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Assessing the repeatability, robustness to disturbance, and parent–offspring colony resemblance of collective behavior

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Abstract

Groups of animals possess phenotypes such as collective behaviour, which may determine the fitness of group members. However, the stability and robustness to perturbations of collective phenotypes in natural conditions is not established. Furthermore, whether group phenotypes are transmitted from parent to offspring groups with fidelity is required for understanding how selection on group phenotypes contributes to evolution, but parent–offspring resemblance at the group level is rarely estimated. We evaluated the repeatability, robustness to perturbation and parent–offspring resemblance of collective foraging aggressiveness in colonies of the social spider *Anelosimus eximius*. Among-colony differences in foraging aggressiveness were consistent over time but changed if the colony was perturbed through the removal of individuals or via individuals' removal and subsequent return. Offspring and parent colony behaviour were correlated at the phenotypic level, but only once the offspring colony had settled after being translocated, and the correlation overlapped with zero at the among-colony level. The parent–offspring resemblance was not driven by a shared elevation but could be due to other environmental factors. The behaviour of offspring colonies in a common garden laboratory setting was not correlated with the behaviour of the parent colony nor with the same colony's behaviour once it was returned to the field. The phenotypes of groups represent a potentially important tier of biological organization, and assessing the stability and heritability of such phenotypes helps us better understand their role in evolution.

KEYWORDS
Anelosimus, behavioural state, collective behaviour, heritability, perturbation

1 | INTRODUCTION

Many organisms form groups (Ward & Webster, 2016). These aggregations can help individuals avoid predation, acquire resources, find mates and so on (Almberg et al., 2015; Bilde et al., 2007; Dobson, Viblanc, Arnaud, & Murie, 2012; Frank, 2007; Groenewoud et al., 2016). For

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many of these purposes, groups use collective behaviour, where individuals act in a co-ordinated or synchronized manner (Sumpter, 2006). Collective behaviours can depend on synergistic interactions, or the actions of a single "keystone individual" (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014; Pruitt & Keiser, 2014), and so cannot always be understood in terms of a simple sum of the actions of individuals, whereas groups can possess phenotypes that simply do not exist at the individual level, such as the level of cohesion in a flock or shoal (Farine,

Strandburg-Peshkin, Couzin, Berger-Wolf, & Crofoot, 2017; Parrish & Edelstein-Keshet, 1999). Group phenotypes are therefore a tier of biological organization that require direct study, both in terms of how they relate to selection and evolution at the individual level, as well as in and of themselves (Couzin, 2009).

Individual traits can range from being highly consistent within an individual to highly variable (Bell, Hankison, & Laskowski, 2009). An individual might retain its behaviour in spite of a disturbance, or it might find its behaviour changed as a result of a disturbance (Sih, Ferrari, & Harris, 2011; Tuomainen & Candolin, 2010). The same could be true of group phenotypes; the collective behaviour of groups may resist disturbances, or it may be altered by them (Flack, Girvan, Waal, & Krakauer, 2006; Flack, Krakauer, & Waal, 2005; Formica, Wood, Cook, & Brodie, 2016; Kubitza, Suhonen, & Vuorisalo, 2015; Smith et al., 2013). For instance, collective behaviours might be "self-organized," where individuals re-create the same group behaviour after disturbances by following the same set of interaction patterns that created the initial group behaviour (Bonabeau, Theraulaz, Deneubourg, Aron, & Camazine, 1997; Fisher & Pruitt, 2019; Fisher, West, Lomeli, Woodard, & Purcell, 2019). In contrast, groups might change their behaviour following disturbances, if they are shunted into different "states" following a disturbance (Doering, Scharf, Moeller, & Pruitt, 2018; Flack et al., 2006, 2005; Pruitt et al., 2018), or engage in non-linear interactions that give divergent trajectories, and so different group phenotypes, from a similar set of starting conditions (Cole, 1994; Fisher, Brachmann, & Burant, 2018; Honegger & de Bivort, 2018; May & Oster, 1976). However, the robustness of group phenotypes to disturbances is not well documented (but see: Flack et al., 2005, 2006; Formica et al., 2016; Kubitza et al., 2015; Smith et al., 2013).

If group phenotypes are resistant to disturbances and stable over time, then they can influence the survival and reproductive success of individuals within those groups (Keiser & Pruitt, 2014; Pruitt & Goodnight, 2014; Pruitt, Goodnight, & Riechert, 2017; Pruitt, McEwen, Cassidy, Najm, & Pinter-Wollman, 2019; Wray, Mattila, & Seeley, 2011). Stability in group phenotypes is important because it determines the degree to which they can be subject to natural selection (in a population of groups, if all group phenotypes vary widely these phenotypes cannot be associated with relative fitness). One of the most extreme forms of group

disturbance is group fission, whereby a subset of group members disperse or bud off to form a smaller, "offspring" group (Aviles, 1986; Vollrath, 1982). The collective behaviour of these offspring groups can be similar to that of their parent group and so exhibit a crude kind of collective or group-level heritability (Bienefeld & Pirchner, 1990; Pruitt et al., 2017, 2019). However, unlike individual-level traits (Houle, 1992), the heritability of group-level traits is not widely documented. This therefore makes it hard to judge how, if at all, group-level selection can contribute to evolution and adaptation (Gardner & Grafen, 2009; Queller & Strassmann, 2009; Wilson, 1997a; 1997b).

