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Group size and social rank predict inhibitory control in spotted hyaenas

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Inhibitory control is the ability to resist performing a prepotent, but ultimately incorrect, behaviour in situations that demand restraint. Inhibitory control is linked to brain size and intelligence in humans and animals, but it is unclear just how it evolves. Inhibitory control is thought to be particularly important in complex social environments where demands can shift frequently based on the social context and the identities or behaviours of other individuals in a group. Indeed, the social intelligence hypothesis suggests that the demands of living in complex social groups led to the evolution of sophisticated cognition. Here, we tested inhibitory control in wild spotted hyaenas, *Crocuta crocuta*, whose large social groups are structured by linear dominance hierarchies. We tested inhibitory control using the cylinder test, which requires subjects to inhibit going straight for a food reward. In support of our predictions, hyaenas living in larger groups had greater inhibitory control. In particular, the size of the cohort in which young hyaenas grew up, rather than the size of adult groups, had the strongest effect. In addition, the effect of group size was significantly stronger for low-ranking hyaenas, which must frequently inhibit both feeding and aggression in the presence of higher-ranking hyaenas. Contrary to our predictions, adult male hyaenas, which always occupy very low rank positions as adults, did not have better inhibitory control than adult females. This suggests that inhibition is not a canalized trait, but instead may be a flexible one such that its development is influenced by early life social environments.

Inhibitory control is the ability to resist performing a prepotent, but ultimately incorrect, behaviour in situations that demand restraint (Aron, 2007; Bari & Robbins, 2013). This cognitive skill is generally thought to be crucial to complex cognition, problem solving and behavioural flexibility (Diamond, 2013). It has been broadly studied in humans and other animals, and is strongly related to intelligence and measures of life success in humans (Diamond, 2013; Mischel, Shoda, & Rodriguez, 1989) and to brain size in nonhuman animals (Horschler et al., 2019; Kabadayi, Taylor, von Bayern, & Osvath, 2016; MacLean et al., 2014). However, we know very little about the circumstances favouring the evolution of inhibitory control.

One of the most popular hypotheses for the evolution of complex cognition is the social intelligence hypothesis (SIH), which suggests that the demands of living in complex social groups have led to the evolution of large brains and greater intelligence (Byrne & Whiten, 1988; Dunbar, 1998; Humphrey, 1976). Inhibition is thought to be particularly important in complex social environments where demands can shift frequently based on the social context and the identities or behaviours of other group members (Aureli et al., 2008). In social environments like these, restraining impulsive behaviour is necessary to maintain a stable or cohesive social group (Amici, Call, Watzek, Brosnan, & Aureli, 2018; Bjorklund & Harnishfeger, 1995; Byrne, 1995; Byrne & Bates, 2007; de Waal, 2013; Dunbar & Shultz, 2007; Marshall-Pescini, Virányi, & Range, 2015). In particular, the inhibition of feeding and other behaviours when more dominant individuals are present is a common challenge for gregarious animals living in societies structured by dominance hierarchies (Amici et al., 2018). Skills such as tactical deception require a high degree of inhibitory control, and such skills are particularly adaptive in societies where dominance hierarchies determine access to food and mates (Amici et al., 2018; Menzel, 1974; Whiten & Byrne, 1988). For instance, a low-ranking male primate might inhibit his vocalizing during mating to avoid attracting the attention of more dominant males. Indeed, research on primates suggests that living in social systems with steeper dominance hierarchies and higher degrees of fission–fusion dynamics may be associated with better

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inhibitory control (Amici, Aureli, & Call, 2008; Amici, Call, & Aureli, 2009). However, research on the SIH has largely used the comparative approach, which ignores the large amount of observed intraspecific variation in both social demands and cognitive abilities. Recently, there has been growing interest in examining this intraspecific variation in cognitive abilities in wild subjects in order to directly quantify social complexity and cognition in an ecologically valid context (Ashton, Thornton, & Ridley, 2018; Whiten, 2018). Here, we experimentally measured inhibitory control in a population of free-living spotted hyaenas, *Crocuta crocuta*, to test predictions of the SIH in regard to inhibition, and inquire how varying social demands might shape variation in inhibitory control.

Spotted hyaenas live in complex social systems that exhibit a high degree of fission–fusion dynamics (Smith, Kolowski, Graham, Dawes, & Holekamp, 2008) and that are structured by strict linear dominance hierarchies that show remarkable convergence with those structuring the societies of many cercopithicine primates (Holekamp, Sakai, & Lundrigan, 2007). This convergent social complexity makes them ideal subjects for testing hypotheses about the evolution of social intelligence. Spotted hyaena social groups, called clans, range in size from 15 to 130 individuals (Holekamp, Dantzer, Stricker, Shaw Yoshida, & Benson-Amram, 2015) and are composed of multiple matrilines of unrelated females, their offspring and one to several adult immigrant males. Rank is not genetically determined; instead, it is ‘inherited’ behaviourally via maternal interventions and other learning situations, and offspring of both sexes typically rank just below their mothers in the clan's dominance hierarchy (Engh, Esch, Smale, & Holekamp, 2000). Female hyaenas are philopatric whereas males nearly always disperse after reaching sexual maturity (2–5 years of age) to join neighbouring clans (Van Horn, McElhinny, & Holekamp, 2003). Maintenance of rank relationships depends heavily on social support (Strauss & Holekamp, 2019; Vullioud et al., 2019), so the highest-ranking individuals in a hyaena clan are always female because male hyaenas, who lack support from their kin in their new groups after dispersal, join their new clan at the very bottom of its dominance hierarchy. Many male hyaenas must therefore go through the sudden transition of having a relatively high rank at birth in their natal clan to an extremely low rank in adulthood in the clans to which they disperse. Previous research on spotted hyaena cognition suggests that they share many of the same sociocognitive abilities possessed by cercopithecine primates; for example, spotted hyaenas show individual recognition of clanmates through multiple modalities and the ability to recognize third-party relationships, and are able to use their knowledge about their clanmates' rank to make adaptive decisions (Holekamp et al., 2007).

The SIH generates several predictions about inhibitory control that we tested in wild spotted hyaenas. Because low-ranking hyaenas must more frequently inhibit feeding and aggression in the presence of higher-ranking individuals than do their higher-ranked groupmates, and because male hyaenas nearly always attain very low ranks as adults, we predicted that adult male hyaenas would have greater inhibitory control than adult females. This prediction was also based on previous research showing that the volume of the frontal cortex is significantly larger in male spotted hyaenas than in female hyaenas; frontal cortex is an area of the brain thought to be centrally involved in social cognition and inhibitory control (Arsznov, Lundrigan, Holekamp, & Sakai, 2010). Next, if inhibitory control is a plastic trait, rather than a fixed one, low-ranking individuals of either sex should also show higher inhibitory control in standardized tests than high-ranking individuals. In addition, we might expect dispersal status of males to play a role: low-ranking immigrant males should have greater inhibitory control than adult natal male hyaenas, of similar age, who have not yet dispersed and who therefore retain their mothers' ranks in the natal group.

In addition to the demands imposed by social rank, larger numbers of individuals in a group may also demand greater inhibitory control (Ashton, Ridley, Edwards, & Thornton, 2018). Group size is frequently used as measure of social complexity; larger groups may be more cognitively demanding due to increasingly complex social structures and exponential increase in the numbers of relationships and interactions with groupmates (Kappeler, 2019). We therefore predicted that clan size would be positively related to inhibitory control. Finally, most cognitive abilities also show developmental effects; mature individuals typically show enhanced abilities relative to those found in juveniles or subadults (Diamond, 1990, 2013). Therefore, we also predicted that subadult hyaenas would have poorer inhibitory control than adult hyaenas.

METHODS

Subjects and Subject Participation

Subjects were from two populations of wild spotted hyaenas living in the Maasai Mara National Reserve (MMNR), Kenya. The data used in this study were collected between June 2016 and December 2017, but these two populations have been monitored continuously for demographic and behavioural data from 1988 and 2008 onward, respectively. Thus all hyaena ages and social rank positions were known. All hyaenas in these populations are well habituated to the presence of observers in research vehicles and are identifiable individually by their unique spot patterns and ear damage, making it possible to collect detailed information on individuals across their life spans. We selected hyaenas from five different clans containing 66–118 individuals per clan during the study period. Unrelated hyaena cubs within the same clan are raised together at a communal den for protection (Holekamp & Dloniak, 2010). Only hyaenas that were independent of the communal den were used for testing, and within that group, hyaenas self-selected as those choosing to participate in the inhibitory control test. Although self-selection is a source of bias, participation was relatively high and a wide representation of all age, sex and rank classes was obtained. Overall, roughly half of all hyaenas given opportunities to participate in a familiarization trial with the inhibitory control apparatus prior to testing chose to do so (92 out of 195 den-independent individuals). Participation was defined as the completion of a trial by feeding from the apparatus. Sixty-two hyaenas subsequently participated in at least one test trial after passing familiarization trial criteria.

Experimental Apparatus

We measured inhibitory control using the ‘cylinder task’, which is a scaled-down detour-reaching test (Fig. 1). Detour-reaching tests in general, and the cylinder task in particular, are used extensively for measuring sensory–motor inhibitory control (Kabadayi, Bobrowicz, & Osvath, 2018). These tests require the subject to detour around a barrier (such as a fence or transparent wall) to reach a visible reward. Detouring requires the subject to initially move away from the reward and inhibit an impulse to move straight towards the reward. A successful trial, or a ‘pass’, is scored if the subject detours without bumping into or touching the barrier, and an unsuccessful trial or a ‘failure’ of inhibition is scored if the subject bumps into or touches the barrier in an attempt to move towards the reward. Detour tests have high ecological validity because animals must detour around obstacles in nature, and high construct validity because they have been long established as accurately measuring executive control (Kabadayi et al., 2018).

