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Molecular markers reveal reproductive strategies of non-pollinating fig wasps

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Abstract

1. Fig wasps have proved extremely useful study organisms for testing how reproductive decisions evolve in response to population structure. In particular, they provide textbook examples of how natural selection can favour female-biased offspring sex ratios, lethal combat for mates, and dimorphic mating strategies.

2. However, previous work has been challenged, because supposed single species have been discovered to be a number of cryptic species. Consequently, new studies are required to determine population structure and reproductive decisions of individuals unambiguously assigned to species.

3. We used microsatellites to determine species identity and reproductive patterns in three non-pollinating *Sycoscapter* species associated with the same fig species. Foundress number was typically 1-5 and most figs contained more than one *Sycoscapter* species. Foundresses produced very small clutches of about 1-4 offspring, but one foundress may lay eggs in several figs.

4. Overall, the data show poor match to theoretical predictions of solitary male clutches and gregarious clutches with (n-1) females. However, sex ratios are male-biased in solitary clutches and female-biased in gregarious ones.

5. At the brood level (all wasps in a fig), a decrease in sex ratio with increasing brood size is only significant in one species, and sex ratio is unrelated to foundress number. In addition, figs with more foundresses contain more wasp offspring.

6. Finally, 10-22% of females develop in patches without males. As males are wingless, these females disperse unmated and are constrained to produce only sons from unfertilized eggs.

Introduction

Insects display a great diversity of mating systems, providing many opportunities to test evolutionary theory (Choe & Crespi, 1997; Shuker & Simmons, 2014). However, the study of insect mating systems can be challenging. First, insects are typically small and highly mobile, so difficult to study in the field under natural selective regimes. Second, recent studies have found cryptic species – morphologically indistinguishable but genetically distinct - in many insect taxa (Hebert et al., 2004; Bickford et al., 2007; Pfenninger & Schwenk, 2007). This suggests that many previous studies of mating systems may have inadvertently pooled data from multiple species (Molbo et al., 2003). Fortunately, molecular techniques now provide tools to deal with the second problem (Molbo et al., 2003; Cook et al., 2015), while careful selection of study species can address the first.

Fig wasps are tiny insects whose offspring develop, and in most species also mate, inside the figs (inflorescences) of *Ficus* trees (Cook & West, 2005). For this reason, despite their small size (typically <5 mm long), we can collect accurate data on the size and composition of fig wasp mating groups under natural field conditions (Hamilton, 1979; Herre et al., 1997). Moreover, in most *Ficus* species, several wasp species develop and mate alongside each other in a fig, creating excellent opportunities for comparative studies (Hamilton, 1979; Greeff & Ferguson, 1990; Cook, 2005). Each of the >750 *Ficus* species is pollinated by 1-5 species (Darwell et al., 2014) of fig-pollinating wasps (family Agaonidae), most of which are host-specific to a single *Ficus* species (Weiblen, 2002; Cook & Rasplus, 2003;). In addition, a given *Ficus* species may host up to about 30 non-pollinating species from diverse lineages in several other wasp families (Cook & Rasplus, 2003). Most non-pollinators are also associated with just one *Ficus* species (Cook & Segar, 2010), but some lay eggs in a few closely related *Ficus* species (Marussich & Machado, 2007; McLeish et al., 2010).

Female pollinator wasps (foundresses) enter receptive figs through a narrow tunnel, the ostiole, at the apex of the fig. Inside, a foundress lays many eggs (often >100, depending on species) before dying inside the fig. She thus lays “all her eggs in one basket” (Herre et al., 1997). Foundress number is typically only 1-5 (Herre et al., 1997), so figs contain many pollinator offspring from a few mothers. Some weeks later the offspring mature and mate inside the fig. This causes local mate competition (LMC - Hamilton, 1967), leading to selection for female-biased offspring sex ratios that increase (more males) with foundress number per fig. These predictions have been tested in several species by counting live offspring and dead foundresses in the same figs and assuming foundresses produce equal numbers of offspring (Hamilton, 1967; Herre, 1985, 1987; Herre et al., 1997). More recent studies have gone further and used molecular markers to assign offspring to sibships and establish the clutch sizes and sex ratios of individual foundresses (Molbo et al., 2003; Moore et al., 2005). This allows tests of more nuanced LMC models that incorporate clutch size variation, and of predictions for individual foundresses, as well as the emergent patterns at the fig level (Molbo et al., 2003). Importantly, molecular markers have also revealed cryptic genetic species within what was thought in previous work to be a single pollinator species (Molbo et al., 2003; Sutton et al. 2017). Together, these improvements in data quality have increased fit between theory and data considerably.

In contrast, we have limited understanding of individual reproductive strategies in non-pollinating fig wasps, which vary greatly in their sex ratios (West & Herre, 1998; Fellowes et al., 1999). In addition, they may have winged, wingless or dimorphic males (Hamilton, 1979; Cook et al., 1997), and, in some species, lethal male combat (Hamilton, 1979; Murray, 1990). Importantly, most non-pollinators lay eggs through the fig wall, without entering the fig, providing the opportunity to lay “a few eggs in many baskets” (Herre et al., 1997). However, this also removes the possibility for researchers to count foundress bodies inside figs and test for relationships between foundress number, sex ratio and clutch size. Models of optimal strategies for non-pollinator foundresses (Greeff, 1997) allow for very small clutches, which can severely limit offspring sex ratio options (Green et al., 1982; Morgan & Cook, 1994). They predict that, when a foundress lays one egg in a fig (solitary clutch) it should be a male and that larger clutches (gregarious) should generally contain one male and (n-1) females. Broadly similar predictions (more males in smaller clutches) also arise from standard LMC models where clutch size is not limiting (Werren, 1980; Stubblefield & Seger, 1990).

Adaptive allocation of offspring to clutches can also scale up to predictable patterns at the brood level (all conspecifics in a fig). Greeff (1997) developed models for foundresses that either do (informed) or do not (uninformed) use information on other foundresses laying eggs in the same fig. The models predict that brood sex ratio should be correlated positively with brood size for informed females, but negatively for uninformed females. Further, these fig level patterns are important for the evolution of constrained sex allocation (Godfray, 1990). Many fig wasp species have wingless, non-dispersing males, so females developing in a fig without males remain unmated (West et al., 1997), but can still potentially produce male (haploid) offspring from unfertilised eggs. Comparative data support the correlated evolution of large brood size and male winglessness across species (Cook et al., 1997), but unrecognized cryptic species could lead to underestimates of constrained sex allocation and potentially confound this pattern.