We therefore had two questions surrounding collective behaviour. First, is collective behaviour robust to disturbance? Second, is collective behaviour transmitted from parent group to offspring group in staged fission events? If both of these are true, then we might expect group phenotypes such as collective behaviours to play a more important role in evolution than is currently thought. We investigated these questions in a Neotropical social spider, *Anelosimus eximius* (Araneae: Theridiidae). *A. eximius* is classified as "nonterritorial permanent social" (Avilés, 1997), where individuals (sometimes numbering into the 10,000 s; Avilés, 1997) from overlapping generations live together in the same web structure and co-operate in web-building, prey capture and alloparental care (Avilés & Guevara, 2017; Avilés & Harwood, 2012; Avilés & Tufiño, 1998; Ebert, 1998; Pruitt & Avilés, 2017; Vollrath, 1986). This allows them to feed on larger prey than would be expected of a spider of their body size and to endure environments where related species with lower levels of sociality cannot (Avilés & Guevara, 2017; Fernandez-Fournier, Guevara, Hoffman, & Avilés, 2018; Guevara & Avilés, 2015). Once prey contacts the web, social spiders collectively rush to immobilize it. How quickly the colony responds to a potential prey item can be an important determinant of colony success, and so, this is the collective behaviour that we focus on here (hereafter "foraging aggressiveness"; Lichtenstein et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Data collection

Our study took place in June and July 2019, near Tena, Ecuador (Figure 1), under the Ecuadorian Ministry of the Environment permit no. 014-2019-IC-FLO-DNB/MA. We located colonies of *A. eximius* on roadsides, where they are relatively conspicuous on hedgerows, fences and in trees. Their webs are composed of a "basket" at the base, with a sheet and tangle capture web above (Yip, Powers, & Avilés, 2008). Once we found colonies, we marked their location and recorded GPS co-ordinates to allow us to re-locate them. We then recorded their elevation and measured the height, width and depth of the basket. We found 45 colonies that were suitable for our study at elevations between 398 and 1,146 m (see Table S1 for the elevation and volume of each colony), being within reach of an observer and located within a morning's drive of our laboratory. We tested these 45 colonies' foraging
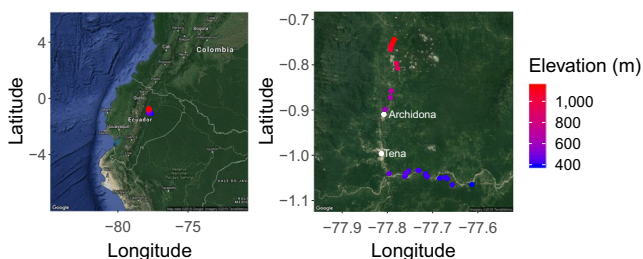

FIGURE 1 Maps showing the location of each of the *Anelosimus eximius* colonies in the study, with the elevation of the colony indicated by the colour (red = high elevation, blue = low elevation). In the right map, the towns of Tena and Archidona are indicated with white points

aggressiveness three times over 6 days (every other day). Our test for foraging aggressiveness was the colony's speed to attack a vibrating stimulus (Lichtenstein et al., 2019). We stimulated colonies to attack by touching a piece of wire fixed to a modified handheld vibratory device (8" Vibrating Jelly Dong, Top Cat Toys) to a small piece of leaf placed in the web. The leaf was always placed on the edge of the basket of the web, and we waited at least 60 s from the placement of the leaf before introducing the vibrations. The vibrations running through the leaf simulate a prey item caught in the web; assays similar to this are often used to estimate foraging aggressiveness in social (e.g. Grinsted, Pruitt, Settepani, & Bilde, 2013; Lichtenstein et al., 2019) and solitary (Dirienzo & Montiglio, 2016; Montiglio & DiRienzo, 2016) spiders. We timed the number of seconds from the start of the vibrations until a spider touched the leaf. Although the attack of a single spider was sufficient for us to halt the trial, we still consider the assay a measure of colony behaviour as typically multiple individuals (mean = 4.28, SD = 5.63) approached the stimulus, and more individuals approached when colonies attacked more quickly ($r = -.417$, $p < .001$). If the colony did not respond within 10 min, the score was set at 600 (2.3% of all trials). The latency to attack the stimulus has previously been shown to be a repeatable trait among-colonies over 4 days ($r = .26$) and, at high elevations, influences colony survival over a 11-month period (Lichtenstein et al., 2019), indicating it captures relatively stable aspects of colony collective behaviour. We typically carried out trials in the morning, but never before 9:00 and never after 17:00 (mean time = 11:37, min = 9:05, max = 16:45). These times correspond to when *A. eximius* individuals are typically not outside of retreats engaged in web-building and maintenance (the "active period"; Ebert, 1998; Pasquet & Krafft, 1992), and so, our assay should not conflate a quick response to prey due to many spiders being engaged web-building activity with a quick response due to high foraging aggressiveness.

After these three baseline collective aggressiveness tests, we assigned each colony randomly to one of three treatments. Fifteen colonies were "removal," 15 "procedural control" and 15 "control." For the removal and procedural control colonies, we returned three days after the 3rd behavioural test and removed a subset of spiders from each colony, placed them in sealed plastic boxes (190 × 190 × 90 mm) with sticks to support web-building and transported them back to our laboratory. Colonies of *A. eximius* at different elevations differ in their foraging aggression (Lichtenstein et al., 2019), so while moving our high elevation colonies (some over 1,000 m) to the laboratory (elevation = 432 m) represented a larger change in the environment for them than the lower elevation colonies, it was necessary to provide a common garden within which to assay foraging aggression. Individuals were collected either by gently shaking the web and caching spiders that dropped or by scooping a small bit of webbing into a large plastic box. We aimed to remove an approximately equal proportion of spiders from each colony, but since we did not have counts of the number of spiders in each colony, we judged this by colony volume, and so removed few spiders from small colonies, and more spiders from larger colonies. We could not identify the specific

instar of each individual removed, but instead counted the number of individuals that were large (>2 mm in body length), medium sized (<2 and >1 mm in body length) or small (<1 mm in body length), with size being estimated by eye (counts of spiders in each size class given in Table S1). We endeavoured not to destroy any vegetation the web was built on, in order to preserve the web's structure. Control colonies were left undisturbed.

Each subset of spiders that we collected was left undisturbed to acclimatize to captivity in their box for 2 days. Boxes had four airholes to provide oxygen, and spiders were provided a moist piece of paper on the 4th day of their captivity for hydration; they were not fed. We then tested the foraging aggressiveness of each of the 30 captive colonies three times over six days (every other day; the 1st laboratory test beginning five days after the last predisturbance test). We typically carried out trials in the morning, but never before 9:00 and never after 12:10 (mean time = 10:20, min = 9:10, max = 12:07). We modified the assay slightly to account for the new setting: we reduced the power of the vibrations to avoid over-amplification in the small box, and the wire was touched directly to the web rather than to a small leaf. These laboratory assays were used to assess the resemblance of parent and offspring colonies in a common garden environment. Although we might expect behaviour in the laboratory to differ substantially from that in the field due to the lack of all natural cues (but see: Boon, Réale, & Boutin, 2008; Fisher, James, Rodriguez-Munoz, & Tregenza, 2015; Herborn et al., 2010; Yuen, Pillay, Heinrichs, Schoepf, & Schradin, 2016), we might still expect the ranking of colonies in terms of their foraging aggression to be similar in both the laboratory and in the field. In this case, a positive correlation would be expected.

