanzee partners through gestures or communication (Crawford 1937; Chalmeau and Gallo 1995; Hirata et al. 2010). Disrupting communication in these cases, for example with a visual barrier between the subjects, should disrupt cooperation, as was indeed observed in a study of capuchin monkeys (Mendres and de Waal 2000). However, evidence in this regard is mixed. In some cases, chimpanzees have failed to recruit other chimpanzees or humans and no gesturing was observed (Warneken et al. 2006; Povinelli and O'Neill 2000). Chimpanzees can also recruit partners in more concrete ways, such as physically opening a door to allow a partner to join them (Melis et al. 2006a). In one study, not only did the chimpanzees spontaneously allow a partner in, they only did so when the circumstances required it; if they could solve the task themselves, they did not open the door. Furthermore, Melis et al. (2006a) demonstrated that when given a choice between partners of differing expertise, the chimpanzees recruited the better partner. Thus, chimpanzees may be sensitive to the expertise and knowledge of a partner.

Compared to coordination, little work has been done on the role of expertise and the learning of task contingencies. In nature, becoming an effective hunter may take a chimpanzee upwards of 25 years and relies on the presence of experts in the group (Boesch 2002). In the laboratory, this can be examined by measuring changes in understanding over time and in the presence of experts. In a study of cooperation in hyenas, the success and efficiency of experts paired with a novice fell midway between that obtained by two experts working together or two novices working together, suggesting that experts were facilitating the novice hyena's performance on the task (Drea and Carter 2009). A study of chimpanzees found that while a pair of trained, experienced chimpanzees successfully cooperated five out of six times, out of 10 expert–novice pairs only two solved the task (Povinelli and O'Neill 2000). The focus of this study was on communication between the experts and novices, and not one single solicitation gesture was observed. However, they did find that novices looked more at the experts than vice versa, suggesting that in a cooperative situation any learning that novices are engaging in may be done through passive observation, rather than active facilitation by the experts.

Although rarely studied in the cooperative context, the presence of experts readily facilitates noncooperative problem solving in a variety of species in a similar fashion (e.g., pigeons: Bouchard et al. 2007; bees: Alem et al. 2016; lions: Borrego and Dowling 2016). Chimpanzees are excellent candidates to further examine the influence of experts on novices' performance on a cooperative task as they are attentive to individual differences in competence at cooperative tasks (Melis et al. 2006a) and are widely known for social learning outside of cooperative contexts (e.g., Whiten et al. 2005; Price et al. 2009). Focusing on the behavior of the novices, rather than the experts, may help shed light on what, if anything, novice chimpanzees learn from observing and working with experts in a cooperative task.

In the current study, we examined the acquisition of a cooperative task in a group of chimpanzees of mixed expertise. We hypothesized that the presence of experts would facilitate success, understanding of the need for a partner, and coordination with a partner for novice individuals, and that these effects should be noticeable over time. We further hypothesized that if the experts facilitated the understanding of the novices, the *mixed-expertise* group would perform better on measures of understanding than the group of *all-novices* in an earlier study using the same task.

Methods

Subjects

Subjects were two groups of adult chimpanzees housed in an indoor/outdoor corral at the Field Station of the Yerkes National Primate Research Center (YNPRC) of Emory University. The corral was 711 m^2 and contained a large climbing structure and several enrichment items. Testing occurred in the outdoor area with the entire group present. Access to the indoor area was always available and at no time were individuals separated from the group for testing. Chimpanzees were fed two daily meals consisting of fruits and vegetables at approximately 8h30 and 15h00 and had access to water and primate chow ad libitum. Food obtained as part of this study was supplemental to the regular diet and at no time were individuals food or water restricted.

The *mixed-expertise* group ($N = 15$, 3 males, 12 females) was formed from preexisting subgroups 3 months prior to testing. One subgroup ($N = 4$) had more than 90 h of experience with the cooperation apparatus used in this study and were considered "experts." Collectively, these four individuals had obtained 3882 rewards from cooperatively pulling at the apparatus as part of a previous study (Suchak et al. 2014). The rest of the group had no experience with this or any similar apparatus and were considered "novices." The novices in the *mixed-expertise* group did not have any visual access to the *all-novice* group during the previous study.

We compared the performance and understanding of novices in this *mixed-expertise* group to data from a previous study of an *all-novice* group ($N = 11$, 1 male, 10 females, described in Suchak et al. 2014). No individuals in the *all-novice* group, from the previous study, had experience with this or any similar apparatus prior to that study.

Apparatus

This study used a cooperative pulling apparatus, which required one chimpanzee to pull a bar to remove a barrier in order for a second chimpanzee to pull on a second bar to bring in a tray with food (Fig. 1, see also Suchak et al. 2014). The apparatus was mounted on the outside of the enclosure, with the pull bars extending into the enclosure. The two bars were too far apart (~ 1.6 m) for one individual to pull both. Once the tray was pulled in, rewards dropped into a funnel and were delivered to each chimpanzee individually. Food rewards were one small slice of banana, one grape, or two raisins and were varied randomly across trials to maintain a high level of interest. For each trial, all of the chimpanzees received the same reward. The chimpanzees were not trained on how the apparatus worked, but rather had to figure it out through trial and error or by watching others.

Procedure

Chimpanzees could approach or leave the apparatus as they desired throughout each test session. Test sessions were 1 h long and consisted of as many trials as could be accomplished during that time. A trial began when the tray was baited with a food reward in each food cup. One chimpanzee needed to pull to move and hold the barrier down and a second chimpanzee could then pull on the bar to move the tray in. A trial ended if two chimpanzees successfully obtained the rewards, and the tray was reset and a new trial began immediately. If the chimpanzees did not solve the task within 5 min, the trial was ended and the food removed for a 1-min time out. Following the time out, the tray was baited for a new trial. We ran 28 test sessions to directly compare the acquisition of the task to the previous study. These procedures, as outlined here, exactly followed Phase 1 of Suchak et al. (2014).

