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Evidence of sweepstakes reproductive success in a broadcast-spawning coral and its implications for coral metapopulation persistence

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Abstract

Processes governing genetic diversity and adaptive potential in reef-building corals are of interest both for fundamental evolutionary biology and for reef conservation. Here, we investigated the possibility of "sweepstakes reproductive success" (SRS) in a broadcast spawning coral, *Acropora hyacinthus*, at Yap Island, Micronesia. SRS is an extreme yearly variation in the number of surviving offspring among parents. It is predicted to generate genetically differentiated, low-genetic-diversity recruit cohorts, containing close kin individuals. We have tested these predictions by comparing genetic composition of size classes (adults and juveniles) at several sites on the island of Yap. We did see the genome-wide dip in genetic diversity in juveniles compared to adults at two of the four sites; however, both adults and juveniles varied in genetic diversity across sites, and there was no detectable genetic structure among juveniles, which does not conform to the classical SRS scenario. Yet, we have identified a pair of juvenile siblings at the site where juveniles had the lowest genetic diversity compared to adults, an observation that is hard to explain without invoking SRS. While further support for SRS is needed to fully settle the issue, we show that incorporating SRS into the Indo-West Pacific coral metapopulation adaptation model had surprisingly little effect on mean rates of coral cover decline during warming. Still, SRS notably increases year-to-year variation in coral cover throughout the simulation.

KEYWORDS
cnidarians, conservation genetics, ecological genetics, population genetics – empirical

1 | INTRODUCTION

In many highly fecund marine species reproduction and recruitment dynamics can be highly stochastic, involving extreme year-to-year variation in the number of surviving offspring per parent. As a result, in a given year nearly all the recruits at a specific location may be the offspring of just a few "lucky winner" individuals out of an orders of magnitude larger adult population, which has been termed "sweepstakes reproductive success" (SRS; Hedgecock, 1994). Since in terms of genetics this implies very small effective population size, SRS dramatically accelerates genetic drift relative to the expectations based on the census sizes, and thus can be the major force shaping genetic diversity and adaptive potential of wild populations. Adaptive capacity of reef-building corals is of particular interest, due to worldwide reef decline driven by the effects of climate change (Eddy et al., 2021; Global Coral Reef Monitoring Network, 2021). Existing models of coral adaptation (e.g., Bay et al., 2017; Kleypas et al., 2016; Matz et al., 2020) assume that equally fit corals are equally likely to produce surviving offspring, which may be an oversimplification if coral recruitment actually follows the SRS pattern. Here, we studied adult and juvenile cohorts of the broadcast-spawning coral *Acropora hyacinthus* across reef sites at the island of Yap, Micronesia (Figure 1a), to look for the following three

predictions of the SRS hypothesis (Hedgecock & Pudovkin, 2011). First, since "lucky winners" in a given year are different among locations, SRS is expected to generate transient (or "chaotic") genetic differentiation among recruits at different sites (Johnson & Black, 1982). This variation may not necessarily translate into differentiation of adult populations since these assemble over multiple years, integrating over yearly variation in recruit sources (Broquet et al., 2013). Second, since under the SRS the recruits are produced by far fewer parents than the whole adult population, their genetic diversity should be lower than in adults. Third, SRS predicts that at least some recruits at a given site will be close relatives. We found evidence for the second and, most notably, the third of these predictions. We then modelled the effect

of SRS on coral persistence in the Indo-West Pacific metapopulation model we have developed previously (Matz et al., 2020).