Following their 3rd test (on the same day), the spiders from procedural control colonies were placed directly back into their source (parental) colony. The colonies in this treatment group therefore lost no spiders but experienced the physical disturbance of the sampling event. Spiders from the removal treatment were placed in vegetation similar to what the parent colony had built its web on, but 5–10 m away from the parent colony. This was designed to mimic the fission of a colony and the foundation of a new colony by a subset of individuals (sociotomy), which occurs naturally in *A. eximius* as colonies grow in size (Avilés, 1997; Venticinque, Fowler, & Silva, 1993; Vollrath, 1982). These "bud colonies" were used to assess the heritability of colony behaviours when in the same environment as their parent colony. At this point, we discovered that eight of the parent colonies had been destroyed by workers clearing roadsides. Two of these colonies were in the procedural control group, but we could not return the previously removed spiders to a now destroyed colony, so we placed these spiders into vegetation 5–10 m away as bud colonies.

Two days after returning them to the wild, we tested the collective aggressiveness of each surviving parent colony ($n = 37$) and each bud colony three times over six days (every other day) using the same method as before. We typically carried out trials in the morning, but never before 9:00 and never after 13:05 (mean time = 10:35, min = 9:09, max = 13:02). In three instances, the bud

colony was completely abandoned, leaving 14 bud colonies (including the additional two colonies that were originally part of the procedural control group) to assay for foraging aggressiveness. To evaluate the robustness of *A. eximius* colonies to disturbance, we tested for a correlation between parent colonies' predisturbance and post-disturbance behaviours. We evaluated transmission of aggressiveness from parent to offspring group by testing for a correlation between the predisturbance behaviour of parent colonies and the behaviour of bud colonies in a common garden setting (the laboratory) and a natural setting (the bud colony behaviours). During the three tests of the bud colony foraging aggressiveness, we observed the bud colonies frequently changing position and orientation in the vegetation. We thought it was likely that there was an initial "settling" phase after returning the bud colonies to the wild from captivity. Therefore, starting eight days after their 3rd test, we tested each bud colony another three times over six days (every other day). As before, we typically did this in the morning, but never before 9:10

and never after 12:45 (mean = 10:18, min = 9:12, max = 12:42). This procedure was meant to capture bud colony behaviour following a settlement period ("settled bud behaviour," the initial three tests hereafter being referred to as "initial bud behaviour"). A schematic outlining the sampling regime for the study is shown in Figure 2.

2.2 | Data analysis

To assess the stability of colony behaviour over time in face of the disturbance, we initially estimated the phenotypic correlation (Pearson's correlations in all cases) between the log of predisturbance foraging aggressiveness and the log of post-disturbance foraging aggressiveness, with a colony's first measure predisturbance paired with its first measured post-disturbance, and so on. However, this does not estimate the among-colony correlation between predisturbance and post-disturbance behaviours; instead,
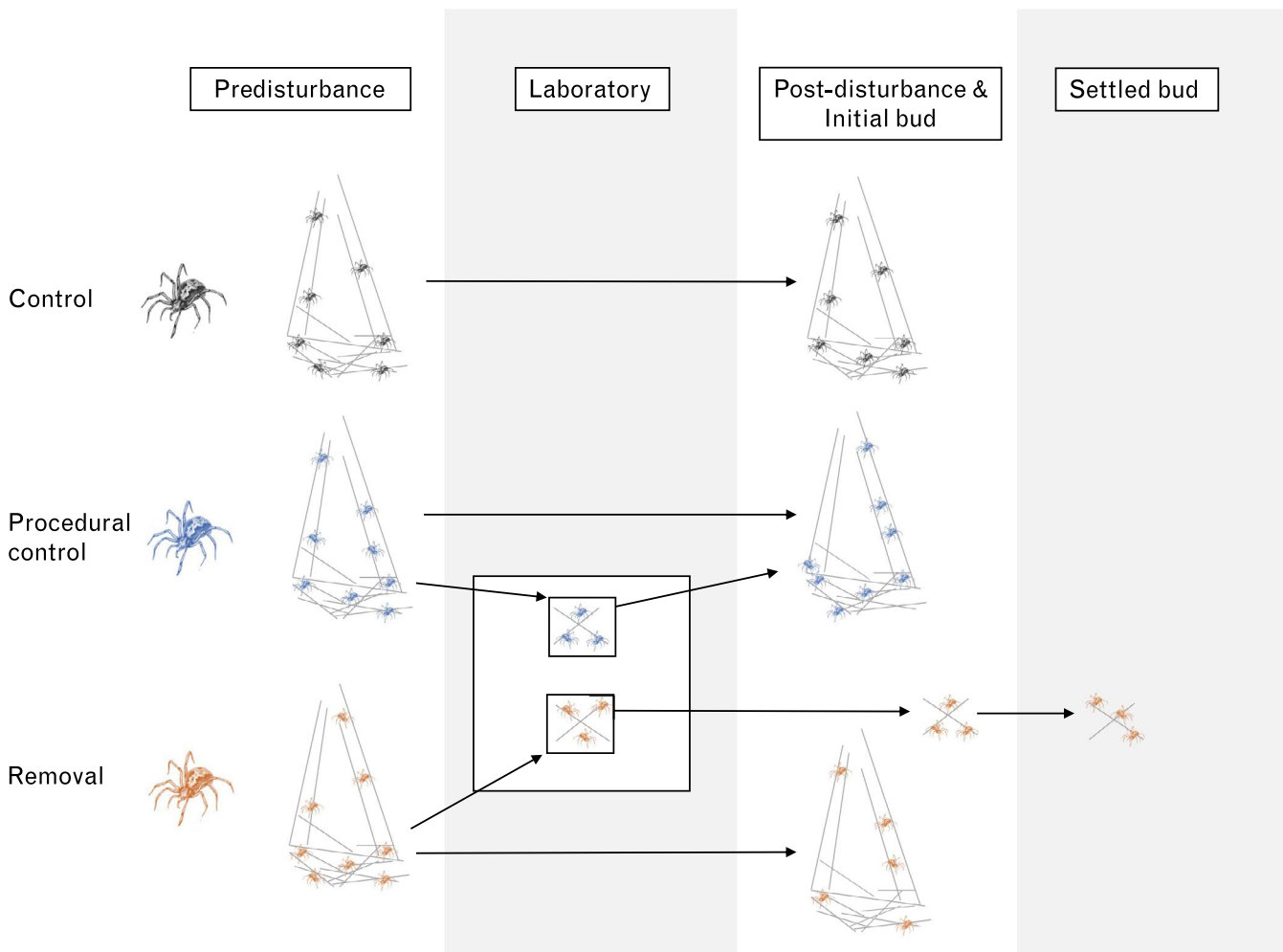

