

CORRECTION

Correction: Behavioral and physiological evidence that increasing group size ameliorates the impacts of social disturbance

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There were several errors in *J. Exp. Biol.* (2020) **223**, jeb217075 (doi:10.1242/jeb.217075).

There was a discrepancy between the terms used to describe the statistical model outputs in the paper and the column names for the raw data published in the supplementary material. Specifically, the terms ‘class’ and ‘time point’ in the paper referred to ‘subject’ and ‘hours’ in the supplementary material, respectively. The paper and supplementary material have now been updated to correct for these discrepancies.

As noted in Materials and Methods, ‘Tank’ and ‘male ID’ were included as random effects in the behavioural analyses. However, the statistical output values for random effects were not included in the original publication. These are now shown as part of Table 1.

There were also three typographical errors in the statistical outputs in Table 2. For the maximum dominance analysis, the partial eta squared (η_p^2) value (0.059) for body mass as a main effect was mistakenly entered as the *P*-value for body mass as a main effect; this should have been 0.252. The total SS value (5307) was mistakenly entered as the residual SS value; this should have been 3925. For the liver LDH analysis, the residual SS value should read 4.510, rather than 4.541. These typographical errors have now been corrected.

The assumption test for ‘affiliation’ failed normality of residuals. These data were reanalysed using a $\log(\text{source}+1)$ transformation but note that ‘Male ID’ was removed as a random component because of a singularity in the data. The Materials and Methods section and Table 1 have been updated to reflect this.

Both the online full text and PDF versions of the paper and the supplementary material have been corrected. The authors apologise to the readers for these errors, which do not impact the results or conclusions of the paper.

RESEARCH ARTICLE

Behavioral and physiological evidence that increasing group size ameliorates the impacts of social disturbance

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ABSTRACT

Intra-group social stability is important for the long-term productivity and health of social organisms. We evaluated the effect of group size on group stability in the face of repeated social perturbations using a cooperatively breeding fish, *Neolamprologus pulcher*. In a laboratory study, we compared both the social and physiological responses of individuals from small versus large groups to the repeated removal and replacement of the most dominant group member (the breeder male), either with a new male (treatment condition) or with the same male (control condition). Individuals living in large groups were overall more resistant to instability but were seemingly slower to recover from perturbation. Members of small groups were more vulnerable to instability but recovered faster. Breeder females in smaller groups also showed greater physiological preparedness for instability following social perturbations. In sum, we discover both behavioral and physiological evidence that living in larger groups helps to dampen the impacts of social instability in this system.

KEY WORDS: Complex system, Cooperation, Dominance hierarchy, Social perturbation, Social scaling, Sociality

INTRODUCTION

Living in groups has various costs and benefits. For instance, group living can increase foraging efficiency (Berger, 1978), decrease predation risk (Foster and Treherne, 1981) and increase collective reproductive output (Modlmeier et al., 2012). In contrast, living in groups can sometimes decrease average per capita reproductive output (Bilde et al., 2007), promote disease transmission (Kappeler et al., 2015) and increase competition for food (Symington, 1988). For group living to evolve, the weight of the combined benefits of grouping must exceed the costs, and any factor that maximizes benefits whilst minimizing the costs of living in groups should promote the evolution of group-living and help to optimize sociality once it has evolved.

Social stability is one factor thought to help maximize benefits while minimizing the costs of group living. For instance, increased familiarity among group members can create a stabilizing effect

caused by increased predictability (Dall et al., 2004) and increase group productivity (Modlmeier et al., 2012; Pruitt and Riechert, 2011). Further, familiarity may be a mechanism for reducing within-group competition (Laskowski and Bell, 2013). Familiarity among groupmates can also enhance the effects of social buffering against environmental challenges (Hennessy et al., 2000; Livia Terranova et al., 1999) and decrease overall stress levels (Culbert et al., 2018; Kikusui et al., 2006; Nadler et al., 2016). Group stability also helps to reduce the costs of group living. For example, stable groups composed of familiar individuals experience less internal conflict, and so experience less stress from the threat of aggression or eviction (Pardon et al., 2004), reduced risk of injury, and waste fewer resources in competition (Marler et al., 1995). Even in non-cooperative territorial species, familiarity among neighbors commonly begets reduced aggression via dear enemy effects (e.g. Getty, 1987; Siracusa et al., 2017).

Despite the common finding that group stability helps to maximize group success, all groups in nature must endure some level of instability. Immigration/emigration, birth/death and alterations to dominance hierarchies, for example, result in alterations in group membership, and thus decrease within-group familiarity and stability. Many social species have therefore evolved mechanisms to help mitigate the negative impacts of such disruptive forces. For instance, some groups exhibit social rules that allow dominance hierarchies to swiftly reorganize following perturbation (Goldenberg et al., 2016). In other cases, reconciliatory communication mechanisms (e.g. specialized vocalization) aid in re-galvanizing damaged social bonds (Reddon et al., 2011; De Waal, 2000) and even particular individuals can help to dampen the negative impacts of group instability (Flack et al., 2005, 2006; McCowan et al., 2011). The traits that enable groups to dampen the acute impacts of social instability and to resume their former predictable states swiftly are important, because (1) stabilizing traits are potentially important targets for selection and (2) forces that compromise these traits risk imperiling the integrity and function of the social system.

Here, we examined how one group trait, group size, impacts the acute behavioral and physiological responses of group members to social disturbances and recoverability from them. We elected to focus on group size because it is known to mediate many costs and benefits associated with group living (Avilés and Tufiño, 1998), and because natural groups vary considerably in their size, with profound impacts on social selection (Brown et al., 2016). We predicted that living in large groups would diminish the acute impacts of social perturbations and increase group recoverability by distributing the negative impacts of social disturbance (e.g. acts of aggression) across more individuals. Larger groups may also recover more swiftly via enhanced affiliative behavior following social perturbations. We term this the ‘distributed perturbation hypothesis’ here. Alternatively, living in larger groups might increase the negative impacts of social perturbations (e.g. via

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increased aggression) or prevent groups from resuming quiescent behavioral states following disturbance. For instance, aggressive acts might initiate positive feedback fostering additional aggressive interactions in high-density environments and thus prevent groups from resuming their former stable states. We term this the 'aggressive feedback hypothesis'.

The impacts of social disturbances are likely to be evidenced physiologically as well. We therefore evaluated whether group size alters the degree to which group members are metabolically poised for intense bouts of acute or sustained physical activity following social perturbation. A higher capacity for intense activity might be necessary in preparation for, or as a training effect of, increased aggression. Many studies have identified links between various social behaviors and metabolic rates (see Huntingford et al., 2012 for review). However, reliance on oxygen consumption as a proxy for energy metabolism neglects the anaerobic processes that fuel burst-type movements typically associated with dominance behaviors (Plaut, 2001). Thus, a more refined focus on the biochemical pathways that underlie metabolic phenotypes should help elucidate links between physiology and behavior.

Enzymes are catalytic proteins that regulate biochemical reaction rates (Boyer and Krebs, 1986). Their expression is often plastic and can change in response to environmental stressors over a period of days to weeks (Beaman et al., 2016). Enzymes that catalyze regulatory steps of greater biochemical pathways can thus be plastically adjusted to meet an organism's peak metabolic demands in contrasting environments. Thus, *in vitro* measures of regulatory enzyme activities can represent upper thresholds for their respective pathways, and reflect the maximal capacity for these pathways to fuel peak activity *in vivo* (e.g. Vigelsø et al., 2014). Indeed, a number of studies have shown that activities of specific metabolic enzymes correlate strongly with intense social behaviors in a range of animal systems (AMP-activated protein kinase, Gilmour et al., 2017; lactate dehydrogenase, citrate synthase, cytochrome oxidase, Guderley, 2009; lactate dehydrogenase, citrate synthase, cytochrome oxidase, Guderley and Couture, 2005; citrate synthase, Kasumovic and Seebacher, 2013; lactate dehydrogenase, pyruvate kinase, Le François et al., 2005; citrate synthase, Regan et al., 2015). In this study, we focused on a key regulatory glycolytic enzyme (lactate dehydrogenase, LDH) and a key regulatory oxidative enzyme (citrate synthase, CS) that have been shown to reflect capacities for quick burst movements and more sustained aerobic activities, respectively (e.g. Alp et al., 1976; Childress and Somero, 1979; Johnston and Moon, 1981). We hypothesized that LDH and CS activities would scale with the most intense bouts of dominant actions displayed by an individual, and that these activities would be highest in individuals from destabilized groups.

To address these questions, we used the cooperative breeding cichlid *Neolamprologus pulcher*, endemic to Lake Tanganyika in the African Rift Valley. In the wild, groups usually comprise one dominant male–female breeding pair and one to 20 smaller, subordinate, non-breeding helpers (Balshine et al., 2001; Heg et al., 2005). Groups cooperate to care for the young of the dominant pair, maintain the group's territory, and defend the territory from both competitors and predators (Taborsky and Limberger, 1981; Wong and Balshine, 2011a). These fish also have a clear linear size-based dominance hierarchy, with increasing body size associated with increasing rank (Balshine-Earn et al., 1998). Natural groups regularly experience turnover of group members as helpers join or leave a group, or when group members perish (Heg et al., 2005; Stiver et al., 2004; Wong and Balshine, 2011b), with breeders estimated to be replaced a median of every 198–274 days (Dierkes

et al., 2005). Thus, this system provides a convenient evolutionary context to evaluate the impacts of group size on behavioral and metabolic responses to social instability and recoverability.

MATERIALS AND METHODS

Ethics

All experimental protocols were approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol no. 18-04-16), and were in compliance with the guidelines set by the Canadian Council on Animal Care (CCAC) regarding the use of animals in research.

Behavioral methods

Focal fish were haphazardly selected from a laboratory population containing approximately third-generation descendants of wild-caught *Neolamprologus pulcher* (Poll 1974) captured in 2014. Each social group was formed with a dominant pair (the largest male and female in each social group), and either four (small groups) or eight (large groups) subordinate helper fish. Thus there were a total of six fish in each 'small group' and 10 fish in each 'large group'. These group sizes reflect natural variation seen in the wild (Balshine et al., 2001; Heg et al., 2005). In total, we formed 12 small groups and 14 large groups. Small and large social groups were randomly allocated to either control (large, $n=6$; small, $n=6$) or treatment (large, $n=8$; small, $n=6$) conditions. Unbalanced group distribution was due to excessive aggression of some groups during the habituation period. To help reduce aggression and mortality, established breeding pairs were used. All helpers were unfamiliar to the dominant pair and had not previously cohabitated with them. Following group formation, the social groups were given 5 weeks to habituate and stabilize.

Each social group was maintained in a separate 189 liter aquarium containing two terracotta pot halves and two small PVC tubes (that served as both shelter and breeding substrate), two 10×10 cm mirrors, two sponge aeration filters, a heater and 3 cm deep coral sand as substrate. The mirrors served as a target of aggression to reduce within-group conflict. A water temperature of 27°C and 13 h:11 h light:dark photoperiod was maintained throughout the study. Each dominant male and female received an identifying dorsal fin clip, which has a minimal effect on behavior (Stiver et al., 2004). Fish were fed 6 days a week *ad libitum* with Nutrafin® basix large cichlid flakes.

The dominant male (standard length, SL: mean±s.e.m.=7.57±0.92 cm) and dominant female (SL: 6.66±0.86 cm) were measured at the start of the experiment. To avoid confusion with later measures of dominance, these fish will subsequently be referred to as the breeder male and breeder female, though not all of these fish were observed breeding prior to the end of the experiment. The standard lengths of all helpers were estimated by an experienced observer (S.B.) (SL: mean=2.5 cm). Helper size was used only for group standardization purposes and not included in the analyses, and so estimation was used in place of physical measurement to reduce the need for further capture and minimize the stress experienced by the fish during group stabilization. In the treatment condition, the social perturbation consisted of the removal of the breeder male from one social group and replacing him with a new, unfamiliar breeder male. Breeder males were only exchanged with other males of the same group size. Therefore, breeder male fish in the treatment groups were swapped between tanks, and throughout the course of the experiment no treatment group experienced the same male twice. We ensured that the breeder males were always larger than the females, as is observed in the wild (Balshine et al., 2001; Desjardins et al., 2008; Wong et al., 2012). In

the control condition, the breeder male fish were removed from their tanks, handled for the same duration as the treatment males, but then returned to their home tank. This social disturbance procedure occurred twice (trial 1 and trial 2), with the manipulations conducted 1 week apart. All tanks were perturbed on the same day. Physiological Acclimation responses occur over a period of hours to weeks. Thus, as a conservative measure, perturbations were conducted twice to permit group members time to deploy morphological and enzymatic responses to reliably stable versus perturbed social conditions.

Behavioral observations were recorded using Canon VIXIA HF r-series cameras immediately before the manipulation, immediately following the manipulation, and then 4 and 24 h following the manipulation. Focal observation recordings were all 15 min long. The first 5 min of each recording were discarded to account for potential disturbance on remaining group members from capturing and returning the breeder male fish and human presence. All videos were scored by the same observer (H.M.A.), who was blind to treatment condition and time recording session. Behaviors were coded using McMaster University's Aquatic Behavioural Ecology Laboratory (ABEL) *N. pulcher* ethogram (Sopinka et al., 2009) and Behavioural Observation Research Interactive Software (BORIS) (Friard and Gamba, 2016). Behaviors were subdivided into the following categories: 'aggression' (chase, bite, ram, puffed throat, mouth-fighting, pseudo-mouth-fighting and head shake), 'submission' (submissive posture, submissive display, flee/chased and bitten) and 'affiliation' (soft touch, following and parallel swim).

We calculated a dominance index for each breeder male, breeder female, and for each group of helpers divided per capita, for each recording session. The dominance index is a well-established method for calculating dominance rank and is calculated as $\text{dominance index} = (\text{sum of aggressive acts given} + \text{sum of submissive acts received}) - (\text{sum of aggressive acts received} + \text{sum of submissive acts given})$ (Aubin-Horth et al., 2007). We also calculated an affiliation index for each breeder male and female, as well as a collective, per capita affiliation index across all helpers within a group, for each recording session, where $\text{affiliation index} = \text{sum of social acts given} + \text{sum of social acts received}$. We also recorded the observation period containing the highest dominance index score for breeder females in each tank, herein referred to as the maximum dominance index observed. Specifically, the maximum dominance index observed represents the dominance index of the time period with the highest levels of aggressive behavior in relation to submissive behaviors. This term therefore reflects what are presumably the most stressful and metabolically demanding moments we observed (Grantner and Taborsky, 1998).

The breeder female of each group was captured and rapidly (≤ 3 min) euthanized via overdose of benzocaine 2 days after the final perturbation; all breeder females were euthanized within a 5-h time frame. Females were measured and their heart, liver, and skeletal muscle just posterior to the dorsal fin were harvested and massed for further analyses. Breeder females were targeted for this analysis owing to their importance to the reproduction of the group, their high care activity and also their key position as both a breeder and a subordinate (Fitzpatrick et al., 2008).

Enzyme assays

In short, tissues were homogenized in 1:10 (m/v) homogenization buffer (0.1% Triton, 50 mmol l⁻¹ Hepes, 1 mmol l⁻¹ EDTA, pH 7.4; CAT: 100 mmol l⁻¹ K phosphate buffer, 100 mmol l⁻¹ KCl, 1 mmol l⁻¹ EDTA, pH 7.4) on ice. Skeletal muscle homogenates were further diluted to 1:400 for the LDH activity

assay, whereas liver homogenates were diluted to 1:20 for both LDH and CS activity assays. Skeletal muscle homogenates were not further diluted for CS activity assays. All assays were run at 27°C in 96-well format on a Spectramax Plus 384 microplate reader (Molecular Devices, Sunnyvale, CA, USA). We used a wavelength of 340 nm to measure the disappearance of NADH (for LDH activity), and a wavelength of 412 nm to measure the production of 2-nitro-5-thiobenzoic acid (TNB; as a proxy of CS activity). For LDH and CS, extinction coefficients of 6.22 and 13.6 (mmol l⁻¹)⁻¹ cm⁻¹ were used, respectively.

Analyses and statistical methods

Dominance and affiliation indices were analyzed using a general linear mixed model (GLMM) fit by restricted maximum likelihood using the free and open software JAMOVI (Version 0.9, GAMLj module; <https://www.jamovi.org>). We fitted tank number and male ID as a random effect, and focal subject (i.e. breeder female, breeder male, helpers), treatment type (i.e. control versus treatment), group size, trial number (i.e. trial 1 or trial 2) and timepoint (i.e. immediately before the manipulation, immediately after, 4 h after and 24 h after the manipulation) as fixed effects. We started with maximal models and pruned non-significant terms (starting with high-order interactions) until we arrived at models where all highest-order fixed effects were significant (Crawley, 2012; but see Harrison et al., 2018 for limitations to this approach). We re-analyzed our affiliation index data using a log(source+1) transformation to account for non-normality of residuals. 'Male ID' was subsequently removed as a random effect because of a singularity. *Post hoc* analyses consisted of Bonferroni-corrected pairwise comparisons. We note here that with six to eight groups per treatment, our power to test higher-order interactions may be low. However, we have nonetheless opted for the statistical model that best reflects our experimental design.

To analyze the relationship between morphology (mass, relative heart mass, liver mass), maximum dominance index, and metabolic capacity (glycolytic and aerobic) across breeder females, we used general linear models (GLMs) fitted by ordinary least squares. For the maximum dominance index observed, we fitted treatment type and group size (factors), body mass, relative heart mass and liver mass (continuous covariates) as fixed effects. For metabolic capacity, LDH activity in either the skeletal muscle or the liver, or CS activity in either the skeletal muscle or the liver represented the dependent variable. Treatment type, group size (factors), maximum dominance index observed, body mass and other enzyme activity levels (continuous covariates) were fitted as fixed effects. We used the maximum dominance index observed as a fixed effect because LDH and CS measures convey individuals' capacities for peak activity. Thus, in addition to generalized locomotor activity, these effects also likely determine maximum capacities for social activities (e.g. aggression, flight and dominance), rather than baseline averages. We again started with a maximal model and pruned non-significant terms (starting with high-order interactions) until we arrived at a model where all fixed effects were significant. As a *post hoc* approach to test whether the effects of maximum dominance on enzyme activities were a potential effect of activity levels, we fitted respective models using mean activity measures as a covariate in place of maximum dominance. For all statistical tests, we used a significance threshold of $\alpha=0.05$.

RESULTS

Behavioral responses

We detected a significant four-way interaction between subject, treatment type, group size and timepoint on individuals' dominance scores (Table 1, Fig. 1A–D). We note again that our relatively

Table 1. Statistical parameters for final (minimal) GLMM for dominance and affiliation indices

	Fixed factor	<i>F</i>	Numerator d.f.	Denominator d.f.	<i>P</i>	
Dominance	Treatment	5.431	1	21	0.030	
	Timepoint	1.137	3	552	0.334	
	Group size	8.089	1	22	0.009	
	Subject	146.421	2	552	<0.001	
	Treatment×Timepoint	0.440	3	552	0.724	
	Treatment×Group size	4.746	1	22	0.040	
	Timepoint×Group size	0.514	3	552	0.673	
	Treatment×Subject	31.269	2	552	<0.001	
	Timepoint×Subject	3.944	6	552	<0.001	
	Group size×Subject	4.463	2	552	0.012	
	Treatment×Timepoint×Group size	0.527	3	552	0.664	
	Treatment×Timepoint×Subject	3.809	6	552	<0.001	
	Treatment×Group size×Subject	2.242	2	552	0.107	
	Timepoint×Group size×Subject	5.069	6	552	<0.001	
Treatment×Timepoint×Group size×Subject	3.686	6	552	0.001		
Random effects		Name	s.d.	Variance	ICC	
Male ID		(intercept)	0.050	0.003	0.002	
Tank number		(intercept)	0.296	0.088	0.070	
Residual			1.081	1.168		
	Fixed factor	<i>F</i>	Numerator d.f.	Denominator d.f.	<i>P</i>	
Affiliation	Group size	0.359	1	22	0.555	
	Treatment	1.880	1	22	0.184	
	Trial number	18.342	1	579	<0.001	
	Subject	10.336	2	579	<0.001	
	Timepoint	2.567	3	579	0.054	
	Group size×Trial number	6.879	1	579	0.009	
	Group size×Treatment	1.184	1	22	0.288	
	Treatment×Timepoint	0.804	3	579	0.492	
	Trial number×Timepoint	5.417	3	579	0.001	
	Group size×Timepoint	2.121	3	579	0.096	
	Group size×Treatment×Timepoint	6.105	3	579	<0.001	
	Random effects		Name	s.d.	Variance	ICC
	Tank number		(intercept)	0.056	0.003	0.105
	Residual			0.164	0.027	

Subject (i.e. female, male, helpers), treatment type (i.e. control versus treatment), group size, trial number (i.e. trial 1 or trial 2), and timepoint type (i.e. immediately before the manipulation, immediately after, 4 h after and 24 h after the manipulation). d.f., degrees of freedom; s.d., standard deviation; Var, variance; ICC, intraclass correlation coefficient. Bold indicates $P < 0.05$.

limited power to test this effect means that results should be interpreted with caution. Consideration of the effect size (Table 1) and examination of the figures (Fig. 1A–D) gives a guide as to the biological importance of this term. In control tanks housing small groups, breeder male dominance was consistently more than five-fold greater than that of breeder females, although this trend was significant only immediately after the control perturbation (Fig. 1A; Table S1 for pairwise comparisons). In control tanks housing large groups, there were no significant differences in dominance between the breeder males, breeder females and helpers, although the helpers consistently had a five-fold lower dominance score than both the breeder males and breeder females (Fig. 1B; Table S1). These results suggest that male aggression is more pronounced in small control groups and that breeder females display more submissive acts in response.

In treatment tanks housing small groups, we found that the dominance indices of the breeder females were significantly lower than those of the breeder males at all timepoints, especially immediately following the perturbation (Fig. 1C; Table S1). However, in treatment tanks housing large groups, there was a delayed spike in breeder male dominance relative to breeder females, in that no significant difference in dominance between breeder males and females was apparent until 4 h after the perturbation (Fig. 1D; Table S1). Helper dominance remained significantly lower than

breeder male dominance in treatment groups across all timepoints and for both group sizes. There was no significant effect of trial number (i.e. perturbation 1 versus perturbation 2) in any of the analyses.

There was a significant interaction term between group size, treatment and timepoint on social affiliation scores. We further detected a significant interaction term between trial number and timepoint, and a main effect of subject (breeder female, breeder male, helper) on social affiliation scores (Table 1, Fig. 1E–H). Although there was no effect of group size on affiliation scores in the control groups, affiliation conspicuously increased following perturbation in the large treatment groups relative to the small treatment groups. Groups gradually increased affiliative behaviors following the introduction of a new breeder male, but somewhat decreased affiliative behavior following the introduction of a second new breeder male (Table 1; Table S2 for pairwise comparisons). Finally, breeder females had the highest affiliation index followed by breeder males, and then by helpers in the treatment groups (Fig. 1E–H, Table 1; Table S2 for pairwise comparisons).