Behavioral coding

Sessions were recorded from two angles (a side angle taken from an observation tower and a front view from the experimenter's perspective) using HD digital video cameras. We recorded which chimpanzees successfully solved the task, the time at which the tray was baited, the timing of any chimpanzees approaching or leaving the apparatus, and the time at which they solved the task. We also recorded all pulls on either bar, which included any pull that moved the tray or barrier, as well as any bodily pulling motion that did not result in movement (such as would occur if a chimpanzee tried to pull in the tray without the barrier having

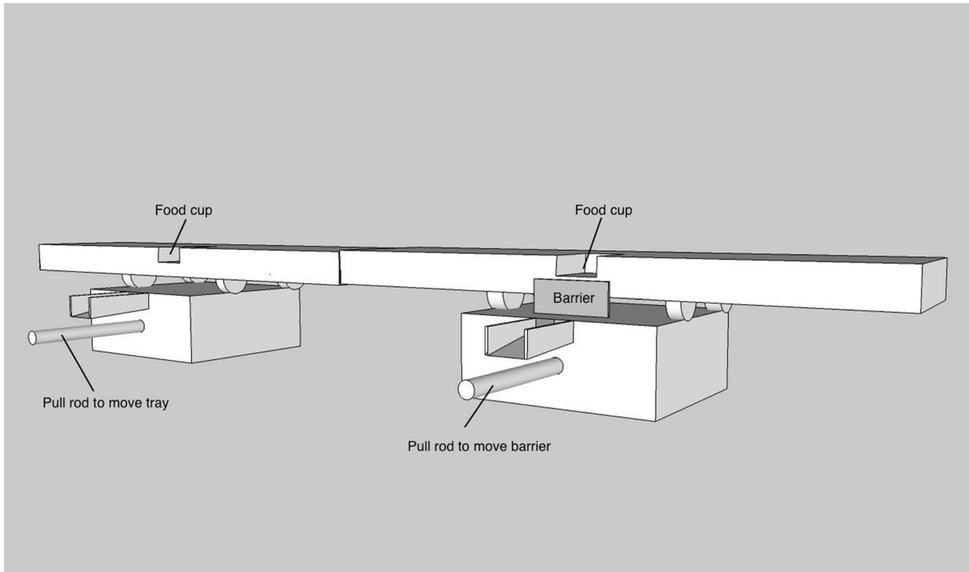

Fig. 1 Test apparatus. The apparatus was mounted on the outside of the enclosure such that only the pull bars were within reach of the chimpanzees. One chimpanzee needed to pull the bar attached to the barrier (right) to move the spring-loaded barrier down, and a second chimpanzee could then pull the second bar (left) to move the tray in. Once the tray was pulled in, the food would drop into the delivery tunnels and roll toward the chimpanzees

been removed first). A second rater coded 10% of the videos and inter-rater reliability was excellent for success (Cohen's kappa = 0.99), latency ($r = 0.99$), and pulling ($r = 0.99$).

Analyses

We used the following measures (a–e) to calculate several variables related to proficiency and understanding of the task. We used parametric statistics for our analyses as most variables were normally distributed.

(a) Success occurred when one chimpanzee pulled the barrier and a second pulled the tray in, delivering food to both chimpanzees.
(b) Latency to succeed was calculated as the time from when both chimpanzees arrived at the baited tray to the time the chimpanzees successfully moved the tray in.
(c) Efficiency was calculated as the number of pulls made by each dyad between approach and success. Note that a lower number of pulls indicates higher efficiency (fewer extraneous pulls prior to success). Perfect efficiency would be two pulls (one at the tray and one at the barrier) and would indicate precise coordination between individuals. Both total number of pulls and pulling rate (pulls per minute) were analyzed.
(d) Uncoordinated Pulling was measured as any pulling that occurred when two chimpanzees were present, but that did not lead to success. This occurred both during failed trials (when the chimpanzees reached the 5-min limit without solving the task) or if two chimpanzees were attempting to solve the task, but one got up and left before they succeeded. Both total number of pulls and pulling rate (pulls per minute) were analyzed.
(e) Partner Presence. We compared the pulling rate when a partner was present at the apparatus against the pulling rate when no partner was present. A chimpanzee was only considered present if they were sitting at the bar "ready" to pull; chimpanzees who were moving toward or away from the apparatus were not counted as present. This measure was calculated as a rate to compensate for the fact that each individual spent differing amounts of time at the apparatus when a partner was present versus absent.

Success, latency, efficiency, and uncoordinated pulling were compared across pair types: expert–expert (E–E) pairs, expert–novice (E–N) pairs, and novice–novice (N–N) pairs. Differences in the occurrence of success (a binomial, yes/no variable) and, if yes, number of successes (a count variable) were analyzed using a zero-inflated generalized linear mixed model (ZIGLMM) using a Poisson error structure. This procedure allowed us to model the large number of zero successes, both because two-thirds of all possible dyads (70 out of 105) did not succeed at all and because the 35 dyads that did succeed, did not necessarily do so every session. For latency, efficiency, and uncoordinated pulling, we used linear mixed models (LMMs). For all of these models, we included pair type (dummy coded with reference category expert–expert), session, and their interaction as fixed effects, and individual identities of the two chimpanzees in a dyad as random effects to account for different baseline proficiencies. Partner Presence was similarly analyzed using an LMM, but comparing experts and novices across sessions on an individual (as opposed to dyadic) level. Pulling rate was the dependent variable, and the fixed effects were expertise level, session, and partner presence and individual identity was the random effect. We also fitted full models, containing all fixed effects, and null models, containing only the intercept and the random effect. We used likelihood ratio tests (LRT) to assess whether a factor significantly improved model fit over a reduced model without that factor. We compared Akaike's information criterion (AIC) to select the most parsimonious model with the best fit for the data. These analyses were done using the glmmTMB (Brooks et al. 2017) and lme4 packages (Bates et al. 2015) in R version 3.3.3 (R Core Team 2017).