In this study, we use microsatellites on three *Sycoscapter* species that co-exist and mate in the same figs and provide the first genetic estimates of reproductive patterns for any non-pollinating fig wasp species. We have two broad aims. First, we estimate the aspects of population structure that are expected to influence the evolution of reproduction behaviour. Specifically, we measure foundress numbers, clutch sizes, and offspring sex ratios, as well as the proportion of females that will disperse unmated. Second, we use our data to establish the reproductive decisions of individual females, to test whether females adjust their offspring sex ratio in response to their own clutch sizes and to the number of females laying eggs in a fruit. These analyses would be impossible without molecular markers, since we cannot place individuals in sibships, or even identify species based on morphology alone.

Materials and methods

Study species and field sampling

We studied three *Sycoscapter* species that develop only in the syconia of *Ficus rubiginosa* and are endemic to eastern Australia. These species have not been described formally and, following (Moore et al., 2008) we refer to them as *Sycoscapter* species A, B and C. Females of species A are distinguished by their longer ovipositors, but we cannot distinguish between B and C based on morphology. The males are wingless and very difficult to identify, because there is great intraspecific variation in morphology (Moore et al., 2008). However, all wasps are identified consistently into the three species using either mtDNA sequences (Moore et al., 2008) or multilocus microsatellite genotypes (Bouteiller Reuter et al., 2009; Cook et al., 2015).

We collected 55 figs from four *Ficus rubiginosa* trees in Brisbane, Queensland, Australia in 2004-2005. Female wasps were allowed to emerge from figs and then preserved in 80% ethanol. Each fig was then placed in 80% ethanol and dissected under a light microscope to count the males and any remaining female wasps. All wasps were subsequently genotyped using the nine microsatellite markers described in (Bouteiller Reuter et al., 2009). In this paper, we use the term clutch to refer to the offspring of one female in one fig, and brood to refer to all conspecific wasp offspring developing in one fig (i.e. mating patch).

Molecular methods

DNA was extracted from the abdomen of each insect in a 100 ul volume of extraction solution (5% Chelex, 0.01% proteinase K) on 96-well plates. We incubated the plates at 56°C for 35 min then at 96°C for 15min and centrifuged for 5 min at 3500 rpm. We genotyped the 387 *Sycoscapter* wasps at nine microsatellite markers (locus 5, 48, 68, 71, 82, 85, 89, 95, 96) developed by Bioprofiles (Newcastle) and described in (Bouteiller Reuter et al., 2009). PCR was carried out on 96-well microplates in 15 ul volumes containing 5 ul of DNA extract, 0.4 U of Taq polymerase (Qiagen), 0.4uM of each primer, 0.2 mM of dNTPs (Qiagen), 1x Buffer (Qiagen) and 2.5 mM of MgCl2. Two negative controls containing the PCR mix without DNA were set on each plate. PCR cycling conditions were 12 min of initial denaturation at 95°C followed by 10 cycles of 15 sec at 94°C, 15 sec at specific annealing T°C (50C for all loci except locus 68 (48°C), loci 48, 82 and 96 (52°) and locus 5 (54°C)), 15 sec at 72°C and 30 cycles of 15 sec at 89°C, 15 sec at specific annealing T°C (same as above), 15 sec at 72°C and a final extension at 72°C for 10 min in Techgene and Eppendorf thermal cyclers. Samples were analysed on an ABI3700 machine and fragment sizes scored using Genescan3.5 and Genotyper 2.5 software (ABI).

Basic population genetics

Basic characteristics of these loci for our three study species have already been described in (Bouteiller Reuter et al., 2009). However, we report here the number of alleles per locus (Na) and their mean polymorphic informative content (PIC). PIC measures the information content of the loci for parentage analysis and is related to their expected heterozygosity (Marshall et al., 1998). We also calculated F_{IS} values for each species and F_{ST} between the different pairs of species using the *Fstat* software (Goudet, 1995). F_{IS} is the inbreeding coefficient and we compared this between the three *Sycoscapter* species. F_{ST} was used to measure genetic differentiation between the three co-habiting *Sycoscapter* species. PIC and *F* statistics were calculated based on n = 140, 47 and 54 females for species A, B, C respectively.

Matriline reconstruction

We first used STRUCTURE to assign each individual *Sycoscapter* wasp to species, as in a study of male fighting behaviour in these species (Cook et al., 2015). We then estimated the number of matrilines (sibships; i.e. offspring of one foundress) in the population (for each species) using a maximum likelihood method in COLONY (Wang, 2004). This software uses a group-likelihood approach to reconstruct matrilines allowing for typing errors in marker data. Genotyping errors can cause severe biases in sibship inference if they are ignored (Wang, 2004) and two classes of errors are taken into account. Class I errors are allelic dropouts; i.e. when PCR fails to amplify one of an individual's two alleles at a locus. Class II errors include a variety of possible stochastic typing errors. These can come from various sources including mutations, false alleles, miscalling, contaminant DNA and data entry (Wang, 2004). We reconstructed the matrilines for each species separately with an allelic dropout rate for the nine loci varying between 0.001 and 0.2 and a stochastic error rate between 0 and 0.1.

Foundress numbers, clutch size and clutch sex ratios

After assigning individuals to matrilines, we then determined offspring production patterns for individual foundresses. This allowed us to calculate foundress number distributions for each species and also how many offspring (clutch size), and what sex ratio, each foundress produced in a given fig.

Statistical analyses of sex ratios and offspring numbers

We explored reproductive patterns at different biological levels – species, clutch (offspring of one female in a fig) and brood (all conspecific wasps in a fig). For each species, we determined the foundress number distribution and sex ratio at the population level and tested for sex ratio bias. We also calculated the proportion of females developing in patches without conspecific males.

At the clutch level, we tested whether individual females adjust their sex ratios to their own clutch sizes to produce solitary male clutches and gregarious clutches with (n-1) females, as predicted by models (Greeff, 1997). Due to poor support for these predictions, we further tested a simpler model of whether mean clutch sex ratio (proportion males) decreased with the transition from solitary to gregarious clutches.

At the brood (fig) level, we tested whether sex ratio increased or decreased with brood size – alternative predictions of models that assume females are either informed (increase) or uninformed (decrease) about other foundresses laying eggs in a fig (Greeff, 1997). In addition, we tested if the overall brood size increased with the number of foundresses per fig.