Morphometric and enzyme responses

We found an interaction between body mass and group size on the maximum dominance index observed (Table 2, Fig. 2A). Here,

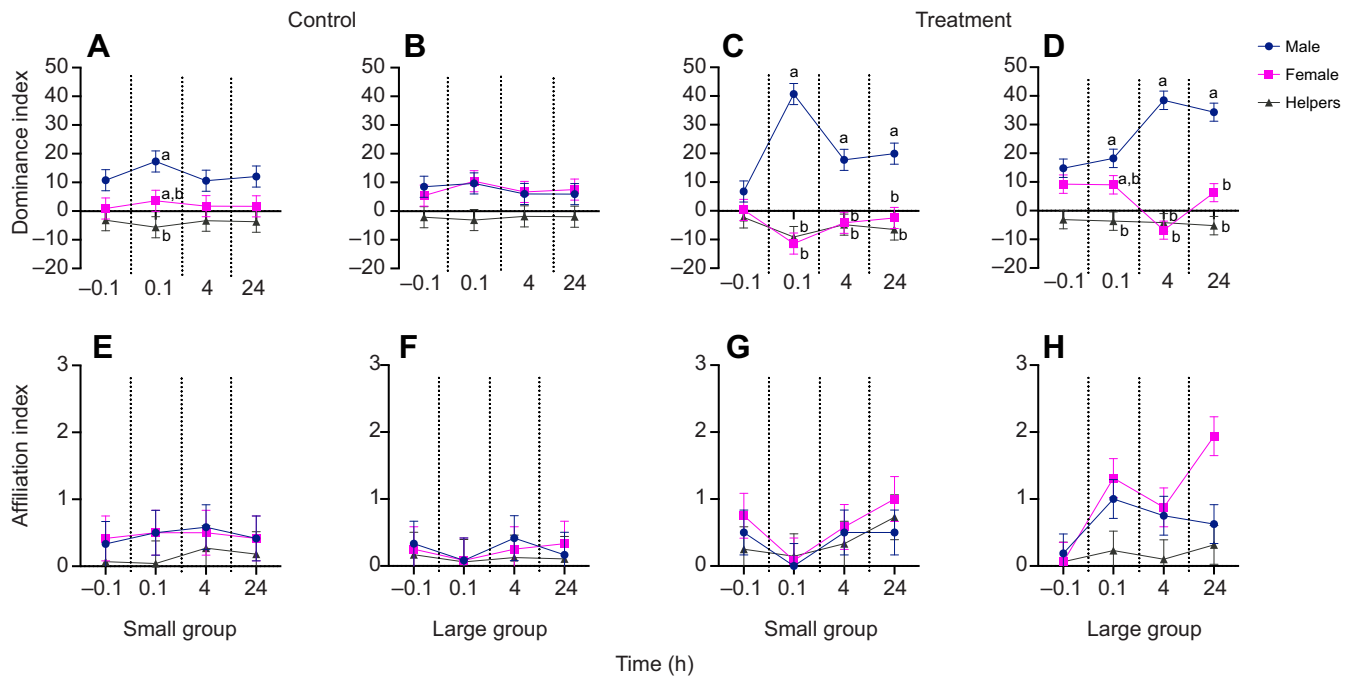


Fig. 1. Time courses for mean dominance and affiliation indices. (A–D) Mean dominance indices in males (blue), females (pink) and helpers (gray) from small and large control (A and B, respectively) and treatment (C and D, respectively) groups. (E–H) Mean affiliation indices from small and large control (E and F, respectively) and treatment (G and H, respectively) groups. Different letters represent significant ($P < 0.05$) differences between males, females and helpers within each respective timepoint, as determined by *post hoc* comparisons.

maximum scores for dominance increased with breeder female body size in small groups and decreased with body size in large groups. There were no significant effects of heart tissue in relation to body mass; however, there was a significant interaction between treatment and group size on relative liver size (hepatosomatic index, HSI; Table 2, Fig. 2B). Specifically, the mean HSI was elevated in breeder females of small groups in control tanks and large groups in treatment tanks.

There was a significant interaction between the dominance indices of breeder females and treatment on liver LDH activity (Table 2, Fig. 2C). Liver LDH activity scaled negatively with breeder female dominance in control groups, and positively with breeder female dominance in treatment groups. This result suggests that our social perturbation treatment was successful in priming breeder females to be more enzymatically prepared for sudden bursts of activity. We found no significant effects of dominance on muscle LDH activity, or liver and skeletal muscle CS activity (Table 2). *Post hoc*, we found no significant effects of mean level of breeder female activity on liver LDH activities (see Dataset 1 for the liver model, which is identical to Table 2 but with ‘mean activity’ replacing ‘maximum dominance’ as a covariate), suggesting that maximum dominance affects glycolytic capacity independently from greater levels of general locomotor activity.

DISCUSSION

Group stability tends to increase the benefits and decrease the costs of social living (Berger, 1978; Modlmeier et al., 2012; Pruitt and Riechert, 2011), and groups often exhibit mechanisms to return to a stable state following disturbance (Goldenberg et al., 2016; McCowan et al., 2011; De Waal, 2000). We sought to determine the effects of group size on the group’s ability to return to social homeostasis in the face of a repeated social stressor. Specifically, we hypothesized a large group would either reduce overall aggression,

through the distributed perturbation hypothesis, or increase and sustain overall aggression, through the aggressive feedback hypothesis. Here, we found more support for the distributed perturbation hypothesis, though additional moderating forces are also likely at play.

Small groups showed more disparate dominance indices between the most dominant fish (breeder males) and the subordinate fish (breeder females and helpers). This is most obvious when comparing the control groups (Fig. 1A,B). Previous work has found large groups benefitting from larger territories with increased shelter and more opportunities to feed (Balshine et al., 2001). Our results further imply that small groups may be inherently more polarized (and less stable) than large groups, even when social conditions remain relatively steady. In other words, large groups likely benefit from both material and non-material social advantages. The timing of dominance index spikes varied with group size in our treatment groups: in small groups, changes to and inequality of dominance indices appeared immediately following the perturbation (Fig. 1C), while in large groups change in the indices lagged following perturbation (Fig. 1D). Small groups also appear to return to baseline states faster, as observed in the apparent reduction in breeder male dominance 24 h following the perturbations, while the dominance of large group breeder males remain elevated. Together, these results suggest that large groups are more resistant to social state change and/or that state change in large groups is slower than in small groups. This could be because new breeder males delay asserting their dominance in larger groups until they have had time to evaluate their new social setting and potential competitors. Regardless of the mechanism, this conveys that larger groups might offer their constituents buffering effects against ephemeral social perturbations in a manner that small groups do not.

Additional circumstantial evidence from affiliation indices and body mass hint that smaller groups are more stressful social

Table 2. Statistical parameters for final (minimal) GLM for female-level effects

	SS	d.f.	F	P
Morphometrics on max. dominance				
Body mass	247	1	1.38	0.252
Group size	621	1	3.48	0.075
Group size×Body mass	866	1	4.85	0.038
Residuals	3925	22		
Relative liver size (HSI)				
Group size	0.007	1	0.04	0.846
Treatment	0.105	1	0.54	0.469
Group size×Treatment	0.831	1	4.31	0.050
Residuals	4.239	22		
Liver LDH				
Body mass	0.174	1	0.73	0.402
Treatment	0.238	1	1.00	0.329
Max. dominance	0.212	1	0.89	0.357
Muscle LDH	1.094	1	4.61	0.045
Treatment×max. dominance	1.732	1	7.30	0.014
Residuals	4.510	19		
Muscle LDH				
Body mass	154	1	1.647	0.212
Residuals	2256	24		
Liver CS				
Body mass	0.004	1	0.184	0.672
Residuals	0.531	22		
Muscle CS				
Body mass	0.300	1	0.211	0.650
Residuals	34.19	24		

CS, citrate synthase; HSI, hepatosomatic index; LDH, lactate dehydrogenase. Max. dominance is the maximum dominance index observed. Bold indicates $P < 0.05$.

environments following perturbation. One can observe an increase in the affiliative behaviors of breeder males and especially breeder females following social perturbations in large groups (Fig. 1H). This conveys that the new breeder pair begins establishing a social bond in these groups. If this happens in small groups too, then it is certainly less conspicuous (Fig. 1G). We further note that large breeder females exhibited higher dominance in small groups, irrespective of control versus treatment, whereas no relationship between body size and dominance was observed in large social groups. This group-size-dependent relationship conveys that more acts of dominance transpire in small groups occupied by large breeder females, whereas the dominance indices of breeder females in large groups are near uniformly low (Fig. 2A). This lack of variation in large groups provides further evidence that large social groups are less volatile and more stable social environments than small groups. In *N. pulcher*, the strength of social buffering is largely managed by aggression rates (Culbert et al., 2019), so the decreased aggression found in these large groups might facilitate recovery from social perturbation.

The significant interaction of treatment type and group size on HSI further reveals that social disturbance affects breeder female physiology as a factor of group size. Decreased liver size in treated females from small groups and enhanced liver size in treated females from large groups may indicate changes in metabolic energy demands, short-term nutritional status, growth rates, synthesis of vitellogenin and eggshell proteins, or a combination thereof (e.g. Adams and McLean, 1985; Berg et al., 2004; Everaarts et al., 1993; Korsgaard et al., 1986; Larsen et al., 1992). Although we lack the resolution to disentangle the mechanisms affecting treatment- and group-size-driven differences in HSI here, higher HSI has been linked to increased dominance in sticklebacks

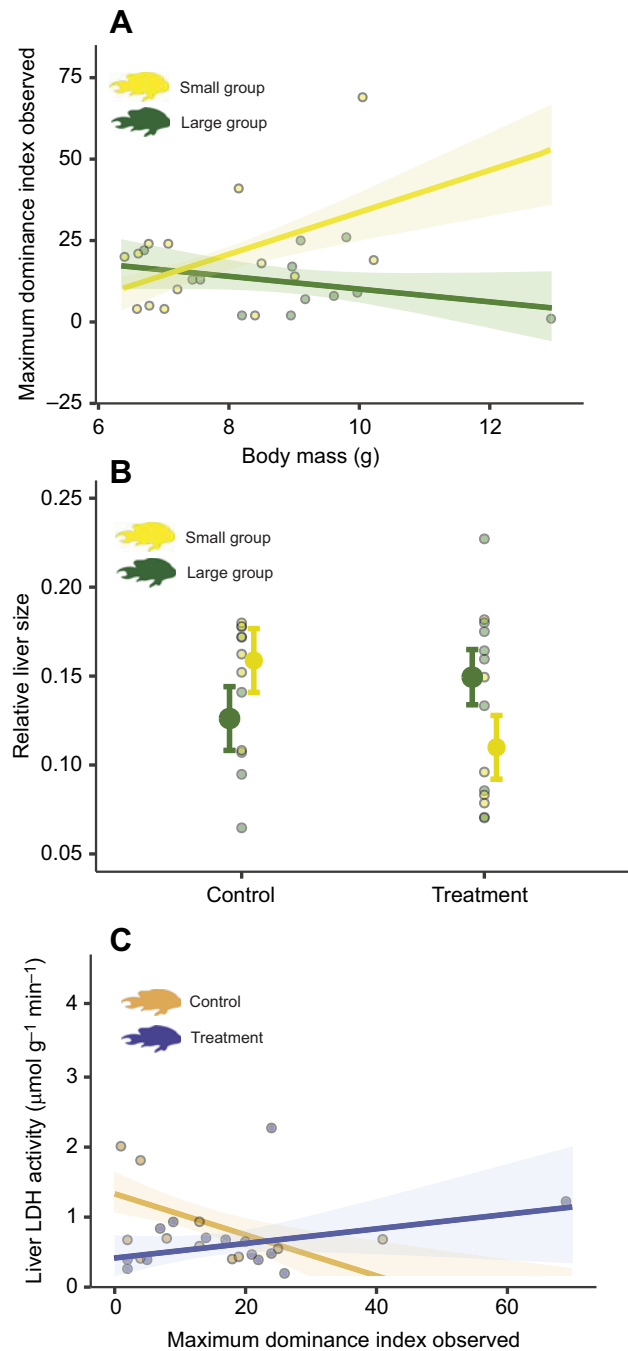


Fig. 2. Relationships between behavioral, morphometric and enzymatic traits. Maximum dominance index observed scales with body mass depending on group size (A), hepatosomatic index (HSI) changes as a function of group size depending on treatment type (B), and liver LDH activity scales with maximum dominance index observed depending on treatment type (C). Small and large groups (A,B) are represented by yellow and green, respectively, whereas treatment and control groups (C) are represented by violet and orange, respectively. Enclosed circles represent observed scores. Note, the directionality and patterns of the relationship remain when we remove the two most extreme data points.

(Guderley and Couture, 2005). Furthermore, concurrent changes in liver LDH activities can indicate that metabolic energy demands, at least in part, contribute to this effect. Specifically, we show that treatment type directionally mediates the relationship between dominance and glycolytic capacity.

The divergent relationship between dominance and LDH activity provides evidence that our social perturbations were successful in instigating an enzymatic response in breeder females. Liver LDH activity increased with breeder female dominance in treatment groups, which were characterized by the largest gaps in dominance between breeder males and females. This further suggests that breeder female dominance increases metabolic preparedness for aggression in these groups relative to controls. By contrast, in the control condition, LDH activity levels decreased with breeder female dominance, suggesting that greater dominance is associated with reduced glycolytic capacity and potentially greater stability in these groups. Because the control perturbation was characterized by a familiar breeder male, we suggest that pre-established social relationships dampen the aggressive actions that foster glycolytic capacity. Whether these phenotypic differences reflect a regulated response to social stress, a positive feedback effect of training, or a combination of the two, remains to be examined. However, the lack of relationship between liver LDH activity and greater breeder female activity levels suggests that these trends are not simply a feedback effect of exercise training.

Overall, we found more support for the distributed perturbation hypothesis from both behavioral and physiological indicators. Physiologically, breeder females elevated their glycolytic capacity in small groups and when faced with strong social perturbations (treatment). Behaviorally, small groups also showed a larger difference in dominance indices across group members, whereas in large groups, dominance indices were slower to polarize following a perturbation and were associated with a surge of affiliative behaviors as well, both observations circumstantially supporting the distributed perturbation hypothesis. In contrast, the gap in dominance indices shrunk faster following the perturbation in small groups compared with large groups, potentially supporting the aggressive feedback hypothesis. It therefore appears that different group sizes create different responses to the forces of instability: small groups experience larger instability following a social perturbation but recover more rapidly and appear physiologically primed for more instability, whereas large groups are more resistant to the instability of perturbation but appear to recover more slowly. In aggregate, these results convey that the demographic traits of social groups can play a large role in shaping group susceptibility to and recoverability from social disturbance, and that larger groups could exhibit greater levels of social stability and social inertia.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: H.M.A., A.G.L., D.N.F., B.L.M., B.M.C., S.B., J.N.P.; Methodology: H.M.A., A.G.L., D.N.F., B.L.M., B.M.C., S.B., J.N.P.; Formal analysis: A.G.L., J.N.P.; Investigation: H.M.A., A.G.L., D.N.F., B.L.M., B.M.C., S.B.; Resources: S.B., J.N.P.; Data curation: H.M.A., A.G.L.; Writing - original draft: H.M.A., A.G.L., J.N.P.; Writing - review & editing: H.M.A., A.G.L., D.N.F., B.L.M., B.M.C., S.B., J.N.P.; Visualization: A.G.L.; Supervision: H.M.A., A.G.L., B.M.C., S.B., J.N.P.; Project administration: H.M.A., A.G.L., S.B., J.N.P.; Funding acquisition: S.B., J.N.P.

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Supplementary information

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Dataset 1.

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Table S1. Post-hoc Comparisons for Dominance Index Analysis – Treatment×Timepoint×Group Size×Subject