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Figure 1. The apparatuses used to test inhibitory control: (a) the white cylinder used during familiarization trials; (b) the transparent cylinder used during test trials.

We also thought a detour task would be particularly appropriate for testing inhibitory control in spotted hyaenas because it specifically measures the ability to inhibit approach towards a food reward, just as low-ranking hyaenas must inhibit approaching food when a higher-ranking hyaena is present. The cylinder detour task is also well suited for testing in the field because its apparatus is easy to deploy; we have also used this task successfully with captive hyaenas (Johnson-Ulrich, Johnson-Ulrich, & Holekamp, 2018). The relatively small size of the cylinder means that it does not create an artificial requirement for spatial reasoning, and unlike nondetour tests of inhibitory control, it requires no knowledge of object permanence or other object affordances (Jelbert, Taylor, & Gray, 2016). Variation in experience with clear objects can influence subjects' performance with the cylinder task (van Horik et al., 2018), but all subjects in the current study were wild hyaenas that were all completely inexperienced with clear objects.

The cylinders used here measured 30.5 cm in diameter and 46 cm in length and were constructed of 1 cm thick plastic. A white PVC cylinder was used for familiarization trials (Fig. 1a), and a clear cast acrylic cylinder (Fig. 1b) was used for test trials. Spotted hyaenas have a keen sense of smell, so unlike previous studies with the cylinder task, we bored 15 holes (2.5 cm diameter) into the wall of each cylinder to control for the fact that the scent of a food reward might lead the hyaenas to successfully retrieve food without inhibiting their approach to the food directly.

Test Protocol

Focal hyaenas were located during daily observation periods from 0530 to 0930 hours and again from 1700 to 2000 hours, which are the periods each day when spotted hyaenas are most active. Hyaenas were only tested when they were alone, which was determined if no other hyaenas were in sight or known to be present within approximately 200 m. The cylinder was baited with a piece of meat weighing approximately 200 g, placed directly in the centre of the cylinder. Bait was nearly always goat meat, but some trials were conducted with beef or mutton. Participation in trials with the baited apparatus appeared unaffected by the type of bait used (Appendix Table A1). Our research vehicle served as a mobile blind from which the cylinder was placed horizontally on the ground with the long side facing the hyaena. After deployment, the research vehicle was driven 20–50 m away, and the entire trial was videotaped. Trials began when the cylinder was deployed. Trials ended when either the bait was retrieved, or when the focal hyaena failed to participate by going of sight, moving outside the 200 m test radius, or lying down for at least 15 min. Trials where hyaenas failed to participate were not included in our analysis. Average (± SD) trial duration was 2.85 ± 2.76 min (median = 2 min, range 0–23 min). If other hyaenas arrived during a trial we collected the still-baited apparatus and paused testing until the other hyaena(s) moved to more than approximately 200 m from the focal hyaena or went out of sight. If the newly arrived hyaena(s) did not leave within 20 min, we ended testing with the focal hyaena for the day.

All hyaenas were initially given familiarization trials using the opaque white PVC cylinder. A 'pass' was recorded if the hyaena successfully retrieved the meat without touching the outside of the cylinder (Supplementary Video S1). A 'fail' was recorded if the hyaena touched the outside of the cylinder with its nose (Supplementary Video S2). Hyaenas sometimes sniffed the outer rim of the cylinder before they inserted their heads inside the cylinder to retrieve the food, especially during familiarization trials; this touching of the outer rim only was considered exploratory behaviour (see Kabadayi et al., 2017). Therefore, touching just the outer rim, which was immediately before the hyaena inserted its head into the cylinder to retrieve the meat, was not recorded as a fail (Supplementary Video S3). After a hyaena passed four out of five consecutive familiarization trials (with a minimum of five trials), it was given a maximum of 11 test trials with the transparent acrylic cylinder. While all attempts were made to give every hyaena at least 10 test trials, the difficulties of field testing meant that not all hyaenas received this number of trials (mean ± SD = 8.92 ± 3.09 trials, median = 10 trials, range 1–11 trials). Only 12 out of 60 hyaenas received fewer than 10 trials. If a hyaena retrieved and ate the bait, and if it had moved at least 5 m away from the cylinder, the cylinder was immediately rebaited for successive trials. Successive trials were administered to a hyaena as long as conditions allowed researchers to do so. For example, successive testing was discontinued if the hyaena stopped participating (as described above), bait supply was exhausted, or rain, other inclement weather or darkness made testing impracticable. Mean (± SD) test session duration was 10.62 ± 10.63 min (median = 8 min, range 0–57 min). Hyaenas were given an average (± SD) of 4.64 ± 2.96 trials per session (median = 4 trials, range 1–10 trials) and completed testing in 1.92 ± 0.96 sessions (median = 2 sessions, range 1–5 sessions). Most test trials were completed less than 1 day apart ($N = 479$ out of 539 trials); however, some hyaenas were not located again for further testing for extended periods. The average (± SD) number of days between trials was 5.32 ± 30.74 days (median = 0 days, range 0–280 days). Only 10 trials were conducted with more than 100 days separating them from the last trial with the same hyaena and these 10 trials did not appear to differ in any measurable way from all other trials. Specifically, removing these 10 trials from our analyses did not alter the significance of any independent variables in our final models.

Because hyaenas were given 360-degree access to the tube, we also recorded the direction of their approach as perpendicular, parallel or 'other' if the approach did not follow a straight line

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(Supplementary Video S4). In addition, hyaenas approached the cylinder at variable speeds, potentially indicating variation in motivation. Therefore, we recorded their latency to approach from 5 m to 1 m of the cylinder in seconds. Both latency to approach and direction of approach were included as extraneous variables in our statistical analysis. All videos were coded by L.J.U.; videos were named with a unique trial number.

Supplementary video related to this article can be found at https://doi.org/10.1016/j.anbehav.2019.11.020

Predictor Variables and Extraneous Variables

We had five main predictions about intraspecific variation in inhibitory control regarding social rank, sex, dispersal status, clan size and age of spotted hyaenas. Social rank was treated as a continuous variable; all individuals in a clan were assigned a numeric rank based on their position in the hierarchy. Ranks used in the current analysis were assigned based on the clan hierarchy at the start of the study in June 2016. This hierarchy was generated using a dominance matrix ordering observations of aggressive or submissive behaviours within dyads of hyaenas over the age of 24 months (Holekamp, Smith, Strelioff, Van Horn, & Watts, 2012; Martin, Bateson, & Bateson, 1993). Hyaenas younger than 24 months of age were assigned a rank directly below that of their mother. Although an individual hyaena's rank may vary across time, most rank changes are small and caused by births and deaths such that rank relative to other clan members remains stable even if the numeric value fluctuates slightly (Strauss & Holekamp, 2019). Rank reversals are rare in this species (Vullioud et al., 2019), and none are known to have occurred during the study period. In our analysis, each hyaena's numeric rank was scaled and centred, with a score of 1 for the highest-ranking individual in a clan and a score of −1 for the lowest. Scaling and centering was done in order to obtain a relative, rather than absolute, value for social rank that was independent of clan size. Hyaenas were sexed based on the morphology of the penis in males or pseudopenis in females. Dispersal status was described either as ‘natal’, for hyaenas born in the current clan, or as ‘immigrant’, for immigrant males. Group size was measured in two different ways. First, overall clan size was approximated as the total number of individuals in a clan at the time of testing. Group size is also known to have effects on cognition during early life development (Ashton, Ridley, et al., 2018); we therefore also measured group size as the number of individuals in each hyaena's communal den cohort. The size of the communal den cohort was calculated as the number of cubs whose period of residence at the communal den overlapped for at least 4 months with that of every other young hyaena present at the den. In our sample, sizes of these communal den cohorts ranged from 4 to 31 cubs. We initially calculated age as a continuous variable rounded to the nearest month; however, age appeared to have a nonlinear relationship with inhibitory control (see Statistical Analysis) and it was therefore binned into three categories: subadults (0–2 years), young adults (2–5 years) and adults (>5 years).

We also measured several extraneous variables that were related to the conditions of each trial, other characteristics of each hyaena subject, or characteristics of the testing environment that might have affected trial success independent of a hyaena's inhibitory control. Hyaena body condition was included with three levels (gaunt, unremarkable or fat); body condition generally indicates how recently a hyaena has eaten (Kruuk, 1972) and might affect motivation to obtain a food reward. Likewise, the annual wildebeest migration in the MMNR represents a massive influx of prey for spotted hyaenas (Holekamp, Smale, Berg, & Cooper, 1997) and this too could potentially affect motivation. Therefore, we also included ‘season/migration’ to indicate whether or not the migration was present in the Reserve when a particular trial was conducted. Although every possible attempt was made to test hyaenas only when they were alone, during 48 of 539 trials, one or two other individuals also showed up. Because this number of additional hyaenas present only varied from one to two, we included testing group size as a categorical variable of either one or more than one. We also included a variable to indicate the number of these additional hyaenas that were higher ranking than the hyaena being tested, and this variable was likewise binned as a categorical variable of either one or more than one additional higher-ranking hyaena. Some studies using the cylinder task have reported an effect of learning across trials, which can positively bias results (Kabadayi et al., 2017). To control for any potential learning effects, we recorded trial number both across all trials and within each testing session. Because the amount of time between trials and between testing sessions varied, we also included a variable for the number of days elapsed since a hyaena's last trial (see Test Protocol). The number of days elapsed since a hyaena's last trial also appeared to have a nonlinear relationship with inhibitory control; because nearly all trials occurred on the same day, we binned this variable into a binary variable of zero days and one or more days. Last, we included variables for the latency to approach and direction of approach, as described above in Test Protocol. Latency to approach was binned into a categorical variable of either fast or slow because it appeared to have a nonlinear relationship with inhibitory control and was highly left-skewed. The median latency to approach was 6 s (mean ± SD = 11.96 ± 23.62), so we classified fast approaches as those in which the hyaena's latency to get from 5 m to within 1 m of the cylinder was less than or equal to 6 s, and slow approaches as those in which the hyaena's latency was greater than 6 s.