2 | METHODS

2.1 | Coral sampling

In November 2015, adult and juvenile *Acropora hyacinthus* colonies were sampled from four separate sites on Yap Island: South Tip (9°26′3.1992″N, 138°2′13.9488″E; n = 48 juveniles, n = 38 adults), West Outer Reef (9°33′33.9336″N, 138°5′22.1496″E;
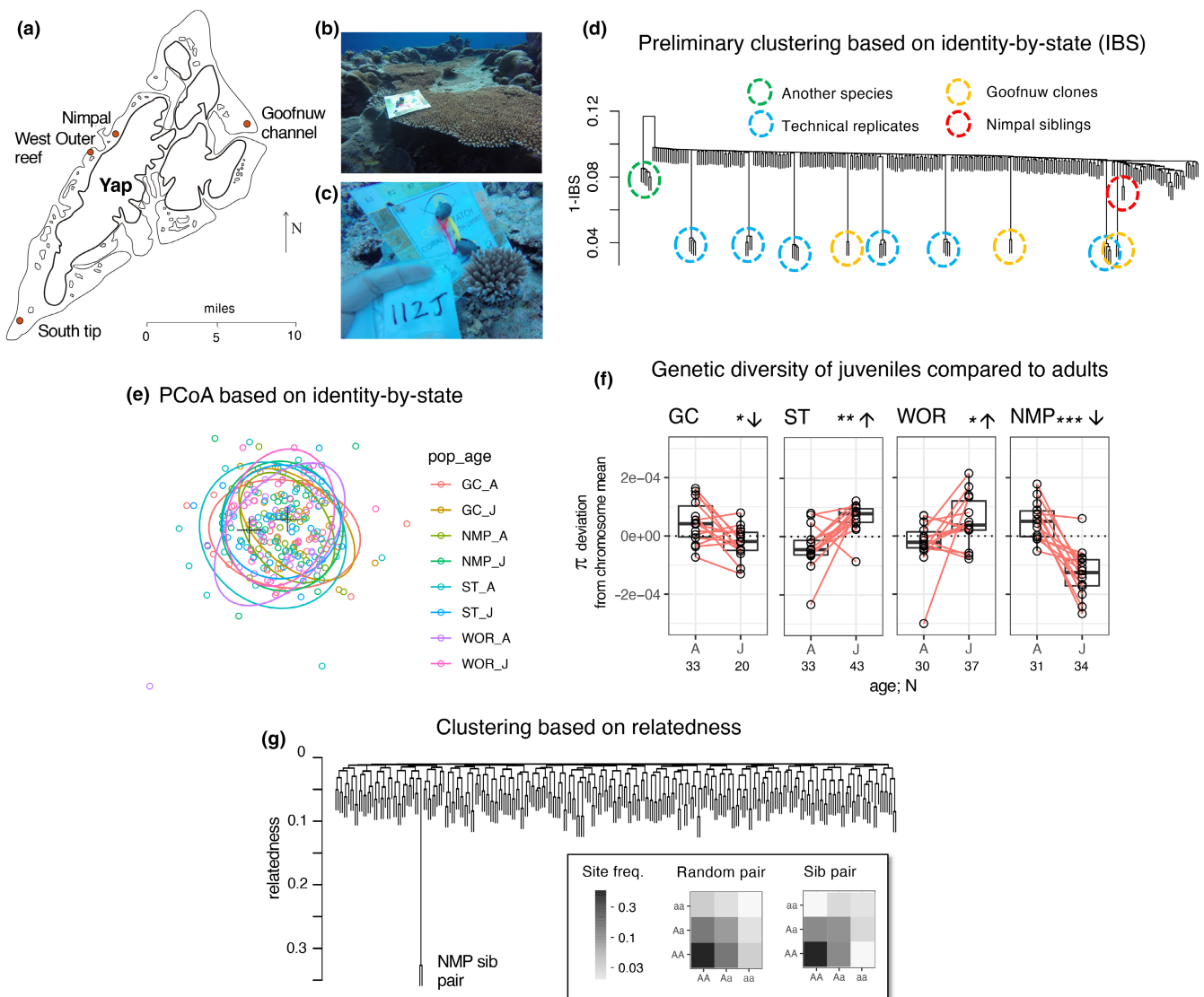

