Ants work harder during consensus decision-making in small groups

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Individuals derive many benefits from being social, one of which is improved accuracy of decision-making, the so-called ‘wisdom of the crowds’ effect. This advantage arises because larger groups can pool information from more individuals. At present, limited empirical data indicate that larger groups outperform smaller ones during consensus decision-making in human and non-human animals. Inaccurate decisions can lead to significant costs, and we might therefore expect individuals in small groups to employ mechanisms to compensate for the lack of numbers. Small groups may be able to maintain decision accuracy if individuals are better informed than those in larger groups and/or by increasing the proportion of the group involved in collective decision-making relative to larger groups. In this study, we use interactive computer vision software to investigate individual contributions to consensus decision-making during house-hunting in different sized groups of the ant Myrmecina nipponica. We show that individuals in small colonies invest greater effort in the consensus decision process than those in large colonies and should be better informed as a result. This may act to ameliorate the limitations of group size, but could leave smaller groups more susceptible to additional stresses.

1. Introduction

Animals benefit in a variety of ways from being social, but must overcome challenges associated with coordinating group members during collective actions [1,2]. During tasks such as collective movements, groups must reach a consensus over which action to pursue if group integrity is to be maintained [1,3–6]. These decisions may be shared, with all group members contributing to the outcome, or unshared, with a distinct leader always initiating the decision [7]. In a wide range of animals including fish [8], some primates [5] and insects [9,10], decisions are shared among a variable proportion of the group, and a group-level consensus manifests as an emergent product of the combined actions of multiple individuals [1,4]. Shared decisions allow information to be pooled, and this ‘wisdom of the crowds’ effect has long been recognized as a means by which groups can make more accurate decisions than individuals [3,11–16]. Group size varies markedly between and within animal societies, however, raising the question of how small groups perform relative to large groups, and how investment in decision-making varies with group size. While modelling studies predict larger groups will outperform smaller ones during decision-making, there are few empirical studies to support this, and fewer still that shed any light on how this benefit is achieved at the individual level [17–19].

During consensus decision-making, individuals with information regarding a possible course of action advertise their preference by ‘voting’ through a range of means designed to recruit other group members. This voting behaviour is exemplified by the waggle-dance of honeybees [10], but includes chemical trails [20], vocalizations [21], posturing [5] and a range of other means [22–24]. These votes are mimetically reinforced by other group members or countered by votes for alternative options, though eventually one option emerges as the one favoured by the majority. The response to this feedback is often step-like, such that the propensity for an individual to perform an action increases markedly once a threshold number of individuals, a quorum, is already performing that action [6]. Quorum decisions are a widespread and effective means of collective decision-making.
[4,6] and can be tuned to environmental conditions to emphasize decision accuracy or speed [25]. Consensus decisions are predicted to be more accurate in larger groups because more individuals can collect more information regarding the environment per unit time and are better able to process this information [6,26,27]. However, empirical data demonstrate that in some cases the proportion of the group involved in decision-making may be quite low (e.g. only around 5% of the colony act as scouts during house-hunting in honeybees and Temnothorax ants [28,29]). There may thus be considerable scope for adaptive variation in the proportion of the group that contributes to the decision process [30]. Furthermore, in addition to the question of how many individuals contribute to the consensus process, there is the question of who contributes. Information quality can vary between individuals, and decision accuracy can be maintained in smaller groups if the individuals that contribute to the decision are better informed [1,31]. In the extreme case, a single expert can outperform a poorly informed collective [32]. In shared decisions, empirical data indicate that the contribution of individuals can be shared equally among all individuals or reside predominantly in a subset of the group [5,33–36]. The strength of individual influence may also vary with group size, with individuals having a greater potential influence in smaller groups [37]. This scope for variation in the proportion of individuals involved in decisions, and the magnitude of the contribution that individuals make to the decision process, may give smaller groups some capacity to ameliorate the limitations of group size. Indeed, Franks et al. [38] showed that small and large colonies of Temnothorax ants were equally adept at solving a nest selection problem, though in contrast, Ward et al. [18] showed that larger groups made better and faster decisions in fish. Understanding how individual contributions to consensus decision-making vary in conjunction with group size should provide valuable insights into the mechanics underpinning collective processes, but this can only be elucidated with detailed quantifications of individual contributions to the decision process.