FIGURE 2 A schematic demonstrating our study design. In the predisturbance phase, 45 colonies were tested three times over 6 days for foraging aggressiveness. For two-thirds of these colonies (in the "removal" and "procedural control" groups), spiders were then removed to the laboratory, where they were tested three times over 6 days for foraging aggressiveness. Following this, spiders in the procedural control groups were returned to their original colony, whereas spiders in the removal groups were placed near the original colony as "bud colonies." We then tested all original colonies and all bud colonies three times over 6 days. Following this, we tested each bud colony another three times over 6 days to measure "settled" behaviour

it conflates within- and among-subject variation (analogous to the "individual gambit"; Brommer, 2013; Dingemanse & Dochtermann, 2013). To directly estimate the among-colony correlation between predisturbance and post-disturbance foraging aggressiveness, we built multivariate models in the R package MCMCglmm (Hadfield, 2010) with the logs of predisturbance foraging aggressiveness and post-disturbance foraging aggressiveness as response variables. We entered "NA" for the post-disturbance trials for colonies that had been destroyed. This allowed us to include their scores for the predisturbance trials in the model, which should improve the estimate of the among-colony variance in predisturbance foraging aggressiveness. We estimated the among-colony variances and covariance between predisturbance and post-disturbance foraging aggressiveness, the among-date variances for these traits (but no covariance as the two behaviours were never tested on the same day) and the residual variances for each behaviour (but no covariance as the two behaviours were never measured at the same time). We included the log of colony basket volume (height*depth*width, mean = 206,977 cm^3, range = 1,008 to 2,025,600 cm^3), mean centred and scaled to a variance of one, and the trial number (1–3), mean centred, as fixed effects for each behaviour. This was done in case colony foraging aggressiveness covaried with size (Pruitt, Iturralde, Avilés, & Riechert, 2011; Yip et al., 2008) and in case the colonies changed their behaviour over time.

To test whether the disturbed colonies changed their behaviour more than the control colonies, we estimated the raw phenotypic correlations for each of the three treatment groups. We then we fitted the multivariate model described above to each of the three treatment groups separately and compared the magnitude and distributions of the among-colony correlations. If the control group had a stronger correlation between predisturbance and post-disturbance foraging aggressiveness than the removal or the procedural control groups, we could conclude that the disturbance disrupted colony collective behaviour.

To assess the resemblance of collective behaviour between parent and offspring colonies, we first estimated the phenotypic correlations between log-transformed predisturbance foraging aggressiveness, log-transformed laboratory foraging aggressiveness and log-transformed bud colony foraging aggressiveness, associating the first predisturbance trial, the first laboratory trial and the first bud trial and so on. However, phenotypic correlations such as those based on only a single measure of parents and offspring (e.g. Pruitt et al., 2017) or those based on averages of parent and offspring colony traits (e.g. Pruitt et al., 2019) conflate among- and within-subject covariance, when only the former is relevant for assessing whether more aggressive parent colonies have more aggressive offspring colonies (Brommer, 2013; Dingemanse & Dochtermann, 2013; see also Niemela & Dingemanse, 2018 for a discussion of the issues with using a single measure of behaviour to estimate covariances). To estimate the among-colony correlation, we built multivariate models in MCMCglmm, with the logs of predisturbance foraging aggressiveness, laboratory foraging aggressiveness and bud foraging aggressiveness as response

variables. We estimated the among-colony variances and covariance between these three traits. This is analogous to a parent–offspring regression, which overestimates heritability compared to estimates from an "animal model" (Kruuk, 2004). We did not have a colony-level pedigree nor could we calculate the relatedness among colonies by some other means. Therefore, the parent–offspring covariance we estimate here should be taken as an upper limit for half the additive genetic variance in the trait.

We also estimated among-date variances for each behaviour (but no covariance as the behaviours were never tested on the same day) and the residual variance for each behaviour (but no covariance as the behaviours were never measured at the same time). We included the log of colony volume as a fixed effect for predisturbance behaviour, and the number of adults removed from the colony and so tested in both the laboratory and as a bud colony (summing large and medium spiders, so any greater than 1 mm in body length; mean = 44.3, range = 4–124) as fixed effects for laboratory and bud behaviour. This was done in case colony size impacted foraging aggressiveness. These fixed effects were scaled to a mean of zero and a variance of one. We also include trial number (1–3) as a fixed effect, mean centred, in case the colonies changed their behaviour over time.

We estimated the raw phenotypic correlations once with the 1st-3rd tests on the bud colonies (initial bud behaviour) and once with the 4th-6th tests (settled bud behaviour). We also re-fitted the multivariate model using the 4th-6th tests instead of the 1st-3rd tests. If collective behaviour was inherited from parent colony to offspring colony, we expected a positive among-colony correlation between the predisturbance and bud behaviours. If behaviour in the laboratory reflects behaviour in the field, then there would also be a positive among-colony correlation between the predisturbance and laboratory foraging aggressiveness. Further, if the 4th-6th tests on the bud colonies reflect settled behaviour, we expected the among-colony correlation between predisturbance foraging aggressiveness and the settled bud foraging aggressiveness to be stronger than the correlation between predisturbance foraging aggressiveness and the initial bud foraging aggressiveness.