In order to identify if social factors were playing a role in the partnerships observed in the *mixed-expertise* group, we analyzed the impact of dominance and familiarity on success and time spent at the apparatus. Ad lib data collection of pant grunts prior to and during the experiment were used to establish a dominance hierarchy using an Elo-rating (Albers and de Vries 2001; Neumann et al. 2011). Individuals were classified in equal groups as high, medium, or low ranking based on their Elo-rating. An ANOVA was used to compare the number of successes and time spent at the apparatus across rank groups. To assess the impact of familiarity, dyads were classified as either in-group (individuals who were previously in the same social group) or out-group (individuals who were newly introduced when the current group was formed). Independent samples *t* tests were used to compare the number of successes and time spent at the apparatus by group membership. These analyses were done using R version 3.3.3 (R Core Team 2017).

To compare acquisition of the task in the *mixed-expertise* group to that in the *all-novice* group, we used data from the novices in each group only. All analyses in this section were done at the individual level, that is, individuals in the *all-novice* group were compared to the individual novices in the *mixed-expertise* group. That means that data from the four experts (who once were novices in the *all-novice* group) were excluded from the *mixed-expertise* group. Data were compared using independent samples *t* tests for success, latency, efficiency, and uncoordinated pulling, with the group as the independent variable. Need for a partner was analyzed using a two-way ANOVA with partner presence and group as the independent variables and pulling rate as the dependent variable. Success, uncoordinated pulling, and pulling rate when a partner was present versus absent were not normally distributed, so the data were log-transformed and re-checked for normality prior to analysis. The analyses comparing the groups were done using IBM SPSS version 24.

Results

Success

Across the 28 1-h sessions, 12 out of 15 chimpanzees solved the task (combined in 4 of 6 possible E–E pairs, 17 of 44 E–N pairs, and 14 of 55 N–N pairs), engaging in 962 cooperative acts overall (an average of 34 per test session). The zero-inflated Poisson model revealed significant effects of session, pair type, and their interaction on the number of successes ($\chi^2(8) = 3402.2$, $P < 0.001$; Table 1). Dyads of all three pair types were roughly equally likely to succeed at least once per session (occurrence of success: $\chi^2(4) = 4.38$, $P = 0.112$), but there were differences across pair types in *how often* successful dyads cooperated ($\chi^2(2) = 36.67$, $P < 0.001$). Dyads that included at least one expert were initially responsible for the majority of successes, with N–N pairs but not E–N pairs succeeding significantly less than E–E pairs (Table 1). However, the pattern of successes changed over time ($\chi^2(2) = 141.72$, $P < 0.001$; Fig. 2). Both E–E pairs and particularly N–N pairs increased the number of successes, but successes decreased for E–N pairs. That is, over time, experts and novices tended to work together less and more with individuals of their own experience level. However, note that N–N pairs did not succeed until session 6 at all, and E–E pairs stopped after session 20.

Latency to success

A linear mixed model including session, pair type, and their interaction was the best model to predict latency ($\chi^2(5) = 103.0$, $P < 0.001$; Table 2). Specifically, the latency for both N–N and E–N pairs was initially significantly greater than that of E–E pairs ($\chi^2(2) = 8.15$, $P = 0.017$); however, only N–N latencies significantly decreased over time, whereas E–N and E–E latencies did not significantly change over time ($\chi^2(2) = 35.46$, $P < 0.001$; Fig. 3).

Efficiency (pulls to success)

Similarly, a linear mixed model including session, pair type, and their interaction was the best model to explain efficiency ($\chi^2(5) = 51.69$, $P < 0.001$; Table 2). The pattern followed that of latency described above, where N–N pairs were initially less efficient than E–E pairs ($\chi^2(2) = 8.05$, $P = 0.018$). There was no significant difference in initial efficiency between E–N and E–E pairs. Again, only N–N pairs, but neither E–N nor E–E pairs became more efficient over time ($\chi^2(2) = 22.92$, $P < 0.001$; Fig. 4).

Table 1 ZIGLMM predicting the occurrence and number of successes

Variable	b	SE	95% CI	OR	95% CI OR
Number of successes					
Intercept	0.70	1.69	(− 2.61, 4.02)	2.02	(0.07, 55.75)
Session	**0.06*** **	**0.02**	**(0.03, 0.09)**	**1.07**	**(1.03, 1.10)**
Pair type[a]					
Expert–novice (E–N)	*− 1.85*	*1.08*	(*− 3.97*, *0.26*)	*0.16*	(*0.02*, *1.30*)
Novice–novice (N–N)	**− 6.08** **	**2.14**	**(− 10.28, − 1.89)**	**0.00**	**(0.00, 0.15)**
Session × E–N	**− 0.10*** **	**0.02**	**(− 0.14, − 0.06)**	**0.90**	**(0.87, 0.94)**
Session × N–N	**0.09*** **	**0.02**	**(0.05, 0.13)**	**1.09**	**(1.05, 1.13)**
Occurrence of success					
Intercept	**2.32*** **	**0.29**	**(1.74, 2.89)**	**10.14**	**(5.71, 18.01)**
Pair type[a]					
Expert–novice (E–N)	0.24	0.34	(− 0.43, 0.91)	1.27	(0.65, 2.47)
Novice–novice (N–N)	− 0.27	0.35	(− 0.95, 0.40)	0.76	(0.39, 1.50)
Random effects					
Partner 1	SD	2.04			
Partner 2	SD	2.48			