FIGURE 1 Sampling and genetic analyses. (a) Map of sampled locations around Yap Island. In the rest of the figure and in the main text names of locations are abbreviated with their initial letters. (b, c) examples of sampled adult (b) and juvenile (c) colonies. (d) Initial hierarchical clustering of all samples based on identity-by-state (IBS), to detect clones and incorrect collections. (e) Ordination plot of the first two principal coordinates of the identity-by-state matrix (filtered data set). Age classes are identified by indices "a" (adults) and "J" (juveniles) added to the abbreviation of reef site. Ellipses show 75% confidence limits of the data (multivariate normal distribution model). None of the population: age groups are significantly different from any others. Crosses identify positions of the two Nimpal siblings. (f) Deviation of nucleotide diversity (π) from global mean in adults and juveniles from each reef site, computed separately for each chromosome (red lines). The x-axis labels identify age class and give the number of genotyped individuals within each group. (g) Hierarchical clustering tree of the filtered data (same as on panel e) based on relatedness. Insets show site frequency spectra of the detected siblings ("sib pair") and two randomly chosen individuals ("random pair").

n = 38 juveniles, n = 34 adults), Nimpal (9°34′0.2496″N, 138°5′50.1324″E; n = 35 juveniles, n = 31 adults), and Goofnuw Channel (9°34′16.41″N, 9°34′16.41″N, 9°34′16.41″N, 138°12′10.3284″E; n = 24 juveniles, n = 33 adults) (Figure 1a–c). At each reef site, all corals were collected within close proximity such that the collection area did not extend beyond an ~100-m radius.

Only juveniles were collected from South Tip during November 2015 as no adults were present on the reef following the crown-of-thorns starfish outbreak in 2010. Adult *A. hyacinthus* samples from the South Tip site (2009) were collected by Davies et al. (2015) a year prior to the outbreak. The number of samples per age cohort and location are given on the *x*-axis labels on Figure 1(f).

Small branches 1–2 cm in length were removed from *A. hyacinthus* colonies using pliers and stored in 100% ethanol at −20°C until they could be processed to extract DNA. Juveniles were classified as individuals less than 20 cm in diameter and adults as individuals >30 cm in diameter. The median diameter was 8.9 cm for juveniles and 60.2 cm for adults (Figure 1b,c).

2.2 | Sample preparation and sequencing

DNA was extracted using a modified phenol–chloroform extraction method (Davies et al., 2013) and genotyped with the original version of the 2b-RAD protocol as described by Wang et al. (2012). Six randomly chosen samples were genotyped four times to provide a reference of what genetically identical samples should look like in subsequent analyses. The libraries were individually barcoded, pooled and sequenced on six lanes of the Illumina HiSeq 4000 at UT Austin. Adapter-trimmed reads have been deposited at the NCBI-SRA, bioproject PRJNA565239.

2.3 | Genetic analysis

Reads were quality filtered with FASTX TOOLKIT such that only reads in which 90% or more of the bases with a Phred score of at least 20 were retained (Gordon et al., 2010). These reads were mapped to the well-assembled genome of the congener, *Acropora millepora* (Fuller et al., 2020), with BOWTIE2 (Langmead & Salzberg, 2012). Of the 299 samples sequenced, 291 passed the initial filter of not being more than three standard deviations below mean log(depth-quality). Depth-quality is the proportion of sites covered at 5× or higher; it is calculated by the script plotQC.R, which is part of the 2b-RAD analytical pipeline (https://github.com/z0on/2bRAD_denovo). The retained samples have depth-quality exceeding 24%. We then calculated individual heterozygosities using ANGSD version 0.921 (Korneliussen et al., 2014) and removed three high-heterozygosity outliers that were more than five standard deviations above the average (the next-highest sample is 1.4 standard deviations above the average). Such high-heterozygosity outliers are probably mixtures of two or more genotypes, possibly due to accidental mixing