All statistical analyses were performed in R (http://www.Rproject.org). We used general linear models (GLMs), with binomial errors for sex ratio (proportion) data and Poisson errors for low offspring number counts. We checked for over-dispersion by comparing the residual deviance with residual degrees of freedom. If necessary, we then applied quasi-binomial or quasi-poisson error structure and tested significance using F-tests or t-tests (Crawley, 2005). Finally, we used (a) exact binomial tests to test if predicted clutch compositions for solitary (prediction = male) and gregarious clutches (prediction = one male plus (n-1) females) were more or less likely than alternatives, and (b) a 2-sample test for equality of proportions (the the prop.test function in R) to test if sex ratios differed between solitary and gregarious clutches.

Results

Basic population genetics

All nine loci were amplified and used successfully in all three species and the number of alleles per locus varied from 3 to 21 (Supporting Information). The mean polymorphic informative content (PIC) of loci was high for *Sycoscapter* species B (0.60) and C (0.68) and medium (0.42) for species A. Genetic differentiation (F_{ST}) was significant between all species pairs (randomisation tests with Bonferroni correction, all $p < 0.001$). It was similar and very high between species A and either B (0.44) or C (0.41), and reduced but still high (0.23) between the two short ovipositor species, B and C. All three species also showed significant inbreeding (randomisation tests, all $p < 0.001$), with F_{IS} values of 0.31 for A, 0.24 for B and 0.30 for C.

Species level results

Our sample of 55 figs contained 202 *Sycoscapter* A wasps (1-25 per occupied fig) in 39 syconia, 82 *Sycoscapter* B wasps (1-10 per fig) in 29 figs, and 103 *Sycoscapter* C wasps (1-7 per fig) in 39 figs (Table 1). Roughly equal numbers of figs contained wasps from one (n=19), two (n=20) or all three (n=16) *Sycoscapter* species (Supporting Information).

Consequently, most wasps occurred in figs that also contained close congeners, making molecular species delimitation an essential first step.

The sibship reconstruction revealed 104 (A), 54 (B), and 68 (C) matrilines respectively and we estimated mean foundress numbers (SE) to be: A=2.7 (2.0), B=1.9 (1.4), C=1.7 (0.8). Typically, there were 2-3 foundresses per fig (Figure 1), but with up to ten for A, seven for B and four for C. All three species have female-biased population sex ratios (Table 2), but the bias is only significant in *Sycoscapter* A (sex ratio = 0.31, $p<0.001$, binomial test; *Sycoscapter* B, $p=0.43$, NS; *Sycoscapter* C, $p=0.48$, NS). The distribution of males and females across figs results in 10-22% of females developing in patches without mates, leading to constrained sex allocation (Tables 1 & S2).

Clutch sizes and sex ratios

In all three species females lay very small clutches, typically only 1 to 3 eggs per fig (Table 2), and solitary clutches are more common than gregarious ones. Clutches very rarely contained more than one male (Tables 2 & Supporting Information). The mean number of females per clutch was also very low (Table 2 & Supporting Information), but reached maxima of 11/8/5 for species A/B/C (Supporting Information).

Observed clutch sex ratios differ considerably from the basic predictions of solitary male clutches and gregarious clutches with n-1 females (Table 2 & Supporting Information). In fact, solitary clutches are only more likely to contain a male (33/47 cases) than a female in species C (Table 2). In gregarious clutches, cases with (n-1) females are actually significantly less common than alternative compositions in species A (Table 2). Deviation from the (n-1) prediction can be due to either no males or multiple males (Supporting Information).

Mean sex ratio does, however, differ between solitary and gregarious clutches (Table 3), and this leads to a decrease in sex ratio with clutch size when tested with logistic regressions: species A (t=-2.75; p=0.007; 7% deviance explained; n=103 clutches); species B (t=-2.36; p=0.02; 11% deviance explained; n=53 clutches); species C (t=-3.66; p=0.0005; 19% deviance explained; n=67 clutches). In all cases, there was slight over-dispersion so we used quasi-binomial errors and t-tests for significance.

In addition, females may lay eggs in more than one fig. Females of species A/B/C were found to have laid eggs in up to 3/2/4 figs on the same tree (Supporting Information). These are minimum estimates, as the number of figs sampled is far lower than the number of figs on a tree.

Brood sizes and sex ratios

At the brood (fig) level, there is considerable sex ratio variation, but no correlation with foundress number for any of the species: A (z=-0.32; p=0.75; df=1,37); B (z=-0.07; p=0.95; df=1,27); C (z=0.06; p=0.95; df=1,37). Brood sex ratio decreases with brood size (all conspecifics in a fig) in all three species (Figure 2), but the relationship is only significant in species C: A (t=-1.41; p=0.17; df=1,37); B (t=-1.53; p=0.13; df=1,27); C (t=-2.582; p= 0.014; df=1,37). In addition, there is a highly significant positive correlation between brood size and foundress number (Figure 3) in all three species: A (z=5.83; p<0.0001; 58% deviance explained); B (z=3.67; p<0.001; 49% deviance explained); C (z=2.78; p<0.006; 51% deviance explained).

Discussion

We applied microsatellite markers to three species of *Sycoscapter* wasps that co-exist in *Ficus rubiginosa* figs to establish their offspring allocation patterns. Foundresses of all three species produced very small clutches, typically laying only 2-3 eggs per fig (Tables 1 & 2). Theoretical models by Greeff (1997) predict that solitary clutches should be male and gregarious clutches contain (n-1) females. These predictions were not met by species A and B, although solitary clutches were more likely to be male in species C (Table 3). Brood level patterns result from combined offspring allocation by multiple foundresses. The emergent patterns are a strong increase in brood size with foundress number in all species (Figure 3), and a weaker decrease in sex ratio with brood size, significant only in species C (Figure 2). Brood sex ratio is not correlated with foundress number. At the population level, all three species have female-biased population sex ratios (Table 1), but the bias (sex ratio = 0.31) is only significant in species A. Meanwhile, 10-22% of females develop in patches without mates (Table 1), leading to a corresponding level of constrained sex allocation by females dispersing unmated.