Statistical Analysis

We analysed the factors affecting inhibitory control using generalized linear mixed models (GLMMs) with a logarithmic link function. All statistical analysis was done using R v.3.5.0 (R Core Team, 2018). Inhibitory control, our dependent variable, was recorded binarily as ‘pass’ or ‘fail’. One assumption of binomial models is that independent variables show a linear relationship with the dependent variable on a log-odds scale (Burnham & Anderson, 2002). Therefore, prior to the creation of any model, all continuous variables were examined to determine whether they met this assumption. Integer count variables with less than four unique values were treated as categorical. This was done for age, clan size, test group size and number of days passing between a hyaena's trials (see Predictor Variables and Extraneous Variables). We also examined evidence for multicollinearity using variance inflation factors (VIFs) prior to creating our global models. Any variable with a VIF >3 was excluded (Zuur, Ieno, & Elphick, 2010). Ultimately, all VIFs were <3.

We created three models, the first to test predictions about sex, rank, age effects and clan size effects ($N = 60$ subjects), the second included data only from male hyaenas to test predictions about dispersal status ($N = 26$ subjects), and the third included only data from hyaenas for whom we were able to calculate cohort size ($N = 42$ subjects) to test predictions about effects of this form of group size. All three models included rank, age and clan size. Model 2 did not include sex because only males were included in this model, but it did include a binary natal versus immigrant variable. Model 3 added the variable cohort size. All three models included a random effect of hyaena identity.

To investigate the effect of extraneous variables on inhibitory control, we also created three ‘global’ models that added every extraneous variable we measured to our initial three models (see

Predictor Variables and Extraneous Variables above). Because we had no a priori expectations about the size or direction of the effect of these extraneous variables, we initially used exploratory model analysis to identify which extraneous variables were actually important (Whittingham, Stephens, Bradbury, & Freckleton, 2006). For exploratory model analysis, we used the Dredge function in the R package MuMIn (Bartoń, 2019). Dredge is a model selection function that systematically examined models containing all possible combinations of the extraneous variables included in our three global models. Variables for which we had specific predictions (e.g. rank and sex) were always included in every variable combination examined across models. Models were ranked by Dredge for their goodness of fit using Akaike's information criterion with a correction for small sample sizes (AICc). Top models were defined as those for which the improvement in AICc was <4 (Burnham & Anderson, 2002; Wisnieski et al., 2019). Although Dredge did not produce a single top model from any of our three global models, only two extraneous variables, latency to approach and direction of approach, were included in all top models for each of our three global models (Appendix Table A2). These were also the only two variables to have large and significant effects in every top model. None of our other extraneous variables had significant effects. Therefore, we decided to include only latency to approach and direction of approach in our three final models along with the variables for which we had specific predictions. Finally, we assessed the repeatability of successful trials across individual hyaenas using the rptR package. We calculated repeatability for hyaena identity (ID) using a null model that included only the trial number as a fixed effect and hyaena ID as a random effect with a binary response variable (pass/fail).

Ethical Note

All research procedures were designed to adhere to the ASAB/ABS Guidelines for the use of animals in research. Utmost care was taken to minimize the impact of our presence on our subjects. All subjects are part of a population of spotted hyaenas that are habituated to the presence of research vehicles and tourists. Subject participation was voluntary and cylinders were only collected once a subject had moved at least 5 m from the cylinder. Research vehicles were used as mobile blinds to hide researchers from view of all spotted hyaenas during deployment and collection of the cylinder. While subjects may experience some distress from neophobia during initial trials, the meat that was used as a reward usually offset this neophobia quite rapidly. Testing was discontinued after five trials for any subjects that continued to show any neophobia towards the cylinders. This work was conducted under research permit number NACOSTI/P/16/35513/10422, issued by the Kenyan National Commission on Science, Technology and Innovation. The data collection procedure followed here was also approved by the Michigan State University Institutional Animal Care and Use Committee (IACUC): AUF number 04/16-050-00.

RESULTS

We conducted 539 test trials with 62 hyaenas in five different clans. Two hyaenas were of unknown sex and their trials were dropped from the analysis, resulting in a final data set of 529 trials involving 60 hyaenas. Within these 60 hyaenas, ages ranged from 7 to 188 months. These hyaenas included 34 female and 26 male hyaenas (20 subadults, 19 young adults and 24 adults). Five hyaenas moved from one age class to the next during testing, and their trials were assigned to their age class at the time of each trial. Overall, the mean (± SD) proportion of correct responses with the opaque cylinder used in familiarization trials by hyaenas was 0.85 ± 0.15 (median = 0.8, range 0.33–1, $N = 60$) and the mean proportion of correct responses with the transparent cylinder used in test trials by hyaenas was 0.76 ± 0.21 (median = 0.8, range 0–1, $N = 60$). On average, hyaenas had nearly one fewer successful trial with the clear tube than with the white out of ten trials (paired two-tailed t test: $\text{mean}_{\text{diff}} = 0.09$, $t_{59} = -2.62$, $P = 0.01$). This suggests that the transparent cylinder presented more of an inhibitory challenge for hyaenas than the opaque tube. Repeatability of success on individual trials with the transparent cylinder was significant but low ($r = 0.07$, SE = 0.03, 95% CI = 0.005–0.13, $P = 0.001$).

We created three models to examine the relationship between sex, age, rank, clan size (Model 1), immigration status (Model 2) and cohort size (Model 3) on inhibitory control. We included two extraneous variables, latency to approach and direction of approach, and one random effect of hyaena ID in all three models. We also added an interaction between rank and clan size to all three models even though we had no a priori predictions about an interaction between these two variables. We added this variable post hoc because in Model 2 (male subset) clan size was initially strongly significant, whereas in Models 1 and 3 it was not. The average rank of hyaenas in our male subset was somewhat lower than the overall average because immigrant males are always very low ranking. This led us to suspect that there might be an interaction between clan size and rank, and this interaction was subsequently added to all three models. We conducted residual diagnostics and evaluated model fit using the R package Dharma (Hartig, 2019). We examined fit by plotting the scaled residuals, a residual dispersion test and the Durbin–Watson test for temporal autocorrelation in the residuals. Model fit was good for all three final models (Appendix Figs A1–A3). Scaled residuals did not significantly deviate from expected values and their distribution was generally uniform without skew. There was no significant dispersion or temporal autocorrelation in the residuals. The results from these tests indicated that model fit was adequate.

Model 1 investigated factors influencing inhibitory control using our full data set (Table 1, Model 1). We found no effect of sex on the odds of a successful trial (GLMM: $z = 0.21$, $P = 0.83$). Young adults had slightly higher odds of success than older or younger hyaenas, but this effect was marginally nonsignificant (GLMM: $z = 1.91$, $P = 0.056$; Fig. 2). Hyaenas who had shorter latencies to approach the cylinder had much lower odds of success (GLMM: $z = -2.90$, $P = 0.004$), whereas hyaenas who used an ‘other’ approach, such as diagonal or circling approach, had higher odds of success (GLMM: $z = 3.43$, $P = 0.001$; Supplementary Video S4). Hyaenas living in larger clans had modestly but significantly better odds of success than those living in smaller clans (GLMM: $z = 2.04$, $P = 0.04$; Fig. 3). Finally, although rank alone was not significant (GLMM: $z = -0.52$, $P = 0.60$; Table 1), we found a significant interaction between rank and clan size (GLMM: $z = -2.82$, $P = 0.005$). At a very low social rank, the coefficient for clan size was large and significant, which shows that for low-ranking hyaenas, living in larger clans was correlated with higher odds of a successful trial and greater inhibitory control (Fig. 4). However, as social rank increased, the effect of clan size became weaker and nonsignificant, such that for high-ranking hyaenas, the size of the clan had little effect on their odds of success. There also appeared to be no effect of presentation order or learning across all trials or across trials within a testing session. Trial number was included in only six out of 18 top models for Model 1 produced by Dredge (GLMM conditional average: $z = 0.91$, $P = 0.37$; Appendix Table A2, Appendix Fig. A4). Session trial number was also included in only six out of 18 top models for Model 1 produced by Dredge (GLMM conditional average: $z = 0.72$, $P = 0.47$, Appendix Table A2, Appendix Fig. A5).