OR odds ratio

** $P < 0.01$; *** $P < 0.001$. Coefficients significant at $P < 0.05$ indicated in bold, Ps < 0.10 in italics

[a] Dummy coded with reference category: expert–expert (E–E)

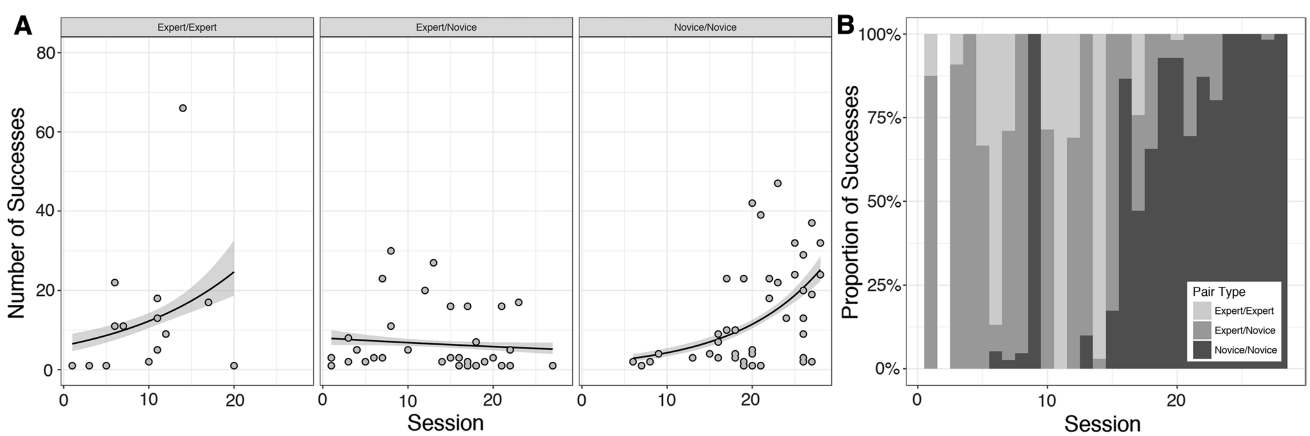

Fig. 2 **a** Number of successes by session and pair type. Black line indicates Poisson regression line, shaded area indicates 95% confidence bands. **b** Proportion of successes by session and pair type. Note that there were no successes in Session 2

Uncoordinated pulling

For uncoordinated pulling (pulling that did not lead to success), the best model only included pair type ($\chi^2(2) = 10.48$, $P = 0.005$; Fig. 5). Specifically, N–N pairs had more uncoordinated pulls than E–E pairs ($b = 11.17$, SE = 3.47, 95% CI (3.54, 18.81), $Z = 3.22$, $P = 0.002$), whereas there was no significant difference between E–N pairs and E–E ($b = 5.90$, SE = 3.38, 95% CI (− 1.54, 13.33), $Z = 1.75$, $P = 0.135$).

Partner presence

We compared rates of pulling when a partner was present and ready to pull versus when no partner was present or a chimpanzee was nearby but was not “ready” to pull. The best model only included partner presence ($\chi^2(1) = 28.84$, $P < 0.001$; Fig. 6, panels 1 and 2). Across both experts and novices, the chimpanzees pulled more when a partner was present and ready at the apparatus than when no partner

Table 2 LMMs predicting latency and efficiency

	Latency to success			Efficiency (pulls to success)		
	b	SE	95% CI	*b*	SE	95% CI
Fixed effects						
Intercept	0.33	0.18	(− 0.11, 0.77)	*7.64*	*3.24*	(*− 0.46*, *15.75*)
Session	0.01	0.01	(− 0.01, 0.03)	0.09	0.14	(− 0.25, 0.44)
Pair type[a]						
Expert–novice (E–N)	**0.31***	**0.12**	**(0.00, 0.62)**	3.02	2.02	(− 2.03, 8.08)
Novice–novice (N–N)	**0.57***	**0.20**	**(0.07, 1.07)**	**9.48***	**3.32**	**(1.16, 17.80)**
Session × E–N	− 0.02	0.01	(− 0.04, 0.00)	− 0.19	0.15	(− 0.58, 0.20)
Session × N–N	**− 0.05*****	**0.01**	**(− 0.08, − 0.03)**	**− 0.67*****	**0.16**	**(− 1.07, − 0.26)**
Random effects						
Partner 1	SD	0.10		SD	1.31	
Partner 2	SD	0.35		SD	7.15	

* $P < 0.05$; *** $P < 0.001$. Coefficients significant at $P < 0.05$ indicated in bold, Ps < 0.10 in italics

[a] Dummy coded with reference group: expert–expert (E–E)