Group Size	Treatment	Subject	Comparison				Difference	SE	t	df	Pbonferroni		
			Time Point	Group Size	Treatment	Subject							
Large	Control	Breeding Female	-0.1	-	Large	Control	Breeding Male	-0.1	-3.0833	5.19	-0.59398	549	1.000
Large	Control	Breeding Female	-0.1	-	Large	Control	Helpers	-0.1	7.5211	5.19	1.44889	549	1.000
Large	Control	Breeding Female	-0.1	-	Large	Treatment	Breeding Male	-0.1	-9.3881	4.86	-1.93024	538	1.000
Large	Control	Breeding Female	-0.1	-	Large	Treatment	Helpers	-0.1	8.5516	4.86	1.75826	538	1.000
Large	Control	Breeding Female	-0.1	-	Small	Control	Breeding Male	-0.1	-5.3333	5.20	-1.02623	536	1.000
Large	Control	Breeding Female	-0.1	-	Small	Control	Helpers	-0.1	8.5694	5.20	1.64892	536	1.000
Large	Control	Breeding Female	-0.1	-	Small	Treatment	Breeding Male	-0.1	-1.3436	5.20	-0.25835	539	1.000
Large	Control	Breeding Female	-0.1	-	Small	Treatment	Helpers	-0.1	7.6772	5.20	1.47613	539	1.000
Large	Control	Breeding Female	0.1	-	Large	Control	Breeding Female	-0.1	5.0000	5.19	0.96322	549	1.000
Large	Control	Breeding Female	0.1	-	Large	Control	Breeding Male	-0.1	1.9167	5.19	0.36923	549	1.000
Large	Control	Breeding Female	0.1	-	Large	Control	Breeding Male	0.1	0.7500	5.19	0.14448	549	1.000
Large	Control	Breeding Female	0.1	-	Large	Control	Helpers	-0.1	12.5211	5.19	2.41211	549	1.000
Large	Control	Breeding Female	0.1	-	Large	Control	Helpers	0.1	13.5054	5.19	2.60171	549	1.000
Large	Control	Breeding Female	0.1	-	Large	Treatment	Breeding Female	-0.1	1.1744	4.86	0.24146	538	1.000
Large	Control	Breeding Female	0.1	-	Large	Treatment	Breeding Male	-0.1	-4.3881	4.86	-0.90222	538	1.000
Large	Control	Breeding Female	0.1	-	Large	Treatment	Breeding Male	0.1	-7.8269	4.86	-1.60948	538	1.000
Large	Control	Breeding Female	0.1	-	Large	Treatment	Helpers	-0.1	13.5516	4.86	2.78628	538	1.000
Large	Control	Breeding Female	0.1	-	Large	Treatment	Helpers	0.1	14.0488	4.86	2.88889	538	1.000
Large	Control	Breeding Female	0.1	-	Small	Control	Breeding Female	-0.1	9.5000	5.20	1.82798	536	1.000
Large	Control	Breeding Female	0.1	-	Small	Control	Breeding Male	-0.1	-0.3333	5.20	-0.06414	536	1.000
Large	Control	Breeding Female	0.1	-	Small	Control	Breeding Male	0.1	-6.9167	5.20	-1.33090	536	1.000
Large	Control	Breeding Female	0.1	-	Small	Control	Helpers	-0.1	13.5694	5.20	2.61102	536	1.000
Large	Control	Breeding Female	0.1	-	Small	Control	Helpers	0.1	16.0625	5.20	3.09073	536	1.000
Large	Control	Breeding Female	0.1	-	Small	Treatment	Breeding Female	-0.1	10.0730	5.20	1.93679	539	1.000
Large	Control	Breeding Female	0.1	-	Small	Treatment	Breeding Male	-0.1	3.6564	5.20	0.70303	539	1.000
Large	Control	Breeding Female	0.1	-	Small	Treatment	Breeding Male	0.1	-30.2585	5.20	-5.81916	539	<.001
Large	Control	Breeding Female	0.1	-	Small	Treatment	Helpers	-0.1	12.6772	5.20	2.43750	539	1.000
Large	Control	Breeding Female	0.1	-	Small	Treatment	Helpers	0.1	19.5332	5.20	3.75651	539	0.216
Large	Control	Breeding Female	24	-	Large	Control	Breeding Female	-0.1	2.0833	5.19	0.40134	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Breeding Female	0.1	-2.9167	5.19	-0.56188	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Breeding Female	4	0.8333	5.19	0.16054	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Breeding Male	-0.1	-1.0000	5.19	-0.19264	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Breeding Male	0.1	-2.1667	5.19	-0.41739	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Breeding Male	24	1.5833	5.19	0.30502	549	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Control	Breeding Female	24	-	Large	Control	Breeding Male	4	1.5000	5.19	0.28896	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Helpers	-0.1	9.6045	5.19	1.85023	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Helpers	0.1	10.5887	5.19	2.03984	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Helpers	24	9.4280	5.19	1.81623	549	1.000
Large	Control	Breeding Female	24	-	Large	Control	Helpers	4	9.3485	5.19	1.80093	549	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Breeding Female	-0.1	-1.7423	4.86	-0.35822	538	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Breeding Female	0.1	-1.4936	4.86	-0.30714	538	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Breeding Female	4	14.3189	4.86	2.94443	538	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Breeding Male	-0.1	-7.3048	4.86	-1.50190	538	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Breeding Male	0.1	-10.7436	4.86	-2.20924	538	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Breeding Male	24	-26.8061	4.86	-5.51222	538	<.001
Large	Control	Breeding Female	24	-	Large	Treatment	Breeding Male	4	-30.9936	4.86	-6.37330	538	<.001
Large	Control	Breeding Female	24	-	Large	Treatment	Helpers	-0.1	10.6350	4.86	2.18660	538	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Helpers	0.1	11.1321	4.86	2.28913	538	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Helpers	24	12.7277	4.86	2.61724	538	1.000
Large	Control	Breeding Female	24	-	Large	Treatment	Helpers	4	11.6433	4.86	2.39424	538	1.000
Large	Control	Breeding Female	24	-	Small	Control	Breeding Female	-0.1	6.5833	5.20	1.26676	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Breeding Female	0.1	3.9167	5.20	0.75364	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Breeding Female	4	5.7500	5.20	1.10641	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Breeding Male	-0.1	-3.2500	5.20	-0.62536	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Breeding Male	0.1	-9.8333	5.20	-1.89212	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Breeding Male	24	-4.5833	5.20	-0.88192	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Breeding Male	4	-3.0833	5.20	-0.59329	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Helpers	-0.1	10.6528	5.20	2.04979	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Helpers	0.1	13.1458	5.20	2.52950	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Helpers	24	11.2153	5.20	2.15803	536	1.000
Large	Control	Breeding Female	24	-	Small	Control	Helpers	4	10.8403	5.20	2.08587	536	1.000
Large	Control	Breeding Female	24	-	Small	Treatment	Breeding Female	-0.1	7.1564	5.20	1.37599	539	1.000
Large	Control	Breeding Female	24	-	Small	Treatment	Breeding Female	0.1	18.9082	5.20	3.63632	539	0.342
Large	Control	Breeding Female	24	-	Small	Treatment	Breeding Female	4	11.6582	5.20	2.24204	539	1.000
Large	Control	Breeding Female	24	-	Small	Treatment	Breeding Male	-0.1	0.7397	5.20	0.14223	539	1.000
Large	Control	Breeding Female	24	-	Small	Treatment	Breeding Male	0.1	-33.1752	5.20	-6.38008	539	<.001
Large	Control	Breeding Female	24	-	Small	Treatment	Breeding Male	24	-12.4252	5.20	-2.38955	539	1.000
Large	Control	Breeding Female	24	-	Small	Treatment	Breeding Male	4	-10.2585	5.20	-1.97286	539	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Control	Breeding Female	24	-	Small	Treatment	Helpers	-0.1	9.7605	5.20	1.87670	539	1.000
Large	Control	Breeding Female	24	-	Small	Treatment	Helpers	0.1	16.6165	5.20	3.19560	539	1.000
Large	Control	Breeding Female	24	-	Small	Treatment	Helpers	24	13.9915	5.20	2.69077	539	1.000
Large	Control	Breeding Female	24	-	Small	Treatment	Helpers	4	12.3040	5.20	2.36624	539	1.000
Large	Control	Breeding Female	4	-	Large	Control	Breeding Female	-0.1	1.2500	5.19	0.24080	549	1.000
Large	Control	Breeding Female	4	-	Large	Control	Breeding Female	0.1	-3.7500	5.19	-0.72241	549	1.000
Large	Control	Breeding Female	4	-	Large	Control	Breeding Male	-0.1	-1.8333	5.19	-0.35318	549	1.000
Large	Control	Breeding Female	4	-	Large	Control	Breeding Male	0.1	-3.0000	5.19	-0.57793	549	1.000
Large	Control	Breeding Female	4	-	Large	Control	Breeding Male	4	0.6667	5.19	0.12843	549	1.000
Large	Control	Breeding Female	4	-	Large	Control	Helpers	-0.1	8.7711	5.19	1.68970	549	1.000
Large	Control	Breeding Female	4	-	Large	Control	Helpers	0.1	9.7554	5.19	1.87930	549	1.000
Large	Control	Breeding Female	4	-	Large	Control	Helpers	4	8.5152	5.19	1.64039	549	1.000
Large	Control	Breeding Female	4	-	Large	Treatment	Breeding Female	-0.1	-2.5756	4.86	-0.52956	538	1.000
Large	Control	Breeding Female	4	-	Large	Treatment	Breeding Female	0.1	-2.3269	4.86	-0.47850	538	1.000
Large	Control	Breeding Female	4	-	Large	Treatment	Breeding Male	-0.1	-8.1381	4.86	-1.67324	538	1.000
Large	Control	Breeding Female	4	-	Large	Treatment	Breeding Male	0.1	-11.5769	4.86	-2.38060	538	1.000
Large	Control	Breeding Female	4	-	Large	Treatment	Breeding Male	4	-31.8269	4.86	-6.54467	538	<.001
Large	Control	Breeding Female	4	-	Large	Treatment	Helpers	-0.1	9.8016	4.86	2.01526	538	1.000
Large	Control	Breeding Female	4	-	Large	Treatment	Helpers	0.1	10.2988	4.86	2.11777	538	1.000
Large	Control	Breeding Female	4	-	Large	Treatment	Helpers	4	10.8100	4.86	2.22288	538	1.000
Large	Control	Breeding Female	4	-	Small	Control	Breeding Female	-0.1	5.7500	5.20	1.10641	536	1.000
Large	Control	Breeding Female	4	-	Small	Control	Breeding Female	0.1	3.0833	5.20	0.59329	536	1.000
Large	Control	Breeding Female	4	-	Small	Control	Breeding Male	-0.1	-4.0833	5.20	-0.78571	536	1.000
Large	Control	Breeding Female	4	-	Small	Control	Breeding Male	0.1	-10.6667	5.20	-2.05247	536	1.000
Large	Control	Breeding Female	4	-	Small	Control	Breeding Male	4	-3.9167	5.20	-0.75364	536	1.000
Large	Control	Breeding Female	4	-	Small	Control	Helpers	-0.1	9.8194	5.20	1.88945	536	1.000
Large	Control	Breeding Female	4	-	Small	Control	Helpers	0.1	12.3125	5.20	2.36916	536	1.000
Large	Control	Breeding Female	4	-	Small	Control	Helpers	4	10.0069	5.20	1.92552	536	1.000
Large	Control	Breeding Female	4	-	Small	Treatment	Breeding Female	-0.1	6.3230	5.20	1.21576	539	1.000
Large	Control	Breeding Female	4	-	Small	Treatment	Breeding Female	0.1	18.0748	5.20	3.47606	539	0.620
Large	Control	Breeding Female	4	-	Small	Treatment	Breeding Male	-0.1	-0.0936	5.20	-0.01800	539	1.000
Large	Control	Breeding Female	4	-	Small	Treatment	Breeding Male	0.1	-34.0085	5.20	-6.54034	539	<.001
Large	Control	Breeding Female	4	-	Small	Treatment	Breeding Male	4	-11.0918	5.20	-2.13313	539	1.000
Large	Control	Breeding Female	4	-	Small	Treatment	Helpers	-0.1	8.9272	5.20	1.71647	539	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison												
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point	Difference	SE	t	df	Pbonferroni
Large	Control	Breeding Female	4	- Small	Treatment	Helpers	0.1	15.7832	5.20	3.03533	539	1.000
Large	Control	Breeding Female	4	- Small	Treatment	Helpers	4	11.4707	5.20	2.20598	539	1.000
Large	Control	Breeding Male	-0.1	- Large	Control	Helpers	-0.1	10.6045	5.19	2.04288	549	1.000
Large	Control	Breeding Male	-0.1	- Large	Treatment	Helpers	-0.1	11.6350	4.86	2.39221	538	1.000
Large	Control	Breeding Male	-0.1	- Small	Control	Helpers	-0.1	11.6528	5.20	2.24221	536	1.000
Large	Control	Breeding Male	-0.1	- Small	Treatment	Helpers	-0.1	10.7605	5.20	2.06898	539	1.000
Large	Control	Breeding Male	0.1	- Large	Control	Breeding Female	-0.1	4.2500	5.19	0.81873	549	1.000
Large	Control	Breeding Male	0.1	- Large	Control	Breeding Male	-0.1	1.1667	5.19	0.22475	549	1.000
Large	Control	Breeding Male	0.1	- Large	Control	Helpers	-0.1	11.7711	5.19	2.26763	549	1.000
Large	Control	Breeding Male	0.1	- Large	Control	Helpers	0.1	12.7554	5.19	2.45723	549	1.000
Large	Control	Breeding Male	0.1	- Large	Treatment	Breeding Female	-0.1	0.4244	4.86	0.08726	538	1.000
Large	Control	Breeding Male	0.1	- Large	Treatment	Breeding Male	-0.1	-5.1381	4.86	-1.05642	538	1.000
Large	Control	Breeding Male	0.1	- Large	Treatment	Helpers	-0.1	12.8016	4.86	2.63208	538	1.000
Large	Control	Breeding Male	0.1	- Large	Treatment	Helpers	0.1	13.2988	4.86	2.73467	538	1.000
Large	Control	Breeding Male	0.1	- Small	Control	Breeding Female	-0.1	8.7500	5.20	1.68366	536	1.000
Large	Control	Breeding Male	0.1	- Small	Control	Breeding Male	-0.1	-1.0833	5.20	-0.20845	536	1.000
Large	Control	Breeding Male	0.1	- Small	Control	Helpers	-0.1	12.8194	5.20	2.46670	536	1.000
Large	Control	Breeding Male	0.1	- Small	Control	Helpers	0.1	15.3125	5.20	2.94641	536	1.000
Large	Control	Breeding Male	0.1	- Small	Treatment	Breeding Female	-0.1	9.3230	5.20	1.79258	539	1.000
Large	Control	Breeding Male	0.1	- Small	Treatment	Breeding Male	-0.1	2.9064	5.20	0.55882	539	1.000
Large	Control	Breeding Male	0.1	- Small	Treatment	Helpers	-0.1	11.9272	5.20	2.29330	539	1.000
Large	Control	Breeding Male	0.1	- Small	Treatment	Helpers	0.1	18.7832	5.20	3.61228	539	0.374
Large	Control	Breeding Male	24	- Large	Control	Breeding Female	-0.1	0.5000	5.19	0.09632	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Breeding Female	0.1	-4.5000	5.19	-0.86689	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Breeding Female	4	-0.7500	5.19	-0.14448	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Breeding Male	-0.1	-2.5833	5.19	-0.49766	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Breeding Male	0.1	-3.7500	5.19	-0.72241	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Breeding Male	4	-0.0833	5.19	-0.01605	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Helpers	-0.1	8.0211	5.19	1.54521	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Helpers	0.1	9.0054	5.19	1.73482	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Helpers	24	7.8446	5.19	1.51122	549	1.000
Large	Control	Breeding Male	24	- Large	Control	Helpers	4	7.7652	5.19	1.49591	549	1.000
Large	Control	Breeding Male	24	- Large	Treatment	Breeding Female	-0.1	-3.3256	4.86	-0.68376	538	1.000
Large	Control	Breeding Male	24	- Large	Treatment	Breeding Female	0.1	-3.0769	4.86	-0.63272	538	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Control	Breeding Male	24	-	Large	Treatment	Breeding Female	4	12.7356	4.86	2.61885	538	1.000
Large	Control	Breeding Male	24	-	Large	Treatment	Breeding Male	-0.1	-8.8881	4.86	-1.82744	538	1.000
Large	Control	Breeding Male	24	-	Large	Treatment	Breeding Male	0.1	-12.3269	4.86	-2.53483	538	1.000
Large	Control	Breeding Male	24	-	Large	Treatment	Breeding Male	4	-32.5769	4.86	-6.69889	538	<.001
Large	Control	Breeding Male	24	-	Large	Treatment	Helpers	-0.1	9.0516	4.86	1.86106	538	1.000
Large	Control	Breeding Male	24	-	Large	Treatment	Helpers	0.1	9.5488	4.86	1.96355	538	1.000
Large	Control	Breeding Male	24	-	Large	Treatment	Helpers	24	11.1444	4.86	2.29166	538	1.000
Large	Control	Breeding Male	24	-	Large	Treatment	Helpers	4	10.0600	4.86	2.06866	538	1.000
Large	Control	Breeding Male	24	-	Small	Control	Breeding Female	-0.1	5.0000	5.20	0.96209	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Breeding Female	0.1	2.3333	5.20	0.44898	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Breeding Female	4	4.1667	5.20	0.80174	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Breeding Male	-0.1	-4.8333	5.20	-0.93002	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Breeding Male	0.1	-11.4167	5.20	-2.19678	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Breeding Male	4	-4.6667	5.20	-0.89795	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Helpers	-0.1	9.0694	5.20	1.74513	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Helpers	0.1	11.5625	5.20	2.22484	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Helpers	24	9.6319	5.20	1.85337	536	1.000
Large	Control	Breeding Male	24	-	Small	Control	Helpers	4	9.2569	5.20	1.78121	536	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Breeding Female	-0.1	5.5730	5.20	1.07155	539	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Breeding Female	0.1	17.3248	5.20	3.33182	539	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Breeding Female	4	10.0748	5.20	1.93754	539	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Breeding Male	-0.1	-0.8436	5.20	-0.16221	539	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Breeding Male	0.1	-34.7585	5.20	-6.68458	539	<.001
Large	Control	Breeding Male	24	-	Small	Treatment	Breeding Male	4	-11.8418	5.20	-2.27736	539	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Helpers	-0.1	8.1772	5.20	1.57227	539	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Helpers	0.1	15.0332	5.20	2.89110	539	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Helpers	24	12.4082	5.20	2.38627	539	1.000
Large	Control	Breeding Male	24	-	Small	Treatment	Helpers	4	10.7207	5.20	2.06174	539	1.000
Large	Control	Breeding Male	4	-	Large	Control	Breeding Female	-0.1	0.5833	5.19	0.11238	549	1.000
Large	Control	Breeding Male	4	-	Large	Control	Breeding Female	0.1	-4.4167	5.19	-0.85084	549	1.000
Large	Control	Breeding Male	4	-	Large	Control	Breeding Male	-0.1	-2.5000	5.19	-0.48161	549	1.000
Large	Control	Breeding Male	4	-	Large	Control	Breeding Male	0.1	-3.6667	5.19	-0.70636	549	1.000
Large	Control	Breeding Male	4	-	Large	Control	Helpers	-0.1	8.1045	5.19	1.56127	549	1.000
Large	Control	Breeding Male	4	-	Large	Control	Helpers	0.1	9.0887	5.19	1.75087	549	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison								Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Control	Breeding Male	4	-	Large	Control	Helpers	4	7.8485	5.19	1.51196	549	1.000
Large	Control	Breeding Male	4	-	Large	Treatment	Breeding Female	-0.1	-3.2423	4.86	-0.66663	538	1.000
Large	Control	Breeding Male	4	-	Large	Treatment	Breeding Female	0.1	-2.9936	4.86	-0.61559	538	1.000
Large	Control	Breeding Male	4	-	Large	Treatment	Breeding Male	-0.1	-8.8048	4.86	-1.81031	538	1.000
Large	Control	Breeding Male	4	-	Large	Treatment	Breeding Male	0.1	-12.2436	4.86	-2.51769	538	1.000
Large	Control	Breeding Male	4	-	Large	Treatment	Helpers	-0.1	9.1350	4.86	1.87819	538	1.000
Large	Control	Breeding Male	4	-	Large	Treatment	Helpers	0.1	9.6321	4.86	1.98068	538	1.000
Large	Control	Breeding Male	4	-	Large	Treatment	Helpers	4	10.1433	4.86	2.08579	538	1.000
Large	Control	Breeding Male	4	-	Small	Control	Breeding Female	-0.1	5.0833	5.20	0.97813	536	1.000
Large	Control	Breeding Male	4	-	Small	Control	Breeding Female	0.1	2.4167	5.20	0.46501	536	1.000
Large	Control	Breeding Male	4	-	Small	Control	Breeding Male	-0.1	-4.7500	5.20	-0.91399	536	1.000
Large	Control	Breeding Male	4	-	Small	Control	Breeding Male	0.1	-11.3333	5.20	-2.18075	536	1.000
Large	Control	Breeding Male	4	-	Small	Control	Helpers	-0.1	9.1528	5.20	1.76117	536	1.000
Large	Control	Breeding Male	4	-	Small	Control	Helpers	0.1	11.6458	5.20	2.24088	536	1.000
Large	Control	Breeding Male	4	-	Small	Control	Helpers	4	9.3403	5.20	1.79724	536	1.000
Large	Control	Breeding Male	4	-	Small	Treatment	Breeding Female	-0.1	5.6564	5.20	1.08758	539	1.000
Large	Control	Breeding Male	4	-	Small	Treatment	Breeding Female	0.1	17.4082	5.20	3.34785	539	0.983
Large	Control	Breeding Male	4	-	Small	Treatment	Breeding Male	-0.1	-0.7603	5.20	-0.14619	539	1.000
Large	Control	Breeding Male	4	-	Small	Treatment	Breeding Male	0.1	-34.6752	5.20	-6.66855	539	<.001
Large	Control	Breeding Male	4	-	Small	Treatment	Helpers	-0.1	8.2605	5.20	1.58829	539	1.000
Large	Control	Breeding Male	4	-	Small	Treatment	Helpers	0.1	15.1165	5.20	2.90712	539	1.000
Large	Control	Breeding Male	4	-	Small	Treatment	Helpers	4	10.8040	5.20	2.07777	539	1.000
Large	Control	Helpers	0.1	-	Large	Control	Breeding Female	-0.1	-8.5054	5.19	-1.63850	549	1.000
Large	Control	Helpers	0.1	-	Large	Control	Breeding Male	-0.1	-11.5887	5.19	-2.23248	549	1.000
Large	Control	Helpers	0.1	-	Large	Control	Helpers	-0.1	-0.9842	5.19	-0.18960	549	1.000
Large	Control	Helpers	0.1	-	Large	Treatment	Breeding Female	-0.1	-12.3310	4.86	-2.53531	538	1.000
Large	Control	Helpers	0.1	-	Large	Treatment	Breeding Male	-0.1	-17.8935	4.86	-3.67899	538	0.291
Large	Control	Helpers	0.1	-	Large	Treatment	Helpers	-0.1	0.0463	4.86	0.00951	538	1.000
Large	Control	Helpers	0.1	-	Small	Control	Breeding Female	-0.1	-4.0054	5.20	-0.77071	536	1.000
Large	Control	Helpers	0.1	-	Small	Control	Breeding Male	-0.1	-13.8387	5.20	-2.66282	536	1.000
Large	Control	Helpers	0.1	-	Small	Control	Helpers	-0.1	0.0641	5.20	0.01233	536	1.000
Large	Control	Helpers	0.1	-	Small	Treatment	Breeding Female	-0.1	-3.4323	5.20	-0.65995	539	1.000
Large	Control	Helpers	0.1	-	Small	Treatment	Breeding Male	-0.1	-9.8490	5.20	-1.89371	539	1.000
Large	Control	Helpers	0.1	-	Small	Treatment	Helpers	-0.1	-0.8282	5.20	-0.15923	539	1.000
Large	Control	Helpers	24	-	Large	Control	Breeding Female	-0.1	-7.3446	5.19	-1.41489	549	1.000
Large	Control	Helpers	24	-	Large	Control	Breeding Female	0.1	-12.3446	5.19	-2.37811	549	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Control	Helpers	24	-	Large	Control	Breeding Female	4	-8.5946	5.19	-1.65570	549	1.000
Large	Control	Helpers	24	-	Large	Control	Breeding Male	-0.1	-10.4280	5.19	-2.00888	549	1.000
Large	Control	Helpers	24	-	Large	Control	Breeding Male	0.1	-11.5946	5.19	-2.23363	549	1.000
Large	Control	Helpers	24	-	Large	Control	Breeding Male	4	-7.9280	5.19	-1.52727	549	1.000
Large	Control	Helpers	24	-	Large	Control	Helpers	-0.1	0.1765	5.19	0.03400	549	1.000
Large	Control	Helpers	24	-	Large	Control	Helpers	0.1	1.1607	5.19	0.22360	549	1.000
Large	Control	Helpers	24	-	Large	Control	Helpers	4	-0.0795	5.19	-0.01531	549	1.000
Large	Control	Helpers	24	-	Large	Treatment	Breeding Female	-0.1	-11.1703	4.86	-2.29666	538	1.000
Large	Control	Helpers	24	-	Large	Treatment	Breeding Female	0.1	-10.9216	4.86	-2.24584	538	1.000
Large	Control	Helpers	24	-	Large	Treatment	Breeding Female	4	4.8909	4.86	1.00573	538	1.000
Large	Control	Helpers	24	-	Large	Treatment	Breeding Male	-0.1	-16.7328	4.86	-3.44034	538	0.706
Large	Control	Helpers	24	-	Large	Treatment	Breeding Male	0.1	-20.1716	4.86	-4.14794	538	0.044
Large	Control	Helpers	24	-	Large	Treatment	Breeding Male	4	-40.4216	4.86	-8.31201	538	<.001
Large	Control	Helpers	24	-	Large	Treatment	Helpers	-0.1	1.2070	4.86	0.24816	538	1.000
Large	Control	Helpers	24	-	Large	Treatment	Helpers	0.1	1.7042	4.86	0.35043	538	1.000
Large	Control	Helpers	24	-	Large	Treatment	Helpers	4	2.2153	4.86	0.45554	538	1.000
Large	Control	Helpers	24	-	Small	Control	Breeding Female	-0.1	-2.8446	5.20	-0.54736	536	1.000
Large	Control	Helpers	24	-	Small	Control	Breeding Female	0.1	-5.5113	5.20	-1.06048	536	1.000
Large	Control	Helpers	24	-	Small	Control	Breeding Female	4	-3.6780	5.20	-0.70771	536	1.000
Large	Control	Helpers	24	-	Small	Control	Breeding Male	-0.1	-12.6780	5.20	-2.43948	536	1.000
Large	Control	Helpers	24	-	Small	Control	Breeding Male	0.1	-19.2613	5.20	-3.70624	536	0.262
Large	Control	Helpers	24	-	Small	Control	Breeding Male	4	-12.5113	5.20	-2.40741	536	1.000
Large	Control	Helpers	24	-	Small	Control	Helpers	-0.1	1.2248	5.20	0.23567	536	1.000
Large	Control	Helpers	24	-	Small	Control	Helpers	0.1	3.7179	5.20	0.71539	536	1.000
Large	Control	Helpers	24	-	Small	Control	Helpers	4	1.4123	5.20	0.27175	536	1.000
Large	Control	Helpers	24	-	Small	Treatment	Breeding Female	-0.1	-2.2716	5.20	-0.43677	539	1.000
Large	Control	Helpers	24	-	Small	Treatment	Breeding Female	0.1	9.4802	5.20	1.82318	539	1.000
Large	Control	Helpers	24	-	Small	Treatment	Breeding Female	4	2.2302	5.20	0.42890	539	1.000
Large	Control	Helpers	24	-	Small	Treatment	Breeding Male	-0.1	-8.6883	5.20	-1.67053	539	1.000
Large	Control	Helpers	24	-	Small	Treatment	Breeding Male	0.1	-42.6032	5.20	-8.19322	539	<.001
Large	Control	Helpers	24	-	Small	Treatment	Breeding Male	4	-19.6865	5.20	-3.78600	539	0.192
Large	Control	Helpers	24	-	Small	Treatment	Helpers	-0.1	0.3326	5.20	0.06394	539	1.000
Large	Control	Helpers	24	-	Small	Treatment	Helpers	0.1	7.1885	5.20	1.38246	539	1.000
Large	Control	Helpers	24	-	Small	Treatment	Helpers	4	2.8760	5.20	0.55310	539	1.000
Large	Control	Helpers	4	-	Large	Control	Breeding Female	-0.1	-7.2652	5.19	-1.39959	549	1.000
Large	Control	Helpers	4	-	Large	Control	Breeding Female	0.1	-12.2652	5.19	-2.36280	549	1.000
Large	Control	Helpers	4	-	Large	Control	Breeding Male	-0.1	-10.3485	5.19	-1.99357	549	1.000
Large	Control	Helpers	4	-	Large	Control	Breeding Male	0.1	-11.5152	5.19	-2.21832	549	1.000
Large	Control	Helpers	4	-	Large	Control	Helpers	-0.1	0.2560	5.19	0.04931	549	1.000
Large	Control	Helpers	4	-	Large	Control	Helpers	0.1	1.2402	5.19	0.23891	549	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Control	Helpers	4	-	Large	Treatment	Breeding Female	-0.1	-11.0908	4.86	-2.28032	538	1.000
Large	Control	Helpers	4	-	Large	Treatment	Breeding Female	0.1	-10.8421	4.86	-2.22950	538	1.000
Large	Control	Helpers	4	-	Large	Treatment	Breeding Male	-0.1	-16.6533	4.86	-3.42400	538	0.749
Large	Control	Helpers	4	-	Large	Treatment	Breeding Male	0.1	-20.0921	4.86	-4.13160	538	0.047
Large	Control	Helpers	4	-	Large	Treatment	Helpers	-0.1	1.2864	4.86	0.26450	538	1.000
Large	Control	Helpers	4	-	Large	Treatment	Helpers	0.1	1.7836	4.86	0.36677	538	1.000
Large	Control	Helpers	4	-	Small	Control	Breeding Female	-0.1	-2.7652	5.20	-0.53207	536	1.000
Large	Control	Helpers	4	-	Small	Control	Breeding Female	0.1	-5.4318	5.20	-1.04519	536	1.000
Large	Control	Helpers	4	-	Small	Control	Breeding Male	-0.1	-12.5985	5.20	-2.42419	536	1.000
Large	Control	Helpers	4	-	Small	Control	Breeding Male	0.1	-19.1818	5.20	-3.69095	536	0.278
Large	Control	Helpers	4	-	Small	Control	Helpers	-0.1	1.3043	5.20	0.25097	536	1.000
Large	Control	Helpers	4	-	Small	Control	Helpers	0.1	3.7973	5.20	0.73068	536	1.000
Large	Control	Helpers	4	-	Small	Treatment	Breeding Female	-0.1	-2.1921	5.20	-0.42149	539	1.000
Large	Control	Helpers	4	-	Small	Treatment	Breeding Female	0.1	9.5596	5.20	1.83846	539	1.000
Large	Control	Helpers	4	-	Small	Treatment	Breeding Male	-0.1	-8.6088	5.20	-1.65526	539	1.000
Large	Control	Helpers	4	-	Small	Treatment	Breeding Male	0.1	-42.5237	5.20	-8.17794	539	<.001
Large	Control	Helpers	4	-	Small	Treatment	Helpers	-0.1	0.4120	5.20	0.07922	539	1.000
Large	Control	Helpers	4	-	Small	Treatment	Helpers	0.1	7.2680	5.20	1.39774	539	1.000
Large	Treatment	Breeding Female	-0.1	-	Large	Control	Breeding Female	-0.1	3.8256	4.86	0.78656	538	1.000
Large	Treatment	Breeding Female	-0.1	-	Large	Control	Breeding Male	-0.1	0.7423	4.86	0.15262	538	1.000
Large	Treatment	Breeding Female	-0.1	-	Large	Control	Helpers	-0.1	11.3467	4.86	2.33295	538	1.000
Large	Treatment	Breeding Female	-0.1	-	Large	Treatment	Breeding Male	-0.1	-5.5625	4.50	-1.23735	549	1.000
Large	Treatment	Breeding Female	-0.1	-	Large	Treatment	Helpers	-0.1	12.3772	4.50	2.75325	549	1.000
Large	Treatment	Breeding Female	-0.1	-	Small	Control	Breeding Female	-0.1	8.3256	4.86	1.71179	538	1.000
Large	Treatment	Breeding Female	-0.1	-	Small	Control	Breeding Male	-0.1	-1.5077	4.86	-0.31000	538	1.000
Large	Treatment	Breeding Female	-0.1	-	Small	Control	Helpers	-0.1	12.3951	4.86	2.54849	538	1.000
Large	Treatment	Breeding Female	-0.1	-	Small	Treatment	Breeding Male	-0.1	2.4820	4.87	0.50922	543	1.000
Large	Treatment	Breeding Female	-0.1	-	Small	Treatment	Helpers	-0.1	11.5028	4.87	2.35999	543	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Control	Breeding Female	-0.1	3.5769	4.86	0.73554	538	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Control	Breeding Female	0.1	-1.4231	4.86	-0.29263	538	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Control	Breeding Male	-0.1	0.4936	4.86	0.10150	538	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Control	Breeding Male	0.1	-0.6731	4.86	-0.13840	538	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Control	Helpers	-0.1	11.0981	4.86	2.28213	538	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Control	Helpers	0.1	12.0823	4.86	2.48452	538	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Treatment	Breeding Female	-0.1	-0.2487	4.50	-0.05529	550	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Treatment	Breeding Male	-0.1	-5.8112	4.50	-1.29214	550	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Treatment	Breeding Male	0.1	-9.2500	4.50	-2.05762	549	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