Model 2 investigated the effect of immigration status on inhibitory control in a subset of subjects that included only males

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Table 1
Model results for three final models looking at the factors affecting inhibitory control

	Model 1: Full				Model 2: Male subjects				Model 3: Natal subjects			
	Odds ratio	SE	*z*	*P*	Odds ratio	SE	*z*	*P*	Odds ratio	SE	*z*	*P*
Sex (male)	1.06	0.28	0.21	0.833	–	–	–	–	1.40	0.31	1.10	0.273
Rank	0.87	0.26	−0.52	0.603	0.57	0.83	−0.68	0.497	0.92	0.28	−0.31	0.756
Age (subadult)	1.41	0.33	1.03	0.305	0.36	1.16	−0.87	0.383	1.44	0.36	1.02	0.309
Age (young adult)	1.83	0.32	1.91	**0.056**	1.07	0.89	0.08	0.935	1.84	0.34	1.78	**0.075**
Clan size	1.32	0.14	2.04	**0.041**	1.74	0.31	1.77	**0.077**	1.06	0.18	0.30	0.762
Latency	0.47	0.26	−2.90	**0.004**	0.61	0.44	−1.12	0.261	0.53	0.31	−2.10	**0.036**
Approach (other)	2.93	0.31	3.43	**0.001**	2.56	0.53	1.76	**0.078**	3.68	0.37	3.52	**0.0004**
Approach (parallel)	6.82	0.75	2.55	**0.011**	9.43	1.10	2.04	**0.041**	3.70	0.77	1.70	0.090
Rank × clan size	0.52	0.23	−2.82	**0.005**	0.54	0.54	−1.16	0.246	0.67	0.27	−1.50	0.133
Immigrant	–	–	–	–	0.26	1.48	−0.91	0.363	–	–	–	–
Cohort size	–	–	–	–	–	–	–	–	1.05	0.02	2.09	**0.036**

All models were built using binomial generalized linear mixed models with a log link function and included random effect of hyaena identity (ID). Model 1 used our full data set ($n = 529$, $N = 60$), Model 2 used only male hyaenas ($n = 230$, $N = 26$) and Model 3 used only hyaenas for which we had natal data ($n = 384$, $N = 42$). Bold *P* values indicate significant or near-significant effects. The reference categories were adult, female and a perpendicular approach for sex, age and approach.

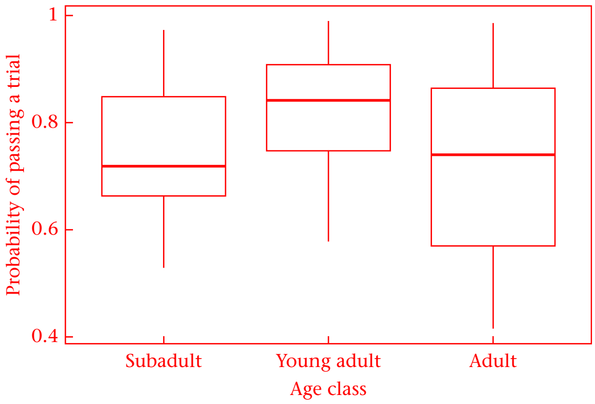

Figure 2. Predicted probability of success for subadult ($N = 20$), young adult ($N = 19$) and adult ($N = 24$) spotted hyaenas from Model 1. Box plots show median values and interquartile ranges.

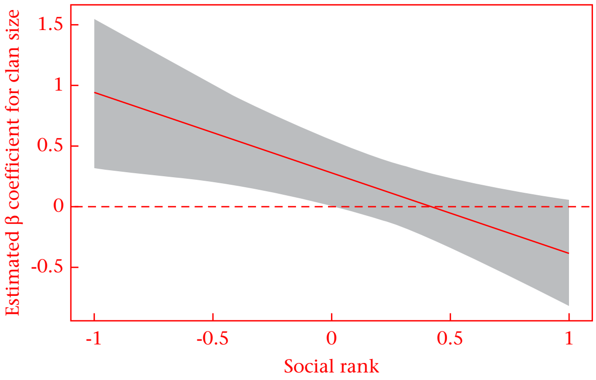

Figure 4. Interaction plot between rank and clan size. Figure shows the effect of rank on the estimated coefficient (log odds) of clan size.

(Table 1, Model 2). Immigrant males did not have significantly higher odds of success than natal males (GLMM: $z = -0.91$, $P = 0.36$). Model 3 investigated the effect of cohort size on inhibitory control in a subset that included natal animals for which cohort size was known (Table 1, Model 3). In this model cohort size had a significant positive effect on the odds of a successful trial (GLMM: $z = 2.09$, $P = 0.036$). Hyaenas that grew up in larger cohorts of cubs at the communal den had significantly better odds of success than those that grew up in smaller cohorts (Fig. 5).

DISCUSSION

Testing the Social Intelligence Hypothesis

This study examined intraspecific variation in inhibitory control in wild spotted hyaenas in relation to social factors in order to test predictions of the social intelligence hypothesis (SIH) (Dunbar,

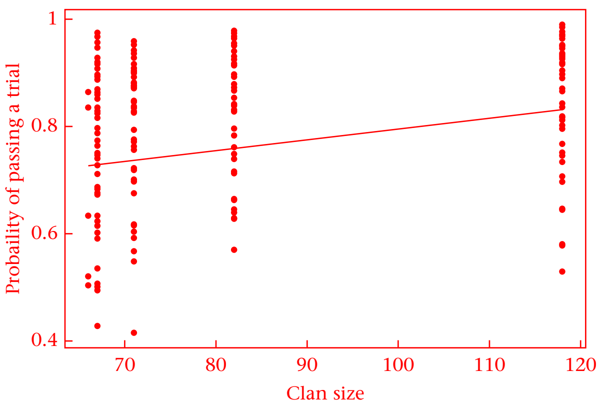

Figure 3. Predicted probability of success for hyaenas living in clans of different sizes from Model 1.

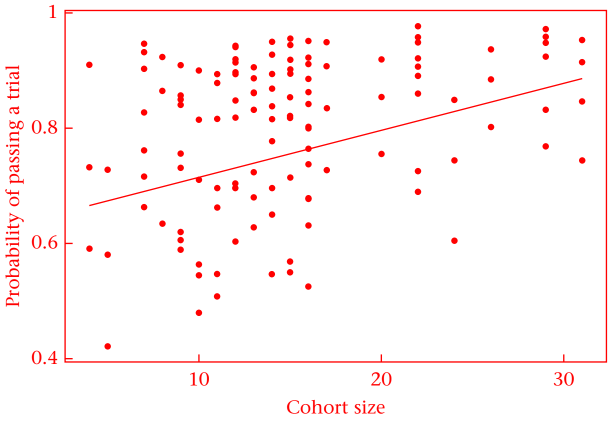

Figure 5. Predicted probability of success for hyaenas growing up in den cohorts of different sizes.

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1998; Dunbar & Shultz, 2017; Humphrey, 1976; Shultz & Dunbar, 2010). Although the SIH is one of the most popular hypotheses forwarded to explain the evolution of intelligence in animals, it is still somewhat controversial, with some interspecific comparative studies finding strong support and others finding no support at all for the SIH (Barrett, Henzi, & Rendall, 2007; DeCasien, Williams, & Higham, 2017; Fedorova, Evans, & Byrne, 2017; Powell, Isler, & Barton, 2017; Rosati, 2017). In particular, how to define and quantify social complexity is still debated (Bergman & Beehner, 2015; Boucherie, Loretto, Massen, & Bugnyar, 2019; Kappeler, 2019). Here, we attempted to directly quantify intraspecific variation in social demands on cognition and compare this variation to variation in inhibitory control, an executive function thought to be particularly important in gregarious species. Although we found that inhibitory control did not vary with sex, both clan size and cohort size, which was the size of the group of peers in which hyaenas spent their early life, were significant predictors of inhibitory control, with hyaenas in larger clans (Fig. 2) and hyaenas raised in larger cohorts (Fig. 4) exhibiting greater inhibitory control. In addition, we found a significant interaction between rank and clan size, with low-ranking hyaenas exhibiting higher levels of inhibitory control in larger clans (Fig. 3).

Group size has frequently been used as a measure of social complexity in interspecific studies. Spotted hyaenas live in large groups relative to those of other social carnivores, but in groups of similar size to those of cercopithicine primates. Importantly, there is a great deal of intraspecific variation in group size within spotted hyaenas, with clans ranging in size from 22 to 126 individuals in the MMNR (Green, Johnson-Ulrich, Couraud, & Holekamp, 2018). Comparing this variation in clan size to variation in cognition within the species provides a powerful tool for directly testing the effect of group size on cognition. In the present, study clan sizes ranged from 66 to 118 total members (Fig. 2) and clan size was significantly and positively correlated with inhibitory control (Table 1, Model 1). Social relationships during development may also be of particular importance in social animals (Ashton, Thornton, et al., 2018). Until approximately 1 year of age, spotted hyaenas live at a communal den with other unrelated juvenile spotted hyaenas, and it is here that cubs begin to learn their dominance ranks and acquire crucial social and physical skills (Holekamp & Dloniak, 2010; Holekamp & Smale, 1991). We therefore also tested the effect of cohort size in the subset of our subjects for which cohort size was known. In this model, cohort size strongly and positively predicted inhibitory control, with hyaenas that grew up in larger cohorts of cubs possessing higher levels of inhibitory control. Interestingly, cohort seemed to provide a stronger fit than clan size; when cohort size was added to Model 3, clan size became nonsignificant (Table 1). This suggests that the effect of group size may be most important during early development, when both social and cognitive skills are still developing. A study in Australian magpies, *Gymnorhina tibicen*, where general intelligence was measured by a cognition test battery that included the cylinder test, also found evidence for a relationship between group size and general intelligence that emerged very early in development (Ashton, Ridley, et al., 2018). Our results replicate and support the findings of Ashton et al. in a mammalian carnivore, greatly strengthening the argument for a relationship between cognitive ability and complexity in the early life social environment.

We had also predicted that rank would influence inhibitory control because low-ranking individuals must inhibit feeding from carcasses whenever higher-ranking hyaenas are present, but instead found that the effect of rank was contingent on clan size. While unpredicted, this result is not entirely surprising. Scaling rank relative to the other members of a group is standard practice, but it does not necessarily capture the difference in social demands between a low-ranking hyaena in a small clan and a low-ranking hyaena in a large clan. In a small clan, a low-ranking hyaena might rank below only 20 other hyaenas, whereas in a large clan, a low-ranking hyaena may rank below 120 other hyaenas. The significant interaction between rank and clan size suggests that low-ranking hyaenas in larger clans may experience greater demands for better inhibitory control, perhaps due to the larger number of individuals ranked above them. Our findings suggest that both the size and social structure of a group are important aspects of social complexity in spotted hyaenas. Therefore, this result not only supports previous work reporting a relationship between group size and cognition but also expands our understanding of how and why variation in group size can affect demands on cognitive abilities.