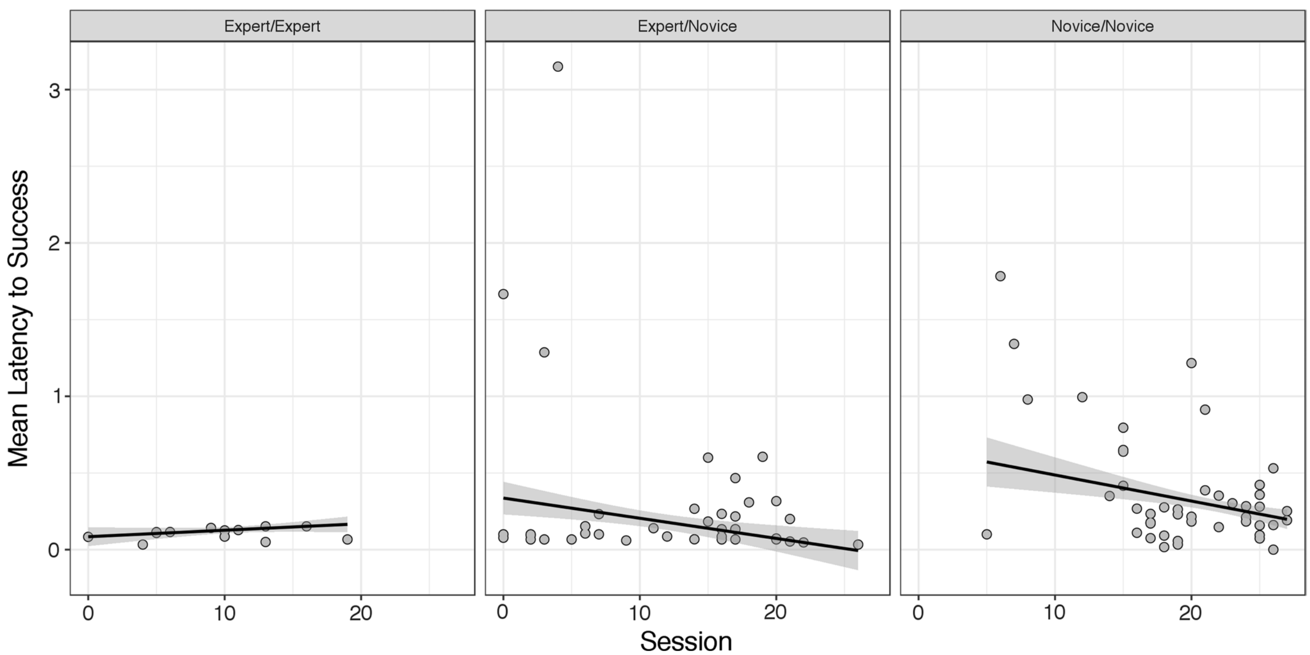

Fig. 3 Mean latency to success (in minutes) over time by pair type

was present ($b = 7.00$, SE = 1.26, 95% CI (4.21, 9.80), $Z = 5.55$, $P < 0.001$).

Social factors

Dominance rank had no significant impact on the amount of time individuals spent at the apparatus ($F(2,12) = 0.19$, $P = 0.826$). Descriptively, low-ranking (rather than high-ranking) individuals spent the most time at the apparatus, on average (low: $M \pm SD = 102.05 \pm 78.06$ min, middle: $M \pm SD = 92.12 \pm 160.27$, high: $M \pm SD = 60.16 \pm 72.30$). Similarly, there was no significant effect of rank group on the amount of success (low: $M \pm SD = 158.4 \pm 138.64$, middle: $M \pm SD = 131.2 \pm 212.08$, high: $M \pm SD = 116.80 \pm 163.77$; $F(2, 12) = 0.07$, $P = 0.93$). Familiarity, or whether individuals were members of the same group prior to the current study, similarly had no significant effect on the amount of time dyads spent at the apparatus (in-group: $M \pm SD = 5.67 \pm 8.25$ min, out-group: $M \pm SD = 4.84 \pm 14.00$; $t(103) = -0.20$, $P = 0.843$) or success (in-group: $M \pm SD = 19.17 \pm 34.54$, out-group: $M \pm SD = 8.45 \pm 29.17$; $t(103) = -1.17$, $P = 0.244$).