For all multivariate models, we used a Gaussian error structure for each response variable, 550,000 iterations, a burn in of 50,000 and a thinning interval of 100. Priors were set to be flat and relatively uninformative, with 70% of the phenotypic variance for the logged values of each trait placed on the residual variance, 20% on the among-colony variance and 10% on the among-date variance (following: Brommer, 2017). All statistics were performed in the R software (R Development Core Team, 2016).

3 | RESULTS

3.1 | Robustness to disturbance

In the predisturbance trials across all treatments, the majority of colonies responded to the stimulus and attacked (131/135 trials, 97%)
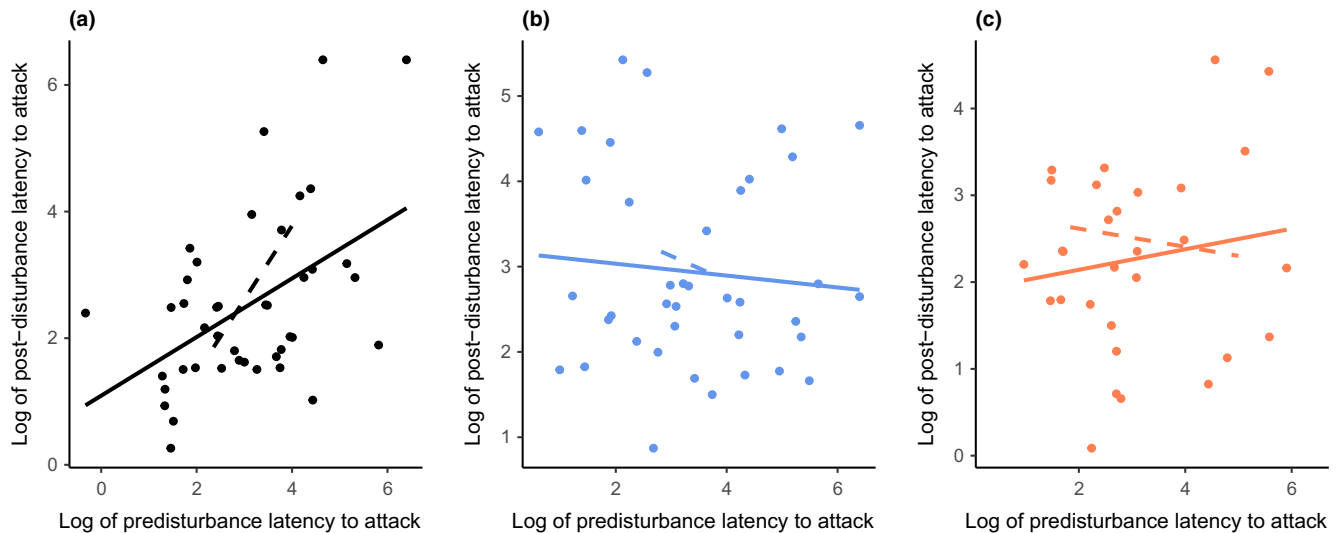
FIGURE 3 The relationship between the logs of predisturbance and post-disturbance foraging aggressiveness in the three treatment groups ((a) control, (b) procedural control, (c) removal). Solid lines show the phenotypic correlations, whereas dashed lines show the estimated among-colony correlations from the multivariate model
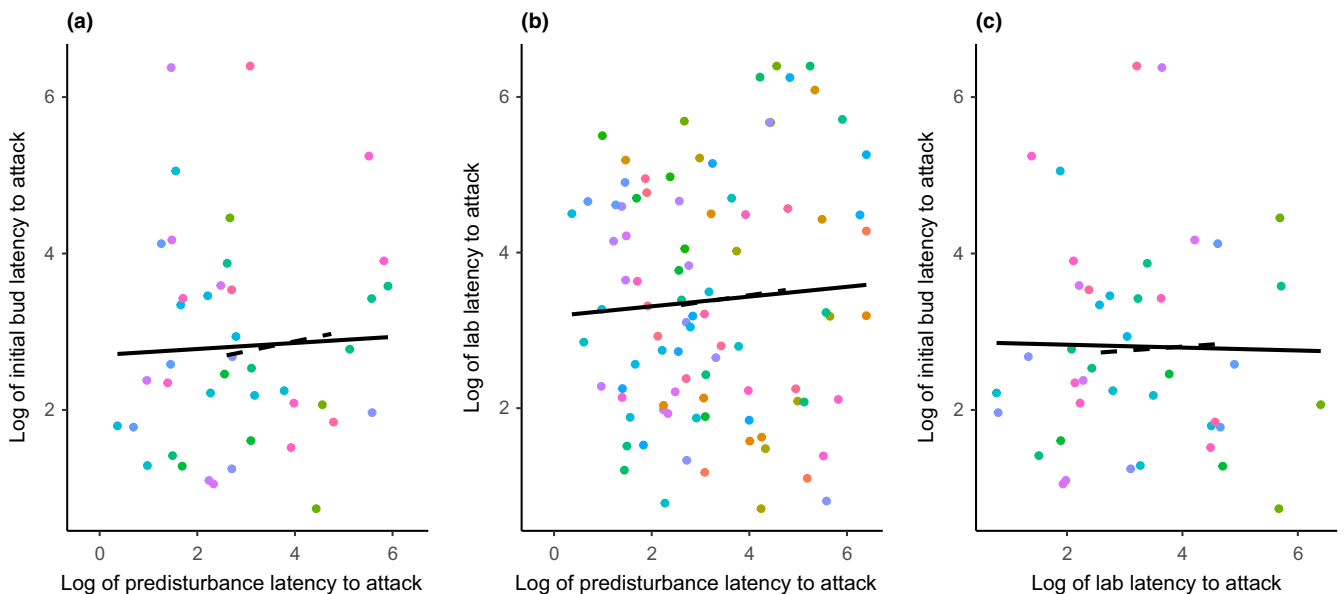