The very small clutches produced by *Sycoscapter* wasps severely constrain their sex allocation options relative to fig-pollinating wasps, which typically have large clutch sizes of 10s or even >100 eggs. Greeff's (1997) offspring allocation models for non-pollinating fig wasps assume that they lay a few eggs in each of several figs. Our data provide supporting evidence for both very small clutches and several cases where a given female laid clutches in 2-4 different figs (Supporting Information). Although parameter values such as fecundity and foundress distributions across patches influence the details, Greeff's models essentially predict two types of clutches: (a) solitary males and (b) larger clutches with one male and (n-1) females. Overall, our data do not support prediction (a) since singletons were equally likely to be male or female in species A and B, and there were still many singleton females in species C (Table 3). The fit to prediction (b) is worse, with a significant excess of clutches that do not have (n-1) females in species A (Table 3).

The above patterns may reflect a genuine lack of fit to model predictions, e.g. because wasps adopt strategies that differ in detail from the alternatives considered in the game theoretic simulations. Another possibility is that developmental mortality may lead to a difference between primary and secondary sex ratios; e.g. singleton females may have originally had a brother in the same fig, but he died. Such patterns have been detected and explored considerably in distantly related bethylid wasps (Hardy & Cook, 1995; Hardy et al., 1998) that also have small clutches and local mating. A further possibility is sex allocation “mistakes” by ovipositing females, and the three explanations considered in this paragraph are not mutually exclusive.

At the brood level, sex ratio decreased with brood size in all three species (Figure 2), but the decrease was only significant for species C. This decrease is predicted by Greeff’s (1997) model for uninformed foundresses, whereas his model for informed foundresses predicts an increase. The limited correlation with brood level model predictions is unsurprising given that these are driven by underlying clutch allocation patterns that are also weak or absent in our data. Overall, species C shows some fit to predictions of the model for uninformed females, while species A and B do not.

Small brood sizes resulted in 10-22% of female wasps (Table 2) developing in patches without mates. These unmated females are subject to constrained sex allocation but can still potentially produce male offspring from unfertilised eggs (Godfray, 1990). However, Bean &

Cook (2001) estimated that 17% of males exit from their natal fig in *Sycoscapter australis.* A few might successfully enter other figs to search for mates, but the likelihood of dispersing and obtaining mates successfully appears very low. The high incidence of single sex patches should favour winged males (Hamilton, 1979) and this is supported by a comparative study across fig wasp species (Cook et al., 1997). However, winged males are unknown in the genus *Sycoscapter* and these wasps may be subject to phylogenetic inertia and unable to respond to this selection pressure (Cook et al., 1997; West et al., 1997).

Our data revealed very few clutches of more than four eggs (Tables S2, Supporting Information). *Sycoscapter* wasps are thought to be synovigenic, continually maturing eggs, so immediate fecundity might limit their clutch sizes. However, dissections revealed that females typically have 10-25 eggs available (JMM, unpubl. data) and other factors could also favour small clutches; e.g. bet-hedging on offspring survival by spreading risk of offspring mortality across patches (Rubenstein, 1982; Greeff, 1997). Additionally, adult females may be selected to make only short visits to each fig to reduce their own risk of predation by spiders, and especially ants, a pervasive threat to ovipositing fig wasps (Schatz et al., 2006; Wang et al., 2014).

In conclusion, we believe this to be the first study to use molecular markers to determine sex ratio and clutch sizes patterns in non-pollinating fig wasps and test directly predictions from theory. Molecular markers were crucial to assign individual wasps both to cryptic species and to sibships within these. We show that clutches are very small in all three species. Species A and B show little fit to predictions of sex ratio models, although gregarious broods are more female-biased than solitary ones. Species C fits some predictions of a model of sex allocation by uninformed foundresses. There are several taxonomically disparate non-pollinating fig wasp lineages (Cook & Rasplus, 2003) and similar molecular ecology studies of other species could test how clutch size varies across taxa, and if species less constrained by small clutch sizes display different sex allocation patterns.

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Contribution of authors

JMC, CR, JCM and SAW conceived the study. JCM conducted the field sampling and insect sorting. CR conducted the microsatellite studies. CR and JMC analysed the data. JMC wrote the paper with input from CR, JCM and SAW.

Supporting Information Short Legends

Table S1. Contents of each occupied fig for each of the three *Sycoscapter* species. Mating is constrained (Constraint=1) when females are in a fig with no conspecific males.

Table S2. Microsatellite genotypes for all wasps. NB males have only one allele per locus as they are haploid.

Conflict of Interest

The authors have no conflicts of interest to declare.

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Figure and Table Legends

Figure 1. The distribution of foundress number per fig (Species A hatched, B white and C black).