during library preparation. Such samples should be removed since they could create false signal of relatedness. The initial hierarchical clustering was based on the identity-by-state (IBS) distance matrix generated by ANGSD. Genetic structure was analysed using PCANGSD (Meisner & Albrechtsen, 2018), and using the functions *capscale* and *adonis2* from the R package *vegan* (Oksanen et al., 2007) based on the IBS matrix for nonclonal samples. PCANGSD initially detected spurious genetic structure (K = 2) that was strongly correlated with the number of sites passing filters (minimum mapping quality = 20, minimum base call quality = 20, *p*-value for being a true single nucleotide polymorphism [SNP] = 1 e-6, genotyping rate across individuals = 80%), which was probably an artefact of PCR (polymerase chain reaction) duplicates retained in the original version of the 2b-RAD protocol used here. We therefore restricted the analysis to only the 257,264 sites (both variable and invariable) that were shared among the three samples that had the least number of sites passing the mapping quality filter and the base call quality filter. After additional filtering (80% genotyping rate in the whole dataset and *p*-value for being a true SNP = 1 e-5, strand bias *p*-value cutoff 1 e-3, heterozygote bias *p*-value cutoff 1 e-3) 11,089 variable sites were retained, and no genetic structure was any longer detectable by PCANGSD. These sites were used to construct the updated IBS distance matrix in ANGSD and to calculate relatedness and pairwise site frequency spectra in NGSRELATE version 2 (Korneliussen & Moltke, 2015). To avoid distortion of the ordination space due to the presence of highly similar siblings, only one sibling was included in the ordination construction. Coordinates of the left-out sibling were then predicted based on their distance to other samples using the *predict.cca* function of the *vegan* package in R. Nucleotide diversity (π) was calculated as per-chromosome theta (expected number of differences between two chromosome copies) estimated by ANGSD utilities *realSFS* and *thetaStat*, divided by the number of genotyped sites in the chromosome. Significance of the genetic diversity difference between adults and juveniles was inferred using a linear mixed model with fixed effect of age class and scalar random effect of chromosome, using the R package *lme4* (Bates et al., 2015). For plotting Figure 1(f), we computed deviations of π from each chrtomosome's mean, to better illustrate which groups were unusual in their diversity. The code to reproduce these analyses is available at the github repository: https://github.com/z0on/Yap_siblings.git.

2.4 | Metapopulation modelling

We incorporated SRS as an adjustable parameter within our Indo-West Pacific coral metapopulation model (Matz et al., 2020). The SRS parameter takes values between 0 and 1 and sets the proportion of individuals that get to reproduce. This SRS fraction of individuals each make 1/SRS number of offspring, so the average number of offspring that a stable-size subpopulation makes over multiple years is the same as in the base model.

3 | RESULTS AND DISCUSSION

3.1 | Natural clones

Hierarchical clustering analysis of the whole dataset (Figure 1d) revealed six samples from a different cryptic species (Ladner & Palumbi, 2012), which were removed from subsequent analyses. It also identified three pairs of natural clones, which were as genetically similar to each other as technical replicates (Figure 1d). All three of these pairs were from Goofnuw channel, which experiences the most wave action due to windward exposure. These clones are therefore likely to be the product of colony fragmentation by storms. Clonal replicates (natural or technical) were removed from subsequent analyses, leaving a single best-covered sample as a representative of a clonal group.

3.2 | Overall genetic structure

Principal coordinates analysis (PCoA) of retained samples based on pairwise identity-by-state did not identify any significantly genetically distinct population:age groups (PERMANOVA $p > .1$, Figure 1e). Lack of genetic differentiation between adults indicates that, on the island scale, larval dispersal and recruitment are unrestricted, as is expected for broadcast-spawning corals (Davies et al., 2015). Yet, we do not have support for the first prediction of the SRS, that juveniles would show some genetic structure, or "chaotic genetic patchiness" sensu Johnson and Black (1982), due to different parents "winning the sweepstakes" at different locations.

3.3 | Genetic diversity variation among age groups

SRS predicts low and possibly variable genetic diversity in juveniles but at the same time high and uniform genetic diversity in adults, because of summation of multiple recruitment events. The null hypothesis would have no difference in genetic diversity between any population:age groups. What we observed did not conform to either of these hypotheses: in our case, we detected small (on the order of 2% of the global mean of 0.005) but significant variation in genetic diversity between all population:age groups (Figure 1f). Compared to adults from the same site, juveniles were significantly less diverse at Goofnuw Channel (GC) and especially at Nimpal (NMP), as SRS would predict; however, they were more diverse at the South Tip (ST) and the West Outer Reef (WOR). Moreover, adults also appeared to vary in genetic diversity across sites (Figure 1f). To check if all this variation was somehow an artefact of our workflow, we have randomized the content of population:age groups before computing per-group genetic diversity; none of the randomized comparisons were significant.