FIGURE 4 The relationship between (a) predisturbance foraging aggressiveness and laboratory foraging aggressiveness; (b) predisturbance foraging aggressiveness and initial bud foraging aggressiveness; and (c) laboratory foraging aggressiveness and initial bud foraging aggressiveness. Point colours indicate different colonies. Solid lines show the phenotypic correlations, whereas the dashed lines show the estimated among-colony correlations from the multivariate model

with the mean attack speed being 54.98 s. Predisturbance foraging aggressiveness showed consistent differences among colonies, (repeatability [r] of logged values = 0.152, credible intervals [CIs] = 0.60 to 0.348). The majority of colonies attacked in the post-disturbance trials (109/111 trials, 98%), with a mean attack speed of 25.41 s. Post-disturbance foraging aggressiveness was also consistently different among-colonies (r = .376, CIs = 0.158–0.555). We therefore conclude that each colony is in a relatively stable behavioural "state" of a particular level of foraging aggressiveness during the 6 days we measured them. The phenotypic correlation between predisturbance and post-disturbance foraging aggressiveness was significant and positive

(r = .217, t = 2.321, df = 109, p = .022). At the among-colony level, predisturbance foraging aggressiveness positively covaried with post-disturbance foraging aggressiveness, although the 95% CIs of the among-colony covariance overlapped zero (covariance mode = 0.167, CIs = −0.103 to 0.598, correlation mode = 0.547, CIs = −0.124 to 0.850). Full model results are provided in the supplementary materials (Table S2). These findings suggest that colony collective behaviour is stable over time.

The phenotypic correlation between predisturbance and post-disturbance foraging aggressiveness in the control group was quite strong and positive (Figure 3a, r = .482, t = 3.483, df = 40,

p = .001), absent in the procedural control group (Figure 3b, r = −.093, t = −0.567, df = 37, p = .574) and weakly positive but nonsignificant in the removal group (Figure 3c, r = .151, t = 0.809, df = 28, p = .425). At the among-colony level, for the control group, there was a positive correlation between predisturbance and post-disturbance foraging aggressiveness (Figure 3a, covariance mode = 0.245, CIs = −0.240 to 1.080, correlation mode = 0.701, CIs = −0.177 to 0.953), no correlation at all in the procedural control group (Figure 3b, covariance mode = −0.001, CIs = −0.621 to 0.464, correlation mode = 0.051, CIs = −0.773 to 0.726) and a weak positive correlation in the removal group (Figure 3c, covariance mode = 0.094, CIs = −0.547 to 1.086, correlation mode = 0.637, CIs = −0.595 to 0.925). Note that the CIs of all of these correlations overlap zero and hence each other. See Tables S3–S5 in the supplementary materials for full model results. Among-colony correlations therefore largely matched the phenotypic correlations (Figure 3a–c). These results collectively convey that perturbing colonies by removing individuals disrupted colony collective behaviour, especially if the individuals were subsequently returned.

3.2 | Transmission of collective behaviour

In the laboratory assays, colonies almost always attacked the stimulus (41/42 trials, 98%) with a mean attacked speed of 73.08 s. Colonies showed consistent differences in foraging aggressiveness in the laboratory (r = .282, CIs = 0.080 to 0.472). Of the bud colonies that could be tested, the vast majority attacked the stimulus (41/42 trials, 98%), with a mean attack speed of 41.07 s. Bud colonies showed a small amount of consistent differences in the initial three measures of foraging aggressiveness (r = .082, CIs = 0.024 to 0.332). There was no phenotypic correlation between predisturbance foraging aggressiveness and initial bud foraging aggressiveness (Figure 4a, r = .043, t = 0.272, df = 40, p = .787) or laboratory foraging aggressiveness (Figure 4b, r = .065, t = 0.610, df = 88, p = .543). Laboratory and initial bud behaviour were also not correlated (Figure 4c, r = −.019, t = −0.120, df = 40, p = .905). Correlations were also absent at the among-colony level (predisturbance and initial bud foraging aggressiveness: Figure 4a, covariance mode = 0.042, CIs = −0.314 to 0.502, correlation mode = 0.143, CIs = −0.553 to 0.814; predisturbance and laboratory foraging aggressiveness: Figure 4b, covariance mode = 0.004, CIs = −0.342 to 0.431, correlation mode = 0.133, CIs = −0.504 to 0.651; laboratory and initial bud foraging aggressiveness: Figure4c, covariance mode = 0.008, CIs = −0.462 to 0.560, correlation mode = 0.386, CIs = −0.631 to 0.779). Full model results are given in the supplementary materials (Table S6).

Settled bud colonies were also likely to attack the stimulus (41/42 trials, 98%), with a mean attack speed on 31.87 s. Settled bud colonies showed consistent differences among-colonies in foraging aggressiveness (r = .161, CIs = 0.044 to 0.464). There was a phenotypic correlation between settled bud behaviour and predisturbance foraging aggressiveness (Figure 5a, r = .464, t = 3.317, df = 40, p = .002), but not between settled bud behaviour and laboratory foraging aggressiveness

(Figure 5b, r = −.117, t = −0.743, df = 40, p = .462). At the among-colony level, settled bud foraging aggressiveness was positively correlated with predisturbance foraging aggressiveness, although the 95% CIs overlapped zero (Figure 5a, covariance mode = 0.136, CIs = −0.214 to 0.696, correlation mode = 0.576, CIs = −0.269 to 0.896). Laboratory foraging aggressiveness was not correlated with settled bud foraging aggressiveness (Figure 5b, covariance mode = 0.005, CIs = −0.534 to 0.549, correlation mode = 0.133, CIs = −0.675 to 0.736). Full model results are given in the supplementary materials (Table S7). Therefore, as for the robustness to disturbance, phenotypic correlations matched the among-colony correlations. These results suggest that parent and offspring colony collective behaviours can resemble each other, but only once the offspring colony had settled into an environment close to that of the parental colony's, and it remains uncertain whether this relationship exists at the among-colony level.

The volume of the colony's basket, number of adults and trial number did not influence foraging aggressiveness in any of the models. There was some variation among days in foraging aggression, see Tables S2–S8 for estimates.