Social insects are excellent subjects for studies of collective behaviour and the influence of group size on consensus decision-making. Colony size varies over several orders of magnitude, and the diversity of social systems represented is unrivalled. Insects need to find a new home when their present nest becomes unsuitable or during colony reproduction by fission [27,39], and studies of the consensus decision process during house-hunting by bees and ants have been particularly illuminating (reviewed in [4,9,10]). While leadership can be highly variable in vertebrate groups, social insects are typically regarded as being self-organized, such that group behaviour emerges as the collective product of individual responses to local information without the need for global control [3]. However, social insect colonies are often characterized by distinct classes of individuals derived from different age groups, genetic lineages and behavioural or morphological castes, each of which has the opportunity to contribute differentially to the decision process. Indeed, it has long been recognized that ‘elites’ or ‘key individuals’ may contribute disproportionately to collective processes [28,40–42]. On the other hand, for effective exploitation of the ‘wisdom of the crowds’ effect in decision-making, individual contributions should be independent, and increasing the diversity of individual contributors can be more beneficial than adding expertise [43,44]. It thus remains unclear to what degree decision-making in social insects relies on specialists. Furthermore, colony size can influence the efficiency of a wide range of group tasks in social insects [45], but see [46], and individual contributions might also vary with group size.

In this study, we shed light on these questions using interactive computer vision software to analyse in detail the consensus decision and colony relocation process at the individual level. We employ as our model system the small colony Japanese ant Myrmica nipponica. This species is ideally suited to this purpose as entire colonies can be observed under controlled laboratory conditions, and previous studies have indicated that large and small colonies perform relocations with similar efficiency [47], suggesting a capacity for adaptive optimization of decision-making in colonies of different size. Here, we explore three main questions: (i) how is individual input to decision-making distributed within colonies, (ii) does this differ in large and smaller colonies, and (iii) does the decision process rely on specialists, that is, ants that consistently take a majority role, or are roles flexible? We estimate individual ‘effort’ by quantifying ant movement and behaviour during the house-hunting process, and contrast individual roles in colonies of different natural and manipulated sizes.

2. Material and methods

2.1. Colony collection and maintenance

Entire colonies of M. nipponica were collected from patches of moss and the bases of ferns in broadleaf forest near Chitose City in Hokkaido, northern Japan (42°47’ N 141°34’ E, altitude approx. 100 m) in September 2012 and 2013. A total of 68 colonies were collected overall, with a mean colony size of 33 ± 18 individuals. Colonies were housed in 10 × 10 × 3 cm plastic boxes floored with plaster that was kept moist. Each box contained a single nest consisting of a microscope slide covered with a red filter mounted on a 2.2 mm high circle of foam with a small (3 mm) opening. Ants were kept at room temperature (approx. 20°C) and provided with ad libitum water and sugar/water solution, and fed mealworm pieces every few days. All ants were individually marked with different coloured spots on the head, thorax and gaster using Mitsubishi paint-marker pen paint applied with a fine brush. See also [47,48] for basic housing and experimental methods.

2.2. Tracking of individuals during relocations

Colonies of M. nipponica can be induced to relocate to a new nest site by removing their artificial home nest (which sits atop the plaster). An identical nest was provided in a new box separated by an empty navigation chamber (figure 1). Colonies rendered homeless send out scouts to find a new nesting site. These scouts ‘vote’ on available sites by laying chemical trails to their favoured site, which in turn attracts further scouts [47]. Once the number of scouts at one site reaches a threshold, a ‘quorum’ is achieved [6]. This triggers a phase shift, and individuals rapidly undergo a behavioural switch to conclude the relocation marked by the transport of brood to the new site. Brood transport does not begin until a consensus decision has been achieved, and this is dependent on achievement of a quorum of individuals at the new site [47,48]. The relocation process in M. nipponica can be divided into three phases [48]. The ‘discovery’ phase is defined as the time from removal of the home nest to the first ant entering the new nest. The ‘assessment’ phase is defined as the time from first entry to the new nest until the first quorum response. The quorum point is defined as the moment at which the first ant to switch to brood transport departs from the destination nest immediately.

\[ E, altitude \approx 0 \]
Figure 1. Experimental set-up for relocations. The apparatus consisted of three nesting boxes (10 × 10 × 3 cm) linked via small holes. Ants relocated from the source nest-box (S) to the destination nest (D) via the navigation box (N). Ants were prevented from accessing other parts of the destination nest-box other than the nest itself. Web cameras (a) recorded exit and entrance events while a further high-resolution camera (b) recorded all movements in the navigation box (see also main text). The area available to ants during the relocations is indicated in grey: the area in the destination box (D) was enclosed within the artificial nest.

prior to her maiden transport voyage. From the quorum point until the end of the relocation is termed the ‘transport’ phase. Relocations were deemed completed when all brood had been transported.