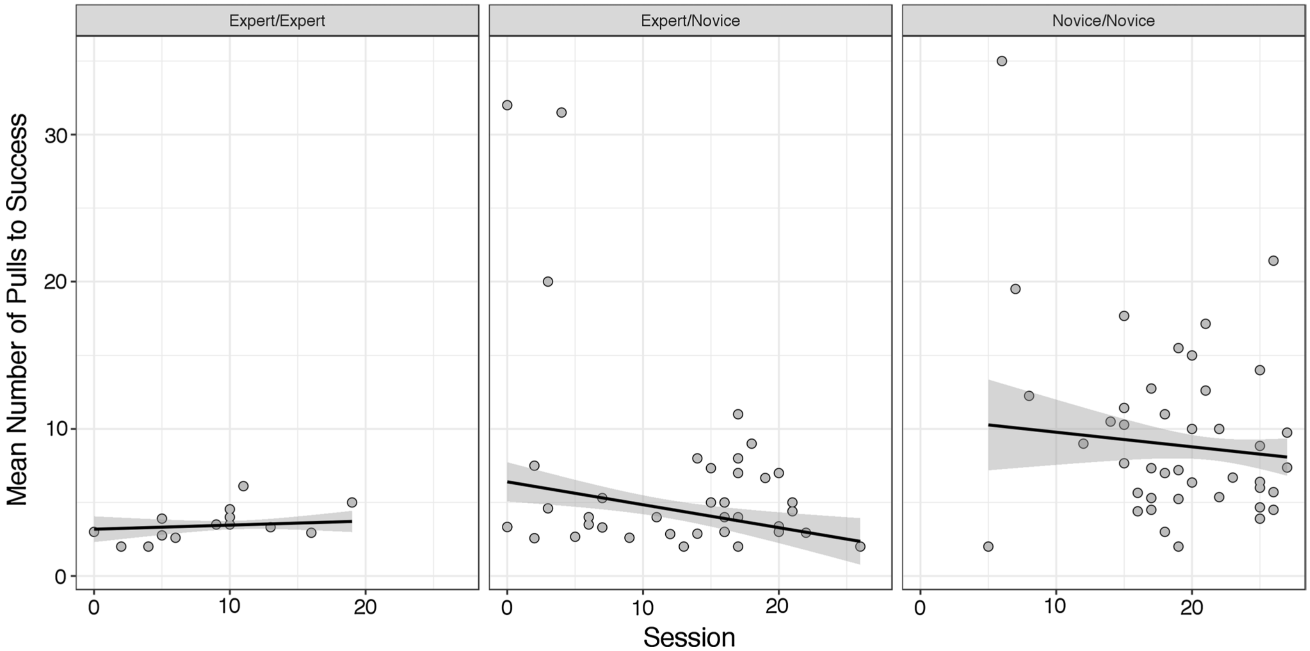

Fig. 4 Mean efficiency (total number of pulls to success for each dyad) over time by pair type. Note that a lower number of pulls indicates higher efficiency (fewer extraneous pulls prior to success)

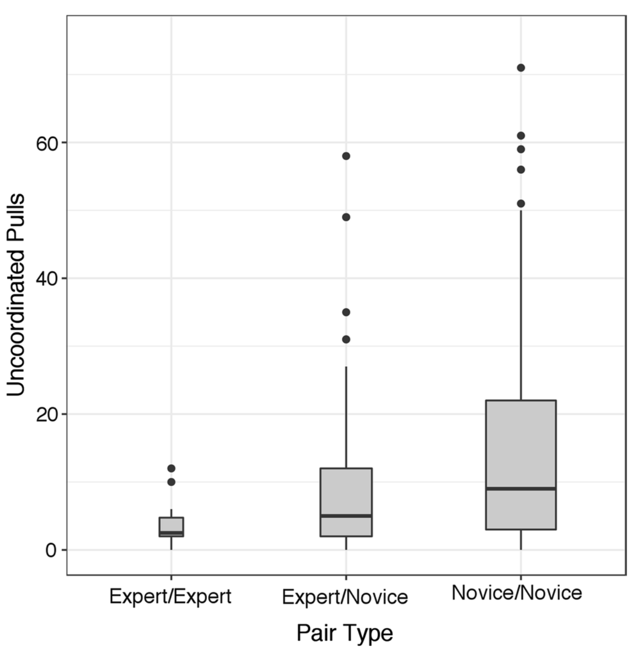

Fig. 5 Number of uncoordinated pulls by pair type, i.e., total number of pulls while a partner was present that did not lead to success. Box plots show the median (solid horizontal line), inter-quartile range (IQR; hinges), values within 1.5 × IQR (whiskers), and outliers (solid circles). Box width is proportional to square root of the number of observations

Comparison between the all-novice and mixed-expertise groups

There was no significant difference in the number of successes by individual novices in the *mixed-expertise* group ($M \pm$ SD = 163.88 ± 179.39) compared to individuals in the original *all-novice* group ($M \pm$ SD = 148.40 ± 194.49; $t(16) = 0.10$, $P = 0.92$). However, the *mixed-expertise* group had a significantly lower latency to success across all individuals (*mixed-expertise*: $M \pm$ SD = 0.19 ± 0.09 min, *all-novice*: $M \pm$ SD = 0.40 ± 0.18 min; $t(16) = 3.01$, $P = 0.008$). The total number of pulls each dyad needed to succeed were relatively similar across groups (*mixed-expertise:* $M \pm$ SD = 3.58 ± 1.36, *all-novice:* $M \pm$ SD = 3.00 ± 0.82; $t(16) = 1.11$, $P = 0.29$), but novices in the *mixed-expertise* group had a significantly higher pulling *rate* (pulls per minute) than novices in the *all-novice* group ($M \pm$ SD = 17.81 ± 2.41 vs. 7.24 ± 1.03 pulls per minute; $t(16) = 4.35$, $P < 0.001$, Fig. 7a). This is likely due to the average lower latency to success in the *mixed-expertise* group; because it took them less time to succeed but the same number of pulls, they were pulling at a higher rate. Similarly, the total number of uncoordinated pulls for each dyad were relatively similar across groups (*mixed-expertise:* $M \pm$ SD = 261.00 ± 268.11, *all-novice:* $M \pm$ SD = 208.09 ± 174.96; $t(19) = -0.36$, $P = 0.72$). However, as with pulls that led to success (efficiency), novices in the *mixed-expertise* group again had a significantly higher uncoordinated pulling rate (pulls per minute) than novices in