4 | DISCUSSION

Organisms in groups often possess collective behaviours, which can be subject to selection. How robust these collective behaviours are to disturbance, and whether they are transmitted from parent groups to offspring groups, is, however, not well known. Here, we show that the foraging aggressiveness of *A. eximius* colonies is consistent over a period of several weeks. Presumably, it is consistent for even longer than this, given that at high elevations foraging aggressiveness can influence colony survival over many months (Lichtenstein et al., 2019). Yet, colony behaviour is not robust to perturbation, especially if individuals are removed from the colony and then returned. We further found that bud colonies
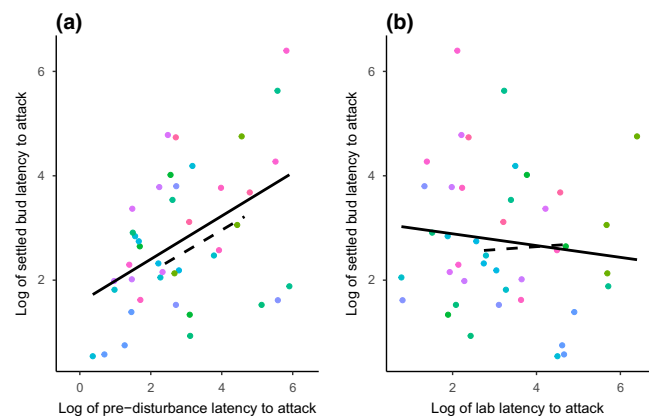

FIGURE 5 The relationship between (a) predisturbance foraging aggressiveness and settled bud foraging aggressiveness and (b) laboratory foraging aggressiveness and settled bud foraging aggressiveness. Point colours indicate different colonies. Solid lines show the phenotypic correlations, whereas the dashed lines show the estimated among-colony correlations

had collective behaviour that resembled that of their parent colony, but this was only apparent once the bud colony had spent over a week settling after the translocation and was not apparent when comparing laboratory measures of the bud colony with the parent colony.

First, we note here that, although all the patterns we detected in the study were qualitatively the same at the among-colony level as at the phenotypic level, the 95% credible intervals of all among-colony correlations overlapped zero. From inspection of the correlation coefficients (see also Figures 3, 4 and 5), we can see the among-colony correlations are often stronger than the phenotypic correlations. Therefore, the overlap with zero is likely due to high uncertainty, probably due to our study using fewer than 50 colonies, and fewer than 20 colonies in each treatment group, rather than a small effect size. We therefore consider the results likely to represent meaningful biological trends rather than statistical error, but uncertainty is clearly high, and therefore, caution should be taken when interpreting the among-colony correlations.

4.1 | Collective behaviour is vulnerable to disturbance

There were consistent differences among colonies in both predisturbance and post-disturbance behaviour, but no covariance between predisturbance and post-disturbance behaviours in the procedural control and removal treatment groups. This suggests that foraging aggressiveness represents a semi-stable state that a colony is in, but that the colony is shifted to a different state by perturbations, as colonies did not retain the same level of foraging aggressiveness when individuals were removed or when the colony was disturbed by the removal and then return of individuals. Discussing populations or ecosystems as "systems" that can exist in different states has a long history in ecology (May, 1974; Solé & Goodwin, 2000). Referring to social groups in this way is less common, but interest in the utility of this viewpoint is growing (Doering et al., 2018; Flack et al., 2006, 2005; Pruitt et al., 2018). Social systems have previously been shown to be vulnerable to shifts from calm to antagonistic states due to the removal of key individuals (in pigtailed macaques, *Macaca nemestrina*; Flack et al., 2005; Flack et al., 2006) or due to gradual heating (in a subsocial spider, *A. studiosus*; Doering et al., 2018). Meanwhile, simulation studies based on killer whale (*Orcinus orca*) and Columbian ground squirrel (*Spermophilus columbianus*) social groups show that groups are quickly fragmented by the removal of key individuals (Manno, 2008; Williams & Lusseau, 2006). Here, we have found that the removal of individuals combined with a physical disturbance to the colony causes the colony to shift from one state of foraging aggression to another, although we did not observe a general increase in aggression due to the perturbations. In fact, mean foraging aggressiveness was equal in the control and removal treatment groups, and lower (longer latencies) in the procedural control group. We concluded this based on comparing the intercepts for

post-disturbance foraging aggressiveness between the models for each treatment (although note that the 95% credible intervals overlapped in all cases, see Tables S3–S5). Instead, we have observed that a colony adopts a different, yet still repeatable, behaviour to what it displayed before the disturbance.

As spider colonies did not return to their original foraging aggressiveness after the disturbance, consistent differences in behaviour among-colonies probably do not rely on some underlying stable trait of the colony (as is suggested for "pace of life syndrome" hypotheses for consistent among-individual differences in behaviour; Réale et al., 2010). Instead, consistent differences among colonies may depend on social interactions that generate positive feedback loops that cause colonies to diverge in behaviour (e.g. Luttbeg & Sih, 2010). Such multiplicative interactions can give systems that are highly sensitive to initial conditions and hence give variable trajectories and final states (Boyce, 1992; Cole, 1994; Hastings, Hom, Ellner, Turchin, & Godfray, 1993). Therefore, following the perturbation, *A. eximius* colonies may engage in interactions that, despite being deterministic and so giving rise to consistent behaviour, nevertheless follow divergent trajectories and so do not give the same behavioural trait as the colony previously possessed (Fisher et al., 2018). Interactions between individual *A. eximius* within the colony that catalyse increased aggression could give this dynamic, whereas interactions between the whole colony and its environment might also generate sufficient feedback. Currently, our understanding of the development of *A. eximius* colony collective behaviour is insufficient to allow us to infer the relative contributions of these two possibilities. However, social network analysis on the distantly related social spider *Stegodypus dumicola* hint that positive feedback within colonies can cause the accentuation of individual differences within groups (Hunt et al., 2018), raising the possibility something similar could happen in *A. eximius*.

Removing individuals and then adding them back to the colony (as occurred in the procedural control group) completely removed any relationship between predisturbance and post-disturbance foraging aggressiveness. This suggests that removing individuals for a time and then returning them destabilizes collective behaviour much more than simply removing them. The returning spiders may not have been recognized by their old colony-mates, and a period of antagonism may have disrupted colony behaviour. There is mixed evidence that social and subsocial spiders discriminate between kin and nonkin (Beavis, Rowell, & Evans, 2007; Bilde & Lubin, 2001; Evans, 1999; Grinsted, Bilde, & d'Ettorre, 2011; Schneider & Bilde, 2008). However, *A. eximius* is known to accept intruders from different colonies as well as from the same colony (Pasquet, Trabalon, Bagnères, & Leborgne, 1997), suggesting there would have been limited antagonism towards the returning spiders. Instead, Pasquet et al., 1997) observed that the presence of an intruder increases the nearest neighbour distance within a colony. This change could then influence collective foraging aggressiveness. For now, we propose that the especially destabilized foraging behaviour of these colonies stems from their effectively experiencing two social disturbance as opposed to just one: having both lost a subset of group members and regained them, regardless of the familiarity of these group members.