Web cameras (Elecom Ucam-DLA200H) positioned above the nest entrances were used with the motion-detection software iSpy (www.ispyconnect.com) to track entry/exit events (figure 1). The identity and timing of individual ants entering and exiting the nest(s) and transporting brood were manually scored from videos. Ant movements in the navigation chamber were recorded for the duration of the relocation using a high-resolution web-camera (Logitech C920). These videos were used to quantify individual ant movements in detail using the software ANTRACKS (www.antracks.org). This software accurately tracks individual movements (x/y pixel coordinates for each video frame) as ‘trajectories’ representing one voyage (here from entry to exit of the navigation chamber). Each trajectory was matched with data from entry/exit events and assigned to an individually marked ant, and then scored as whether or not it involved transport of a brood item and whether or not it followed the pheromone trail. Trajectories were considered to follow the trail if at least 80% of the trajectory followed the most frequently used path in the navigation chamber. The most frequented path in each relocation was inferred using the ‘density map’ function in ANTRACKS, which in all cases clearly indicated the most frequently used path in the navigation box between the source and destination nests (see the electronic supplementary material).

2.3. Experimental approach

Relocations were performed with the goal of quantifying the relative contribution of all individuals to the decision-making process, exploring the influence of colony size on this distribution and investigating the adaptability of individual roles. To this end, nine relocations were analysed in detail for six colonies. Relocations were divided into three classes: large colonies, small colonies and split colonies. The former two categories were natural colonies of varying size (34 ants for large colonies and 15–18 ants for small colonies; table 1). Because natural colonies of different sizes can differ in other size-correlated attributes such as experience [49] we also performed relocations with manipulated (split) colonies. Split colonies were the same colonies as those used in large relocations, but were halved in size (17 ants), such that small and split colonies were of equivalent size. To standardize which individuals were removed and control for possible stochastic effects of the removal of key individuals, we deliberately selected the most active ants (as adjudged by distance covered during full-size relocations) to be removed.

2.4. Data analysis

Data from ANTRACKS were converted into spatial objects using the sp and trip packages in R v. 3.0.2 [50,51] after manual scaling of distances. The mean speed and distance of individual trajectories were obtained from these spatial objects. Individual contributions to the relocation process were assessed using two metrics, (i) the distance covered by individuals and (ii) the number of brood transports undertaken. The distance covered by each individual (hereafter termed effort) was recorded only in the central navigation chamber, and an assumption of our analysis is that activity beyond this area was directly proportional to activity within it. Observations suggest that this is reasonable as the activity level of individual ants was consistent across regions. Activity outside the navigation chamber was only a small proportion of overall activity as movement in the source nest-box was largely limited to between the site of the old nest and the entrance to the navigation chamber, and the area of the new nest was small. To account for variation in the duration of phases when comparing relocation events, distance was scaled by relative duration of the relocation or phase (i.e. divided by the proportionate difference between the focal and longest relocation). This metric was termed ‘scaled effort’ and was our primary measure of individual contributions to the decision and relocation process.

Generalized linear mixed models (GLMM) were implemented using the lme4 package in R v. 3.0.2 [51] with colony identity as a random factor. Analyses of quorum thresholds, scout and transporters numbers were modelled using a Poisson errors, whereas binary data such as trail following were treated assuming a binomial error distribution. Other data including speeds and durations were treated as Gaussian, and log transformed when plots of residuals indicated a violation of the assumption of equal variance. Scaled effort data were continuous and zero-inflated and thus we employed a compound Poisson linear mixed model using the cphm package in R [52]. In analyses of speed, individual identity was added as a nested random factor within colony. In analyses of overall trends during relocations (§3.1), all potential explanatory factors were initially fitted and removed in a stepwise fashion until the minimal adequate model was achieved following Zuur et al. [53]. Factors included transport status (carrying brood or not), experience (number of trips by each individual), trail fidelity (following the trail or not) and time (seconds since start of the relocation). In analyses of group effects (§3.2), we used only group (large, small and split) as a factor, with colony identity as a random factor. These latter models were followed by Tukey post-hoc comparisons between groups using the glht function of the multcomp package in R. Means are given as arithmetic mean ± s.d. unless otherwise stated.