Last, we also predicted that male hyaenas, which are nearly always extremely low ranking as adults, and which have larger frontal cortices than females (Arsznov et al., 2010), would have the highest levels of inhibitory control. However, sex was not significant in our final model (Table 1). It is worth noting that, although the size of the frontal cortex varies between male and female hyaenas (Arsznov et al., 2010) and although the relative size of the entire neocortex has consistently been linked to social intelligence (summarized in Holekamp & Benson-Amram, 2017), previous researchers using the cylinder task found that performance was more closely correlated with overall brain size than with frontal cortex or neocortex size alone (Horschler et al., 2019; MacLean et al., 2014). The lack of significant sex differences in this study suggests that inhibitory control may not be a canalized trait, and may instead be a plastic trait contingent on developmental conditions (e.g. the social environment). Because rank, cohort size and clan size, none of which are genetically determined, are all strongly related to inhibitory control in hyaenas, our findings also support this notion that inhibitory control is a plastic trait.

Taken together, our results provide strong support for the social intelligence hypothesis; by demonstrating that both measures of social group size and a rank∗clan size interaction predict inhibitory control, this study provides direct support for the hypothesis that social complexity favours the development of enhanced cognitive abilities. The size of the group and an individual's social rank within it both appear to place cognitive demands on hyaenas, favouring the development of greater inhibitory control. Direct evidence for such a relationship between greater social complexity and enhanced cognition has been surprisingly rare. Most support for the SIH comes from studies that use average group size and average brain size of each species, rather than direct measures of cognition, across various species in comparative analyses (Dunbar, 1998; Dunbar & Shultz, 2007; Shultz & Dunbar, 2010). Interestingly, interspecific studies of captive animals in which cognitive ability was directly measured have generally failed to find a link between cognitive performance and group size (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016; MacLean et al., 2014; Reddy, MacLean, Sandel, & Hare, 2015; Rudolph & Fichtel, 2017). Indeed, it is still unclear just how or why a larger group increases cognitive demands, although the SIH offers many suggestions (Aureli & Schino, 2019; Barrett, Henzi, & Dunbar, 2003; Boucherie et al., 2019; Emery, Seed, von Bayern, & Clayton, 2007; Kappeler, 2019). For example, it may be that managing a greater number of differentiated social relationships requires greater intelligence (Bergman & Beehner, 2015), but it might also be that living in a larger group exposes individuals to more frequent opportunities to learn socially about their physical environment; under these circumstances social living is a facilitator rather than a selective force for intelligence (van Schaik, Isler, & Burkart, 2012) as proposed in the cultural intelligence hypothesis (CIH). Although we are

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currently unable to differentiate between these two hypotheses, captive spotted hyaenas show only very limited social learning of physical skills (Benson-Amram, Heinen, Gessner, Weldele, & Holekamp, 2014). In addition, previous research with spotted hyaenas found that rates of social play are related to cohort size and that rates of social play, but not object play, peak while cubs live at the communal den (Tanner, Smale, & Holekamp, 2007). Because social play is thought to be critical to development of social skills in hyaenas (Drea, Hawk, & Glickman, 1997), these previous studies certainly suggest that aspects of sociality itself are more likely to directly mediate the relationship between cohort size and inhibitory control, rather than indirectly as the CIH suggests. Indeed, the interaction between clan size and rank found in the present study certainly suggests that navigating the social hierarchy is particularly challenging for low-ranking hyaenas. This finding also supports the idea that managing a large number of differentiated social relationships is a critical aspect of social complexity. Ultimately, more research is needed to test these possibilities. Potential areas for future research include using social network analyses to quantify the strength of social relationships, or using experimental paradigms to directly measure social learning and cultural diffusion in wild hyaenas.

Developmental Effects on Inhibitory Control

Many cognitive abilities are developmentally plastic, and individuals tend to show improved cognition as they approach adulthood due to learning and brain development (Casey, Tottenham, Liston, & Durston, 2005; Greenough, Black, & Wallace, 1993; Johnson, Munakata, & Gilmore, 2008; Kolb & Gibb, 2011; Snell-Rood, 2013). Executive functions, such as inhibitory control, are typically among the last to become fully developed during ontogeny (Diamond, 1990, 2013). We therefore had predicted that adult spotted hyaenas would show better inhibitory control than subadults. However, we found that young adult hyaenas 2—4 years of age had higher levels of inhibitory control than other age groups ($P = 0.055$). This effect was not driven by male hyaenas (which disperse during this age interval), as age was not a significant predictor of inhibitory control in our male-only model. Instead, this effect may simply be a product of the way the brain develops, rather than driven by life history or environmental circumstances. Research on human and animal cognition suggests that many cognitive abilities peak in young adulthood (Craik & Bialystok, 2006; Feyereisen & Charlot, 2008; Matzel, Grossman, Light, Townsend, & Kolata, 2008; Salthouse, 2009; Whitley et al., 2016). Whereas crystallized intelligence, a facet of general intelligence that represents accumulated knowledge across the life span, continues to improve across the entire life span, fluid intelligence, which is akin to behavioural flexibility in the animal literature, tends to peak during young adulthood. However, the exact age at which this peak occurs varies tremendously among different cognitive abilities (Hartshorne & Germine, 2015). Although our sample included only den-independent cubs, which are usually older than 8 months of age, it would be extremely interesting to test young hyaenas at the den to examine how inhibitory control might improve from a very young age.

Inhibitory Control Task Design Considerations

The cylinder task is fairly well established as a tool for studying inhibitory control, but performance with the cylinder task has been found to be susceptible to several sources of bias. For one, prior experience with clear objects can significantly improve performance on detour tasks that use clear barriers (van Horik et al., 2018; but see Santacà, Busatta, Savaşçı, Lucon-Xiccato, & Bisazza, 2019) and several studies have also found that subjects tend to improve in their success rate across trials (Kabadayi et al., 2017), suggesting that individuals may be learning the affordances of the clear cylinder, which would make the inhibitory challenge decrease across trials. This can bias results by making it look like individuals have higher levels of inhibitory control than they really do (Kabadayi et al., 2017). Here, all of our subjects were equally inexperienced with transparent objects. To observe and control for any potential learning effects, we recorded trial number both across all trials and within each testing session. Neither of these measures was significant, suggesting that our hyaenas were not learning to perform better with the cylinder across trials. Aspects of test set-up, such as distance and direction of approach can also influence trial success (Kabadayi et al., 2018). Here, hyaenas who had an approach other than perpendicular or parallel to the tube were much more likely to pass a trial. This ‘other’ category included diagonal and circling approaches, which may have given hyaenas more time to detect the food and locate the openings on either end of the cylinder than more direct approaches, improving their ability to inhibit bumping into the wall of cylinder (Supplementary Video S4). Likewise, hyaenas who approached the cylinder more slowly were much more likely to pass a trial. Although latency to and direction of approach may also be measures of a hyaena's inhibitory control, latency to approach is often used as a measure of motivation in studies of animal personality and cognition. Motivation is a known confound in studies of inhibitory control and problem solving (van Horik et al., 2018; van Horik, Langley, Whiteside, & Madden, 2017), and one study with the cylinder found that temperament and arousal levels affect inhibitory control in domestic dogs (Bray, MacLean, & Hare, 2015). Therefore, we included both of these approach measures in our models to control for their potentially confounding effects. Our results confirm the need to statistically control for such variables, particularly in studies with wild subjects where numerous factors cannot be controlled experimentally. We also controlled for olfaction in our study because, although spotted hyaenas have good visual acuity (Kruuk, 1972), they are highly olfactory animals. Therefore, we drilled holes into the wall of the cylinder so that scent could not draw hyaenas to a successful detour.

Although there is little doubt that detour tasks, like the cylinder test, do measure inhibitory control, inhibitory control on the whole appears to be both task and context specific. Previous research with captive spotted hyaenas did not detect a relationship between inhibition with the cylinder task and inhibition with a multi-access problem-solving box (Johnson-Ulrich et al., 2018). During the cylinder task, individuals must remember their previously learned response with the white cylinder and inhibit an impulse with the clear cylinder, whereas with the multi-access box, individuals are required to inhibit their previously learned solution in order to learn a new one. In general, studies that have used different tasks to measure inhibitory control in animals find that inhibitory control does not correlate across tasks that make different behavioural demands (Bray, Maclean, & Hare, 2014; Brucks, Marshall-Pescini, & Range, 2019; Brucks, Marshall-Pescini, Wallis, Huber, & Range, 2017; Fagnani, Barrera, Carballo, & Bentosela, 2016; Marshall-Pescini et al., 2015; Müller, Riemer, Virányi, Huber, & Range, 2016; Völter, Tinklenberg, Call, & Seed, 2018). Indeed, it is likely that inhibitory control is a multifaceted cognitive ability with many underlying processes (Bari & Robbins, 2013). Because of this task specificity, we chose the cylinder test because it most closely approximated the type of inhibitory control we aimed to test in hyaenas: the ability to resist feeding in circumstances that demand restraint (i.e. response inhibition in the context of feeding). It is possible that feeding response inhibition in the presence of a physical barrier, i.e. the cylinder test, might not actually

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approximate feeding response inhibition in the presence of a ‘social barrier’ (i.e. a higher-ranking individual), because the costs and benefits of inhibition differs dramatically between these scenarios. This possibility is supported by previous studies showing that social tasks involving inhibitory control do not always correlate with physical tasks involving inhibitory control (Bray et al., 2014; MacLean et al., 2013). However, the inhibitory control tests in these studies not only differed in the physical and social context, but also differed dramatically in task demands. Although we cannot rule out the possibility that our results are biased by using a physical, rather than social, test of inhibitory control, we would expect our results to be biased towards our null hypothesis. For example, if social and physical feeding inhibition were only weakly related or unrelated, we would not have expected to find a significant correlation between our social measures and performance on the cylinder test. However, we did find a significant correlation between our social measures and performance on the cylinder test, which implies that the cylinder test likely does, to some degree, approximate social inhibitory control.