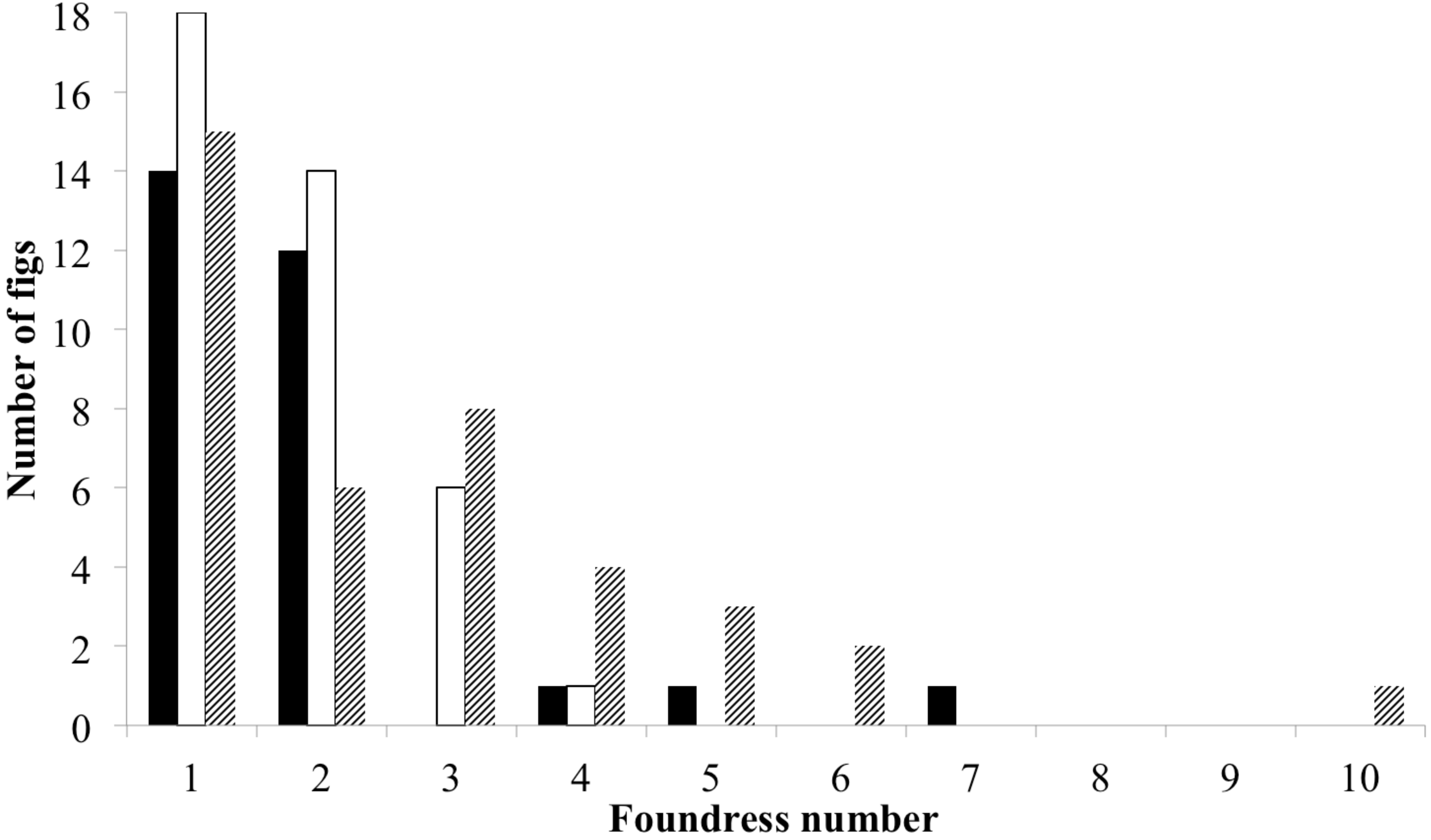
Figure 2. Brood sex ratio (proportion males) decreases with brood size number in Sycoscapter sp. A (top, triangles), B (middle, squares) and C (bottom, circles). The relationship is only significant in species C – see text for details.

Figure 3. Brood size increases significantly with foundress number in Sycoscapter sp. A (top, triangles), B (middle, squares) and C (bottom, circles) – see text for details.

Table 1. Population and fig level data for the three wasp species.

Table 2. Clutch sizes and sex ratios in the three wasp species.
Solitary clutches containing males and gregarious clutches with n-1 females are predictions from theoretical models. A significant ($p < 0.05$*, 0.01**, 0.001***) excess (*) or deficit ($^{\#}$) of the predicted clutch sex ratio compared to alternatives occurs in some cases.

Table 3. Comparison of sex ratios (SR) of solitary and gregarious clutches.
$P < 0.05$ (*), 0.001 (***).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14
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6
4
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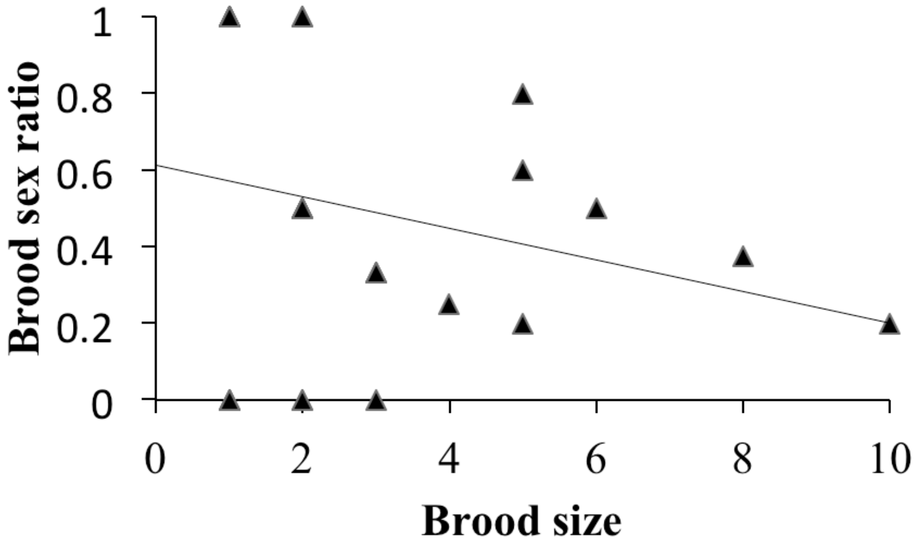
0
1
2
3
4
5
6
7
8
9
10
Foundress number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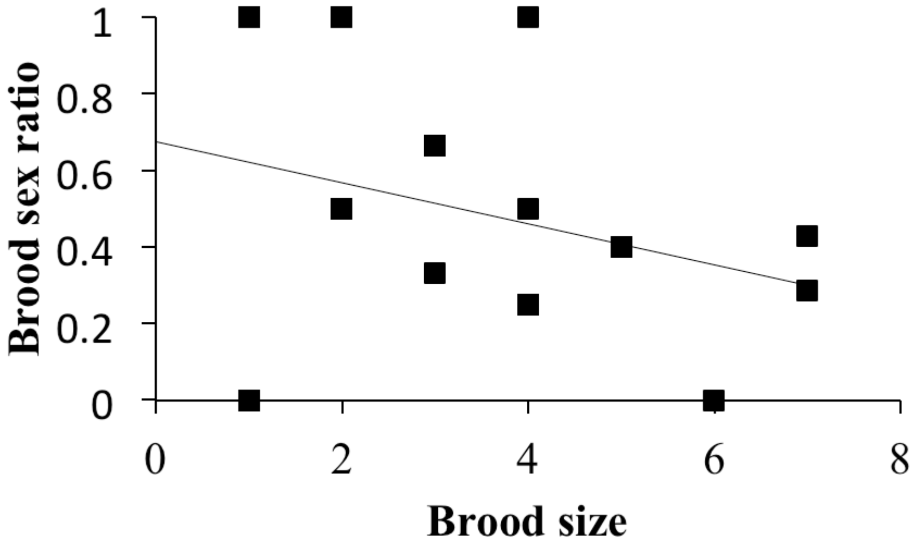
0.4
0.2
0
0
2
4
6
8
10
Brood size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0.2
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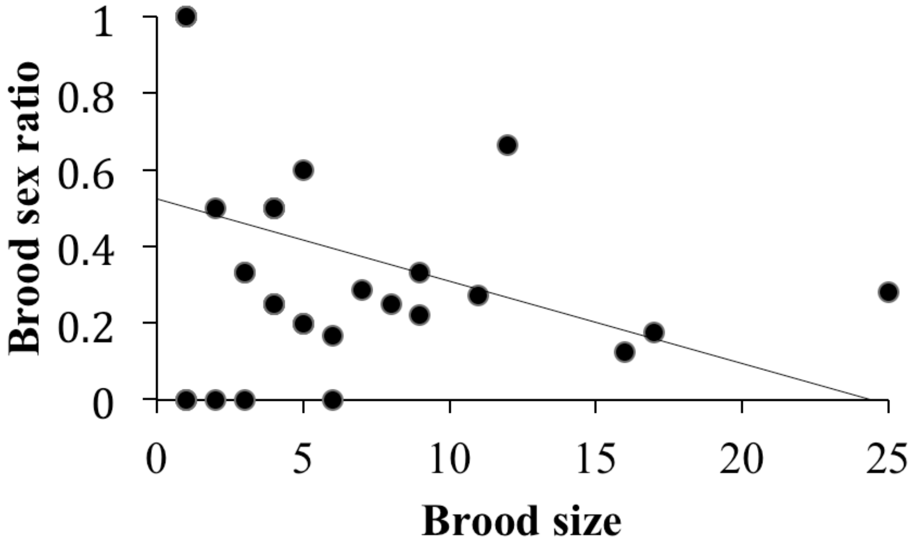
4
6
8
Brood size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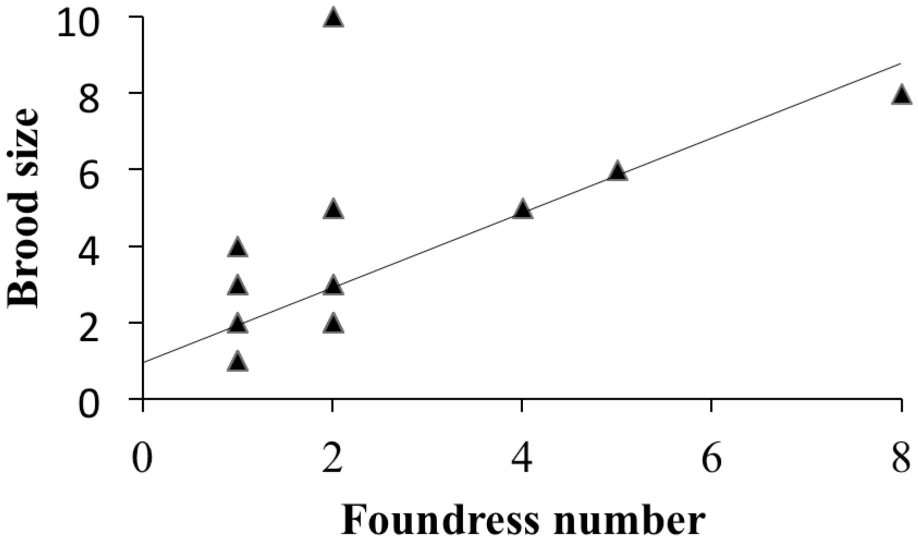
0.2
0
0
5
10
15
20
25
Brood size