3. Results

All nine relocations were completed successfully, with a total of between 119 and 469 trajectories recorded (mean = 260 ± 98; table 1). As might be expected from the greater number of individuals, large colonies tended to generate more trajectories than split or small colonies (means: large = 347 ± 112, split = 189 ± 77 and small = 245 ± 20; table 1), though this difference was significant only between large and split colonies (table 2).

3.1. Relocation mechanics and distribution of effort

3.1.1. Trajectory alignment, speed and distance

Trajectory speed increased both with time (t12157 = 8.09, p < 0.001) and individual experience (t2136 = 5.60, p < 0.001),
and there was a corresponding decrease in distance of trajectories with time ($t_{2140} = -7.57$, $p < 0.001$) though not with experience ($t_{2137} = 0.22$, $p = 0.823$). Trajectories associated with the trail were on average faster ($t_{2137} = 3.36$, $p < 0.001$) and shorter ($t_{2140} = 9.20$, $p < 0.001$). There was no influence of brood transport on speed ($t_{2135} = 1.51$, $p = 0.131$) or distance ($t_{2138} = -0.005$, $p = 0.996$) of individual trajectories. Trail fidelity increased over time ($z = 19.07$, $p < 0.001$) though not with experience ($z = -1.30$, $p = 0.192$), and while only 18% ($n = 1539$) of trajectories followed the trail prior to the quorum point, this was markedly higher (85%; $n = 802$) after the quorum point (range: 3–70% before
versus 64–97% after, by relocation event). Ants in one relocation closely followed the box edge and this lead to an unusually high-level pre-quorum trail fidelity (70%), whereas the next highest was 28% for the split version of the same colony. Trajectories in which ants were carrying brood were more likely to be associated with the trail (93% versus 82% following the quorum point: \(z = 4.82, p < 0.001\)). Of 38 trips made by naive ants (those undertaking their first trajectory) following the quorum point, all but one was aligned with the trail.

### 3.1.2. Distribution of effort within colonies

An average of 78% (range 65–93%) of colony members recorded at least one trajectory prior to the quorum point (i.e. functioned as scouts), whereas 48% (range 13–76%) of the colony contributed to brood transport. Scaled effort for the entire relocation was higher in scouts than non-scouts (\(z = 11.31, p < 0.001\)) and transporters than non-transporters (\(z = 4.50, p < 0.001\)). The high trail fidelity following the quorum point suggests that a functional trail was present when a consensus decision was reached. As it is not possible to observe trail laying in this species, we estimated trail-laying effort by quantifying the number of trajectories aligned to the final trail prior to the quorum point. This value varied from 6 to 75 (mean 24 + 23) and suggests that very low numbers of passages (6, 7 and 8 passages in the three lowest cases) are sufficient to generate a functional trail. The high passage rate in some colonies prior to the quorum point (43 and 75) suggests that trail establishment is not the principal requirement of the assessment phase, in agreement with a previous study which showed that colonies provided with pre-formed trails retained a long assessment phase [47]. The route followed by trails varied from being closely aligned to one side of the navigation box to a more or less straight line through the centre (see the electronic supplementary material). As for scouting and transporting, there was no evidence that trail laying was monopolized by one or few individuals, as pre-quorum trail oriented trajectories were shared among individuals, with 1–11 trajectories per individual (mean: 2.5 ± 1.9) and at least four separate individuals following a trajectory aligned to the trail before the quorum point in all relocations.