		Comparison							Difference	SE	t	df	Pbonferroni
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Treatment	Breeding Female	0.1	-	Large	Treatment	Helpers	-0.1	12.1286	4.50	2.69685	550	1.000
Large	Treatment	Breeding Female	0.1	-	Large	Treatment	Helpers	0.1	12.6257	4.50	2.80853	549	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Control	Breeding Female	-0.1	8.0769	4.86	1.66089	538	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Control	Breeding Female	0.1	5.4103	4.86	1.11253	538	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Control	Breeding Male	-0.1	-1.7564	4.86	-0.36117	538	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Control	Breeding Male	0.1	-8.3397	4.86	-1.71492	538	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Control	Helpers	-0.1	12.1464	4.86	2.49770	538	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Control	Helpers	0.1	14.6394	4.86	3.01035	538	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Treatment	Breeding Female	-0.1	8.6500	4.87	1.77605	544	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Treatment	Breeding Male	-0.1	2.2333	4.87	0.45855	544	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Treatment	Breeding Male	0.1	-31.6816	4.87	-6.50474	543	<.001
Large	Treatment	Breeding Female	0.1	-	Small	Treatment	Helpers	-0.1	11.2541	4.87	2.31075	544	1.000
Large	Treatment	Breeding Female	0.1	-	Small	Treatment	Helpers	0.1	18.1101	4.87	3.71829	543	0.250
Large	Treatment	Breeding Female	24	-	Large	Control	Breeding Female	-0.1	0.8269	4.86	0.17005	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Breeding Female	0.1	-4.1731	4.86	-0.85812	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Breeding Female	24	-1.2564	4.86	-0.25835	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Breeding Female	4	-0.4231	4.86	-0.08699	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Breeding Male	-0.1	-2.2564	4.86	-0.46399	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Breeding Male	0.1	-3.4231	4.86	-0.70389	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Breeding Male	24	0.3269	4.86	0.06723	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Breeding Male	4	0.2436	4.86	0.05009	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Helpers	-0.1	8.3481	4.86	1.71664	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Helpers	0.1	9.3323	4.86	1.91903	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Helpers	24	8.1716	4.86	1.68035	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Control	Helpers	4	8.0921	4.86	1.66401	538	1.000
Large	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Female	-0.1	-2.9987	4.50	-0.66677	550	1.000
Large	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Female	0.1	-2.7500	4.50	-0.61172	549	1.000
Large	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Female	4	13.0625	4.50	2.90569	549	1.000
Large	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Male	-0.1	-8.5612	4.50	-1.90362	550	1.000
Large	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Male	0.1	-12.0000	4.50	-2.66934	549	1.000
Large	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Male	24	-28.0625	4.50	-6.24236	549	<.001
Large	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Male	4	-32.2500	4.50	-7.17385	549	<.001
Large	Treatment	Breeding Female	24	-	Large	Treatment	Helpers	-0.1	9.3786	4.50	2.08537	550	1.000
Large	Treatment	Breeding Female	24	-	Large	Treatment	Helpers	0.1	9.8757	4.50	2.19681	549	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

		Comparison							Difference	SE	t	df	Pbonferroni
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Treatment	Breeding Female	24	-	Large	Treatment	Helpers	24	11.4714	4.50	2.55175	549	1.000
Large	Treatment	Breeding Female	24	-	Large	Treatment	Helpers	4	10.3869	4.50	2.31051	549	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Breeding Female	-0.1	5.3269	4.86	1.09540	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Breeding Female	0.1	2.6603	4.86	0.54704	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Breeding Female	24	4.5769	4.86	0.94117	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Breeding Female	4	4.4936	4.86	0.92403	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Breeding Male	-0.1	-4.5064	4.86	-0.92666	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Breeding Male	0.1	-11.0897	4.86	-2.28041	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Breeding Male	24	-5.8397	4.86	-1.20084	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Breeding Male	4	-4.3397	4.86	-0.89239	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Helpers	-0.1	9.3964	4.86	1.93221	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Helpers	0.1	11.8894	4.86	2.44486	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Helpers	24	9.9589	4.86	2.04788	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Control	Helpers	4	9.5839	4.86	1.97076	538	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Female	-0.1	5.9000	4.87	1.21141	544	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Female	0.1	17.6518	4.87	3.62419	543	0.358
Large	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Female	4	10.4018	4.87	2.13565	543	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Male	-0.1	-0.5167	4.87	-0.10609	544	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Male	0.1	-34.4316	4.87	-7.06936	543	<.001
Large	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Male	24	-13.6816	4.87	-2.80905	543	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Male	4	-11.5149	4.87	-2.36419	543	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Helpers	-0.1	8.5041	4.87	1.74611	544	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Helpers	0.1	15.3601	4.87	3.15368	543	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Helpers	24	12.7351	4.87	2.61472	543	1.000
Large	Treatment	Breeding Female	24	-	Small	Treatment	Helpers	4	11.0476	4.87	2.26825	543	1.000
Large	Treatment	Breeding Female	4	-	Large	Control	Breeding Female	-0.1	-12.2356	4.86	-2.51603	538	1.000
Large	Treatment	Breeding Female	4	-	Large	Control	Breeding Female	0.1	-17.2356	4.86	-3.54420	538	0.483
Large	Treatment	Breeding Female	4	-	Large	Control	Breeding Female	4	-13.4856	4.86	-2.77307	538	1.000
Large	Treatment	Breeding Female	4	-	Large	Control	Breeding Male	-0.1	-15.3189	4.86	-3.15007	538	1.000
Large	Treatment	Breeding Female	4	-	Large	Control	Breeding Male	0.1	-16.4856	4.86	-3.38997	538	0.846
Large	Treatment	Breeding Female	4	-	Large	Control	Breeding Male	4	-12.8189	4.86	-2.63598	538	1.000
Large	Treatment	Breeding Female	4	-	Large	Control	Helpers	-0.1	-4.7144	4.86	-0.96944	538	1.000
Large	Treatment	Breeding Female	4	-	Large	Control	Helpers	0.1	-3.7302	4.86	-0.76705	538	1.000
Large	Treatment	Breeding Female	4	-	Large	Control	Helpers	4	-4.9704	4.86	-1.02207	538	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Treatment	Breeding Female	4	-	Large	Treatment	Breeding Female	-0.1	-16.0612	4.50	-3.57128	550	0.436
Large	Treatment	Breeding Female	4	-	Large	Treatment	Breeding Female	0.1	-15.8125	4.50	-3.51741	549	0.532
Large	Treatment	Breeding Female	4	-	Large	Treatment	Breeding Male	-0.1	-21.6237	4.50	-4.80813	550	0.002
Large	Treatment	Breeding Female	4	-	Large	Treatment	Breeding Male	0.1	-25.0625	4.50	-5.57503	549	<.001
Large	Treatment	Breeding Female	4	-	Large	Treatment	Breeding Male	4	-45.3125	4.50	-10.07954	549	<.001
Large	Treatment	Breeding Female	4	-	Large	Treatment	Helpers	-0.1	-3.6839	4.50	-0.81914	550	1.000
Large	Treatment	Breeding Female	4	-	Large	Treatment	Helpers	0.1	-3.1868	4.50	-0.70888	549	1.000
Large	Treatment	Breeding Female	4	-	Large	Treatment	Helpers	4	-2.6756	4.50	-0.59517	549	1.000
Large	Treatment	Breeding Female	4	-	Small	Control	Breeding Female	-0.1	-7.7356	4.86	-1.59068	538	1.000
Large	Treatment	Breeding Female	4	-	Small	Control	Breeding Female	0.1	-10.4022	4.86	-2.13904	538	1.000
Large	Treatment	Breeding Female	4	-	Small	Control	Breeding Female	4	-8.5689	4.86	-1.76204	538	1.000
Large	Treatment	Breeding Female	4	-	Small	Control	Breeding Male	-0.1	-17.5689	4.86	-3.61274	538	0.374
Large	Treatment	Breeding Female	4	-	Small	Control	Breeding Male	0.1	-24.1522	4.86	-4.96649	538	0.001
Large	Treatment	Breeding Female	4	-	Small	Control	Breeding Male	4	-17.4022	4.86	-3.57847	538	0.425
Large	Treatment	Breeding Female	4	-	Small	Control	Helpers	-0.1	-3.6661	4.86	-0.75387	538	1.000
Large	Treatment	Breeding Female	4	-	Small	Control	Helpers	0.1	-1.1731	4.86	-0.24122	538	1.000
Large	Treatment	Breeding Female	4	-	Small	Control	Helpers	4	-3.4786	4.86	-0.71532	538	1.000
Large	Treatment	Breeding Female	4	-	Small	Treatment	Breeding Female	-0.1	-7.1625	4.87	-1.47064	544	1.000
Large	Treatment	Breeding Female	4	-	Small	Treatment	Breeding Female	0.1	4.5893	4.87	0.94225	543	1.000
Large	Treatment	Breeding Female	4	-	Small	Treatment	Breeding Male	-0.1	-13.5792	4.87	-2.78814	544	1.000
Large	Treatment	Breeding Female	4	-	Small	Treatment	Breeding Male	0.1	-47.4941	4.87	-9.75130	543	<.001
Large	Treatment	Breeding Female	4	-	Small	Treatment	Breeding Male	4	-24.5774	4.87	-5.04614	543	<.001
Large	Treatment	Breeding Female	4	-	Small	Treatment	Helpers	-0.1	-4.5584	4.87	-0.93594	544	1.000
Large	Treatment	Breeding Female	4	-	Small	Treatment	Helpers	0.1	2.2976	4.87	0.47173	543	1.000
Large	Treatment	Breeding Female	4	-	Small	Treatment	Helpers	4	-2.0149	4.87	-0.41369	543	1.000
Large	Treatment	Breeding Male	-0.1	-	Large	Control	Breeding Male	-0.1	6.3048	4.86	1.29629	538	1.000
Large	Treatment	Breeding Male	-0.1	-	Large	Control	Helpers	-0.1	16.9092	4.86	3.47663	538	0.619
Large	Treatment	Breeding Male	-0.1	-	Large	Treatment	Helpers	-0.1	17.9397	4.50	3.99060	549	0.084
Large	Treatment	Breeding Male	-0.1	-	Small	Control	Breeding Male	-0.1	4.0548	4.86	0.83368	538	1.000
Large	Treatment	Breeding Male	-0.1	-	Small	Control	Helpers	-0.1	17.9576	4.86	3.69217	538	0.276
Large	Treatment	Breeding Male	-0.1	-	Small	Treatment	Helpers	-0.1	17.0653	4.87	3.50122	543	0.565
Large	Treatment	Breeding Male	0.1	-	Large	Control	Breeding Female	-0.1	12.8269	4.86	2.63764	538	1.000
Large	Treatment	Breeding Male	0.1	-	Large	Control	Breeding Male	-0.1	9.7436	4.86	2.00361	538	1.000
Large	Treatment	Breeding Male	0.1	-	Large	Control	Breeding Male	0.1	8.5769	4.86	1.76370	538	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

		Comparison						Difference	SE	t	df	Pbonferroni
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point					
Large	Treatment	Breeding Male	0.1	- Large	Control	Helpers	-0.1	20.3481	4.86	4.18423	538	0.038
Large	Treatment	Breeding Male	0.1	- Large	Control	Helpers	0.1	21.3323	4.86	4.38662	538	0.016
Large	Treatment	Breeding Male	0.1	- Large	Treatment	Breeding Female	-0.1	9.0013	4.50	2.00149	550	1.000
Large	Treatment	Breeding Male	0.1	- Large	Treatment	Breeding Male	-0.1	3.4388	4.50	0.76464	550	1.000
Large	Treatment	Breeding Male	0.1	- Large	Treatment	Helpers	-0.1	21.3786	4.50	4.75364	550	0.003
Large	Treatment	Breeding Male	0.1	- Large	Treatment	Helpers	0.1	21.8757	4.50	4.86615	549	0.002
Large	Treatment	Breeding Male	0.1	- Small	Control	Breeding Female	-0.1	17.3269	4.86	3.56299	538	0.450
Large	Treatment	Breeding Male	0.1	- Small	Control	Breeding Male	-0.1	7.4936	4.86	1.54093	538	1.000
Large	Treatment	Breeding Male	0.1	- Small	Control	Breeding Male	0.1	0.9103	4.86	0.18718	538	1.000
Large	Treatment	Breeding Male	0.1	- Small	Control	Helpers	-0.1	21.3964	4.86	4.39980	538	0.015
Large	Treatment	Breeding Male	0.1	- Small	Control	Helpers	0.1	23.8894	4.86	4.91245	538	0.001
Large	Treatment	Breeding Male	0.1	- Small	Treatment	Breeding Female	-0.1	17.9000	4.87	3.67531	544	0.295
Large	Treatment	Breeding Male	0.1	- Small	Treatment	Breeding Male	-0.1	11.4833	4.87	2.35781	544	1.000
Large	Treatment	Breeding Male	0.1	- Small	Treatment	Helpers	-0.1	20.5041	4.87	4.21000	544	0.034
Large	Treatment	Breeding Male	0.1	- Small	Treatment	Helpers	0.1	27.3601	4.87	5.61747	543	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Breeding Female	-0.1	28.8894	4.86	5.94062	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Breeding Female	0.1	23.8894	4.86	4.91245	538	0.001
Large	Treatment	Breeding Male	24	- Large	Control	Breeding Female	4	27.6394	4.86	5.68358	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Breeding Male	-0.1	25.8061	4.86	5.30658	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Breeding Male	0.1	24.6394	4.86	5.06668	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Breeding Male	24	28.3894	4.86	5.83780	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Breeding Male	4	28.3061	4.86	5.82067	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Helpers	-0.1	36.4106	4.86	7.48721	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Helpers	0.1	37.3948	4.86	7.68960	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Helpers	24	36.2341	4.86	7.45092	538	<.001
Large	Treatment	Breeding Male	24	- Large	Control	Helpers	4	36.1546	4.86	7.43458	538	<.001
Large	Treatment	Breeding Male	24	- Large	Treatment	Breeding Female	-0.1	25.0638	4.50	5.57307	550	<.001
Large	Treatment	Breeding Male	24	- Large	Treatment	Breeding Female	0.1	25.3125	4.50	5.63064	549	<.001
Large	Treatment	Breeding Male	24	- Large	Treatment	Breeding Female	4	41.1250	4.50	9.14805	549	<.001
Large	Treatment	Breeding Male	24	- Large	Treatment	Breeding Male	-0.1	19.5013	4.50	4.33622	550	0.019
Large	Treatment	Breeding Male	24	- Large	Treatment	Breeding Male	0.1	16.0625	4.50	3.57302	549	0.433
Large	Treatment	Breeding Male	24	- Large	Treatment	Breeding Male	4	-4.1875	4.50	-0.93149	549	1.000
Large	Treatment	Breeding Male	24	- Large	Treatment	Helpers	-0.1	37.4411	4.50	8.32522	550	<.001
Large	Treatment	Breeding Male	24	- Large	Treatment	Helpers	0.1	37.9382	4.50	8.43917	549	<.001

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison													
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point	Difference	SE	t	df	Pbonferroni	
Large	Treatment	Breeding Male	24	-	Large	Treatment	Helpers	24	39.5339	4.50	8.79411	549	<.001
Large	Treatment	Breeding Male	24	-	Large	Treatment	Helpers	4	38.4494	4.50	8.55288	549	<.001
Large	Treatment	Breeding Male	24	-	Small	Control	Breeding Female	-0.1	33.3894	4.86	6.86597	538	<.001
Large	Treatment	Breeding Male	24	-	Small	Control	Breeding Female	0.1	30.7228	4.86	6.31761	538	<.001
Large	Treatment	Breeding Male	24	-	Small	Control	Breeding Female	4	32.5561	4.86	6.69461	538	<.001
Large	Treatment	Breeding Male	24	-	Small	Control	Breeding Male	-0.1	23.5561	4.86	4.84391	538	0.002
Large	Treatment	Breeding Male	24	-	Small	Control	Breeding Male	0.1	16.9728	4.86	3.49016	538	0.589
Large	Treatment	Breeding Male	24	-	Small	Control	Breeding Male	24	22.2228	4.86	4.56973	538	0.007
Large	Treatment	Breeding Male	24	-	Small	Control	Breeding Male	4	23.7228	4.86	4.87818	538	0.002
Large	Treatment	Breeding Male	24	-	Small	Control	Helpers	-0.1	37.4589	4.86	7.70278	538	<.001
Large	Treatment	Breeding Male	24	-	Small	Control	Helpers	0.1	39.9519	4.86	8.21543	538	<.001
Large	Treatment	Breeding Male	24	-	Small	Control	Helpers	24	38.0214	4.86	7.81845	538	<.001
Large	Treatment	Breeding Male	24	-	Small	Control	Helpers	4	37.6464	4.86	7.74133	538	<.001
Large	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Female	-0.1	33.9625	4.87	6.97333	544	<.001
Large	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Female	0.1	45.7143	4.87	9.38587	543	<.001
Large	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Female	4	38.4643	4.87	7.89733	543	<.001
Large	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Male	-0.1	27.5458	4.87	5.65583	544	<.001
Large	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Male	0.1	-6.3691	4.87	-1.30767	543	1.000
Large	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Male	4	16.5476	4.87	3.39749	543	0.823
Large	Treatment	Breeding Male	24	-	Small	Treatment	Helpers	-0.1	36.5666	4.87	7.50803	544	<.001
Large	Treatment	Breeding Male	24	-	Small	Treatment	Helpers	0.1	43.4226	4.87	8.91536	543	<.001
Large	Treatment	Breeding Male	24	-	Small	Treatment	Helpers	24	40.7976	4.87	8.37640	543	<.001
Large	Treatment	Breeding Male	24	-	Small	Treatment	Helpers	4	39.1101	4.87	8.02993	543	<.001
Large	Treatment	Breeding Male	4	-	Large	Control	Breeding Female	-0.1	33.0769	4.86	6.80171	538	<.001
Large	Treatment	Breeding Male	4	-	Large	Control	Breeding Female	0.1	28.0769	4.86	5.77354	538	<.001
Large	Treatment	Breeding Male	4	-	Large	Control	Breeding Male	-0.1	29.9936	4.86	6.16767	538	<.001
Large	Treatment	Breeding Male	4	-	Large	Control	Breeding Male	0.1	28.8269	4.86	5.92777	538	<.001
Large	Treatment	Breeding Male	4	-	Large	Control	Breeding Male	4	32.4936	4.86	6.68175	538	<.001
Large	Treatment	Breeding Male	4	-	Large	Control	Helpers	-0.1	40.5981	4.86	8.34830	538	<.001
Large	Treatment	Breeding Male	4	-	Large	Control	Helpers	0.1	41.5823	4.86	8.55069	538	<.001
Large	Treatment	Breeding Male	4	-	Large	Control	Helpers	4	40.3421	4.86	8.29567	538	<.001
Large	Treatment	Breeding Male	4	-	Large	Treatment	Breeding Female	-0.1	29.2513	4.50	6.50419	550	<.001
Large	Treatment	Breeding Male	4	-	Large	Treatment	Breeding Female	0.1	29.5000	4.50	6.56213	549	<.001
Large	Treatment	Breeding Male	4	-	Large	Treatment	Breeding Male	-0.1	23.6888	4.50	5.26734	550	<.001