Conclusion

In summary, our results support the SIH as an explanation for the evolution of inhibitory control and provide some of the first direct evidence for a relationship between the social complexity experienced early in life and cognitive ability later in life. We compared two measures of social complexity, social rank and group size, to inhibitory control. We found no support for the hypothesis that male spotted hyaenas, which must frequently inhibit behaviours in the presence of higher-ranking individuals, have better inhibitory control than female hyaenas. Rather, spotted hyaenas who grew up in larger cohorts, lived in larger clans and were low ranking in larger clans had significantly better inhibitory control than other hyaenas. Our results suggest that both the dominance structure and the size of the group experienced during development may be key aspects of social complexity. We suggest that future research should further investigate the mechanism by which group size and structure are related to enhanced cognition. We also found significant effects of age, latency to approach and direction of approach on inhibitory control. Future work should thus further investigate the effects of context and task demands on inhibitory control. It would be extremely interesting to compare a measure of inhibitory control in a social contex to both performance on the cylinder test and measures of social complexity. Overall, testing cognition in the wild poses unique challenges for controlling a wide variety of extraneous variables, but the intraspecific approach in wild animals also appears to be a powerful tool for testing hypotheses about the evolution of cognition.

Data Availability

R code and generated output used for all analyses are provided as Supplementary material. Full data set is available upon request.

Acknowledgments

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References

Amici, F., Aureli, F., & Call, J. (2008). Fission–fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology, 18*(18), 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020.

Amici, F., Call, J., & Aureli, F. (2009). Variation in withholding of information in three monkey species. *Proceedings of the Royal Society of London Series B Biological Sciences, 276*(1671), 3311–3318.

Amici, F., Call, J., Watzek, J., Brosnan, S., & Aureli, F. (2018). Social inhibition and behavioural flexibility when the context changes: A comparison across six primate species. *Scientific Reports, 8*(1), 3067. https://doi.org/10.1038/s41598-018-21496-6.

Aron, A. R. (2007). The neural basis of inhibition in cognitive control. *Neuroscientist, 13*(3), 214–228. https://doi.org/10.1177/1073858407299288.

Arsznov, B. M., Lundrigan, B. L., Holekamp, K. E., & Sakai, S. T. (2010). Sex and the frontal cortex: A developmental CT study in the spotted hyena. *Brain, Behavior and Evolution, 76*(3–4), 185–197. https://doi.org/10.1159/000321317.

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature, 554*, 364–367. https://doi.org/10.1038/nature25503.

Ashton, B. J., Thornton, A., & Ridley, A. R. (2018). An intraspecific appraisal of the social intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 373*(1756). https://doi.org/10.1098/rstb.2017.0288, 20170288.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., et al. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology, 49*(4), 627–654. https://doi.org/10.1086/586708.

Aureli, F., & Schino, G. (2019). Social complexity from within: How individuals experience the structure and organization of their groups. *Behavioral Ecology and Sociobiology, 73*(1), 6. https://doi.org/10.1007/s00265-018-2604-5.

Bari, A., & Robbins, T. W. (2013). Inhibition and impulsivity: Behavioral and neural basis of response control. *Progress in Neurobiology, 108*, 44–79. https://doi.org/10.1016/j.pneurobio.2013.06.005.

Barrett, L., Henzi, P., & Dunbar, R. I. M. (2003). Primate cognition: From ‘what now?’ to ‘what if? *Trends in Cognitive Sciences, 7*(11), 494–497. https://doi.org/10.1016/j.tics.2003.09.005.

Barrett, L., Henzi, P., & Rendall, D. (2007). Social brains, simple minds: Does social complexity really require cognitive complexity? *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*(1480), 561–575. http://rstb.royalsocietypublishing.org/content/362/1480/561.abstract.

Bartoń, K. (2019). *MuMIn: Multi-Model Inference*. Version 1.43.6 https://cran.r-project.org/package=MuMIn.

Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E. M., & Holekamp, K. E. (2016). Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Sciences of the United States of America, 113*(9), 2532–2537. https://doi.org/10.1073/pnas.1505913113.

Benson-Amram, S., Heinen, V. K., Gessner, A., Weldele, M. L., & Holekamp, K. E. (2014). Limited social learning of a novel technical problem by spotted hyenas. *Behavioural Processes, 109*, 111–120.

Bergman, T. J., & Beehner, J. C. (2015). Measuring social complexity. *Animal Behaviour, 103*, 203–209.

Bjorklund, D. F., & Harnishfeger, K. K. (1995). The evolution of inhibition mechanisms and their role in human cognition and behavior. In F. N. Dempster, & C. J. Brainerd (Eds.), *Interference and inhibition in cognition* (pp. 141–173). San Diego, CA: Academic Press/Elsevier. https://doi.org/10.1016/B978-012208930-5/50006-4.

Boucherie, P. H., Loretto, M.-C., Massen, J. J. M., & Bugnyar, T. (2019). What constitutes ‘social complexity’ and ‘social intelligence’ in birds? Lessons from ravens. *Behavioral Ecology and Sociobiology, 73*(1), 12. https://doi.org/10.1007/s00265-018-2607-2.

Bray, E. E., Maclean, E. L., & Hare, B. A. (2014). Context specificity of inhibitory control in dogs. *Animal Cognition, 17*(1), 15–31. https://doi.org/10.1007/s10071-013-0633-z.

Bray, E. E., MacLean, E. L., & Hare, B. A. (2015). Increasing arousal enhances inhibitory control in calm but not excitable dogs. *Animal Cognition, 18*(6), 1317–1329. https://doi.org/10.1007/s10071-015-0901-1.

Brucks, D., Marshall-Pescini, S., & Range, F. (2019). Dogs and wolves do not differ in their inhibitory control abilities in a non-social test battery. *Animal Cognition, 22*(1), 1–15. https://doi.org/10.1007/s10071-018-1216-9.

Please cite this article in press as: Johnson-Ulrich, L., & Holekamp, K. E., Group size and social rank predict inhibitory control in spotted hyaenas, Animal Behaviour (2019), https://doi.org/10.1016/j.anbehav.2019.11.020

Brucks, D., Marshall-Pescini, S., Wallis, L. J., Huber, L., & Range, F. (2017). Measures of dogs' inhibitory control abilities do not correlate across tasks. *Frontiers in Psychology, 8*, 849. https://doi.org/10.3389/fpsyg.2017.00849.

Burnham, K., & Anderson, D. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, NY: Springer.

Byrne, R. W. (1995). Machiavellian intelligence. *The thinking ape: Evolutionary origins of intelligence* (pp. 195–209). New York, NY: Oxford University Press.

Byrne, R. W., & Bates, L. A. (2007). Sociality, evolution and cognition. *Current Biology, 17*(16), R714–R723. https://doi.org/10.1016/j.cub.2007.05.069.

Byrne, R. W., & Whiten, A. (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford, U.K.: Clarendon Press.

Casey, B. J., Tottenham, N., Liston, C., & Durston, S. (2005). Imaging the developing brain: What have we learned about cognitive development? *Trends in Cognitive Sciences, 9*(3), 104–110. https://doi.org/10.1016/j.tics.2005.01.011.

Craik, F. I. M., & Bialystok, E. (2006). Cognition through the lifespan: Mechanisms of change. *Trends in Cognitive Sciences, 10*(3), 131–138.

DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution, 1*, 0112. https://doi.org/10.1038/s41559-017-0112.

Diamond, A. (1990). Developmental time course in human infants and infant monkeys, and the neural bases of, inhibitory control in reaching. *Annals of the New York Academy of Sciences, 608*(1), 637–676.

Diamond, A. (2013). Executive functions. *Annual Review of Psychology, 64*, 135–168. https://doi.org/10.1146/annurev-psych-113011-143750.

Drea, C. M., Hawk, J. E., & Glickman, S. E. (1997). The emergence of affiliative behavior in infant spotted hyenas (*Crocuta crocuta*). *Annals of the New York Academy of Sciences, 807*(1), 498–500.

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews, 6*(5), 178–190. https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.3.CO;2-P.

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science, 317*(5843), 1344–1347. https://doi.org/10.1126/science.1145463.

Dunbar, R. I. M., & Shultz, S. (2017). Why are there so many explanations for primate brain evolution? *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1727). https://doi.org/10.1098/rstb.2016.0244, 20160244.

Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*(1480), 489–505. https://doi.org/10.1098/rstb.2006.1991.

Engh, A. L., Esch, K., Smale, L., & Holekamp, K. (2000). Mechanisms of maternal rank 'inheritance' in the spotted hyaena, *Crocuta crocuta*. *Animal Behaviour, 60*(3), 323–332. https://doi.org/10.1006/anbe.2000.1502.

Fagnani, J., Barrera, G., Carballo, F., & Bentosela, M. (2016). Is previous experience important for inhibitory control? A comparison between shelter and pet dogs in A-not-B and cylinder tasks. *Animal Cognition, 19*(6), 1165–1172. https://doi.org/10.1007/s10071-016-1024-z.