### 3.2. Group size effects

#### 3.2.1. Duration of relocations and task allocation

The results of inter-group comparisons are presented in table 2. The time taken to locate the new nest site was highly variable, and large colonies in general found new nests more rapidly than small or split colonies (figure 2). Overall, however, relocations times did not differ significantly, as large colonies, having more brood, also spent longer transporting. Analyses of distance covered during each phase support this, with significantly more distance (summed over all trajectories) covered during transport in large colonies when compared with both small and split colonies, and correspondingly higher distance covered overall (figure 2). Larger colonies employed more scouts and transporters, and used higher quorum thresholds than both small and split colonies (table 1 and figure 3). The proportion of scouts, however, did not vary with colony size (means: 84 ± 10 small, 74 ± 5 large and 77 ± 10 split).
3.2.2. Variation in individual contributions

Individuals in large colonies invested more effort in discovery than in small or split colonies (figure 4). However, this trend was reversed during the assessment and transport phases, as split colonies invested significantly more effort per individual than large colonies overall and during assessment and transport. The same was true for small colonies except that there was no difference in effort during the assessment phase. Furthermore, ants moved faster in both small and split colonies relative to large colonies (figure 3). The number of transports per individual did not differ between groups. However, transport efficiency (transport per individual per unit time) was higher in split colonies than large colonies. Finally, the proportion of the total distance covered by each individual was considerably more skewed in small and split colonies relative to large colonies (figure 5), indicating that the increase in effort exhibited in smaller colonies was focused in a few individuals rather than being evenly distributed.

3.3. Role flexibility

Removing the most active ants from split colonies had no observable influence on the performance of colonies during the relocation process, and no significant differences were found in any of the analysed metrics between small and split colonies. This suggests that colonies are readily able to adapt to changes in group size and that roles are highly flexible.

4. Discussion

Relative to their large counterparts, split colonies of *M. nipponica* employed a lower quorum threshold, increased movement speed, had higher transport efficiency, and invested more effort per individual overall and during the assessment and transport phases. In addition and probably because of having less brood, split colonies required less time to relocate brood and covered less distance during brood transport. These patterns were also largely consistent with unmanipulated small colonies, suggesting they are not an artefact of the manipulation (see also [47]), nor related to other colony-size-correlated factors such as experience [28,54].

Colony-size related differences in the discovery and transport phases can be attributed to the likelihood of finding the new nest with more scouts and differences in the number of brood, respectively. However, the bulk of the relocation was spent in information collection and collation during the assessment phase. During the assessment phase, ants accumulate knowledge of potential nesting sites by exploring the accessible area. Colonies may eventually decide to nest anywhere within the nesting box, but show a preference for protected sites such as corners, and in this study we provided an overwhelmingly superior choice in the form of the artificial nest. As a consequence, all colonies made ‘successful’ choices, though sub-optimal decisions can occur when the available options are less distinct [55]. To determine the optimal site and collectively decide to move to it, both small and large colonies had to assess an equivalent area of the experimental arena and, although smaller colonies had fewer scouts with which to do this, assessment time and distance did not differ between groups. If we make the assumption that information accrued is proportional to distance covered, it follows that small colonies are likely to have had a similar collective awareness of their environment to large colonies, though in small colonies this information was vested in fewer individuals. Because individuals in small colonies invested more effort (covered more distance) than individuals...
in large colonies, these individuals should have accrued more information and thus could be considered better informed. Furthermore, the same individuals that perform the greatest scouting effort are likely to be the ones with most opportunity to contribute to trail formation (i.e. generate social information), and thus voting weight will also scale with effort. In this way, small colonies of *M. nipponica* may be able to ameliorate to some degree the disadvantage of small colony size with respect to the ‘wisdom of the crowds’ effect: small colonies have fewer individuals available to contribute to the information pool but, by virtue of their greater effort, it is likely that these individuals are better informed and have higher voting weight. The degree to which this may enhance decision accuracy in small colonies remains unclear but any compensation for the lack of numbers is likely to be partial, as currently available data suggest that smaller colonies of *M. nipponica* suffer from reduced decision accuracy relative to larger colonies (AL Cronin 2014, unpublished data).

Evidence that workers vary effort with colony size in other species is contradictory: Dornhaus et al. [49] show that the most active individual performed proportionately more work in smaller colonies of *Temnothorax albipennis* over a range of tasks, whereas honeybee foragers in large colonies work harder than those in small colonies [56]. However, in many cases, workload is likely to scale with colony size: foraging effort, for example will depend on the number of brood, which in turn is correlated with colony size. In this study, all groups had to perform a similar task (finding a new home) and, while work during the transport phase varied as brood numbers differed, an equivalent amount of work was required to assess possible nesting sites and decide on one of these. If effort is evenly distributed among group members, we would expect a higher proportion of effort per individual in smaller colonies. However, we found that not only proportionate effort, but also absolute effort, was higher in smaller colonies. This suggests that individuals in large colonies may only work ‘hard enough’ to maintain an acceptable level of decision speed and accuracy and may retain a capacity for additional effort if required. Individuals in small colonies, on the other hand, may be at or close to their maximum work limit. This difference could limit the ability of small colonies to cope with additional stresses to the decision and relocation process as might occur under harsh conditions or in complex environments, and small colonies may suffer a higher cost to decision accuracy as a result.