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison												
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point	Difference	SE	t	df	Pbonferroni
Large	Treatment	Breeding Male	4	- Large	Treatment	Breeding Male	0.1	20.2500	4.50	4.50451	549	0.009
Large	Treatment	Breeding Male	4	- Large	Treatment	Helpers	-0.1	41.6286	4.50	9.25633	550	<.001
Large	Treatment	Breeding Male	4	- Large	Treatment	Helpers	0.1	42.1257	4.50	9.37066	549	<.001
Large	Treatment	Breeding Male	4	- Large	Treatment	Helpers	4	42.6369	4.50	9.48437	549	<.001
Large	Treatment	Breeding Male	4	- Small	Control	Breeding Female	-0.1	37.5769	4.86	7.72705	538	<.001
Large	Treatment	Breeding Male	4	- Small	Control	Breeding Female	0.1	34.9103	4.86	7.17870	538	<.001
Large	Treatment	Breeding Male	4	- Small	Control	Breeding Male	-0.1	27.7436	4.86	5.70500	538	<.001
Large	Treatment	Breeding Male	4	- Small	Control	Breeding Male	0.1	21.1603	4.86	4.35125	538	0.018
Large	Treatment	Breeding Male	4	- Small	Control	Breeding Male	4	27.9103	4.86	5.73927	538	<.001
Large	Treatment	Breeding Male	4	- Small	Control	Helpers	-0.1	41.6464	4.86	8.56387	538	<.001
Large	Treatment	Breeding Male	4	- Small	Control	Helpers	0.1	44.1394	4.86	9.07652	538	<.001
Large	Treatment	Breeding Male	4	- Small	Control	Helpers	4	41.8339	4.86	8.60242	538	<.001
Large	Treatment	Breeding Male	4	- Small	Treatment	Breeding Female	-0.1	38.1500	4.87	7.83313	544	<.001
Large	Treatment	Breeding Male	4	- Small	Treatment	Breeding Female	0.1	49.9018	4.87	10.24564	543	<.001
Large	Treatment	Breeding Male	4	- Small	Treatment	Breeding Male	-0.1	31.7333	4.87	6.51563	544	<.001
Large	Treatment	Breeding Male	4	- Small	Treatment	Breeding Male	0.1	-2.1816	4.87	-0.44791	543	1.000
Large	Treatment	Breeding Male	4	- Small	Treatment	Helpers	-0.1	40.7541	4.87	8.36783	544	<.001
Large	Treatment	Breeding Male	4	- Small	Treatment	Helpers	0.1	47.6101	4.87	9.77512	543	<.001
Large	Treatment	Breeding Male	4	- Small	Treatment	Helpers	4	43.2976	4.87	8.88969	543	<.001
Large	Treatment	Helpers	-0.1	- Large	Control	Helpers	-0.1	-1.0305	4.86	-0.21187	538	1.000
Large	Treatment	Helpers	-0.1	- Small	Control	Helpers	-0.1	0.0178	4.86	0.00366	538	1.000
Large	Treatment	Helpers	0.1	- Large	Control	Breeding Female	-0.1	-9.0488	4.86	-1.86073	538	1.000
Large	Treatment	Helpers	0.1	- Large	Control	Breeding Male	-0.1	-12.1321	4.86	-2.49476	538	1.000
Large	Treatment	Helpers	0.1	- Large	Control	Helpers	-0.1	-1.5277	4.86	-0.31414	538	1.000
Large	Treatment	Helpers	0.1	- Large	Control	Helpers	0.1	-0.5434	4.86	-0.11175	538	1.000
Large	Treatment	Helpers	0.1	- Large	Treatment	Breeding Female	-0.1	-12.8744	4.50	-2.86269	550	1.000
Large	Treatment	Helpers	0.1	- Large	Treatment	Breeding Male	-0.1	-18.4369	4.50	-4.09954	550	0.054
Large	Treatment	Helpers	0.1	- Large	Treatment	Helpers	-0.1	-0.4972	4.50	-0.11055	550	1.000
Large	Treatment	Helpers	0.1	- Small	Control	Breeding Female	-0.1	-4.5488	4.86	-0.93538	538	1.000
Large	Treatment	Helpers	0.1	- Small	Control	Breeding Male	-0.1	-14.3821	4.86	-2.95744	538	1.000
Large	Treatment	Helpers	0.1	- Small	Control	Helpers	-0.1	-0.4794	4.86	-0.09857	538	1.000
Large	Treatment	Helpers	0.1	- Small	Control	Helpers	0.1	2.0137	4.86	0.41408	538	1.000
Large	Treatment	Helpers	0.1	- Small	Treatment	Breeding Female	-0.1	-3.9758	4.87	-0.81632	544	1.000
Large	Treatment	Helpers	0.1	- Small	Treatment	Breeding Male	-0.1	-10.3924	4.87	-2.13382	544	1.000
Large	Treatment	Helpers	0.1	- Small	Treatment	Helpers	-0.1	-1.3716	4.87	-0.28162	544	1.000
Large	Treatment	Helpers	24	- Large	Control	Breeding Female	-0.1	-10.6444	4.86	-2.18884	538	1.000
Large	Treatment	Helpers	24	- Large	Control	Breeding Female	0.1	-15.6444	4.86	-3.21700	538	1.000
Large	Treatment	Helpers	24	- Large	Control	Breeding Female	4	-11.8944	4.86	-2.44588	538	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Treatment	Helpers	24	-	Large	Control	-0.1	-13.7277	4.86	-2.82287	538	1.000	
Large	Treatment	Helpers	24	-	Large	Control	Breeding Male	0.1	-14.8944	4.86	-3.06278	538	1.000
Large	Treatment	Helpers	24	-	Large	Control	Breeding Male	4	-11.2277	4.86	-2.30879	538	1.000
Large	Treatment	Helpers	24	-	Large	Control	Helpers	-0.1	-3.1233	4.86	-0.64225	538	1.000
Large	Treatment	Helpers	24	-	Large	Control	Helpers	0.1	-2.1390	4.86	-0.43986	538	1.000
Large	Treatment	Helpers	24	-	Large	Control	Helpers	24	-3.2998	4.86	-0.67854	538	1.000
Large	Treatment	Helpers	24	-	Large	Control	Helpers	4	-3.3792	4.86	-0.69488	538	1.000
Large	Treatment	Helpers	24	-	Large	Treatment	Breeding Female	-0.1	-14.4700	4.50	-3.21748	550	1.000
Large	Treatment	Helpers	24	-	Large	Treatment	Breeding Female	0.1	-14.2214	4.50	-3.16347	549	1.000
Large	Treatment	Helpers	24	-	Large	Treatment	Breeding Female	4	1.5911	4.50	0.35394	549	1.000
Large	Treatment	Helpers	24	-	Large	Treatment	Breeding Male	-0.1	-20.0325	4.50	-4.45433	550	0.012
Large	Treatment	Helpers	24	-	Large	Treatment	Breeding Male	0.1	-23.4714	4.50	-5.22108	549	<.001
Large	Treatment	Helpers	24	-	Large	Treatment	Breeding Male	4	-43.7214	4.50	-9.72560	549	<.001
Large	Treatment	Helpers	24	-	Large	Treatment	Helpers	-0.1	-2.0928	4.50	-0.46534	550	1.000
Large	Treatment	Helpers	24	-	Large	Treatment	Helpers	0.1	-1.5956	4.50	-0.35494	549	1.000
Large	Treatment	Helpers	24	-	Large	Treatment	Helpers	4	-1.0844	4.50	-0.24123	549	1.000
Large	Treatment	Helpers	24	-	Small	Control	Breeding Female	-0.1	-6.1444	4.86	-1.26349	538	1.000
Large	Treatment	Helpers	24	-	Small	Control	Breeding Female	0.1	-8.8111	4.86	-1.81185	538	1.000
Large	Treatment	Helpers	24	-	Small	Control	Breeding Female	4	-6.9777	4.86	-1.43485	538	1.000
Large	Treatment	Helpers	24	-	Small	Control	Breeding Male	-0.1	-15.9777	4.86	-3.28555	538	1.000
Large	Treatment	Helpers	24	-	Small	Control	Breeding Male	0.1	-22.5611	4.86	-4.63930	538	0.005
Large	Treatment	Helpers	24	-	Small	Control	Breeding Male	4	-15.8111	4.86	-3.25128	538	1.000
Large	Treatment	Helpers	24	-	Small	Control	Helpers	-0.1	-2.0750	4.86	-0.42668	538	1.000
Large	Treatment	Helpers	24	-	Small	Control	Helpers	0.1	0.4181	4.86	0.08597	538	1.000
Large	Treatment	Helpers	24	-	Small	Control	Helpers	24	-1.5125	4.86	-0.31101	538	1.000
Large	Treatment	Helpers	24	-	Small	Control	Helpers	4	-1.8875	4.86	-0.38812	538	1.000
Large	Treatment	Helpers	24	-	Small	Treatment	Breeding Female	-0.1	-5.5714	4.87	-1.14394	544	1.000
Large	Treatment	Helpers	24	-	Small	Treatment	Breeding Female	0.1	6.1804	4.87	1.26894	543	1.000
Large	Treatment	Helpers	24	-	Small	Treatment	Breeding Female	4	-1.0696	4.87	-0.21960	543	1.000
Large	Treatment	Helpers	24	-	Small	Treatment	Breeding Male	-0.1	-11.9880	4.87	-2.46144	544	1.000
Large	Treatment	Helpers	24	-	Small	Treatment	Breeding Male	0.1	-45.9029	4.87	-9.42461	543	<.001
Large	Treatment	Helpers	24	-	Small	Treatment	Breeding Male	4	-22.9863	4.87	-4.71945	543	0.003
Large	Treatment	Helpers	24	-	Small	Treatment	Helpers	-0.1	-2.9672	4.87	-0.60924	544	1.000
Large	Treatment	Helpers	24	-	Small	Treatment	Helpers	0.1	3.8887	4.87	0.79842	543	1.000
Large	Treatment	Helpers	24	-	Small	Treatment	Helpers	4	-0.4238	4.87	-0.08700	543	1.000
Large	Treatment	Helpers	4	-	Large	Control	Breeding Female	-0.1	-9.5600	4.86	-1.96584	538	1.000
Large	Treatment	Helpers	4	-	Large	Control	Breeding Female	0.1	-14.5600	4.86	-2.99401	538	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Large	Treatment	Helpers	4	-	Large	Control	Breeding Male	-0.1	-12.6433	4.86	-2.59988	538	1.000
Large	Treatment	Helpers	4	-	Large	Control	Breeding Male	0.1	-13.8100	4.86	-2.83978	538	1.000
Large	Treatment	Helpers	4	-	Large	Control	Helpers	-0.1	-2.0388	4.86	-0.41925	538	1.000
Large	Treatment	Helpers	4	-	Large	Control	Helpers	0.1	-1.0546	4.86	-0.21686	538	1.000
Large	Treatment	Helpers	4	-	Large	Control	Helpers	4	-2.2948	4.86	-0.47188	538	1.000
Large	Treatment	Helpers	4	-	Large	Treatment	Breeding Female	-0.1	-13.3856	4.50	-2.97635	550	1.000
Large	Treatment	Helpers	4	-	Large	Treatment	Breeding Female	0.1	-13.1369	4.50	-2.92224	549	1.000
Large	Treatment	Helpers	4	-	Large	Treatment	Breeding Male	-0.1	-18.9481	4.50	-4.21320	550	0.033
Large	Treatment	Helpers	4	-	Large	Treatment	Breeding Male	0.1	-22.3869	4.50	-4.97985	549	<.001
Large	Treatment	Helpers	4	-	Large	Treatment	Helpers	-0.1	-1.0083	4.50	-0.22421	550	1.000
Large	Treatment	Helpers	4	-	Large	Treatment	Helpers	0.1	-0.5112	4.50	-0.11371	549	1.000
Large	Treatment	Helpers	4	-	Small	Control	Breeding Female	-0.1	-5.0600	4.86	-1.04049	538	1.000
Large	Treatment	Helpers	4	-	Small	Control	Breeding Female	0.1	-7.7266	4.86	-1.58885	538	1.000
Large	Treatment	Helpers	4	-	Small	Control	Breeding Male	-0.1	-14.8933	4.86	-3.06255	538	1.000
Large	Treatment	Helpers	4	-	Small	Control	Breeding Male	0.1	-21.4766	4.86	-4.41630	538	0.014
Large	Treatment	Helpers	4	-	Small	Control	Helpers	-0.1	-0.9905	4.86	-0.20368	538	1.000
Large	Treatment	Helpers	4	-	Small	Control	Helpers	0.1	1.5025	4.86	0.30897	538	1.000
Large	Treatment	Helpers	4	-	Small	Control	Helpers	4	-0.8030	4.86	-0.16513	538	1.000
Large	Treatment	Helpers	4	-	Small	Treatment	Breeding Female	-0.1	-4.4869	4.87	-0.92128	544	1.000
Large	Treatment	Helpers	4	-	Small	Treatment	Breeding Female	0.1	7.2649	4.87	1.49159	543	1.000
Large	Treatment	Helpers	4	-	Small	Treatment	Breeding Male	-0.1	-10.9036	4.87	-2.23877	544	1.000
Large	Treatment	Helpers	4	-	Small	Treatment	Breeding Male	0.1	-44.8185	4.87	-9.20195	543	<.001
Large	Treatment	Helpers	4	-	Small	Treatment	Helpers	-0.1	-1.8828	4.87	-0.38658	544	1.000
Large	Treatment	Helpers	4	-	Small	Treatment	Helpers	0.1	4.9732	4.87	1.02108	543	1.000
Small	Control	Breeding Female	-0.1	-	Large	Control	Breeding Female	-0.1	-4.5000	5.20	-0.86588	536	1.000
Small	Control	Breeding Female	-0.1	-	Large	Control	Breeding Male	-0.1	-7.5833	5.20	-1.45918	536	1.000
Small	Control	Breeding Female	-0.1	-	Large	Control	Helpers	-0.1	3.0211	5.20	0.58132	536	1.000
Small	Control	Breeding Female	-0.1	-	Large	Treatment	Breeding Male	-0.1	-13.8881	4.86	-2.85547	538	1.000
Small	Control	Breeding Female	-0.1	-	Large	Treatment	Helpers	-0.1	4.0516	4.86	0.83303	538	1.000
Small	Control	Breeding Female	-0.1	-	Small	Control	Breeding Male	-0.1	-9.8333	5.19	-1.89432	549	1.000
Small	Control	Breeding Female	-0.1	-	Small	Control	Helpers	-0.1	4.0694	5.19	0.78395	549	1.000
Small	Control	Breeding Female	-0.1	-	Small	Treatment	Breeding Male	-0.1	-5.8436	5.20	-1.12358	539	1.000
Small	Control	Breeding Female	-0.1	-	Small	Treatment	Helpers	-0.1	3.1772	5.20	0.61089	539	1.000
Small	Control	Breeding Female	0.1	-	Large	Control	Breeding Female	-0.1	-1.8333	5.20	-0.35277	536	1.000
Small	Control	Breeding Female	0.1	-	Large	Control	Breeding Female	0.1	-6.8333	5.20	-1.31486	536	1.000
Small	Control	Breeding Female	0.1	-	Large	Control	Breeding Male	-0.1	-4.9167	5.20	-0.94606	536	1.000
Small	Control	Breeding Female	0.1	-	Large	Control	Breeding Male	0.1	-6.0833	5.20	-1.17055	536	1.000
Small	Control	Breeding Female	0.1	-	Large	Control	Helpers	-0.1	5.6878	5.20	1.09444	536	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison								Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Control	Breeding Female	0.1	-	Large	Control	Helpers	0.1	6.6720	5.20	1.28382	536	1.000
Small	Control	Breeding Female	0.1	-	Large	Treatment	Breeding Female	-0.1	-5.6589	4.86	-1.16351	538	1.000
Small	Control	Breeding Female	0.1	-	Large	Treatment	Breeding Male	-0.1	-11.2214	4.86	-2.30719	538	1.000
Small	Control	Breeding Female	0.1	-	Large	Treatment	Breeding Male	0.1	-14.6603	4.86	-3.01464	538	1.000
Small	Control	Breeding Female	0.1	-	Large	Treatment	Helpers	-0.1	6.7183	4.86	1.38132	538	1.000
Small	Control	Breeding Female	0.1	-	Large	Treatment	Helpers	0.1	7.2155	4.86	1.48374	538	1.000
Small	Control	Breeding Female	0.1	-	Small	Control	Breeding Female	-0.1	2.6667	5.19	0.51371	549	1.000
Small	Control	Breeding Female	0.1	-	Small	Control	Breeding Male	-0.1	-7.1667	5.19	-1.38061	549	1.000
Small	Control	Breeding Female	0.1	-	Small	Control	Breeding Male	0.1	-13.7500	5.19	-2.64884	549	1.000
Small	Control	Breeding Female	0.1	-	Small	Control	Helpers	-0.1	6.7361	5.19	1.29766	549	1.000
Small	Control	Breeding Female	0.1	-	Small	Control	Helpers	0.1	9.2292	5.19	1.77793	549	1.000
Small	Control	Breeding Female	0.1	-	Small	Treatment	Breeding Female	-0.1	3.2397	5.20	0.62291	539	1.000
Small	Control	Breeding Female	0.1	-	Small	Treatment	Breeding Male	-0.1	-3.1770	5.20	-0.61085	539	1.000
Small	Control	Breeding Female	0.1	-	Small	Treatment	Breeding Male	0.1	-37.0918	5.20	-7.13331	539	<.001
Small	Control	Breeding Female	0.1	-	Small	Treatment	Helpers	-0.1	5.8439	5.20	1.12363	539	1.000
Small	Control	Breeding Female	0.1	-	Small	Treatment	Helpers	0.1	12.6998	5.20	2.44236	539	1.000
Small	Control	Breeding Female	24	-	Large	Control	Breeding Female	-0.1	-3.7500	5.20	-0.72157	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Breeding Female	0.1	-8.7500	5.20	-1.68366	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Breeding Female	24	-5.8333	5.20	-1.12244	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Breeding Female	4	-5.0000	5.20	-0.96209	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Breeding Male	-0.1	-6.8333	5.20	-1.31486	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Breeding Male	0.1	-8.0000	5.20	-1.53935	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Breeding Male	24	-4.2500	5.20	-0.81778	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Breeding Male	4	-4.3333	5.20	-0.83381	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Helpers	-0.1	3.7711	5.20	0.72564	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Helpers	0.1	4.7554	5.20	0.91502	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Helpers	24	3.5946	5.20	0.69168	536	1.000
Small	Control	Breeding Female	24	-	Large	Control	Helpers	4	3.5152	5.20	0.67639	536	1.000
Small	Control	Breeding Female	24	-	Large	Treatment	Breeding Female	-0.1	-7.5756	4.86	-1.55758	538	1.000
Small	Control	Breeding Female	24	-	Large	Treatment	Breeding Female	0.1	-7.3269	4.86	-1.50666	538	1.000
Small	Control	Breeding Female	24	-	Large	Treatment	Breeding Female	4	8.4856	4.86	1.74491	538	1.000
Small	Control	Breeding Female	24	-	Large	Treatment	Breeding Male	-0.1	-13.1381	4.86	-2.70126	538	1.000
Small	Control	Breeding Female	24	-	Large	Treatment	Breeding Male	0.1	-16.5769	4.86	-3.40876	538	0.791
Small	Control	Breeding Female	24	-	Large	Treatment	Breeding Male	24	-32.6394	4.86	-6.71174	538	<.001

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Control	Breeding Female	24	-	Large	Treatment	Breeding Male	4	-36.8269	4.86	-7.57283	538	<.001
Small	Control	Breeding Female	24	-	Large	Treatment	Helpers	-0.1	4.8016	4.86	0.98724	538	1.000
Small	Control	Breeding Female	24	-	Large	Treatment	Helpers	0.1	5.2988	4.86	1.08961	538	1.000
Small	Control	Breeding Female	24	-	Large	Treatment	Helpers	24	6.8944	4.86	1.41772	538	1.000
Small	Control	Breeding Female	24	-	Large	Treatment	Helpers	4	5.8100	4.86	1.19472	538	1.000
Small	Control	Breeding Female	24	-	Small	Control	Breeding Female	-0.1	0.7500	5.19	0.14448	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Breeding Female	0.1	-1.9167	5.19	-0.36923	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Breeding Female	4	-0.0833	5.19	-0.01605	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Breeding Male	-0.1	-9.0833	5.19	-1.74984	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Breeding Male	0.1	-15.6667	5.19	-3.01807	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Breeding Male	24	-10.4167	5.19	-2.00670	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Breeding Male	4	-8.9167	5.19	-1.71773	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Helpers	-0.1	4.8194	5.19	0.92843	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Helpers	0.1	7.3125	5.19	1.40870	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Helpers	24	5.3819	5.19	1.03679	549	1.000
Small	Control	Breeding Female	24	-	Small	Control	Helpers	4	5.0069	5.19	0.96455	549	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Breeding Female	-0.1	1.3230	5.20	0.25439	539	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Breeding Female	0.1	13.0748	5.20	2.51448	539	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Breeding Female	4	5.8248	5.20	1.12020	539	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Breeding Male	-0.1	-5.0936	5.20	-0.97938	539	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Breeding Male	0.1	-39.0085	5.20	-7.50191	539	<.001
Small	Control	Breeding Female	24	-	Small	Treatment	Breeding Male	24	-18.2585	5.20	-3.51138	539	0.545
Small	Control	Breeding Female	24	-	Small	Treatment	Breeding Male	4	-16.0918	5.20	-3.09470	539	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Helpers	-0.1	3.9272	5.20	0.75510	539	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Helpers	0.1	10.7832	5.20	2.07376	539	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Helpers	24	8.1582	5.20	1.56893	539	1.000
Small	Control	Breeding Female	24	-	Small	Treatment	Helpers	4	6.4707	5.20	1.24440	539	1.000
Small	Control	Breeding Female	4	-	Large	Control	Breeding Female	-0.1	-3.6667	5.20	-0.70554	536	1.000
Small	Control	Breeding Female	4	-	Large	Control	Breeding Female	0.1	-8.6667	5.20	-1.66763	536	1.000
Small	Control	Breeding Female	4	-	Large	Control	Breeding Female	4	-4.9167	5.20	-0.94606	536	1.000
Small	Control	Breeding Female	4	-	Large	Control	Breeding Male	-0.1	-6.7500	5.20	-1.29883	536	1.000
Small	Control	Breeding Female	4	-	Large	Control	Breeding Male	0.1	-7.9167	5.20	-1.52332	536	1.000
Small	Control	Breeding Female	4	-	Large	Control	Breeding Male	4	-4.2500	5.20	-0.81778	536	1.000
Small	Control	Breeding Female	4	-	Large	Control	Helpers	-0.1	3.8545	5.20	0.74167	536	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison												
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point	Difference	SE	t	df	Pbonferroni
Small	Control	Breeding Female	4	- Large	Control	Helpers	0.1	4.8387	5.20	0.93105	536	1.000
Small	Control	Breeding Female	4	- Large	Control	Helpers	4	3.5985	5.20	0.69242	536	1.000
Small	Control	Breeding Female	4	- Large	Treatment	Breeding Female	-0.1	-7.4923	4.86	-1.54045	538	1.000
Small	Control	Breeding Female	4	- Large	Treatment	Breeding Female	0.1	-7.2436	4.86	-1.48952	538	1.000
Small	Control	Breeding Female	4	- Large	Treatment	Breeding Male	-0.1	-13.0548	4.86	-2.68413	538	1.000
Small	Control	Breeding Female	4	- Large	Treatment	Breeding Male	0.1	-16.4936	4.86	-3.39163	538	0.841
Small	Control	Breeding Female	4	- Large	Treatment	Breeding Male	4	-36.7436	4.86	-7.55569	538	<.001
Small	Control	Breeding Female	4	- Large	Treatment	Helpers	-0.1	4.8850	4.86	1.00437	538	1.000
Small	Control	Breeding Female	4	- Large	Treatment	Helpers	0.1	5.3821	4.86	1.10674	538	1.000
Small	Control	Breeding Female	4	- Large	Treatment	Helpers	4	5.8933	4.86	1.21185	538	1.000
Small	Control	Breeding Female	4	- Small	Control	Breeding Female	-0.1	0.8333	5.19	0.16054	549	1.000
Small	Control	Breeding Female	4	- Small	Control	Breeding Female	0.1	-1.8333	5.19	-0.35318	549	1.000
Small	Control	Breeding Female	4	- Small	Control	Breeding Male	-0.1	-9.0000	5.19	-1.73379	549	1.000
Small	Control	Breeding Female	4	- Small	Control	Breeding Male	0.1	-15.5833	5.19	-3.00202	549	1.000
Small	Control	Breeding Female	4	- Small	Control	Breeding Male	4	-8.8333	5.19	-1.70168	549	1.000
Small	Control	Breeding Female	4	- Small	Control	Helpers	-0.1	4.9028	5.19	0.94449	549	1.000
Small	Control	Breeding Female	4	- Small	Control	Helpers	0.1	7.3958	5.19	1.42476	549	1.000
Small	Control	Breeding Female	4	- Small	Control	Helpers	4	5.0903	5.19	0.98061	549	1.000
Small	Control	Breeding Female	4	- Small	Treatment	Breeding Female	-0.1	1.4064	5.20	0.27041	539	1.000
Small	Control	Breeding Female	4	- Small	Treatment	Breeding Female	0.1	13.1582	5.20	2.53051	539	1.000
Small	Control	Breeding Female	4	- Small	Treatment	Breeding Male	-0.1	-5.0103	5.20	-0.96335	539	1.000
Small	Control	Breeding Female	4	- Small	Treatment	Breeding Male	0.1	-38.9252	5.20	-7.48589	539	<.001
Small	Control	Breeding Female	4	- Small	Treatment	Breeding Male	4	-16.0085	5.20	-3.07867	539	1.000
Small	Control	Breeding Female	4	- Small	Treatment	Helpers	-0.1	4.0105	5.20	0.77112	539	1.000
Small	Control	Breeding Female	4	- Small	Treatment	Helpers	0.1	10.8665	5.20	2.08979	539	1.000
Small	Control	Breeding Female	4	- Small	Treatment	Helpers	4	6.5540	5.20	1.26043	539	1.000
Small	Control	Breeding Male	-0.1	- Large	Control	Breeding Male	-0.1	2.2500	5.20	0.43294	536	1.000
Small	Control	Breeding Male	-0.1	- Large	Control	Helpers	-0.1	12.8545	5.20	2.47344	536	1.000
Small	Control	Breeding Male	-0.1	- Large	Treatment	Helpers	-0.1	13.8850	4.86	2.85482	538	1.000
Small	Control	Breeding Male	-0.1	- Small	Control	Helpers	-0.1	13.9028	5.19	2.67827	549	1.000
Small	Control	Breeding Male	-0.1	- Small	Treatment	Helpers	-0.1	13.0105	5.20	2.50159	539	1.000
Small	Control	Breeding Male	0.1	- Large	Control	Breeding Female	-0.1	11.9167	5.20	2.29299	536	1.000
Small	Control	Breeding Male	0.1	- Large	Control	Breeding Male	-0.1	8.8333	5.20	1.69970	536	1.000
Small	Control	Breeding Male	0.1	- Large	Control	Breeding Male	0.1	7.6667	5.20	1.47521	536	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

		Comparison						Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Control	Breeding Male	0.1	-	Large	Control	Helpers	-0.1	19.4378	5.20	3.74020	536	0.230
Small	Control	Breeding Male	0.1	-	Large	Control	Helpers	0.1	20.4220	5.20	3.92958	536	0.109
Small	Control	Breeding Male	0.1	-	Large	Treatment	Breeding Female	-0.1	8.0911	4.86	1.66356	538	1.000
Small	Control	Breeding Male	0.1	-	Large	Treatment	Breeding Male	-0.1	2.5286	4.86	0.51988	538	1.000
Small	Control	Breeding Male	0.1	-	Large	Treatment	Helpers	-0.1	20.4683	4.86	4.20839	538	0.034
Small	Control	Breeding Male	0.1	-	Large	Treatment	Helpers	0.1	20.9655	4.86	4.31119	538	0.022
Small	Control	Breeding Male	0.1	-	Small	Control	Breeding Female	-0.1	16.4167	5.19	3.16256	549	1.000
Small	Control	Breeding Male	0.1	-	Small	Control	Breeding Male	-0.1	6.5833	5.19	1.26823	549	1.000
Small	Control	Breeding Male	0.1	-	Small	Control	Helpers	-0.1	20.4861	5.19	3.94651	549	0.101
Small	Control	Breeding Male	0.1	-	Small	Control	Helpers	0.1	22.9792	5.19	4.42678	549	0.013
Small	Control	Breeding Male	0.1	-	Small	Treatment	Breeding Female	-0.1	16.9897	5.20	3.26669	539	1.000
Small	Control	Breeding Male	0.1	-	Small	Treatment	Breeding Male	-0.1	10.5730	5.20	2.03292	539	1.000
Small	Control	Breeding Male	0.1	-	Small	Treatment	Helpers	-0.1	19.5939	5.20	3.76740	539	0.207
Small	Control	Breeding Male	0.1	-	Small	Treatment	Helpers	0.1	26.4498	5.20	5.08669	539	<.001
Small	Control	Breeding Male	24	-	Large	Control	Breeding Female	-0.1	6.6667	5.20	1.28279	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Breeding Female	0.1	1.6667	5.20	0.32070	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Breeding Female	4	5.4167	5.20	1.04227	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Breeding Male	-0.1	3.5833	5.20	0.68950	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Breeding Male	0.1	2.4167	5.20	0.46501	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Breeding Male	24	6.1667	5.20	1.18658	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Breeding Male	4	6.0833	5.20	1.17055	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Helpers	-0.1	14.1878	5.20	2.73000	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Helpers	0.1	15.1720	5.20	2.91938	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Helpers	24	14.0113	5.20	2.69604	536	1.000
Small	Control	Breeding Male	24	-	Large	Control	Helpers	4	13.9318	5.20	2.68075	536	1.000
Small	Control	Breeding Male	24	-	Large	Treatment	Breeding Female	-0.1	2.8411	4.86	0.58414	538	1.000
Small	Control	Breeding Male	24	-	Large	Treatment	Breeding Female	0.1	3.0897	4.86	0.63535	538	1.000
Small	Control	Breeding Male	24	-	Large	Treatment	Breeding Female	4	18.9022	4.86	3.88692	538	0.129
Small	Control	Breeding Male	24	-	Large	Treatment	Breeding Male	-0.1	-2.7214	4.86	-0.55954	538	1.000
Small	Control	Breeding Male	24	-	Large	Treatment	Breeding Male	0.1	-6.1603	4.86	-1.26676	538	1.000
Small	Control	Breeding Male	24	-	Large	Treatment	Breeding Male	4	-26.4103	4.86	-5.43082	538	<.001
Small	Control	Breeding Male	24	-	Large	Treatment	Helpers	-0.1	15.2183	4.86	3.12896	538	1.000
Small	Control	Breeding Male	24	-	Large	Treatment	Helpers	0.1	15.7155	4.86	3.23162	538	1.000
Small	Control	Breeding Male	24	-	Large	Treatment	Helpers	24	17.3111	4.86	3.55973	538	0.456