3.4 | Siblings

Another key prediction of SRS is occurrence of close kin individuals among same-cohort recruits, and indeed we find a pair of juveniles at Nimpal that were related to each other with pairwise relatedness of 0.33, indicating probable full-sib or half-sib relationship (Figure 1g). Their pairwise site frequency spectrum was clearly different from a typical pair of unrelated corals, with more shared heterozygotes and minor allele homozygotes and fewer sites in alternative homozygote states (*AA* vs. *aa*, Figure 1g, inset). This relatedness is unlikely to be an artefact of genotyping since these samples were not outliers in terms of position in the overall PCoA (Figure 1e) or depth-quality and the number of sites passing filters (Figure S1).

3.5 | Effect of SRS on modelled coral persistence

The effect of SRS on coral cover during warming within the Indo-Pacific metapopulation model (Matz et al., 2020) was surprisingly subtle (Figure 2a–c): diminishing coral cover was only observed at the most severe SRS setting (Figure 2d), where only the 0.001-th fraction of all individuals were allowed to reproduce. The reason for this lack of effect is that SRS did not affect adaptive genetic diversity much (Figure 2e), probably because the model with overlapping generations allowed for accumulation of genetic diversity in populations via multiple rounds of recruitment. Yet, there was a clear effect of SRS on year-to-year variation in the coral cover: even mild SRS of 0.1 already amplifies the coral cover volatility compared to the base model (Figure 2f). This increase is most pronounced at smaller reefs (Figure 2g), which is not surprising since they should be more prone to demographic fluctuations of any kind. Since coral cover in the model depends on the match between genetic thermal optimum of the local population and the environmental setting, SRS probably increased the chance of better-than-average match in some years and worse-than-average match in other years.

While SRS in nature can be well below 0.001 (Dennis Hedgecock & Pudovkin, 2011), it should be noted that the sizes of our modelled subpopulations were much smaller than in nature: the smallest modelled subpopulations had a carrying capacity of only 100. We therefore believe that the emerging effect of severe SRS was predominantly due to the fact that many subpopulations, with carrying capacity near or below 1/SRS, did not reproduce at all except once in several generations. This would have led to their diminishing size due to yearly mortality and thus less reproduction overall than in the base model. This is a rather unrealistic situation since natural census sizes of coral populations are well above 1000, although there are notable exceptions such as the pillar coral *Dendrogyra cylindrus* in the Florida Keys (Neely et al., 2021). Overall, SRS does not seem to hurt coral adaptive capacity too much, at least not within our model. That said, SRS might matter more in more complex models, such as in models
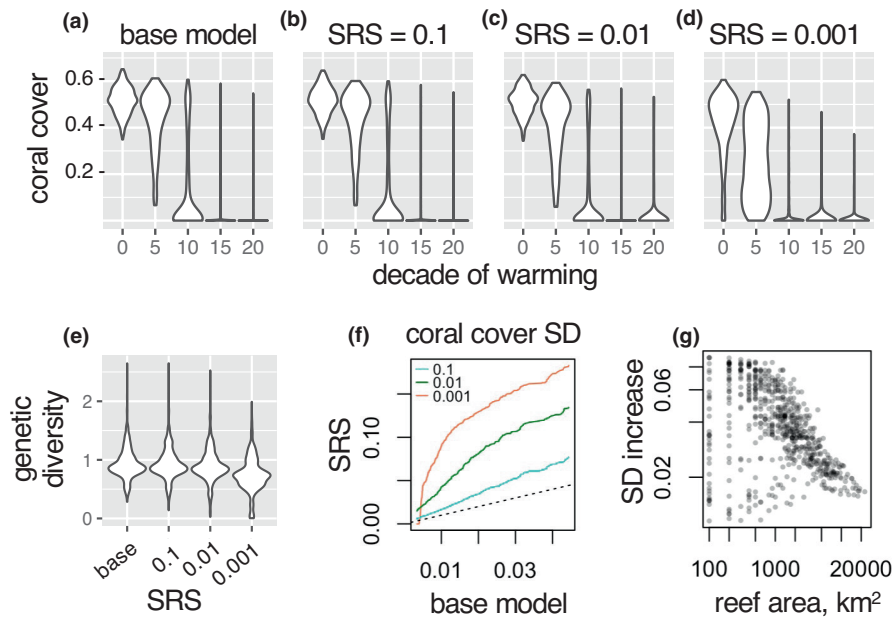
FIGURE 2 Effect of sweepstakes reproductive success (SRS) on coral persistence during warming in the indo-Pacific metapopulation model. (a–d) Violin plots representing the density of decadal mean coral cover across 680 modelled reefs, under increasing SRS severity: From no SRS (a) to SRS = 0.001 (d), when only 0.1% of all individuals get to reproduce. (e) Effect of SRS on adaptive genetic diversity, measured as standard deviation of the breeding value for heat tolerance, calculated for the fifth decade of warming. (f) SRS amplifies within-decade percentage coral cover variation (calculated for the last decade before the onset of warming). Dashed line is 1:1 correspondence, and coloured lines are different SRS settings. (g) Increase of decadal coral cover variation under SRS is the most pronounced at smaller reefs (plotted for SRS = 0.01).