While individual effort was higher in smaller colonies of *M. nipponica*, it appears that other characteristics scale with colony size. As in previous studies of this species, quorum thresholds and the number of scouts and transporters were higher in larger colonies [47,48]. This indicates that while ants increase individual effort in small groups, there is no increase in the proportion of individuals involved in the decision-making process. The number of scouts is likely to be linked to the quorum threshold because colonies cannot increase quorums without increasing the scouting force or they risk achieving no decision at all [3]. Quorum thresholds are thus linked to the number of individuals involved in information gathering, and larger quorums should be associated with better decisions [25]. Why smaller colonies do not allocate more individuals to the decision process is unclear, though the high proportion of scouts in many relocations suggests that these colonies may be at a functional limit while still retaining some individuals for brood protection and maintenance. Indeed the high proportion of scouts found here (78 ± 9% of ants recorded at least one trajectory, and 67 ± 11% entered the new nest prior to the quorum point) supports earlier data indicating that *M. nipponica* has a more equally shared decision process than in other insects so far studied [48] and is in this regard perhaps more akin to some social vertebrates [33,34]. The number of scouts also appears to scale with colony size in *Temnothorax* ants [28,38] and honeybees [57], but is a considerably lower proportion of the colony: Dornhaus et al. [28] report that only 5–7% of ants in *T. albipennis* reach the new nest before commencement of transports and a similarly a low percentage of scouts (5%) is found during nest relocation in honeybees [29]. Having additional resources may allow smaller colonies of these and other species to allocate proportionately more individuals to information collection without (or in conjunction with) increasing individual effort.

Split colonies were able to perform relocations successfully and on par with naturally small colonies despite the most active ants having been removed. Because the impact of individual contributions is expected to be larger in smaller colonies [58], we might expect that removing the most active half of the colony could have a particularly detrimental effect in *M. nipponica*. However, this manipulation did not appear to interfere with the consensus decision-making or relocation process, suggesting both a lack of specialists and highly flexible roles in this species. This is in line with predictions that larger societies of social insects are characterized by greater individual specialization and a loss of individual totipotency [59–61]. *Myrmecina nipponica* is a small-colony ant and thus may exhibit greater flexibility in individual roles than large colony species. By contrast, Möglich & Hölldobler [24] showed that in two species of large-colony formicine ants, a small subset of the colony acted as relocation specialists, and relocation behaviour suffered if these ants were removed. However, Sumana & Sona [42] demonstrated the presence of a single specialist during colony relocations in the small-colony ant *Diacamma indicum*, indicating that colony size is not a reliable predictor of specialist roles.

We demonstrate that individuals in small groups of *M. nipponica* work harder than those in large groups during the information gathering and voting stage of consensus decisions. This may act to ameliorate the limitation of fewer individuals with respect to the ‘wisdom of the crowds’ effect in decision-making because the individuals involved are better informed. To achieve an equivalent task at a comparable rate and standard, individuals in smaller groups should work harder than those in larger groups. For example, to attain the same level of predator awareness, individuals in smaller groups need to invest more effort in collective vigilance [62]. However, at present we have a limited understanding of how the behaviour of individuals is modified and compiled in groups of different size. Our study shows that individuals in smaller groups may employ different strategies during collective actions than those in larger groups. Our findings also raise some additional questions: firstly, it remains unclear to what degree increasing effort can improve decision-making in small groups, and if the scope for increased effort to improve decisions is realized. Secondly, if individuals in small groups are already working harder, this may limit the flexibility they have in responding to additional environmental stresses during decision-making, and as a result we might expect
such stress to have a more marked effect on smaller colonies. These questions are currently under investigation.

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Data accessibility. The datasets supporting this article have been uploaded as part of the Supplementary Material.

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