Fedorova, N., Evans, C. L., & Byrne, R. W. (2017). Living in stable social groups is associated with reduced brain size in woodpeckers (Picidae). *Biology Letters, 13*(3). https://doi.org/10.1098/rsbl.2017.0008, 20170008.

Feyereisen, P., & Charlot, V. (2008). Are there uniform age-related changes across tasks involving inhibitory control through access, deletion, and restraint functions? A preliminary investigation. *Experimental Aging Research, 34*(4), 392–418. https://doi.org/10.1080/03610730802271880.

Green, D. S. S., Johnson-Ulrich, L., Couraud, H. E. E., & Holekamp, K. E. E. (2018). Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. *Biodiversity & Conservation, 27*(4), 871–889. https://doi.org/10.1007/s10531-017-1469-7.

Greenough, W. T., Black, J. E., & Wallace, C. S. (1993). Experience and brain development. In M. H. Johnson, Y. Munakata, & R. O. Gilmore (Eds.), *Brain development and cognition: A reader* (Vol. 2, pp. 186–216). Oxford, U.K.: Blackwell.

Hartig, F. (2019). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. Retrieved from http://florianhartig.github.io/DHARMa/.

Hartshorne, J. K., & Germine, L. T. (2015). When does cognitive functioning peak? The asynchronous rise and fall of different cognitive abilities across the life span. *Psychological Science, 26*(4), 433–443.

Holekamp, K. E., & Benson-Amram, S. (2017). The evolution of intelligence in mammalian carnivores. *Interface Focus, 7*(3). https://doi.org/10.1098/rsfs.2016.0108, 20160108.

Holekamp, K. E., Dantzer, B., Stricker, G., Shaw Yoshida, K. C., & Benson-Amram, S. (2015). Brains, brawn and sociality: A hyaena's tale. *Animal Behaviour, 103*, 237–248. https://doi.org/10.1016/j.anbehav.2015.01.023.

Holekamp, K. E., & Dloniak, S. M. (2010). Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. *Advances in the Study of Behavior, 42*, 189–229. https://doi.org/10.1016/S0065-3454(10)42006-9.

Holekamp, K. E., Sakai, S., & Lundrigan, B. (2007). The spotted hyena (*Crocuta crocuta*) as a model system for study of the evolution of intelligence. *Journal of Mammalogy, 88*(3), 545–554. https://doi.org/10.1644/06-MAMM-S-361R1.1.

Holekamp, K. E., & Smale, L. (1991). Dominance acquisition during mammalian social development: The 'inheritance' of maternal rank. *American Zoologist, 31*(2), 306–317.

Holekamp, K. E., Smale, L., Berg, R., & Cooper, S. M. (1997). Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology, 242*(1), 1–15.

Holekamp, K. E., Smith, J. E., Strelioff, C. C., Van Horn, R. C., & Watts, H. E. (2012). Society, demography and genetic structure in the spotted hyena. *Molecular Ecology, 21*(3), 613–632.

van Horik, J. O., Langley, E. J. G., Whiteside, M. A., Laker, P. R., Beardsworth, C. E., & Madden, J. R. (2018). Do detour tasks provide accurate assays of inhibitory control? *Proceedings of the Royal Society B: Biological Sciences, 285*(1875). https://doi.org/10.1098/rspb.2018.0150, 20180150.

van Horik, J. O., Langley, E. J G., Whiteside, M. A., & Madden, J. R. (2017). Differential participation in cognitive tests is driven by personality, sex, body condition and experience. *Behavioural Processes, 134*, 22–30. https://doi.org/10.1016/j.beproc.2016.07.001.

Horschler, D. J., Hare, B., Call, J., Kaminski, J., Miklósi, Á., & MacLean, E. L. (2019). Absolute brain size predicts dog breed differences in executive function. *Animal Cognition, 22*(2), 187–198. https://doi.org/10.1007/s10071-018-01234-1.

Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson, & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 303–317). Cambridge, U.K.: Cambridge University Press.

Jelbert, S. A., Taylor, A. H., & Gray, R. D. (2016). Does absolute brain size really predict self-control? Hand-tracking training improves performance on the A-not-B task. *Biology Letters, 12*(2). https://doi.org/10.1098/rsbl.2015.0871, 20150871.

Johnson-Ulrich, L., Johnson-Ulrich, Z., & Holekamp, K. (2018). Proactive behavior, but not inhibitory control, predicts repeated innovation by spotted hyenas tested with a multi-access box. *Animal Cognition, 21*(3), 379–392. https://doi.org/10.1007/s10071-018-1174-2.

Johnson, M. H., Munakata, Y., & Gilmore, R. O. (2008). *Brain development and cognition: A reader* (2nd ed.). New York, NY: J. Wiley. e-book.

Kabadayi, C., Bobrowicz, K., & Osvath, M. (2018). The detour paradigm in animal cognition. *Animal Cognition, 21*(1), 21–35. https://doi.org/10.1007/s10071-017-1152-0.

Kabadayi, C., Krasheninnikova, A., O'Neill, L., van de Weijer, J., Osvath, M., & von Bayern, A. M. P. (2017). Are parrots poor at motor self-regulation or is the cylinder task poor at measuring it? *Animal Cognition, 20*(6), 1137–1146. https://doi.org/10.1007/s10071-017-1131-5.

Kabadayi, C., Taylor, L. A., von Bayern, A. M. P., & Osvath, M. (2016). Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. *Royal Society Open Science, 3*(4). https://doi.org/10.1098/rsos.160104, 160104.

Kappeler, P. M. (2019). A framework for studying social complexity. *Behavioral Ecology and Sociobiology, 73*(1), 13. https://doi.org/10.1007/s00265-018-2601-8.

Kolb, B., & Gibb, R. (2011). Brain plasticity and behaviour in the developing brain. *Journal of the Canadian Academy of Child and Adolescent Psychiatry, 20*(4), 265–276.

Kruuk, H. (1972). *The spotted hyena: A study of predation and social behavior*. Chicago, IL: University of Chicago Press.

MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., et al. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences of the United States of America, 111*(20), E2140–E2148. https://doi.org/10.1073/pnas.1323533111.

MacLean, E. L., Sandel, A. A., Bray, J., Oldenkamp, R. E., Reddy, R. B., & Hare, B. A. (2013). Group size predicts social but not nonsocial cognition in lemurs. *PLoS One, 8*(6). e66359.

Marshall-Pescini, S., Virányi, Z., & Range, F. (2015). The effect of domestication on inhibitory control: Wolves and dogs compared. *PLoS One, 10*(2). e0118469.

Martin, P., Bateson, P. P. G., & Bateson, P. (1993). *Measuring behaviour: An introductory guide*. Cambridge, U.K.: Cambridge University Press.

Matzel, L. D., Grossman, H., Light, K., Townsend, D., & Kolata, S. (2008). Age-related declines in general cognitive abilities of Balb/C mice are associated with disparities in working memory, body weight, and general activity. *Learning & Memory, 15*(10), 733–746.

Menzel, E. (1974). A group of chimpanzees in a one-acre field. In A. Shrier, & F. Stollnitz (Eds.), *Behavior of non-human primates* (pp. 83–153). San Diego, CA: Academic Press.

Mischel, W., Shoda, Y., & Rodriguez, M. (1989). Delay of gratification in children. *Science, 244*(4907), 933–938. https://doi.org/10.1126/science.2658056.

Müller, C. A., Riemer, S., Virányi, Z., Huber, L., & Range, F. (2016). Inhibitory control, but not prolonged object-related experience appears to affect physical problem-solving performance of pet dogs. *PLoS One, 11*(2). https://doi.org/10.1371/journal.pone.0147753. e0147753.

Powell, L. E., Isler, K., & Barton, R. A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society B: Biological Sciences, 284*(1865). https://doi.org/10.1098/rspb.2017.1765, 20171765.

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.r-project.org/.

Reddy, R. B., MacLean, E. L., Sandel, A. A., & Hare, B. (2015). Social inhibitory control in five lemur species. *Primates, 56*(3), 241–252.

Rosati, A. G. (2017). Foraging cognition: Reviving the ecological intelligence hypothesis. *Trends in Cognitive Sciences, 21*(9), 691–702. https://doi.org/10.1016/j.tics.2017.05.011.

Rudolph, K., & Fichtel, C. (2017). Inhibitory control in douc langurs (*Pygathrix nemaeus* and *P. cinerea*). *Vietnamese Journal of Primatology, 2*(5), 73–81.

Salthouse, T. A. (2009). When does age-related cognitive decline begin? *Neurobiology of Aging, 30*(4), 507–514. https://doi.org/10.1016/j.neurobiolaging.2008.09.023.

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Santacà, M., Busatta, M., Savaşçı, B. B., Lucon-Xiccato, T., & Bisazza, A. (2019). The effect of experience and olfactory cue in an inhibitory control task in guppies, *Poecilia reticulata*. *Animal Behaviour, 151*, 1–7. https://doi.org/10.1016/j.anbehav.2019.03.003.

van Schaik, C. P., Isler, K., & Burkart, J. M. (2012). Explaining brain size variation: From social to cultural brain. *Trends in Cognitive Sciences, 16*(5), 277–284. https://doi.org/10.1016/j.tics.2012.04.004.

Shultz, S., & Dunbar, R. (2010). Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proceedings of the National Academy of Sciences of the United States of America, 107*(50), 21582–21586. https://doi.org/10.1073/pnas.1005246107.

Smith, J. E., Kolowski, J. M., Graham, K. E., Dawes, S. E., & Holekamp, K. E. (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. *Animal Behaviour, 76*(3), 619–636. https://doi.org/10.1016/j.anbehav.2008.05.001.

Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour, 85*(5), 1004–1011. https://doi.org/10.1016/j.anbehav.2012.12.031.