involving adaptation to multiple stressors or adaptation to local environmental factors that do not change during warming, which should be explored in the future.

3.6 | Do we have SRS?

We have good support for SRS at the Nimpal (NMP) location: lower genome-wide genetic diversity in juveniles compared to adults (Figure 1f) along with the occurrence of close relatives among juveniles (Figure 1g), the latter being particularly hard to explain without invoking SRS. Yet, other results do not conform to the classical SRS hypothesis: we detect variation in genetic diversity not only in juveniles but also in adults (Figure 1f), and we do not see the emergence of "chaotic genetic patchiness" (sensu Johnson & Black, 1982) in juveniles (Figure 1e).

One possible reason why we detect variation in genetic diversity but not divergence between population:age groups could be the difference in power of these two analyses. Our genetic diversity comparison benefits from 14-fold replication across chromosomes, and is capable of revealing very subtle differences on the order of 2% of the mean. The signal of SNP covariance (i.e., genetic divergence) generated by such a minor change may simply not be detectable. Generally, the SRS signal is expected to be weak in our case because all our population:age groups, even juveniles, were probably pooled across several recruitment years, averaging out the SRS signature. In the future, to maximize the power of SRS detection, it would be

advisable to ensure that the compared groups of corals truly represent same-year recruitment cohorts. This should not be too difficult for juveniles of broadcast-spawning corals that only recruit once a year: the youngest corals sampled shortly before the spawning season are probably the same recruitment cohort from the previous year.

Why do we see variation in genetic diversity in every direction in both adults and juveniles (Figure 1f)? While it is tempting to again invoke recruitment stochasticity (i.e., some form of SRS), another viable explanation would be environmental filtering that varies in both space and time. These alternatives (stochasticity vs. selection) could not be resolved with our sparse 2b-RAD data. One would need whole-genome resequencing to look for evidence of temporally and spatially varying selection in the form of regions of lower diversity forming extended haplotypes, rather than being distributed evenly across the genome as is expected in the case or recruitment stochasticity.

Even though the evidence for SRS is still inconclusive, we believe it would be prudent to keep the possibility of SRS in mind, especially when planning efforts aimed at preserving or restoring coral genetic diversity (Baums et al., 2019). While SRS does not seem to affect adaptive potential in long-lived corals (Figure 1a–c), probably because multiple recruitment events per generation help maintain genetic diversity (Figure 2e), it can have stronger effect on adaptive potential when recruitment is very infrequent (Hedgecock & Pudovkin, 2011), as in *Acropora* and *Orbicella* in the Caribbean (van Woesik et al., 2014; Kuffner & Toth, 2016).

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://github.com/z0on/Yap_siblings.git

DATA AVAILABILITY STATEMENT

All sequencing data generated from the project are available from NCIB-SRA, accession no. PRJNA565239. Linux walkthrough, R and SLiM scripts are available at the github repository: https://github.com/z0on/Yap_siblings.git

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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