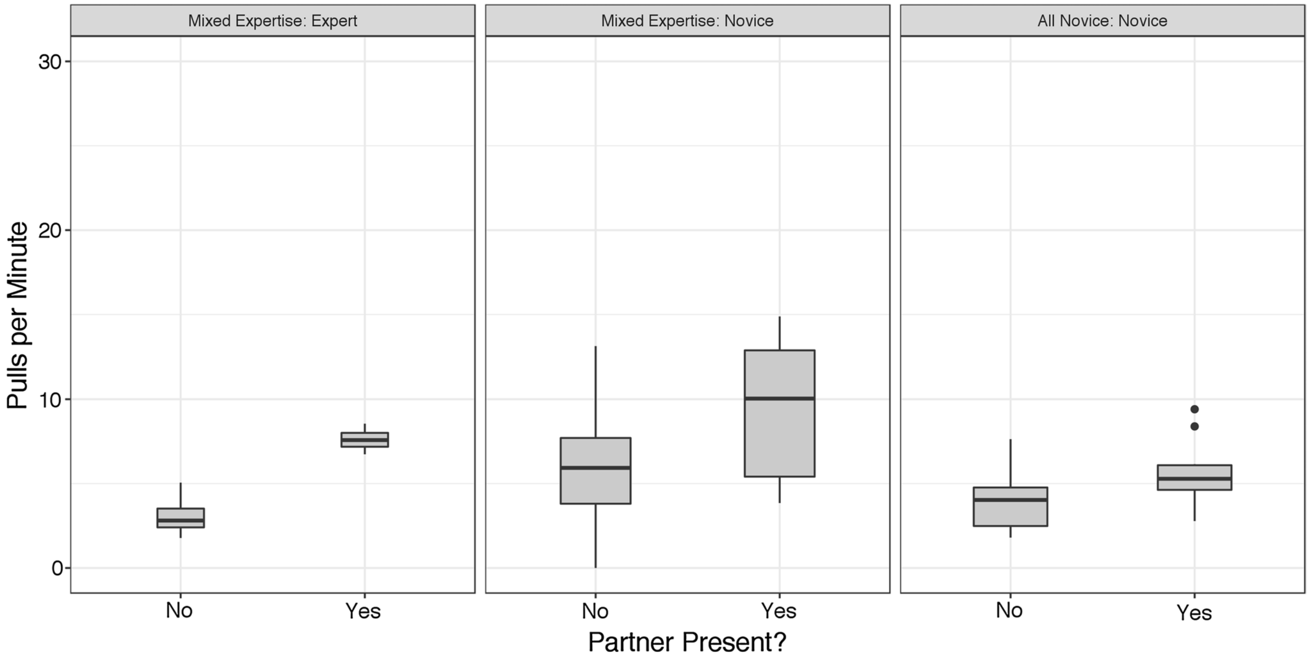

Fig. 6 Pulling rate over time by status and partner presence at the apparatus

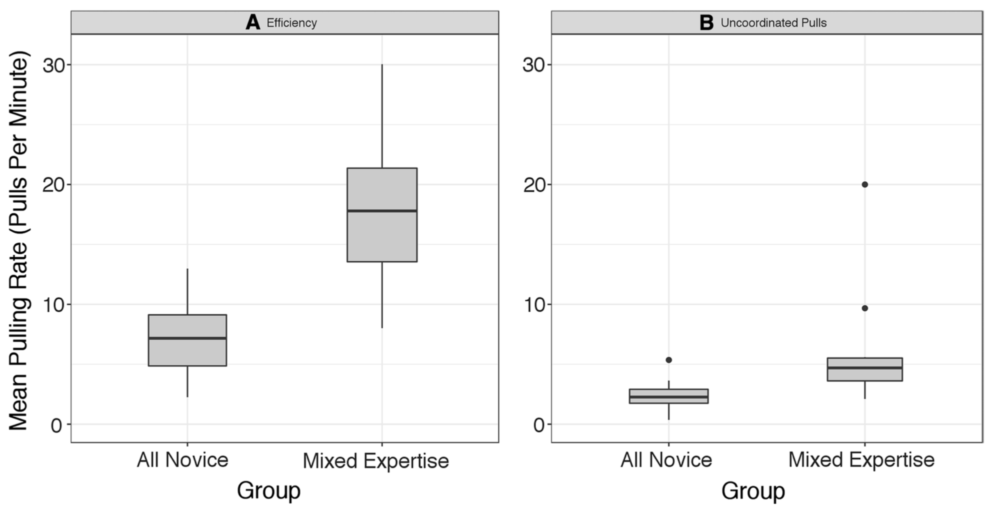

Fig. 7 **a** Mean efficiency rate and **b** uncoordinated pulling rate of novices in the *all-novice* group compared to novices in the *mixed-expertise* group

the *all-novice* group ($M \pm$ SD = 6.22 ± 5.28 vs. 2.38 ± 1.36 pulls per minute; $t(19) = -3.07$, $P = 0.006$, Fig. 7b) when it did not lead to success. Finally, although both the *mixed-expertise* and *all-novice* groups showed a similar pattern with regard to partner presence (Fig. 6; panels 2 and 3), pulling significantly more when a partner was present (*mixed-expertise:* $M \pm$ SD = 9.27 ± 3.99 pulls/min with a partner present vs. 5.84 ± 4.24 with no partner, *all-novice:* $M \pm$ SD = 5.55 ± 2.09 pulls/min with a partner present vs. 4.09 ± 1.89 with no partner; $F(1, 17) = 14.71$, $P = 0.001$), the *mixed-expertise* group had a nonsignificant trend toward a higher rate of pulling overall compared to the *all-novice* group (*mixed-expertise:* $M \pm$ SD = 7.56 ± 4.37, *all-novice:* $M \pm$ SD = 4.82 ± 2.08; $F(1,17) = 4.35$, $P = 0.052$). Thus, across several measures, novices in the mixed-expertise group had a higher pulling rate, but similar overall number of pulls, meaning they were pulling the same amount, but more rapidly and for shorter durations of time.

Discussion

In this study, we examined the impact of the presence of experts on acquisition of a cooperative task. Our hypothesis that experts would facilitate the success of the novices was not supported. The analysis demonstrates that although novices were initially only successful when paired with experts and despite various opportunities for competitive interactions (such as freeloading, displacement, or agonism; Suchak et al. 2016), they quickly developed competency at the task, solving it in novice–novice pairs as early as session 6. It is particularly interesting that there are peaks in latency as well as inefficiency (extraneous pulling prior to success), for N–E pairs in session 5, and for N–N pairs in session 7. Similarly, there was a peak in novices pulling without a partner present in session 5. These sudden spikes may reflect the trial and error learning process occurring for the novices as they learned the contingencies of the apparatus. Most of the successes in the early sessions were from N–E pairs, rather than E–E pairs (Fig. 2b), suggesting that the novices may have learned as they were working, rather than by observing E–E pairs work at the apparatus.