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison													
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point	Difference	SE	t	df	Pbonferroni	
Small	Control	Breeding Male	24	-	Large	Treatment	Helpers	4	16.2266	4.86	3.33673	538	1.000
Small	Control	Breeding Male	24	-	Small	Control	Breeding Female	-0.1	11.1667	5.19	2.15118	549	1.000
Small	Control	Breeding Male	24	-	Small	Control	Breeding Female	0.1	8.5000	5.19	1.63747	549	1.000
Small	Control	Breeding Male	24	-	Small	Control	Breeding Female	4	10.3333	5.19	1.99064	549	1.000
Small	Control	Breeding Male	24	-	Small	Control	Breeding Male	-0.1	1.3333	5.19	0.25686	549	1.000
Small	Control	Breeding Male	24	-	Small	Control	Breeding Male	0.1	-5.2500	5.19	-1.01138	549	1.000
Small	Control	Breeding Male	24	-	Small	Control	Breeding Male	4	1.5000	5.19	0.28896	549	1.000
Small	Control	Breeding Male	24	-	Small	Control	Helpers	-0.1	15.2361	5.19	2.93513	549	1.000
Small	Control	Breeding Male	24	-	Small	Control	Helpers	0.1	17.7292	5.19	3.41540	549	0.772
Small	Control	Breeding Male	24	-	Small	Control	Helpers	24	15.7986	5.19	3.04349	549	1.000
Small	Control	Breeding Male	24	-	Small	Control	Helpers	4	15.4236	5.19	2.97125	549	1.000
Small	Control	Breeding Male	24	-	Small	Treatment	Breeding Female	-0.1	11.7397	5.20	2.25725	539	1.000
Small	Control	Breeding Male	24	-	Small	Treatment	Breeding Female	0.1	23.4915	5.20	4.51776	539	0.009
Small	Control	Breeding Male	24	-	Small	Treatment	Breeding Female	4	16.2415	5.20	3.12348	539	1.000
Small	Control	Breeding Male	24	-	Small	Treatment	Breeding Male	-0.1	5.3230	5.20	1.02348	539	1.000
Small	Control	Breeding Male	24	-	Small	Treatment	Breeding Male	0.1	-28.5918	5.20	-5.49864	539	<.001
Small	Control	Breeding Male	24	-	Small	Treatment	Breeding Male	4	-5.6752	5.20	-1.09142	539	1.000
Small	Control	Breeding Male	24	-	Small	Treatment	Helpers	-0.1	14.3439	5.20	2.75796	539	1.000
Small	Control	Breeding Male	24	-	Small	Treatment	Helpers	0.1	21.1998	5.20	4.07704	539	0.059
Small	Control	Breeding Male	24	-	Small	Treatment	Helpers	24	18.5748	5.20	3.57221	539	0.435
Small	Control	Breeding Male	24	-	Small	Treatment	Helpers	4	16.8873	5.20	3.24768	539	1.000
Small	Control	Breeding Male	4	-	Large	Control	Breeding Female	-0.1	5.1667	5.20	0.99416	536	1.000
Small	Control	Breeding Male	4	-	Large	Control	Breeding Female	0.1	0.1667	5.20	0.03207	536	1.000
Small	Control	Breeding Male	4	-	Large	Control	Breeding Male	-0.1	2.0833	5.20	0.40087	536	1.000
Small	Control	Breeding Male	4	-	Large	Control	Breeding Male	0.1	0.9167	5.20	0.17638	536	1.000
Small	Control	Breeding Male	4	-	Large	Control	Breeding Male	4	4.5833	5.20	0.88192	536	1.000
Small	Control	Breeding Male	4	-	Large	Control	Helpers	-0.1	12.6878	5.20	2.44137	536	1.000
Small	Control	Breeding Male	4	-	Large	Control	Helpers	0.1	13.6720	5.20	2.63075	536	1.000
Small	Control	Breeding Male	4	-	Large	Control	Helpers	4	12.4318	5.20	2.39212	536	1.000
Small	Control	Breeding Male	4	-	Large	Treatment	Breeding Female	-0.1	1.3411	4.86	0.27573	538	1.000
Small	Control	Breeding Male	4	-	Large	Treatment	Breeding Female	0.1	1.5897	4.86	0.32690	538	1.000
Small	Control	Breeding Male	4	-	Large	Treatment	Breeding Male	-0.1	-4.2214	4.86	-0.86795	538	1.000
Small	Control	Breeding Male	4	-	Large	Treatment	Breeding Male	0.1	-7.6603	4.86	-1.57521	538	1.000
Small	Control	Breeding Male	4	-	Large	Treatment	Helpers	-0.1	13.7183	4.86	2.82055	538	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison													
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point	Difference	SE	t	df	Pbonferroni	
Small	Control	Breeding Male	4	-	Large	Treatment	Helpers	0.1	14.2155	4.86	2.92317	538	1.000
Small	Control	Breeding Male	4	-	Large	Treatment	Helpers	4	14.7266	4.86	3.02828	538	1.000
Small	Control	Breeding Male	4	-	Small	Control	Breeding Female	-0.1	9.6667	5.19	1.86222	549	1.000
Small	Control	Breeding Male	4	-	Small	Control	Breeding Female	0.1	7.0000	5.19	1.34850	549	1.000
Small	Control	Breeding Male	4	-	Small	Control	Breeding Male	-0.1	-0.1667	5.19	-0.03211	549	1.000
Small	Control	Breeding Male	4	-	Small	Control	Breeding Male	0.1	-6.7500	5.19	-1.30034	549	1.000
Small	Control	Breeding Male	4	-	Small	Control	Helpers	-0.1	13.7361	5.19	2.64617	549	1.000
Small	Control	Breeding Male	4	-	Small	Control	Helpers	0.1	16.2292	5.19	3.12644	549	1.000
Small	Control	Breeding Male	4	-	Small	Control	Helpers	4	13.9236	5.19	2.68229	549	1.000
Small	Control	Breeding Male	4	-	Small	Treatment	Breeding Female	-0.1	10.2397	5.20	1.96883	539	1.000
Small	Control	Breeding Male	4	-	Small	Treatment	Breeding Female	0.1	21.9915	5.20	4.22929	539	0.031
Small	Control	Breeding Male	4	-	Small	Treatment	Breeding Male	-0.1	3.8230	5.20	0.73507	539	1.000
Small	Control	Breeding Male	4	-	Small	Treatment	Breeding Male	0.1	-30.0918	5.20	-5.78711	539	<.001
Small	Control	Breeding Male	4	-	Small	Treatment	Helpers	-0.1	12.8439	5.20	2.46955	539	1.000
Small	Control	Breeding Male	4	-	Small	Treatment	Helpers	0.1	19.6998	5.20	3.78857	539	0.190
Small	Control	Breeding Male	4	-	Small	Treatment	Helpers	4	15.3873	5.20	2.95921	539	1.000
Small	Control	Helpers	-0.1	-	Large	Control	Helpers	-0.1	-1.0483	5.20	-0.20172	536	1.000
Small	Control	Helpers	0.1	-	Large	Control	Breeding Female	-0.1	-11.0625	5.20	-2.12863	536	1.000
Small	Control	Helpers	0.1	-	Large	Control	Breeding Male	-0.1	-14.1458	5.20	-2.72192	536	1.000
Small	Control	Helpers	0.1	-	Large	Control	Helpers	-0.1	-3.5414	5.20	-0.68143	536	1.000
Small	Control	Helpers	0.1	-	Large	Control	Helpers	0.1	-2.5571	5.20	-0.49204	536	1.000
Small	Control	Helpers	0.1	-	Large	Treatment	Breeding Female	-0.1	-14.8881	4.86	-3.06107	538	1.000
Small	Control	Helpers	0.1	-	Large	Treatment	Breeding Male	-0.1	-20.4506	4.86	-4.20475	538	0.035
Small	Control	Helpers	0.1	-	Large	Treatment	Helpers	-0.1	-2.5109	4.86	-0.51625	538	1.000
Small	Control	Helpers	0.1	-	Small	Control	Breeding Female	-0.1	-6.5625	5.19	-1.26422	549	1.000
Small	Control	Helpers	0.1	-	Small	Control	Breeding Male	-0.1	-16.3958	5.19	-3.15854	549	1.000
Small	Control	Helpers	0.1	-	Small	Control	Helpers	-0.1	-2.4931	5.19	-0.48027	549	1.000
Small	Control	Helpers	0.1	-	Small	Treatment	Breeding Female	-0.1	-5.9895	5.20	-1.15162	539	1.000
Small	Control	Helpers	0.1	-	Small	Treatment	Breeding Male	-0.1	-12.4061	5.20	-2.38538	539	1.000
Small	Control	Helpers	0.1	-	Small	Treatment	Helpers	-0.1	-3.3853	5.20	-0.65091	539	1.000
Small	Control	Helpers	24	-	Large	Control	Breeding Female	-0.1	-9.1319	5.20	-1.75716	536	1.000
Small	Control	Helpers	24	-	Large	Control	Breeding Female	0.1	-14.1319	5.20	-2.71925	536	1.000
Small	Control	Helpers	24	-	Large	Control	Breeding Female	4	-10.3819	5.20	-1.99768	536	1.000
Small	Control	Helpers	24	-	Large	Control	Breeding Male	-0.1	-12.2153	5.20	-2.35045	536	1.000
Small	Control	Helpers	24	-	Large	Control	Breeding Male	0.1	-13.3819	5.20	-2.57494	536	1.000
Small	Control	Helpers	24	-	Large	Control	Breeding Male	4	-9.7153	5.20	-1.86940	536	1.000
Small	Control	Helpers	24	-	Large	Control	Helpers	-0.1	-1.6108	5.20	-0.30995	536	1.000
Small	Control	Helpers	24	-	Large	Control	Helpers	0.1	-0.6266	5.20	-0.12057	536	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison								Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Control	Helpers	24	-	Large	Control	Helpers	24	-1.7873	5.20	-0.34391	536	1.000
Small	Control	Helpers	24	-	Large	Control	Helpers	4	-1.8668	5.20	-0.35920	536	1.000
Small	Control	Helpers	24	-	Large	Treatment	Breeding Female	-0.1	-12.9576	4.86	-2.66414	538	1.000
Small	Control	Helpers	24	-	Large	Treatment	Breeding Female	0.1	-12.7089	4.86	-2.61337	538	1.000
Small	Control	Helpers	24	-	Large	Treatment	Breeding Female	4	3.1036	4.86	0.63820	538	1.000
Small	Control	Helpers	24	-	Large	Treatment	Breeding Male	-0.1	-18.5201	4.86	-3.80782	538	0.176
Small	Control	Helpers	24	-	Large	Treatment	Breeding Male	0.1	-21.9589	4.86	-4.51547	538	0.009
Small	Control	Helpers	24	-	Large	Treatment	Breeding Male	4	-42.2089	4.86	-8.67953	538	<.001
Small	Control	Helpers	24	-	Large	Treatment	Helpers	-0.1	-0.5803	4.86	-0.11932	538	1.000
Small	Control	Helpers	24	-	Large	Treatment	Helpers	0.1	-0.0831	4.86	-0.01710	538	1.000
Small	Control	Helpers	24	-	Large	Treatment	Helpers	4	0.4280	4.86	0.08801	538	1.000
Small	Control	Helpers	24	-	Small	Control	Breeding Female	-0.1	-4.6319	5.19	-0.89231	549	1.000
Small	Control	Helpers	24	-	Small	Control	Breeding Female	0.1	-7.2986	5.19	-1.40603	549	1.000
Small	Control	Helpers	24	-	Small	Control	Breeding Female	4	-5.4653	5.19	-1.05285	549	1.000
Small	Control	Helpers	24	-	Small	Control	Breeding Male	-0.1	-14.4653	5.19	-2.78663	549	1.000
Small	Control	Helpers	24	-	Small	Control	Breeding Male	0.1	-21.0486	5.19	-4.05487	549	0.065
Small	Control	Helpers	24	-	Small	Control	Breeding Male	4	-14.2986	5.19	-2.75453	549	1.000
Small	Control	Helpers	24	-	Small	Control	Helpers	-0.1	-0.5625	5.19	-0.10836	549	1.000
Small	Control	Helpers	24	-	Small	Control	Helpers	0.1	1.9306	5.19	0.37191	549	1.000
Small	Control	Helpers	24	-	Small	Control	Helpers	4	-0.3750	5.19	-0.07224	549	1.000
Small	Control	Helpers	24	-	Small	Treatment	Breeding Female	-0.1	-4.0589	5.20	-0.78043	539	1.000
Small	Control	Helpers	24	-	Small	Treatment	Breeding Female	0.1	7.6929	5.20	1.47945	539	1.000
Small	Control	Helpers	24	-	Small	Treatment	Breeding Female	4	0.4429	5.20	0.08517	539	1.000
Small	Control	Helpers	24	-	Small	Treatment	Breeding Male	-0.1	-10.4756	5.20	-2.01419	539	1.000
Small	Control	Helpers	24	-	Small	Treatment	Breeding Male	0.1	-44.3905	5.20	-8.53694	539	<.001
Small	Control	Helpers	24	-	Small	Treatment	Breeding Male	4	-21.4738	5.20	-4.12973	539	0.047
Small	Control	Helpers	24	-	Small	Treatment	Helpers	-0.1	-1.4547	5.20	-0.27971	539	1.000
Small	Control	Helpers	24	-	Small	Treatment	Helpers	0.1	5.4012	5.20	1.03873	539	1.000
Small	Control	Helpers	24	-	Small	Treatment	Helpers	4	1.0887	5.20	0.20937	539	1.000
Small	Control	Helpers	4	-	Large	Control	Breeding Female	-0.1	-8.7569	5.20	-1.68500	536	1.000
Small	Control	Helpers	4	-	Large	Control	Breeding Female	0.1	-13.7569	5.20	-2.64709	536	1.000
Small	Control	Helpers	4	-	Large	Control	Breeding Male	-0.1	-11.8403	5.20	-2.27829	536	1.000
Small	Control	Helpers	4	-	Large	Control	Breeding Male	0.1	-13.0069	5.20	-2.50278	536	1.000
Small	Control	Helpers	4	-	Large	Control	Helpers	-0.1	-1.2358	5.20	-0.23779	536	1.000
Small	Control	Helpers	4	-	Large	Control	Helpers	0.1	-0.2516	5.20	-0.04841	536	1.000
Small	Control	Helpers	4	-	Large	Control	Helpers	4	-1.4918	5.20	-0.28704	536	1.000
Small	Control	Helpers	4	-	Large	Treatment	Breeding Female	-0.1	-12.5826	4.86	-2.58704	538	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Control	Helpers	4	-	Large	Treatment	Breeding Female	0.1	-12.3339	4.86	-2.53625	538	1.000
Small	Control	Helpers	4	-	Large	Treatment	Breeding Male	-0.1	-18.1451	4.86	-3.73072	538	0.238
Small	Control	Helpers	4	-	Large	Treatment	Breeding Male	0.1	-21.5839	4.86	-4.43836	538	0.012
Small	Control	Helpers	4	-	Large	Treatment	Helpers	-0.1	-0.2053	4.86	-0.04221	538	1.000
Small	Control	Helpers	4	-	Large	Treatment	Helpers	0.1	0.2919	4.86	0.06001	538	1.000
Small	Control	Helpers	4	-	Small	Control	Breeding Female	-0.1	-4.2569	5.19	-0.82007	549	1.000
Small	Control	Helpers	4	-	Small	Control	Breeding Female	0.1	-6.9236	5.19	-1.33379	549	1.000
Small	Control	Helpers	4	-	Small	Control	Breeding Male	-0.1	-14.0903	5.19	-2.71439	549	1.000
Small	Control	Helpers	4	-	Small	Control	Breeding Male	0.1	-20.6736	5.19	-3.98263	549	0.087
Small	Control	Helpers	4	-	Small	Control	Helpers	-0.1	-0.1875	5.19	-0.03612	549	1.000
Small	Control	Helpers	4	-	Small	Control	Helpers	0.1	2.3056	5.19	0.44415	549	1.000
Small	Control	Helpers	4	-	Small	Treatment	Breeding Female	-0.1	-3.6839	5.20	-0.70832	539	1.000
Small	Control	Helpers	4	-	Small	Treatment	Breeding Female	0.1	8.0679	5.20	1.55157	539	1.000
Small	Control	Helpers	4	-	Small	Treatment	Breeding Male	-0.1	-10.1006	5.20	-1.94208	539	1.000
Small	Control	Helpers	4	-	Small	Treatment	Breeding Male	0.1	-44.0155	5.20	-8.46482	539	<.001
Small	Control	Helpers	4	-	Small	Treatment	Helpers	-0.1	-1.0797	5.20	-0.20761	539	1.000
Small	Control	Helpers	4	-	Small	Treatment	Helpers	0.1	5.7762	5.20	1.11085	539	1.000
Small	Treatment	Breeding Female	-0.1	-	Large	Control	Breeding Female	-0.1	-5.0730	5.20	-0.97542	539	1.000
Small	Treatment	Breeding Female	-0.1	-	Large	Control	Breeding Male	-0.1	-8.1564	5.20	-1.56826	539	1.000
Small	Treatment	Breeding Female	-0.1	-	Large	Control	Helpers	-0.1	2.4481	5.20	0.47071	539	1.000
Small	Treatment	Breeding Female	-0.1	-	Large	Treatment	Breeding Female	-0.1	-8.8986	4.87	-1.82570	543	1.000
Small	Treatment	Breeding Female	-0.1	-	Large	Treatment	Breeding Male	-0.1	-14.4611	4.87	-2.96694	543	1.000
Small	Treatment	Breeding Female	-0.1	-	Large	Treatment	Helpers	-0.1	3.4786	4.87	0.71369	543	1.000
Small	Treatment	Breeding Female	-0.1	-	Small	Control	Breeding Female	-0.1	-0.5730	5.20	-0.11018	539	1.000
Small	Treatment	Breeding Female	-0.1	-	Small	Control	Breeding Male	-0.1	-10.4064	5.20	-2.00088	539	1.000
Small	Treatment	Breeding Female	-0.1	-	Small	Control	Helpers	-0.1	3.4964	5.20	0.67227	539	1.000
Small	Treatment	Breeding Female	-0.1	-	Small	Treatment	Breeding Male	-0.1	-6.4167	5.19	-1.23613	549	1.000
Small	Treatment	Breeding Female	-0.1	-	Small	Treatment	Helpers	-0.1	2.6042	5.19	0.50167	549	1.000
Small	Treatment	Breeding Female	0.1	-	Large	Control	Breeding Female	-0.1	-16.8248	5.20	-3.23566	539	1.000
Small	Treatment	Breeding Female	0.1	-	Large	Control	Breeding Female	0.1	-21.8248	5.20	-4.19724	539	0.036
Small	Treatment	Breeding Female	0.1	-	Large	Control	Breeding Male	-0.1	-19.9082	5.20	-3.82863	539	0.162
Small	Treatment	Breeding Female	0.1	-	Large	Control	Breeding Male	0.1	-21.0748	5.20	-4.05300	539	0.065
Small	Treatment	Breeding Female	0.1	-	Large	Control	Helpers	-0.1	-9.3037	5.20	-1.78924	539	1.000
Small	Treatment	Breeding Female	0.1	-	Large	Control	Helpers	0.1	-8.3195	5.20	-1.59996	539	1.000
Small	Treatment	Breeding Female	0.1	-	Large	Treatment	Breeding Female	-0.1	-20.6504	4.87	-4.24048	544	0.030
Small	Treatment	Breeding Female	0.1	-	Large	Treatment	Breeding Female	0.1	-20.4018	4.87	-4.18881	543	0.037
Small	Treatment	Breeding Female	0.1	-	Large	Treatment	Breeding Male	-0.1	-26.2129	4.87	-5.38272	544	<.001

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

		Comparison						Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Treatment	Breeding Female	0.1	-	Large	Treatment	Breeding Male	0.1	-29.6518	4.87	-6.08798	543	<.001
Small	Treatment	Breeding Female	0.1	-	Large	Treatment	Helpers	-0.1	-8.2732	4.87	-1.69887	544	1.000
Small	Treatment	Breeding Female	0.1	-	Large	Treatment	Helpers	0.1	-7.7760	4.87	-1.59654	543	1.000
Small	Treatment	Breeding Female	0.1	-	Small	Control	Breeding Female	-0.1	-12.3248	5.20	-2.37024	539	1.000
Small	Treatment	Breeding Female	0.1	-	Small	Control	Breeding Female	0.1	-14.9915	5.20	-2.88308	539	1.000
Small	Treatment	Breeding Female	0.1	-	Small	Control	Breeding Male	-0.1	-22.1582	5.20	-4.26134	539	0.027
Small	Treatment	Breeding Female	0.1	-	Small	Control	Breeding Male	0.1	-28.7415	5.20	-5.52741	539	<.001
Small	Treatment	Breeding Female	0.1	-	Small	Control	Helpers	-0.1	-8.2554	5.20	-1.58763	539	1.000
Small	Treatment	Breeding Female	0.1	-	Small	Control	Helpers	0.1	-5.7623	5.20	-1.10818	539	1.000
Small	Treatment	Breeding Female	0.1	-	Small	Treatment	Breeding Female	-0.1	-11.7518	5.19	-2.26268	551	1.000
Small	Treatment	Breeding Female	0.1	-	Small	Treatment	Breeding Male	-0.1	-18.1685	5.19	-3.49814	551	0.571
Small	Treatment	Breeding Female	0.1	-	Small	Treatment	Breeding Male	0.1	-52.0833	5.19	-10.03349	549	<.001
Small	Treatment	Breeding Female	0.1	-	Small	Treatment	Helpers	-0.1	-9.1476	5.19	-1.76128	551	1.000
Small	Treatment	Breeding Female	0.1	-	Small	Treatment	Helpers	0.1	-2.2917	5.19	-0.44147	549	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Breeding Female	-0.1	-7.9082	5.20	-1.52085	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Breeding Female	0.1	-12.9082	5.20	-2.48243	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Breeding Female	24	-9.9915	5.20	-1.92151	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Breeding Female	4	-9.1582	5.20	-1.76125	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Breeding Male	-0.1	-10.9915	5.20	-2.11383	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Breeding Male	0.1	-12.1582	5.20	-2.33819	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Breeding Male	24	-8.4082	5.20	-1.61701	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Breeding Male	4	-8.4915	5.20	-1.63304	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Helpers	-0.1	-0.3870	5.20	-0.07443	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Helpers	0.1	0.5972	5.20	0.11485	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Helpers	24	-0.5635	5.20	-0.10837	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Control	Helpers	4	-0.6430	5.20	-0.12365	539	1.000
Small	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Female	-0.1	-11.7338	4.87	-2.40948	544	1.000
Small	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Female	0.1	-11.4851	4.87	-2.35808	543	1.000
Small	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Female	24	-8.7351	4.87	-1.79346	543	1.000
Small	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Female	4	4.3274	4.87	0.88849	543	1.000
Small	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Male	-0.1	-17.2963	4.87	-3.55172	544	0.469
Small	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Male	0.1	-20.7351	4.87	-4.25725	543	0.028
Small	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Male	24	-36.7976	4.87	-7.55514	543	<.001
Small	Treatment	Breeding Female	24	-	Large	Treatment	Breeding Male	4	-40.9851	4.87	-8.41490	543	<.001