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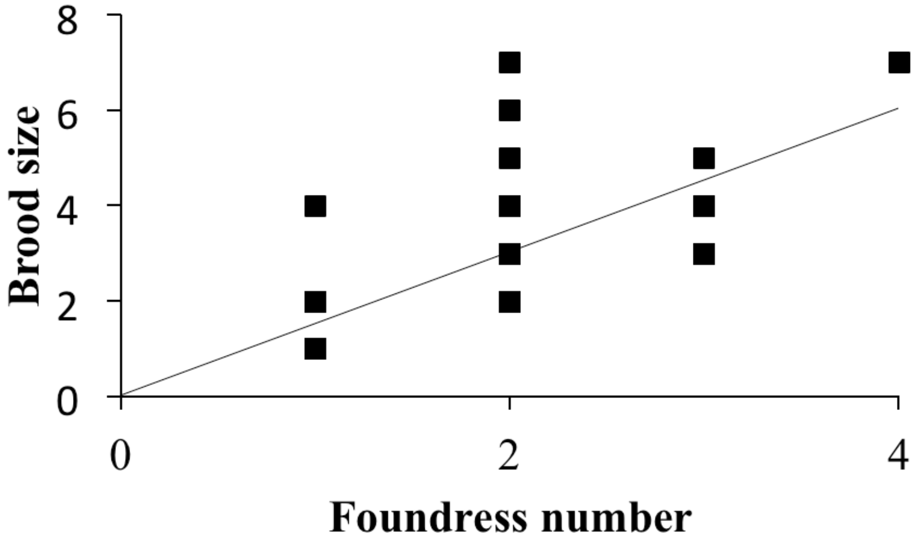
2
0
0
2
4
6
8
Foundress number



Brood size
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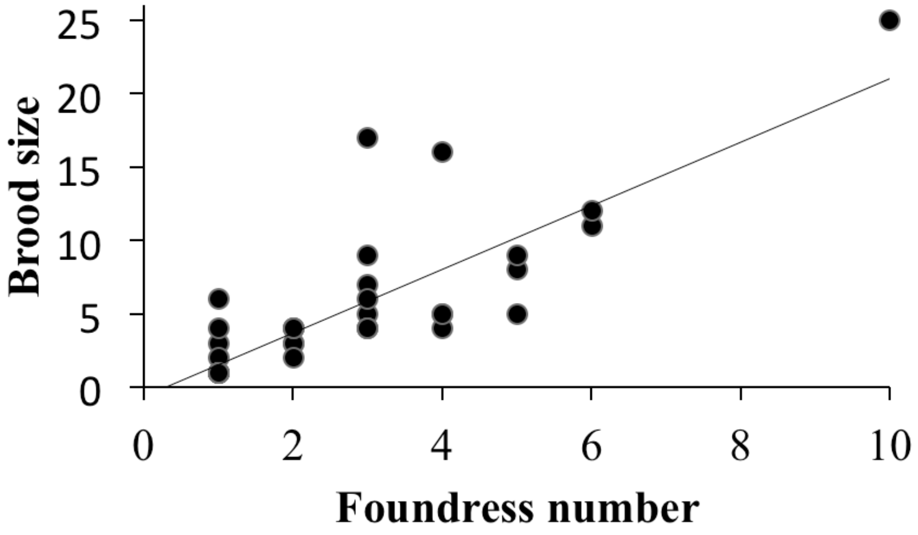
6
4
2
0
0
2
4
Foundress number



Brood size
25
20
15
10
5
0
0
2
4
6
8
10
Foundress number

Supporting information

This document provides detailed supporting information for the main document.