4.2 | Settled offspring colonies resemble their parent colony, but only at the phenotypic level

Parent colony behaviour (predisturbance) only covaried with bud colony behaviour once the bud colony had settled, and only at the phenotypic level, the among-colony correlation still overlapped zero. The suggestion of a correlation implies that a group phenotype can be transmitted from parent to offspring colonies, like individual behaviours often are, but our uncertainty regarding this conclusion is high. The trend here was only apparent over a week after the bud colony was been returned to the wild, suggesting there is an initial settling period is necessary before the bud colony regains the collective behaviour its parent colony showed. Further, parent colony foraging aggressiveness did not covary with laboratory foraging aggressiveness. Behaviour in the laboratory could represent a different trait to behaviour in the wild, perhaps owing to colonies' residing in completely different environments. Therefore, it could be that bud colonies being permitted to reassume a shared environment that drove the phenotypic correlation between parent colonies and bud colonies (Kruuk & Hadfield, 2007). Such a phenomenon often occurs at the individual level in nature. For example, the heritability of laying date between mother and daughter great tits (*Parus major*) that nested near each other dropped from 0.40 to 0.15 when spatial autocorrelation was corrected for (Van Der Jeugd & McCleery, 2002). If a similar spatial autocorrelation drove the similar of parent and offspring colonies in our study, then foraging aggressiveness might not actually be transmitted between parent and offspring groups.

To evaluate the possible influence of a shared environment, we can identify and control for an environmental variable that could drive such a parent–offspring resemblance (Kruuk & Hadfield, 2007). Foraging aggressiveness in *A. eximius* decreases at higher elevations (Lichtenstein et al., 2019), and our study included colonies from 398 to 1,146 m above sea level (Figure 1). We tested whether it was elevation that drove the parent–offspring correlation by re-fitting the model for predisturbance, laboratory and settled bud foraging aggressiveness with the elevation of the colony (mean centred and scaled to a variance of one) as a fixed effect. In this model, predisturbance foraging aggression was lower (latencies tended to be longer) at higher elevations, although the credible intervals for the effect overlapped zero (fixed effect mode = 0.392, CIs = −0.059 to 0.836), but settled bud foraging aggressiveness did not change with elevation (fixed effect mode = 0.034, CIs = −1.001 to 1.261). Behaviour in the laboratory was also not influenced by the original elevation of the parent colony (fixed effect mode = −0.024, CIs = −0.614 to 0.459). In this model, the relationship between predisturbance and settled bud foraging aggressiveness was roughly the same as in the model without elevation (covariance mode = 0.119, CIs = −0.212 to 0.715, correlation mode = 0.583, CIs = −0.283 to 0.892). This therefore suggests that sharing the same elevation was not driving the similarity between parent and offspring colonies. However, it is possible that other environmental variables underpin the resemblance.

The outcome of selection on collective behaviour is quite different if collective behaviour is determined by an environmental variable (other than elevation) versus directly transmitted quality of the parent

colony. Relatedness within *A. eximius* colonies is typically very high (average *r* = .92 across four populations in Suriname, although *r* was estimated as .18 based on two nearby colonies at a site in Panama; Smith & Hagen, 1996), and so, selection at the colony level could be expected to give adaptation at the colony-level (Gardner & Grafen, 2009; Queller & Strassmann, 2009). Selection on group traits is used in animal and plant breeding to maximize the evolution of productivity traits. For example, selection on average body mass in groups of related Japanese quail (*Coturnix japonica*) lead to the evolution of heavier birds (Muir, Bijma, & Schinckel, 2013). Evidence that group adaptation occurs in the wild is however difficult to detect.

If collective behaviour is determined by the environment, then selection will most likely favour colonies that best match their behaviour to the environment. In this case, changes to a population's mean behaviour across generations are more likely to reflect changes in habitat availabilities or selection acting on some aspect of colonies' habitat preferences or dispersal abilities. In contrast, if foraging aggressiveness is genuinely directly passed from parent colony to offspring colony, and given at high elevations we can observe selection against high foraging aggression (Lichtenstein et al., 2019), then we might expect mean aggression at high elevations to decrease across generations by selection acting directly on colony behaviour. However, the parent–offspring colony resemblance was only different from zero at the phenotypic level, not the among-colony level, and so even if not due to a shared environment may not influence evolutionary change. More estimates of trait heritability in different taxa at the level of colonies and groups are required before we can assess how this level of biological organization can contribute to evolutionary change.

5 | CONCLUSIONS

In summary, we found that the foraging aggressiveness of *A. eximius* colonies is relatively stable over time but can be disrupted by perturbations. Returning individuals to their source colony disrupts a colony's collective foraging even more than simply removing individuals from a colony. Offspring colonies have collective behaviour that may resemble that of their parent colony, and this does not appear to be driven by a shared elevation. Instead, other forces like shared microhabitat preferences or the direct transmission of colony interaction rules, genetically determined behaviours, or plastic states (e.g., hunger levels, aggression levels) may drive resemblance of parent and offspring colonies. Appreciating that groups possess behavioural states, and that these states are influenced by external perturbations yet still may be passed from parent group to offspring group, should help us understand the role of group phenotypes in ecological and evolutionary processes.

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CONFLICT OF INTEREST

We have no conflicts of interest.

AUTHOR CONTRIBUTIONS

DNF, JLLL and JNP designed the study. JY acquired the permits. DNF, JLLL and RCP collected the data. DNF analysed the data and drafted the manuscript. All authors contributed to revisions of the manuscript and approved the final version.

DATA AVAILABILITY STATEMENT

All data and R code used for the analysis are available at: https://doi.org/10.5061/dryad.fn2z34tq4

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.