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Treatment	Breeding Female	24	-	Large	Treatment	Helpers	-0.1	0.6435	4.87	0.13213	544	1.000
Small	Treatment	Breeding Female	24	-	Large	Treatment	Helpers	0.1	1.1406	4.87	0.23419	543	1.000
Small	Treatment	Breeding Female	24	-	Large	Treatment	Helpers	24	2.7363	4.87	0.56180	543	1.000
Small	Treatment	Breeding Female	24	-	Large	Treatment	Helpers	4	1.6518	4.87	0.33914	543	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Breeding Female	-0.1	-3.4082	5.20	-0.65544	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Breeding Female	0.1	-6.0748	5.20	-1.16828	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Breeding Female	24	-4.1582	5.20	-0.79967	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Breeding Female	4	-4.2415	5.20	-0.81570	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Breeding Male	-0.1	-13.2415	5.20	-2.54653	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Breeding Male	0.1	-19.8248	5.20	-3.81261	539	0.173
Small	Treatment	Breeding Female	24	-	Small	Control	Breeding Male	24	-14.5748	5.20	-2.80295	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Breeding Male	4	-13.0748	5.20	-2.51448	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Helpers	-0.1	0.6613	5.20	0.12718	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Helpers	0.1	3.1543	5.20	0.60663	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Helpers	24	1.2238	5.20	0.23535	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Control	Helpers	4	0.8488	5.20	0.16324	539	1.000
Small	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Female	-0.1	-2.8351	5.19	-0.54587	551	1.000
Small	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Female	0.1	8.9167	5.19	1.71773	549	1.000
Small	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Female	4	1.6667	5.19	0.32107	549	1.000
Small	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Male	-0.1	-9.2518	5.19	-1.78133	551	1.000
Small	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Male	0.1	-43.1667	5.19	-8.31576	549	<.001
Small	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Male	24	-22.4167	5.19	-4.31841	549	0.021
Small	Treatment	Breeding Female	24	-	Small	Treatment	Breeding Male	4	-20.2500	5.19	-3.90102	549	0.121
Small	Treatment	Breeding Female	24	-	Small	Treatment	Helpers	-0.1	-0.2310	5.19	-0.04447	551	1.000
Small	Treatment	Breeding Female	24	-	Small	Treatment	Helpers	0.1	6.6250	5.19	1.27626	549	1.000
Small	Treatment	Breeding Female	24	-	Small	Treatment	Helpers	24	4.0000	5.19	0.77057	549	1.000
Small	Treatment	Breeding Female	24	-	Small	Treatment	Helpers	4	2.3125	5.19	0.44549	549	1.000
Small	Treatment	Breeding Female	4	-	Large	Control	Breeding Female	-0.1	-9.5748	5.20	-1.84138	539	1.000
Small	Treatment	Breeding Female	4	-	Large	Control	Breeding Female	0.1	-14.5748	5.20	-2.80295	539	1.000
Small	Treatment	Breeding Female	4	-	Large	Control	Breeding Female	4	-10.8248	5.20	-2.08177	539	1.000
Small	Treatment	Breeding Female	4	-	Large	Control	Breeding Male	-0.1	-12.6582	5.20	-2.43435	539	1.000
Small	Treatment	Breeding Female	4	-	Large	Control	Breeding Male	0.1	-13.8248	5.20	-2.65872	539	1.000
Small	Treatment	Breeding Female	4	-	Large	Control	Breeding Male	4	-10.1582	5.20	-1.95356	539	1.000
Small	Treatment	Breeding Female	4	-	Large	Control	Helpers	-0.1	-2.0537	5.20	-0.39495	539	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison												
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point	Difference	SE	t	df	Pbonferroni
Small	Treatment	Breeding Female	4	- Large	Control	Helpers	0.1	-1.0695	5.20	-0.20567	539	1.000
Small	Treatment	Breeding Female	4	- Large	Control	Helpers	4	-2.3096	5.20	-0.44418	539	1.000
Small	Treatment	Breeding Female	4	- Large	Treatment	Breeding Female	-0.1	-13.4004	4.87	-2.75172	544	1.000
Small	Treatment	Breeding Female	4	- Large	Treatment	Breeding Female	0.1	-13.1518	4.87	-2.70027	543	1.000
Small	Treatment	Breeding Female	4	- Large	Treatment	Breeding Female	4	2.6607	4.87	0.54629	543	1.000
Small	Treatment	Breeding Female	4	- Large	Treatment	Breeding Male	-0.1	-18.9629	4.87	-3.89396	544	0.125
Small	Treatment	Breeding Female	4	- Large	Treatment	Breeding Male	0.1	-22.4018	4.87	-4.59944	543	0.006
Small	Treatment	Breeding Female	4	- Large	Treatment	Breeding Male	4	-42.6518	4.87	-8.75709	543	<.001
Small	Treatment	Breeding Female	4	- Large	Treatment	Helpers	-0.1	-1.0232	4.87	-0.21011	544	1.000
Small	Treatment	Breeding Female	4	- Large	Treatment	Helpers	0.1	-0.5260	4.87	-0.10800	543	1.000
Small	Treatment	Breeding Female	4	- Large	Treatment	Helpers	4	-0.0149	4.87	-0.00305	543	1.000
Small	Treatment	Breeding Female	4	- Small	Control	Breeding Female	-0.1	-5.0748	5.20	-0.97596	539	1.000
Small	Treatment	Breeding Female	4	- Small	Control	Breeding Female	0.1	-7.7415	5.20	-1.48880	539	1.000
Small	Treatment	Breeding Female	4	- Small	Control	Breeding Female	4	-5.9082	5.20	-1.13622	539	1.000
Small	Treatment	Breeding Female	4	- Small	Control	Breeding Male	-0.1	-14.9082	5.20	-2.86706	539	1.000
Small	Treatment	Breeding Female	4	- Small	Control	Breeding Male	0.1	-21.4915	5.20	-4.13313	539	0.047
Small	Treatment	Breeding Female	4	- Small	Control	Breeding Male	4	-14.7415	5.20	-2.83501	539	1.000
Small	Treatment	Breeding Female	4	- Small	Control	Helpers	-0.1	-1.0054	5.20	-0.19335	539	1.000
Small	Treatment	Breeding Female	4	- Small	Control	Helpers	0.1	1.4877	5.20	0.28610	539	1.000
Small	Treatment	Breeding Female	4	- Small	Control	Helpers	4	-0.8179	5.20	-0.15729	539	1.000
Small	Treatment	Breeding Female	4	- Small	Treatment	Breeding Female	-0.1	-4.5018	5.19	-0.86677	551	1.000
Small	Treatment	Breeding Female	4	- Small	Treatment	Breeding Female	0.1	7.2500	5.19	1.39666	549	1.000
Small	Treatment	Breeding Female	4	- Small	Treatment	Breeding Male	-0.1	-10.9185	5.19	-2.10223	551	1.000
Small	Treatment	Breeding Female	4	- Small	Treatment	Breeding Male	0.1	-44.8333	5.19	-8.63683	549	<.001
Small	Treatment	Breeding Female	4	- Small	Treatment	Breeding Male	4	-21.9167	5.19	-4.22209	549	0.032
Small	Treatment	Breeding Female	4	- Small	Treatment	Helpers	-0.1	-1.8976	5.19	-0.36537	551	1.000
Small	Treatment	Breeding Female	4	- Small	Treatment	Helpers	0.1	4.9583	5.19	0.95519	549	1.000
Small	Treatment	Breeding Female	4	- Small	Treatment	Helpers	4	0.6458	5.19	0.12442	549	1.000
Small	Treatment	Breeding Male	-0.1	- Large	Control	Breeding Male	-0.1	-1.7397	5.20	-0.33450	539	1.000
Small	Treatment	Breeding Male	-0.1	- Large	Control	Helpers	-0.1	8.8648	5.20	1.70447	539	1.000
Small	Treatment	Breeding Male	-0.1	- Large	Treatment	Breeding Male	-0.1	-8.0445	4.87	-1.65045	543	1.000
Small	Treatment	Breeding Male	-0.1	- Large	Treatment	Helpers	-0.1	9.8953	4.87	2.03017	543	1.000
Small	Treatment	Breeding Male	-0.1	- Small	Control	Breeding Male	-0.1	-3.9897	5.20	-0.76712	539	1.000
Small	Treatment	Breeding Male	-0.1	- Small	Control	Helpers	-0.1	9.9131	5.20	1.90603	539	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

		Comparison							Difference	SE	t	df	Pbonferroni
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Treatment	Breeding Male	-0.1	-	Small	Treatment	Helpers	-0.1	9.0208	5.19	1.73780	549	1.000
Small	Treatment	Breeding Male	0.1	-	Large	Control	Breeding Female	-0.1	35.2585	5.20	6.78073	539	<.001
Small	Treatment	Breeding Male	0.1	-	Large	Control	Breeding Male	-0.1	32.1752	5.20	6.18776	539	<.001
Small	Treatment	Breeding Male	0.1	-	Large	Control	Breeding Male	0.1	31.0085	5.20	5.96340	539	<.001
Small	Treatment	Breeding Male	0.1	-	Large	Control	Helpers	-0.1	42.7796	5.20	8.22716	539	<.001
Small	Treatment	Breeding Male	0.1	-	Large	Control	Helpers	0.1	43.7639	5.20	8.41644	539	<.001
Small	Treatment	Breeding Male	0.1	-	Large	Treatment	Breeding Female	-0.1	31.4329	4.87	6.45462	544	<.001
Small	Treatment	Breeding Male	0.1	-	Large	Treatment	Breeding Male	-0.1	25.8704	4.87	5.31238	544	<.001
Small	Treatment	Breeding Male	0.1	-	Large	Treatment	Breeding Male	0.1	22.4316	4.87	4.60556	543	0.006
Small	Treatment	Breeding Male	0.1	-	Large	Treatment	Helpers	-0.1	43.8101	4.87	8.99624	544	<.001
Small	Treatment	Breeding Male	0.1	-	Large	Treatment	Helpers	0.1	44.3073	4.87	9.09700	543	<.001
Small	Treatment	Breeding Male	0.1	-	Small	Control	Breeding Female	-0.1	39.7585	5.20	7.64615	539	<.001
Small	Treatment	Breeding Male	0.1	-	Small	Control	Breeding Male	-0.1	29.9252	5.20	5.75506	539	<.001
Small	Treatment	Breeding Male	0.1	-	Small	Control	Breeding Male	0.1	23.3418	5.20	4.48898	539	0.010
Small	Treatment	Breeding Male	0.1	-	Small	Control	Helpers	-0.1	43.8280	5.20	8.42877	539	<.001
Small	Treatment	Breeding Male	0.1	-	Small	Control	Helpers	0.1	46.3210	5.20	8.90822	539	<.001
Small	Treatment	Breeding Male	0.1	-	Small	Treatment	Breeding Female	-0.1	40.3315	5.19	7.76541	551	<.001
Small	Treatment	Breeding Male	0.1	-	Small	Treatment	Breeding Male	-0.1	33.9149	5.19	6.52995	551	<.001
Small	Treatment	Breeding Male	0.1	-	Small	Treatment	Helpers	-0.1	42.9357	5.19	8.26681	551	<.001
Small	Treatment	Breeding Male	0.1	-	Small	Treatment	Helpers	0.1	49.7917	5.19	9.59202	549	<.001
Small	Treatment	Breeding Male	24	-	Large	Control	Breeding Female	-0.1	14.5085	5.20	2.79020	539	1.000
Small	Treatment	Breeding Male	24	-	Large	Control	Breeding Female	0.1	9.5085	5.20	1.82863	539	1.000
Small	Treatment	Breeding Male	24	-	Large	Control	Breeding Female	4	13.2585	5.20	2.54981	539	1.000
Small	Treatment	Breeding Male	24	-	Large	Control	Breeding Male	-0.1	11.4252	5.20	2.19723	539	1.000
Small	Treatment	Breeding Male	24	-	Large	Control	Breeding Male	0.1	10.2585	5.20	1.97286	539	1.000
Small	Treatment	Breeding Male	24	-	Large	Control	Breeding Male	24	14.0085	5.20	2.69404	539	1.000
Small	Treatment	Breeding Male	24	-	Large	Control	Breeding Male	4	13.9252	5.20	2.67802	539	1.000
Small	Treatment	Breeding Male	24	-	Large	Control	Helpers	-0.1	22.0296	5.20	4.23663	539	0.030
Small	Treatment	Breeding Male	24	-	Large	Control	Helpers	0.1	23.0139	5.20	4.42591	539	0.013
Small	Treatment	Breeding Male	24	-	Large	Control	Helpers	24	21.8532	5.20	4.20269	539	0.035
Small	Treatment	Breeding Male	24	-	Large	Control	Helpers	4	21.7737	5.20	4.18740	539	0.037
Small	Treatment	Breeding Male	24	-	Large	Treatment	Breeding Female	-0.1	10.6829	4.87	2.19369	544	1.000
Small	Treatment	Breeding Male	24	-	Large	Treatment	Breeding Female	0.1	10.9316	4.87	2.24443	543	1.000
Small	Treatment	Breeding Male	24	-	Large	Treatment	Breeding Female	4	26.7441	4.87	5.49099	543	<.001

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison													
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point	Difference	SE	t	df	Pbonferroni	
Small	Treatment	Breeding Male	24	-	Large	Treatment	Breeding Male	-0.1	5.1204	4.87	1.05146	544	1.000
Small	Treatment	Breeding Male	24	-	Large	Treatment	Breeding Male	0.1	1.6816	4.87	0.34525	543	1.000
Small	Treatment	Breeding Male	24	-	Large	Treatment	Breeding Male	24	-14.3809	4.87	-2.95264	543	1.000
Small	Treatment	Breeding Male	24	-	Large	Treatment	Breeding Male	4	-18.5684	4.87	-3.81240	543	0.173
Small	Treatment	Breeding Male	24	-	Large	Treatment	Helpers	-0.1	23.0601	4.87	4.73531	544	0.003
Small	Treatment	Breeding Male	24	-	Large	Treatment	Helpers	0.1	23.5573	4.87	4.83670	543	0.002
Small	Treatment	Breeding Male	24	-	Large	Treatment	Helpers	24	25.1529	4.87	5.16430	543	<.001
Small	Treatment	Breeding Male	24	-	Large	Treatment	Helpers	4	24.0685	4.87	4.94164	543	0.001
Small	Treatment	Breeding Male	24	-	Small	Control	Breeding Female	-0.1	19.0085	5.20	3.65562	539	0.318
Small	Treatment	Breeding Male	24	-	Small	Control	Breeding Female	0.1	16.3418	5.20	3.14278	539	1.000
Small	Treatment	Breeding Male	24	-	Small	Control	Breeding Female	4	18.1752	5.20	3.49536	539	0.578
Small	Treatment	Breeding Male	24	-	Small	Control	Breeding Male	-0.1	9.1752	5.20	1.76452	539	1.000
Small	Treatment	Breeding Male	24	-	Small	Control	Breeding Male	0.1	2.5918	5.20	0.49845	539	1.000
Small	Treatment	Breeding Male	24	-	Small	Control	Breeding Male	24	7.8418	5.20	1.50810	539	1.000
Small	Treatment	Breeding Male	24	-	Small	Control	Breeding Male	4	9.3418	5.20	1.79658	539	1.000
Small	Treatment	Breeding Male	24	-	Small	Control	Helpers	-0.1	23.0780	5.20	4.43823	539	0.012
Small	Treatment	Breeding Male	24	-	Small	Control	Helpers	0.1	25.5710	5.20	4.91768	539	0.001
Small	Treatment	Breeding Male	24	-	Small	Control	Helpers	24	23.6405	5.20	4.54641	539	0.008
Small	Treatment	Breeding Male	24	-	Small	Control	Helpers	4	23.2655	5.20	4.47429	539	0.011
Small	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Female	-0.1	19.5815	5.19	3.77022	551	0.204
Small	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Female	0.1	31.3333	5.19	6.03615	549	<.001
Small	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Female	4	24.0833	5.19	4.63949	549	0.005
Small	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Male	-0.1	13.1649	5.19	2.53476	551	1.000
Small	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Male	0.1	-20.7500	5.19	-3.99734	549	0.082
Small	Treatment	Breeding Male	24	-	Small	Treatment	Breeding Male	4	2.1667	5.19	0.41739	549	1.000
Small	Treatment	Breeding Male	24	-	Small	Treatment	Helpers	-0.1	22.1857	5.19	4.27162	551	0.026
Small	Treatment	Breeding Male	24	-	Small	Treatment	Helpers	0.1	29.0417	5.19	5.59467	549	<.001
Small	Treatment	Breeding Male	24	-	Small	Treatment	Helpers	24	26.4167	5.19	5.08899	549	<.001
Small	Treatment	Breeding Male	24	-	Small	Treatment	Helpers	4	24.7292	5.19	4.76390	549	0.003
Small	Treatment	Breeding Male	4	-	Large	Control	Breeding Female	-0.1	12.3418	5.20	2.37352	539	1.000
Small	Treatment	Breeding Male	4	-	Large	Control	Breeding Female	0.1	7.3418	5.20	1.41195	539	1.000
Small	Treatment	Breeding Male	4	-	Large	Control	Breeding Male	-0.1	9.2585	5.20	1.78055	539	1.000
Small	Treatment	Breeding Male	4	-	Large	Control	Breeding Male	0.1	8.0918	5.20	1.55618	539	1.000
Small	Treatment	Breeding Male	4	-	Large	Control	Breeding Male	4	11.7585	5.20	2.26134	539	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

		Comparison							Difference	SE	t	df	Pbonferroni
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Treatment	Breeding Male	4	-	Large	Control	Helpers	-0.1	19.8630	5.20	3.81994	539	0.168
Small	Treatment	Breeding Male	4	-	Large	Control	Helpers	0.1	20.8472	5.20	4.00923	539	0.078
Small	Treatment	Breeding Male	4	-	Large	Control	Helpers	4	19.6070	5.20	3.77072	539	0.204
Small	Treatment	Breeding Male	4	-	Large	Treatment	Breeding Female	-0.1	8.5162	4.87	1.74878	544	1.000
Small	Treatment	Breeding Male	4	-	Large	Treatment	Breeding Female	0.1	8.7649	4.87	1.79958	543	1.000
Small	Treatment	Breeding Male	4	-	Large	Treatment	Breeding Male	-0.1	2.9537	4.87	0.60654	544	1.000
Small	Treatment	Breeding Male	4	-	Large	Treatment	Breeding Male	0.1	-0.4851	4.87	-0.09960	543	1.000
Small	Treatment	Breeding Male	4	-	Large	Treatment	Breeding Male	4	-20.7351	4.87	-4.25725	543	0.028
Small	Treatment	Breeding Male	4	-	Large	Treatment	Helpers	-0.1	20.8935	4.87	4.29039	544	0.024
Small	Treatment	Breeding Male	4	-	Large	Treatment	Helpers	0.1	21.3906	4.87	4.39184	543	0.015
Small	Treatment	Breeding Male	4	-	Large	Treatment	Helpers	4	21.9018	4.87	4.49679	543	0.010
Small	Treatment	Breeding Male	4	-	Small	Control	Breeding Female	-0.1	16.8418	5.20	3.23894	539	1.000
Small	Treatment	Breeding Male	4	-	Small	Control	Breeding Female	0.1	14.1752	5.20	2.72610	539	1.000
Small	Treatment	Breeding Male	4	-	Small	Control	Breeding Male	-0.1	7.0085	5.20	1.34784	539	1.000
Small	Treatment	Breeding Male	4	-	Small	Control	Breeding Male	0.1	0.4252	5.20	0.08177	539	1.000
Small	Treatment	Breeding Male	4	-	Small	Control	Breeding Male	4	7.1752	5.20	1.37989	539	1.000
Small	Treatment	Breeding Male	4	-	Small	Control	Helpers	-0.1	20.9113	5.20	4.02155	539	0.075
Small	Treatment	Breeding Male	4	-	Small	Control	Helpers	0.1	23.4043	5.20	4.50100	539	0.009
Small	Treatment	Breeding Male	4	-	Small	Control	Helpers	4	21.0988	5.20	4.05761	539	0.064
Small	Treatment	Breeding Male	4	-	Small	Treatment	Breeding Female	-0.1	17.4149	5.19	3.35305	551	0.964
Small	Treatment	Breeding Male	4	-	Small	Treatment	Breeding Female	0.1	29.1667	5.19	5.61875	549	<.001
Small	Treatment	Breeding Male	4	-	Small	Treatment	Breeding Male	-0.1	10.9982	5.19	2.11759	551	1.000
Small	Treatment	Breeding Male	4	-	Small	Treatment	Breeding Male	0.1	-22.9167	5.19	-4.41474	549	0.014
Small	Treatment	Breeding Male	4	-	Small	Treatment	Helpers	-0.1	20.0190	5.19	3.85445	551	0.146
Small	Treatment	Breeding Male	4	-	Small	Treatment	Helpers	0.1	26.8750	5.19	5.17728	549	<.001
Small	Treatment	Breeding Male	4	-	Small	Treatment	Helpers	4	22.5625	5.19	4.34651	549	0.019
Small	Treatment	Helpers	-0.1	-	Large	Control	Helpers	-0.1	-0.1561	5.20	-0.03001	539	1.000
Small	Treatment	Helpers	-0.1	-	Large	Treatment	Helpers	-0.1	0.8744	4.87	0.17940	543	1.000
Small	Treatment	Helpers	-0.1	-	Small	Control	Helpers	-0.1	0.8922	5.20	0.17156	539	1.000
Small	Treatment	Helpers	0.1	-	Large	Control	Breeding Female	-0.1	-14.5332	5.20	-2.79494	539	1.000
Small	Treatment	Helpers	0.1	-	Large	Control	Breeding Male	-0.1	-17.6165	5.20	-3.38791	539	0.852
Small	Treatment	Helpers	0.1	-	Large	Control	Helpers	-0.1	-7.0120	5.20	-1.34852	539	1.000
Small	Treatment	Helpers	0.1	-	Large	Control	Helpers	0.1	-6.0278	5.20	-1.15923	539	1.000
Small	Treatment	Helpers	0.1	-	Large	Treatment	Breeding Female	-0.1	-18.3588	4.87	-3.76990	544	0.204
Small	Treatment	Helpers	0.1	-	Large	Treatment	Breeding Male	-0.1	-23.9213	4.87	-4.91213	544	0.001
Small	Treatment	Helpers	0.1	-	Large	Treatment	Helpers	-0.1	-5.9815	4.87	-1.22828	544	1.000
Small	Treatment	Helpers	0.1	-	Large	Treatment	Helpers	0.1	-5.4844	4.87	-1.12603	543	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

Comparison								Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Treatment	Helpers	0.1	-	Small	Control	Breeding Female	-0.1	-10.0332	5.20	-1.92952	539	1.000
Small	Treatment	Helpers	0.1	-	Small	Control	Breeding Male	-0.1	-19.8665	5.20	-3.82062	539	0.168
Small	Treatment	Helpers	0.1	-	Small	Control	Helpers	-0.1	-5.9637	5.20	-1.14691	539	1.000
Small	Treatment	Helpers	0.1	-	Small	Control	Helpers	0.1	-3.4707	5.20	-0.66746	539	1.000
Small	Treatment	Helpers	0.1	-	Small	Treatment	Breeding Female	-0.1	-9.4601	5.19	-1.82144	551	1.000
Small	Treatment	Helpers	0.1	-	Small	Treatment	Breeding Male	-0.1	-15.8768	5.19	-3.05691	551	1.000
Small	Treatment	Helpers	0.1	-	Small	Treatment	Helpers	-0.1	-6.8560	5.19	-1.32004	551	1.000
Small	Treatment	Helpers	24	-	Large	Control	Breeding Female	-0.1	-11.9082	5.20	-2.29011	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Breeding Female	0.1	-16.9082	5.20	-3.25169	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Breeding Female	4	-13.1582	5.20	-2.53051	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Breeding Male	-0.1	-14.9915	5.20	-2.88308	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Breeding Male	0.1	-16.1582	5.20	-3.10745	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Breeding Male	4	-12.4915	5.20	-2.40230	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Helpers	-0.1	-4.3870	5.20	-0.84369	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Helpers	0.1	-3.4028	5.20	-0.65441	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Helpers	24	-4.5635	5.20	-0.87763	539	1.000
Small	Treatment	Helpers	24	-	Large	Control	Helpers	4	-4.6430	5.20	-0.89291	539	1.000
Small	Treatment	Helpers	24	-	Large	Treatment	Breeding Female	-0.1	-15.7338	4.87	-3.23086	544	1.000
Small	Treatment	Helpers	24	-	Large	Treatment	Breeding Female	0.1	-15.4851	4.87	-3.17934	543	1.000
Small	Treatment	Helpers	24	-	Large	Treatment	Breeding Female	4	0.3274	4.87	0.06722	543	1.000
Small	Treatment	Helpers	24	-	Large	Treatment	Breeding Male	-0.1	-21.2963	4.87	-4.37310	544	0.017
Small	Treatment	Helpers	24	-	Large	Treatment	Breeding Male	0.1	-24.7351	4.87	-5.07851	543	<.001
Small	Treatment	Helpers	24	-	Large	Treatment	Breeding Male	4	-44.9851	4.87	-9.23616	543	<.001
Small	Treatment	Helpers	24	-	Large	Treatment	Helpers	-0.1	-3.3565	4.87	-0.68925	544	1.000
Small	Treatment	Helpers	24	-	Large	Treatment	Helpers	0.1	-2.8594	4.87	-0.58707	543	1.000
Small	Treatment	Helpers	24	-	Large	Treatment	Helpers	24	-1.2637	4.87	-0.25947	543	1.000
Small	Treatment	Helpers	24	-	Large	Treatment	Helpers	4	-2.3482	4.87	-0.48212	543	1.000
Small	Treatment	Helpers	24	-	Small	Control	Breeding Female	-0.1	-7.4082	5.20	-1.42470	539	1.000
Small	Treatment	Helpers	24	-	Small	Control	Breeding Female	0.1	-10.0748	5.20	-1.93754	539	1.000
Small	Treatment	Helpers	24	-	Small	Control	Breeding Female	4	-8.2415	5.20	-1.58496	539	1.000
Small	Treatment	Helpers	24	-	Small	Control	Breeding Male	-0.1	-17.2415	5.20	-3.31579	539	1.000
Small	Treatment	Helpers	24	-	Small	Control	Breeding Male	0.1	-23.8248	5.20	-4.58187	539	0.006
Small	Treatment	Helpers	24	-	Small	Control	Breeding Male	4	-17.0748	5.20	-3.28374	539	1.000
Small	Treatment	Helpers	24	-	Small	Control	Helpers	-0.1	-3.3387	5.20	-0.64208	539	1.000
Small	Treatment	Helpers	24	-	Small	Control	Helpers	0.1	-0.8457	5.20	-0.16263	539	1.000
Small	Treatment	Helpers	24	-	Small	Control	Helpers	24	-2.7762	5.20	-0.53391	539	1.000
Small	Treatment	Helpers	24	-	Small	Control	Helpers	4	-3.1512	5.20	-0.60602	539	1.000
Small	Treatment	Helpers	24	-	Small	Treatment	Breeding Female	-0.1	-6.8351	5.19	-1.31603	551	1.000
Small	Treatment	Helpers	24	-	Small	Treatment	Breeding Female	0.1	4.9167	5.19	0.94716	549	1.000
Small	Treatment	Helpers	24	-	Small	Treatment	Breeding Female	4	-2.3333	5.19	-0.44950	549	1.000
Small	Treatment	Helpers	24	-	Small	Treatment	Breeding Male	-0.1	-13.2518	5.19	-2.55149	551	1.000