First, we provide a summary of allelic diversity at the microsatellite loci in Table S1. The individual genotypes for all individuals at all loci are then provided in Table S2. Finally, Table S3 provides the raw data on brood composition (all conspecific wasps in a fig) for all three wasp species and all figs.

Table S1. Allele numbers per locus in the three wasp species

Locus	Sp. B	Sp. C	Sp. A
48	6	10	4
68	6	9	3
71	9	15	3
82	9	16	5
85	6	12	9
89	14	8	5
95	8	8	4
96	4	21	16
Average	8.2	14.6	8.8

Table S1b then lists all genotypes for all individual wasps on the following 7 pages.

Fig ID	Ind ID	sex	5a	5b	48a	48b	68a	68b	71a	71b	82a	82b	85a	85b	89a	89b	95a	95b	96a	96b	Fig ID	family ID	Species
1001	5000	m	212	0	156	0	214	0	193	0	224	0	168	0	153	0	99	0	113	0	1001	28	B
1001	5001	m	208	0	142	0	218	0	181	0	209	0	168	0	137	0	97	0	113	0	1001	2012	A
1001	5002	m	212	0	148	0	220	0	203	0	208	0	168	0	151	0	95	0	138	0	1001	1007	C
1001	5003	m	214	0	156	0	214	0	197	0	221	0	170	0	153	0	101	0	115	0	1001	58	B
1001	5004	m	209	0	144	0	218	0	179	0	209	0	174	0	139	0	99	0	0	0	1001	2009	A
1001	5005	m	216	0	154	0	214	0	193	0	226	0	168	0	137	0	97	0	111	0	1001	19	B
1001	5006	f	209	213	142	144	218	218	179	179	209	210	168	168	141	145	97	97	0	0	1001	2009	A
1001	5007	f	213	215	142	144	218	218	179	179	209	209	168	174	139	145	97	99	109	109	1001	2009	A
1001	5008	f	214	214	152	158	214	214	191	195	220	221	168	170	153	163	101	101	111	115	1001	24	B
1001	5009	f	212	212	148	148	212	212	0	0	219	222	168	168	153	153	95	95	134	134	1001	1026	C
1001	5010	f	226	232	148	150	218	218	199	199	222	223	168	170	153	153	97	99	138	138	1001	1002	C
1001	5011	f	215	232	148	150	218	218	199	199	224	224	168	170	153	153	95	97	138	138	1001	1002	C
1001	5113	m	207	0	142	0	218	0	179	0	210	0	170	0	139	0	97	0	0	0	1001	2013	A
1001	5116	f	216	222	154	156	214	214	191	193	221	221	164	168	151	153	95	95	115	115	1001	10	B
1001	5117	f	214	214	152	158	214	214	191	198	220	221	168	170	0	0	0	0	111	111	1001	24	B
1003	5012	m	228	0	156	0	214	0	0	0	221	0	168	0	0	0	99	0	113	0	1003	2	B
1003	5013	m	226	0	150	0	220	0	199	0	225	0	166	0	153	0	95	0	0	0	1003	1015	C
1003	5014	m	216	0	154	0	214	0	0	0	226	0	168	0	137	0	97	0	113	0	1003	19	B
1003	5015	m	216	0	154	0	214	0	193	0	228	0	168	0	155	0	97	0	111	0	1003	19	B
1003	5016	f	218	228	156	156	214	214	191	191	221	221	168	170	137	137	99	99	113	115	1003	2	B
1003	5017	f	220	225	148	150	218	218	199	201	223	225	168	176	151	153	95	97	136	142	1003	1005	C
1003	5018	f	218	218	156	156	214	216	191	193	221	221	168	168	153	155	95	95	113	117	1003	2	B
1003	5019	f	220	225	150	150	218	218	201	201	223	225	168	176	151	153	97	97	0	0	1003	1005	C
1004	5020	m	226	0	148	0	218	0	199	0	224	0	170	0	153	0	99	0	136	0	1004	1002	C
1004	5021	m	213	0	142	0	218	0	179	0	209	0	170	0	137	0	97	0	0	0	1004	2004	A
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1004	5023	f	228	228	148	150	212	216	201	201	219	222	168	168	153	157	93	93	140	140	1004	1006	C
1004	5024	f	214	216	152	152	214	214	193	193	221	232	166	166	153	155	97	97	115	115	1004	27	B
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1004	5109	m	229	0	150	0	218	0	199	0	219	0	168	0	157	0	95	0	140	0	1004	1006	C
1005	5027	m	216	0	152	0	216	0	193	0	221	0	168	0	159	0	103	0	111	0	1005	1	B
1005	5028	m	210	0	150	0	212	0	201	0	224	0	168	0	153	0	95	0	134	0	1005	1009	C
1005	5029	m	214	0	154	0	214	0	0	0	224	0	168	0	153	0	0	0	113	0	1005	7	B
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1005	5035	f	216	218	154	156	214	216	193	193	219	226	168	169	159	159	97	103	111	113	1005	1	B
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1032	5070	m	213	0	142	0	218	0	179	0	210	0	168	0	137	0	97	0	132	0	1032	2003	A
1032	5071	f	213	229	142	142	218	218	179	179	209	210	168	168	137	137	97	97	0	0	1032	2003	A
1032	5072	f	208	208	142	142	218	218	179	179	209	210	168	172	139	141	97	97	0	0	1032	2016	A
1032	5073	f	212	214	156	156	216	216	189	193	226	228	168	170	137	137	97	97	111	111	1032	64	B
1033	5074	m	216	0	148	0	218	0	201	0	226	0	168	0	153	0	95	0	0	0	1033	1026	C
1033	5075	m	214	0	154	0	214	0	189	0	228	0	168	0	137	0	97	0	115	0	1033	22	B
1033	5076	f	214	220	154	154	214	214	189	193	226	228	168	169	165	165	97	97	113	115	1033	22	B
1033	5077	f	234	234	148	150	218	218	201	201	222	222	168	168	155	155	97	97	0	0	1033	1011	C
1033	5078	f	214	220	154	154	214	214	189	193	226	228	168	169	165	165	97	97	113	115	1033	22	B
1033	5115	m	234	0	150	0	218	0	201	0	222	0	166	0	155	0	97	0	138	0	1033	1011	C
1034	2003	f	212	214	156	156	214	214	193	197	219	226	168	168	153	161	99	99	111	115	1034	4	B
1034	2004	f	212	214	156	156	214	214	193	197	219	226	168	168	153	161	99	99	115	115	1034	4	B
1034	2005	f	212	214	156	156	214	214	193	197	219	226	168	168	153	161	99	99	111	115	1034	4	B
1034	5079	m	214	0	156	0	214	0	193	0	219	0	161	0	153	0	99	0	111	0	1034	4	B
1035	5120	m	236	0	150	0	216	0	199	0	224	0	168	0	153	0	95	0	0	0	1035	1010	C
1037	5080	m	207	0	142	0	218	0	179	0	211	0	172	0	143	0	97	0	0	0	1037	2005	A
1037	5081	m	214	0	158	0	214	0	189	0	228	0	168	0	0	0	103	0	0	0	1037	18	B
1037	5082	m	214	0	156	0	214	0	189	0	226	0	168	0	153	0	101	0	115	0	1037	12	B
1037	5083	m	216	0	150	0	218	0	199	0	225	0	166	0	153	0	95	0	0	0	1037	1019	C
1037	5084	m	207	0	142	0	218	0	179	0	209	0	172	0	139	0	97	0	0	0	1037	2006	A
1037	5085	m	212	0	156	0	214	0	0	0	221	0	168	0	153	0	97	0	113	0	1037	28	B
1037	5086	f	213	213	142	142	218	218	179	179	209	211	168	172	137	143	97	97	0	0	1037	2001	A
1037	5087	f	209	213	142	142	218	218	179	179	209	211	168	172	143	143	97	97	0	0	1037	2001	A
1037	5088	f	207	209	142	142	218	218	179	179	209	209	168	172	139	139	97	97	0	0	1037	2006	A
1037	5089	f	209	213	142	142	218	218	179	179	209	211	168	168	143	143	97	97	0	0	1037	2001	A