When compared with an earlier group of all novices, however, it becomes clear that the experts did not necessarily facilitate their understanding of the task and thus our second hypothesis, that this *mixed-expertise* group would have better performance than a previous group of *all-novices* was not supported. The total effort put forth by individuals in each group (as measured by the absolute number of pulls on the apparatus) was relatively similar, resulting in similar efficiency and uncoordinated pulling. Rates of pulling reflect both the absolute effort put in as well as the amount of time, and the novices in the *mixed-expertise* group had higher rates of pulling for both efficiency and uncoordinated pulling, and a trend for a higher pulling rate overall compared to the *all-novice* group. The difference suggests that novices in the *mixed-expertise* group pulled relatively rapidly for shorter periods of time as compared to novices in the *all-novice* group. This may have resulted from their initial pairing with experts in the early sessions, which may have facilitated quick and frequent successes throughout the experiment. This might be interpreted as the novices in the *mixed-expertise* group showing higher proficiency than the *all-novice* group. However, historically, careful coordination has been best exemplified in studies where individuals must inhibit their behavior or perform complementary actions which necessitate waiting for the partner (Melis et al. 2006a, b, 2013; Hirata and Fuwa 2007). Therefore, faster pulling is not necessarily indicative of better understanding and one might argue that the slower pulling rates in the *all-novice* group might indicate a more methodical approach and greater inhibition of behavior. Similar to previous studies of birds and nonhuman primates, success is still possible when there are high pulling rates without precise coordination and the partner becomes a cue to pull at the apparatus (Chalmeau et al. 1997; Visalberghi et al. 2000; Seed et al. 2008; Péron et al. 2011; Jelbert et al. 2015). Thus, novices in the *mixed-expertise* group may have experienced social facilitation to pull when a partner is present, which was less likely in the *all-novice* group.

It is possible that short, rapid interactions with the apparatus seen in the *mixed-expertise* group might result from social intolerance, rather than social facilitation. The need for tolerant cooperative partnerships is well substantiated in the literature (Melis et al. 2006b; Suchak et al. 2014). In our study, it was possible for dominant individuals to monopolize the apparatus, preventing subordinate individuals from spending quality time learning the contingencies. However, this was not the case because we found no impact of dominance on time spent at the apparatus or amount of success. In our previous work, we have also demonstrated that all individuals in a group tend to have access to the apparatus, and while preferred partnerships tend to minimize conflict (by, for example, approaching someone of similar rank), when conflict does arise, the chimpanzees are quite well able to overcome it to favor cooperation (Suchak et al. 2014, 2016).

However, the *mixed-expertise* group was also newly formed, whereas the *all-novice* group had been living together for decades prior to testing. Our previous work demonstrated that, although the newly formed group was engaged in nearly three times more agonism outside of the experimental context than the original group, they actually had fewer displacements at the apparatus and a similar amount of freeloading during the experiment (Suchak et al. 2016). Furthermore, in the current study we found that dyads that were previously members of the same group, which would presumably result in higher comfort working together, did not spend more time at the apparatus or have more success together. Taken together, the social data suggest it is unlikely that the rapid pulling resulted from social intolerance or a lack of comfort with out-group individuals at the apparatus.

We did not see any change in the experts' behavior over time when paired with other experts, which is to be expected since there should have been little to no learning during this experiment for them. A previous study by Povinelli and O'Neill (2000) also found that experts did not change their behavior in response to working with novices. However, in their study, expert–novice pairs routinely failed to succeed at the cooperative task. In contrast, in our study, not only were expert–novice pairs quite successful, but so were novice–novice pairs. In fact, our results look similar to a study examining cooperation in mixed-expertise groups of hyenas, where expert–novice pairs fell midway between the performance of two experts or two novices together (Drea and Carter 2009).

Together, these findings suggest that although the *mixed-expertise* group experienced a great deal of success, novices may not have been closely coordinating with their partners due to their rapid interactions. The question remains why the novices did not appear to benefit from the presence of experts. One possibility is that the task was not difficult enough to require social learning. Although most cooperative pulling studies have required extensive training, and therefore it would be expected that novices might benefit from social learning, novices in the *mixed-expertise* group may have had sufficient productivity such that asocial learning was the preferred strategy (Laland 2004). A more difficult task or a task with less obvious causality might elicit a greater reliance on social learning. Another possibility is that experience with others of the same skill level would have benefited the novices prior to being tested with the experts. In studies of elite human performance in areas such as chess, music, and sports, researchers have suggested that most experts started by engaging with other novices before moving onto practice with individuals of higher expertise (Ericcson et al. 1993). This early phase of learning with other novices provides the individual with feedback and the opportunity to correct errors. Future studies may want to investigate the role of experts once novices have had some baseline exposure to the task.

What is peculiar about our studies is that despite both groups appearing to primarily use trial and error learning, the two groups spontaneously developed different pulling rates, which resulted from different amounts of time spent at the apparatus. This suggests that there may be flexibility in developing proficiency in a task such as this one and the failure of one individual or a group of individuals may not be indicative of that species' capabilities as a whole.

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Compliance with ethical standards

Conflict of interest Malini Suchak, Julia Watzek, Luke F. Quarles, and Frans B.M. de Waal declare that they have no conflict of interest.

Ethical standard All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures were approved by Emory University's Institutional Animal Care and Use Committee (IACUC), protocol #YER-2000180-53114GA prior to commencement of the study. The YNPRC is furthermore fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AAALAC).

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