Post Hoc Comparisons - Group Size * Treatment * Subject * Time Point

				Comparison				Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Subject	Time Point	Group Size	Treatment	Subject	Time Point						
Small	Treatment	Helpers	24	-	Small	Treatment	Breeding Male	0.1	-47.1667	5.19	-9.08633	549	<.001
Small	Treatment	Helpers	24	-	Small	Treatment	Breeding Male	4	-24.2500	5.19	-4.67159	549	0.004
Small	Treatment	Helpers	24	-	Small	Treatment	Helpers	-0.1	-4.2310	5.19	-0.81462	551	1.000
Small	Treatment	Helpers	24	-	Small	Treatment	Helpers	0.1	2.6250	5.19	0.50569	549	1.000
Small	Treatment	Helpers	24	-	Small	Treatment	Helpers	4	-1.6875	5.19	-0.32509	549	1.000
Small	Treatment	Helpers	4	-	Large	Control	Breeding Female	-0.1	-10.2207	5.20	-1.96558	539	1.000
Small	Treatment	Helpers	4	-	Large	Control	Breeding Female	0.1	-15.2207	5.20	-2.92716	539	1.000
Small	Treatment	Helpers	4	-	Large	Control	Breeding Male	-0.1	-13.3040	5.20	-2.55855	539	1.000
Small	Treatment	Helpers	4	-	Large	Control	Breeding Male	0.1	-14.4707	5.20	-2.78292	539	1.000
Small	Treatment	Helpers	4	-	Large	Control	Helpers	-0.1	-2.6995	5.20	-0.51916	539	1.000
Small	Treatment	Helpers	4	-	Large	Control	Helpers	0.1	-1.7153	5.20	-0.32988	539	1.000
Small	Treatment	Helpers	4	-	Large	Control	Helpers	4	-2.9555	5.20	-0.56838	539	1.000
Small	Treatment	Helpers	4	-	Large	Treatment	Breeding Female	-0.1	-14.0463	4.87	-2.88434	544	1.000
Small	Treatment	Helpers	4	-	Large	Treatment	Breeding Female	0.1	-13.7976	4.87	-2.83287	543	1.000
Small	Treatment	Helpers	4	-	Large	Treatment	Breeding Male	-0.1	-19.6088	4.87	-4.02658	544	0.073
Small	Treatment	Helpers	4	-	Large	Treatment	Breeding Male	0.1	-23.0476	4.87	-4.73204	543	0.003
Small	Treatment	Helpers	4	-	Large	Treatment	Helpers	-0.1	-1.6690	4.87	-0.34273	544	1.000
Small	Treatment	Helpers	4	-	Large	Treatment	Helpers	0.1	-1.1719	4.87	-0.24060	543	1.000
Small	Treatment	Helpers	4	-	Large	Treatment	Helpers	4	-0.6607	4.87	-0.13565	543	1.000
Small	Treatment	Helpers	4	-	Small	Control	Breeding Female	-0.1	-5.7207	5.20	-1.10017	539	1.000
Small	Treatment	Helpers	4	-	Small	Control	Breeding Female	0.1	-8.3873	5.20	-1.61301	539	1.000
Small	Treatment	Helpers	4	-	Small	Control	Breeding Male	-0.1	-15.5540	5.20	-2.99126	539	1.000
Small	Treatment	Helpers	4	-	Small	Control	Breeding Male	0.1	-22.1373	5.20	-4.25733	539	0.028
Small	Treatment	Helpers	4	-	Small	Control	Helpers	-0.1	-1.6512	5.20	-0.31755	539	1.000
Small	Treatment	Helpers	4	-	Small	Control	Helpers	0.1	0.8418	5.20	0.16190	539	1.000
Small	Treatment	Helpers	4	-	Small	Control	Helpers	4	-1.4637	5.20	-0.28149	539	1.000
Small	Treatment	Helpers	4	-	Small	Treatment	Breeding Female	-0.1	-5.1476	5.19	-0.99112	551	1.000
Small	Treatment	Helpers	4	-	Small	Treatment	Breeding Female	0.1	6.6042	5.19	1.27225	549	1.000
Small	Treatment	Helpers	4	-	Small	Treatment	Breeding Male	-0.1	-11.5643	5.19	-2.22658	551	1.000
Small	Treatment	Helpers	4	-	Small	Treatment	Breeding Male	0.1	-45.4792	5.19	-8.76124	549	<.001
Small	Treatment	Helpers	4	-	Small	Treatment	Helpers	-0.1	-2.5435	5.19	-0.48971	551	1.000
Small	Treatment	Helpers	4	-	Small	Treatment	Helpers	0.1	4.3125	5.19	0.83077	549	1.000

Table S2. Post-hoc Comparisons for Affiliation Index Analysis - Treatment × Group Size × Timepoint

		Comparison					Difference	SE	t	df	Pbonferroni
Group Size	Treatment	Time Point	Group Size	Treatment	Time Point						
Large	Control	0.1	-	Large	Control	-0.1	-0.05066	0.0385	-1.3144	579.0	1.000
Large	Control	0.1	-	Large	Treatment	-0.1	-0.00903	0.0471	-0.1918	68.4	1.000
Large	Control	0.1	-	Small	Control	-0.1	-0.05228	0.0504	-1.0380	68.4	1.000
Large	Control	0.1	-	Small	Treatment	-0.1	-0.11253	0.0504	-2.2344	68.4	1.000
Large	Control	24	-	Large	Control	-0.1	-0.02452	0.0385	-0.6362	579.0	1.000
Large	Control	24	-	Large	Control	0.1	0.02614	0.0385	0.6781	579.0	1.000
Large	Control	24	-	Large	Control	4	-0.02786	0.0385	-0.7227	579.0	1.000
Large	Control	24	-	Large	Treatment	-0.1	0.01710	0.0471	0.3631	68.4	1.000
Large	Control	24	-	Large	Treatment	0.1	-0.11565	0.0471	-2.4548	68.4	1.000
Large	Control	24	-	Large	Treatment	4	-0.09375	0.0471	-1.9900	68.4	1.000
Large	Control	24	-	Small	Control	-0.1	-0.02614	0.0504	-0.5189	68.4	1.000
Large	Control	24	-	Small	Control	0.1	-0.04477	0.0504	-0.8890	68.4	1.000
Large	Control	24	-	Small	Control	4	-0.07661	0.0504	-1.5211	68.4	1.000
Large	Control	24	-	Small	Treatment	-0.1	-0.08639	0.0504	-1.7154	68.4	1.000
Large	Control	24	-	Small	Treatment	0.1	0.02998	0.0504	0.5952	68.4	1.000
Large	Control	24	-	Small	Treatment	4	-0.07475	0.0504	-1.4842	68.4	1.000
Large	Control	4	-	Large	Control	-0.1	0.00333	0.0385	0.0865	579.0	1.000
Large	Control	4	-	Large	Control	0.1	0.05400	0.0385	1.4009	579.0	1.000
Large	Control	4	-	Large	Treatment	-0.1	0.04496	0.0471	0.9544	68.4	1.000
Large	Control	4	-	Large	Treatment	0.1	-0.08779	0.0471	-1.8634	68.4	1.000
Large	Control	4	-	Small	Control	-0.1	0.00172	0.0504	0.0342	68.4	1.000
Large	Control	4	-	Small	Control	0.1	-0.01691	0.0504	-0.3358	68.4	1.000
Large	Control	4	-	Small	Treatment	-0.1	-0.05853	0.0504	-1.1622	68.4	1.000
Large	Control	4	-	Small	Treatment	0.1	0.05784	0.0504	1.1484	68.4	1.000
Large	Treatment	-0.1	-	Large	Control	-0.1	-0.04163	0.0471	-0.8837	68.4	1.000
Large	Treatment	-0.1	-	Small	Control	-0.1	-0.04324	0.0471	-0.9178	68.4	1.000
Large	Treatment	0.1	-	Large	Control	-0.1	0.09112	0.0471	1.9342	68.4	1.000
Large	Treatment	0.1	-	Large	Control	0.1	0.14179	0.0471	3.0096	68.4	0.439
Large	Treatment	0.1	-	Large	Treatment	-0.1	0.13275	0.0334	3.9767	579.0	0.009
Large	Treatment	0.1	-	Small	Control	-0.1	0.08951	0.0471	1.9000	68.4	1.000
Large	Treatment	0.1	-	Small	Control	0.1	0.07087	0.0471	1.5044	68.4	1.000
Large	Treatment	0.1	-	Small	Treatment	-0.1	0.02925	0.0471	0.6210	68.4	1.000
Large	Treatment	24	-	Large	Control	-0.1	0.06344	0.0471	1.3466	68.4	1.000
Large	Treatment	24	-	Large	Control	0.1	0.11411	0.0471	2.4221	68.4	1.000
Large	Treatment	24	-	Large	Control	24	0.08797	0.0471	1.8672	68.4	1.000
Large	Treatment	24	-	Large	Control	4	0.06011	0.0471	1.2759	68.4	1.000
Large	Treatment	24	-	Large	Treatment	-0.1	0.10507	0.0334	3.1475	579.0	0.208
Large	Treatment	24	-	Large	Treatment	0.1	-0.02768	0.0334	-0.8292	579.0	1.000
Large	Treatment	24	-	Large	Treatment	4	-0.00579	0.0334	-0.1733	579.0	1.000
Large	Treatment	24	-	Small	Control	-0.1	0.06183	0.0471	1.3124	68.4	1.000
Large	Treatment	24	-	Small	Control	0.1	0.04319	0.0471	0.9168	68.4	1.000
Large	Treatment	24	-	Small	Control	24	0.03498	0.0471	0.7425	68.4	1.000
Large	Treatment	24	-	Small	Control	4	0.01136	0.0471	0.2411	68.4	1.000
Large	Treatment	24	-	Small	Treatment	-0.1	0.00157	0.0471	0.0334	68.4	1.000
Large	Treatment	24	-	Small	Treatment	0.1	0.11794	0.0471	2.5035	68.4	1.000
Large	Treatment	24	-	Small	Treatment	4	0.01322	0.0471	0.2805	68.4	1.000
Large	Treatment	4	-	Large	Control	-0.1	0.06923	0.0471	1.4694	68.4	1.000
Large	Treatment	4	-	Large	Control	0.1	0.11989	0.0471	2.5449	68.4	1.000
Large	Treatment	4	-	Large	Control	4	0.06589	0.0471	1.3987	68.4	1.000
Large	Treatment	4	-	Large	Treatment	-0.1	0.11086	0.0334	3.3208	579.0	0.114
Large	Treatment	4	-	Large	Treatment	0.1	-0.02190	0.0334	-0.6559	579.0	1.000
Large	Treatment	4	-	Small	Control	-0.1	0.06762	0.0471	1.4352	68.4	1.000

Post Hoc Comparisons - Group Size * Treatment * Time Point

Comparison						Difference	SE	t	df	Pbonferroni	
Group Size	Treatment	Time Point	Group Size	Treatment	Time Point						
Large	Treatment	4	-	Small	Control	0.1	0.04898	0.0471	1.0396	68.4	1.000
Large	Treatment	4	-	Small	Control	4	0.01714	0.0471	0.3639	68.4	1.000
Large	Treatment	4	-	Small	Treatment	-0.1	0.00736	0.0471	0.1562	68.4	1.000
Large	Treatment	4	-	Small	Treatment	0.1	0.12373	0.0471	2.6263	68.4	1.000
Small	Control	-0.1	-	Large	Control	-0.1	0.00161	0.0504	0.0320	68.4	1.000
Small	Control	0.1	-	Large	Control	-0.1	0.02025	0.0504	0.4020	68.4	1.000
Small	Control	0.1	-	Large	Control	0.1	0.07091	0.0504	1.4080	68.4	1.000
Small	Control	0.1	-	Large	Treatment	-0.1	0.06188	0.0471	1.3134	68.4	1.000
Small	Control	0.1	-	Small	Control	-0.1	0.01864	0.0385	0.4835	579.0	1.000
Small	Control	0.1	-	Small	Treatment	-0.1	-0.04162	0.0504	-0.8264	68.4	1.000
Small	Control	24	-	Large	Control	-0.1	0.02846	0.0504	0.5651	68.4	1.000
Small	Control	24	-	Large	Control	0.1	0.07912	0.0504	1.5711	68.4	1.000
Small	Control	24	-	Large	Control	24	0.05298	0.0504	1.0520	68.4	1.000
Small	Control	24	-	Large	Control	4	0.02513	0.0504	0.4989	68.4	1.000
Small	Control	24	-	Large	Treatment	-0.1	0.07009	0.0471	1.4878	68.4	1.000
Small	Control	24	-	Large	Treatment	0.1	-0.06266	0.0471	-1.3301	68.4	1.000
Small	Control	24	-	Large	Treatment	4	-0.04077	0.0471	-0.8653	68.4	1.000
Small	Control	24	-	Small	Control	-0.1	0.02685	0.0385	0.6965	579.0	1.000
Small	Control	24	-	Small	Control	0.1	0.00821	0.0385	0.2130	579.0	1.000
Small	Control	24	-	Small	Control	4	-0.02362	0.0385	-0.6129	579.0	1.000
Small	Control	24	-	Small	Treatment	-0.1	-0.03341	0.0504	-0.6633	68.4	1.000
Small	Control	24	-	Small	Treatment	0.1	0.08296	0.0504	1.6473	68.4	1.000
Small	Control	24	-	Small	Treatment	4	-0.02177	0.0504	-0.4322	68.4	1.000
Small	Control	4	-	Large	Control	-0.1	0.05209	0.0504	1.0342	68.4	1.000
Small	Control	4	-	Large	Control	0.1	0.10275	0.0504	2.0401	68.4	1.000
Small	Control	4	-	Large	Control	4	0.04875	0.0504	0.9680	68.4	1.000
Small	Control	4	-	Large	Treatment	-0.1	0.09371	0.0471	1.9892	68.4	1.000
Small	Control	4	-	Large	Treatment	0.1	-0.03904	0.0471	-0.8286	68.4	1.000
Small	Control	4	-	Small	Control	-0.1	0.05047	0.0385	1.3094	579.0	1.000
Small	Control	4	-	Small	Control	0.1	0.03184	0.0385	0.8259	579.0	1.000
Small	Control	4	-	Small	Treatment	-0.1	-0.00978	0.0504	-0.1942	68.4	1.000
Small	Control	4	-	Small	Treatment	0.1	0.10659	0.0504	2.1164	68.4	1.000
Small	Treatment	-0.1	-	Large	Control	-0.1	0.06187	0.0504	1.2284	68.4	1.000
Small	Treatment	-0.1	-	Large	Treatment	-0.1	0.10350	0.0471	2.1969	68.4	1.000
Small	Treatment	-0.1	-	Small	Control	-0.1	0.06026	0.0504	1.1964	68.4	1.000
Small	Treatment	0.1	-	Large	Control	-0.1	-0.05450	0.0504	-1.0822	68.4	1.000
Small	Treatment	0.1	-	Large	Control	0.1	-0.00384	0.0504	-0.0762	68.4	1.000
Small	Treatment	0.1	-	Large	Treatment	-0.1	-0.01287	0.0471	-0.2732	68.4	1.000
Small	Treatment	0.1	-	Large	Treatment	0.1	-0.14562	0.0471	-3.0911	68.4	0.346
Small	Treatment	0.1	-	Small	Control	-0.1	-0.05611	0.0504	-1.1142	68.4	1.000
Small	Treatment	0.1	-	Small	Control	0.1	-0.07475	0.0504	-1.4842	68.4	1.000
Small	Treatment	0.1	-	Small	Treatment	-0.1	-0.11637	0.0385	-3.0190	579.0	0.318
Small	Treatment	24	-	Large	Control	-0.1	0.07404	0.0504	1.4701	68.4	1.000
Small	Treatment	24	-	Large	Control	0.1	0.12470	0.0504	2.4761	68.4	1.000
Small	Treatment	24	-	Large	Control	24	0.09856	0.0504	1.9571	68.4	1.000
Small	Treatment	24	-	Large	Control	4	0.07071	0.0504	1.4039	68.4	1.000
Small	Treatment	24	-	Large	Treatment	-0.1	0.11567	0.0471	2.4553	68.4	1.000
Small	Treatment	24	-	Large	Treatment	0.1	-0.01708	0.0471	-0.3626	68.4	1.000
Small	Treatment	24	-	Large	Treatment	24	0.01060	0.0471	0.2250	68.4	1.000
Small	Treatment	24	-	Large	Treatment	4	0.00481	0.0471	0.1022	68.4	1.000
Small	Treatment	24	-	Small	Control	-0.1	0.07243	0.0504	1.4381	68.4	1.000
Small	Treatment	24	-	Small	Control	0.1	0.05379	0.0504	1.0681	68.4	1.000
Small	Treatment	24	-	Small	Control	24	0.04558	0.0504	0.9050	68.4	1.000

Post Hoc Comparisons - Group Size * Treatment * Time Point

Comparison											
Group Size	Treatment	Time Point		Group Size	Treatment	Time Point	Difference	SE	t	df	Pbonferroni
Small	Treatment	24	-	Small	Control	4	0.02196	0.0504	0.4359	68.4	1.000
Small	Treatment	24	-	Small	Treatment	-0.1	0.01217	0.0385	0.3158	579.0	1.000
Small	Treatment	24	-	Small	Treatment	0.1	0.12854	0.0385	3.3348	579.0	0.109
Small	Treatment	24	-	Small	Treatment	4	0.02381	0.0385	0.6178	579.0	1.000
Small	Treatment	4	-	Large	Control	-0.1	0.05023	0.0504	0.9973	68.4	1.000
Small	Treatment	4	-	Large	Control	0.1	0.10089	0.0504	2.0032	68.4	1.000
Small	Treatment	4	-	Large	Control	4	0.04689	0.0504	0.9311	68.4	1.000
Small	Treatment	4	-	Large	Treatment	-0.1	0.09185	0.0471	1.9498	68.4	1.000
Small	Treatment	4	-	Large	Treatment	0.1	-0.04090	0.0471	-0.8681	68.4	1.000
Small	Treatment	4	-	Large	Treatment	4	-0.01900	0.0471	-0.4033	68.4	1.000
Small	Treatment	4	-	Small	Control	-0.1	0.04861	0.0504	0.9653	68.4	1.000
Small	Treatment	4	-	Small	Control	0.1	0.02998	0.0504	0.5952	68.4	1.000
Small	Treatment	4	-	Small	Control	4	-0.00186	0.0504	-0.0369	68.4	1.000
Small	Treatment	4	-	Small	Treatment	-0.1	-0.01164	0.0385	-0.3020	579.0	1.000
Small	Treatment	4	-	Small	Treatment	0.1	0.10473	0.0385	2.7169	579.0	0.814

Table S3. Readme file. Behavioral data was collected in McMaster University's Animal Behaviour Ecology Laboratory (ABEL) from February 29, 2019 to March 2, 2020. Video recordings were scored from March 13, 2019 to June 6, 2019. Tissue samples were collected March 3, 2019 and assays were conducted from June 11, 2019 to June 20. All the data for this paper was analyzed from June 27, 2019 to September 16, 2019.

The dataset (Dataset 1) is contained in an Excel worksheet organized by columns. The column labels (variables of interest) and how this data was scored are as follows:

Labels	Factor Values	Meaning
Tank Number_n	1-2, 4-13, 15-16, 18-19, 22, 24-31, 34	Tank ID
Group Size	Small, Large	Binary categorization of group size, with groups either being Small (containing 4 or fewer Helper Fish) or Large (containing 5 or greater Helper Fish).
Treatment	Treatment, Control	Binary categorization of treatment type.
Subject	Breeding Male, Breeding Female, Helpers	Fish class, being Breeding Male (the dominant male of the group), Breeding Female (the dominant female of the group) or Helpers (all of the remaining fish, collectively).
Observation Type	Pre 1, Pre 2, Post 1, Post 2, 4 Hours Post 1, 4 Hours Post 2, 24 Hours Post 1, 24 Hours Post 2	The time step of the observation. The time steps listed are: Pre 1 (recording occurred immediately before the first social perturbation), Pre 2 (recording occurred immediately before the second social perturbation), Post 1 (recording occurred immediately after the first social perturbation), Post 2 (recording occurred immediately after the second social perturbation), 4 Hours Post 1 (recording occurred 4 hours following the first social perturbation), 4 Hours Post 2 (recording occurred 4 hours following the second social perturbation), 24 Hours Post 1 (recording occurred 24 hours following the first social perturbation) and 24 Hours Post 2 (recording occurred 24 hours following the second social perturbation).
Male_ID	A letter/integer combination	A unique combination of a letter and number that identifies each male. The

		number indicates the tank the male started in at the beginning of the experiment.
Helper #_n	Range: 1-8	The number of helpers within the group during experimental treatments.
Trial #_n	1, 2	The observation block, being either 1 (associated with the first social perturbation) or 2 (associated with the second social perturbation).
Hours	-0.1, 0.1, 4, 24	The number of hours before or after the social perturbation the observation occurred, being -0.1 (immediately before the perturbation), 0.1 (immediately after the perturbation), 4 (4 hours after the perturbation) or 24 (24 hours after the perturbation).
Agg_dirac	Continuous integer	Aggressive acts by the focal fish toward another subject, including both other fish in the social group and its own reflection. Was not used in the calculation of Dominance Index.
Agg_dirac_nomirror	Continuous integer	Aggressive acts by the focal fish toward another fish. Excludes aggressive acts toward reflections. Was used in the calculation of Dominance Index.
Social_dirac	Continuous integer	Affiliative acts performed by the focal fish to another fish.
Sub_dirac	Continuous integer	Submissive acts by the focal fish toward another subject, including both other fish and reflections.
Agg_rec	Continuous integer	Aggressive acts received by the focal fish from another fish.
Social_rec	Continuous integer	Affiliative acts received by the focal fish from another fish.
Sub_rec	Continuous integer	Submissive acts received by the focal fish from another fish.
Self_Maintenance	Continuous integer	Personal maintenance behaviors performed by the fish, including the initiation of swimming, remaining still, yawning etc. Not used in any of the analysis.
Territorial Maintenance_n	Continuous integer	Behaviors performed by the focal fish in the maintenance of the group's territory.
Still Duration (s)	Continuous	The duration of time (in seconds) that the focal fish was still (no active locomotion). Does not include time when the fish was not visible to the observer. Was not recorded for helpers.

Swim Duration (s)	Continuous	The duration of time (in seconds) that the focal fish was actively swimming. Does not include time when the fish was not visible to the observer. Was not recorded for helpers.
Activity	Continuous	Calculated by dividing the total time the focal fish was observed swimming in an observation over the total time the fish was observed swimming or still: Swim Duration / (Swim Duration + Still Duration) Not relevant for helpers.
Dominance_Index	Continuous Integer	(Sum of aggressive acts given + sum of submissive acts received) – (sum of aggressive acts received + sum of submissive acts given) (Aubin-Horth et al., 2007) Does not include acts toward reflections.
Dominance per capita for helpers	Continuous	Only relevant for helpers. The dominance index divided by the number of helpers in the group.
Co-op per capita for helpers		Only relevant for helpers. The territorial maintenance actions divided by the number of helpers in the group.
Affiliation per capita for helpers		Only relevant for helpers. The affiliation index divided by the number of helpers in the group.