Strauss, E. D., & Holekamp, K. E. (2019). Social alliances improve rank and fitness in convention-based societies. *Proceedings of the National Academy of Sciences of the United States of America, 116*(18), 8919–8924. https://doi.org/10.1073/pnas.1810384116.

Tanner, J. B., Smale, L., & Holekamp, K. E. (2007). Ontogenetic variation in the play behavior of spotted hyenas. *Journal of Developmental Processes, 2*, 5–30.

Van Horn, R. C., McElhinny, T. L., & Holekamp, K. E. (2003). Age estimation and dispersal in the spotted hyena (*Crocuta crocuta*). *Journal of Mammalogy, 84*, 1019–1030.

Völter, C. J., Tinklenberg, B., Call, J., & Seed, A. M. (2018). Comparative psychometrics: Establishing what differs is central to understanding what evolves. *Philosophical Transactions of the Royal Society B: Biological Sciences, 373*(1756). https://doi.org/10.1098/rstb.2017.0283, 20170283.

Vullioud, C., Davidian, E., Wachter, B., Rousset, F., Courtiol, A., & Höner, O. P. (2019). Social support drives female dominance in the spotted hyaena. *Nature Ecology & Evolution, 3*, 71–76. https://doi.org/10.1038/s41559-018-0718-9.

de Waal, F. B. M. (2013). *The bonobo and the atheist: In search of humanism among the primates*. New York, NY: W. W. Norton.

Whiten, A. (2018). Social, machiavellian and cultural cognition: A golden age of discovery in comparative and evolutionary psychology. *Journal of Comparative Psychology, 132*(4), 437–441.

Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences, 11*(2), 233–273.

Whitley, E., Deary, I. J., Ritchie, S. J., Batty, G. D., Kumari, M., & Benzeval, M. (2016). Variations in cognitive abilities across the life course: Cross-sectional evidence from understanding society: The UK household longitudinal study. *Intelligence, 59*, 39–50.

Whittingham, M. J., Stephens, P. A., Bradbury, R. B., & Freckleton, R. P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology, 75*(5), 1182–1189.

Wisnieski, L., Norby, B., Pierce, S. J., Becker, T., Gandy, J. C., & Sordillo, L. M. (2019). Predictive models for early lactation diseases in transition dairy cattle at dry-off. *Preventive Veterinary Medicine, 163*, 68–78. https://doi.org/10.1016/j.prevetmed.2018.12.014.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution, 1*(1), 3–14.

Appendix

Table A1
Results of a binomial regression model on participation by hyaenas in trials with baited apparatus

	Odds ratio	SE	*z*	*P*
Bait (milk powder)	1.77	0.14	3.91	**<0.001**
Bait (bone)	0.89	0.12	−1.06	0.29
Bait (meat)	0.96	0.16	−0.22	0.83
Bait (offal)	0.83	0.19	−1.05	0.30
Bait (rotten)	1.02	0.14	0.16	0.87

A score of 1 indicated that a hyaena participated in a trial by contacting the apparatus and/or feeding from inside the apparatus, and a score of 0 indicated that a hyaena failed to participate in a trial. Model included a random effect of hyaena identity ($n = 2909$ trials, $N = 300$ subjects). Note that 'milk powder' was not used as bait in cylinder trials. Bold *P* values indicate significant effects.

Table A2
Dredge results showing the number of top models, determined by a ΔAICc of less than 4, containing each variable

	Model 1	Model 2	Model 3
Total top models	18	41	130
Sex	**18**	–	**130**
Rank	**18**	–	**130**
Age class	**18**	**41**	**130**
Clan size	**18**	**41**	**130**
Rank × clan size	18	–	62
Immigrant	–	**41**	–
Cohort size	–	–	**130**
Latency	18	15	89
Approach	18	41	130
Migration	8	17	61
Trial number	6	9	59
Session trial number	6	17	38
Time since last trial	6	16	59
Body condition	2	15	27
Higher rankers present	1	0	38
Trial group size	1	3	10

Bold indicates variables that were 'fixed' for inclusion in every model.

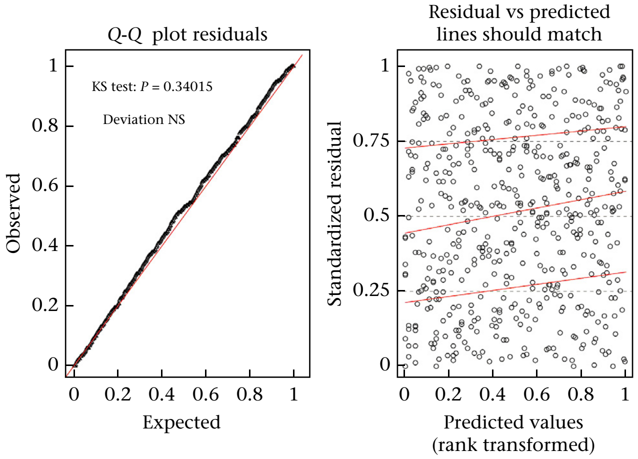

Figure A1. Residual plots showing *Q-Q* plot and a plot of the residuals against the expected values from simulated residuals generated from Model 1 using the R package DHARMa (Hartig, 2019).

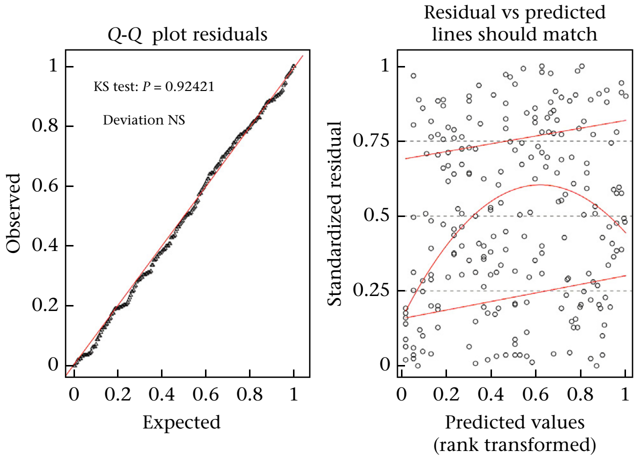

Figure A2. Residual plots showing *Q-Q* plot and a plot of the residuals against the expected values from simulated residuals generated from Model 2 using the R package DHARMa (Hartig, 2019).

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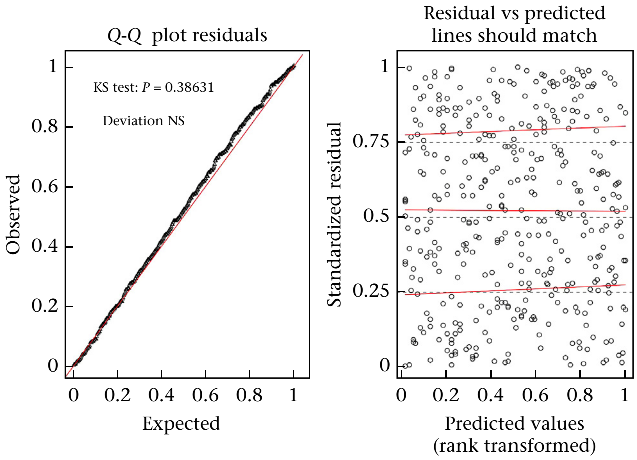

Figure A3. Residual plots showing *Q-Q* plot and a plot of the residuals against the expected values from simulated residuals generated from Model 3 using the R package DHARMa (Hartig, 2019).

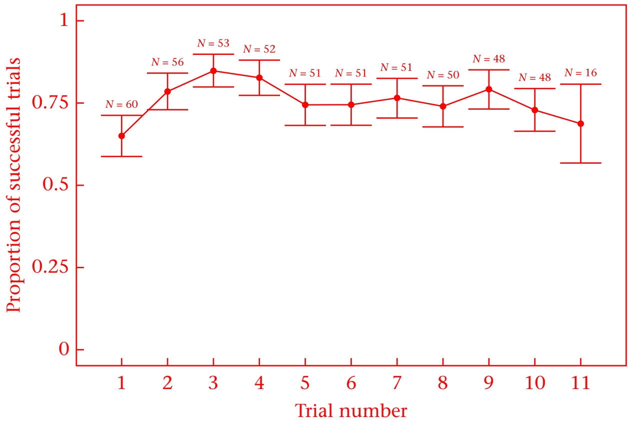

Figure A4. The relationship between overall trial number with the clear cylinder and proportion of successful trials. Error bars show standard errors. Sample sizes indicate the number of subjects that received trials.

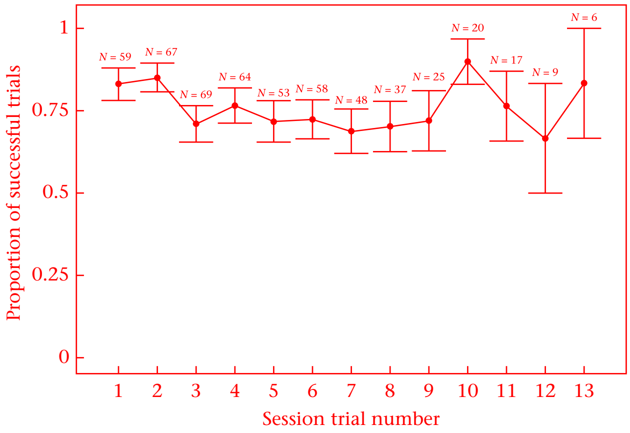

Figure A5. The relationship between trial number within a testing session and proportion of successful trials with the clear cylinder. Error bars show standard errors. Sample sizes indicate the number of subjects that received trials. Session trial number accounts for any trials done with the white cylinder prior to testing with the clear cylinder.

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