1037	5090	f	207	207	142	142	218	218	179	179	209	209	168	168	139	139	97	97	0	0	1037	2006	A
1037	5091	f	216	218	148	150	218	222	199	199	222	225	164	166	153	153	95	95	136	140	1037	1019	C
1037	5092	f	218	220	148	150	220	222	199	199	222	225	164	164	153	153	95	95	136	136	1037	1019	C
1037	5093	f	216	218	148	150	218	222	199	199	222	225	164	166	153	153	95	95	136	140	1037	1019	C
1037	5094	f	214	214	154	156	214	214	189	193	226	226	168	169	137	153	97	101	115	115	1037	12	B
1037	5121	m	212	0	152	0	216	0	193	0	228	0	168	0	155	0	107	0	115	0	1037	43	B
1038	2006	f	218	230	142	142	218	218	179	179	209	209	168	172	139	139	97	97	0	0	1038	2011	A
1038	5095	m	216	0	154	0	214	0	193	0	222	0	168	0	137	0	97	0	113	0	1038	9	B
1038	5096	m	218	0	142	0	218	0	179	0	209	0	168	0	139	0	97	0	0	0	1038	2011	A
1038	5097	m	214	0	144	0	212	0	199	0	221	0	166	0	153	0	93	0	0	0	1038	1017	C
1038	5098	m	218	0	142	0	218	0	179	0	209	0	168	0	139	0	97	0	0	0	1038	2011	A
1038	5099	f	218	230	142	142	218	218	179	179	209	209	168	172	139	139	97	97	0	0	1038	2011	A
1040	2010	f	207	218	142	142	218	218	181	181	209	210	168	170	139	141	97	97	0	0	1040	2010	A
1043	5100	m	229	0	135	0	218	0	179	0	210	0	168	0	137	0	97	0	0	0	1043	2003	A
1043	5101	f	208	221	142	142	218	218	181	181	209	210	168	168	139	139	97	99	153	153	1043	2012	A
1043	5102	f	208	221	142	142	218	218	181	181	209	210	168	168	139	139	97	99	0	0	1043	2012	A
1046	5103	m	214	0	148	0	0	0	198	0	223	0	166	0	155	0	95	0	138	0	1046	1024	C
1048	5104	m	212	0	156	0	214	0	193	0	221	0	168	0	155	0	0	0	113	0	1048	21	B
1048	5105	f	212	214	154	158	214	214	193	193	221	221	168	170	155	155	97	99	113	115	1048	28	B
1048	5106	f	214	216	154	158	214	214	193	193	221	221	168	170	137	155	99	99	113	115	1048	28	B
1048	5107	f	214	216	154	156	214	214	193	193	221	221	168	170	155	155	97	99	113	115	1048	28	B
1048	5108	f	212	214	154	156	214	214	193	193	221	221	168	170	153	153	97	99	113	115	1048	28	B
1101	5137	m	222	0	150	0	212	0	199	0	222	0	170	0	155	0	95	0	0	0	1101	1207	C
1101	5138	m	0	0	144	0	218	0	0	0	0	0	172	0	0	0	97	0	0	0	1101	2207	A
1102	5139	m	209	0	142	0	218	0	179	0	209	0	174	0	137	0	97	0	0	0	1102	2211	A
1102	5140	f	209	230	142	142	218	218	179	179	211	211	168	174	139	143	97	97	132	132	1102	2221	A
1102	5141	f	207	207	142	142	218	218	179	179	209	210	170	170	139	141	95	97	0	0	1102	2208	A
1102	5142	f	209	230	142	142	218	218	179	179	211	211	168	174	139	143	97	97	0	0	1102	2221	A
1102	5143	f	225	231	142	142	218	218	179	179	209	210	172	176	139	145	97	97	0	0	1102	2212	A
1105	5144	m	0	0	142	0	218	0	179	0	209	0	172	0	137	0	0	0	0	0	1105	2205	A
1105	5145	m	214	0	154	0	214	0	193	0	228	0	168	0	161	0	99	0	115	0	1105	116	B
1105	5146	m	223	0	142	0	218	0	179	0	210	0	172	0	139	0	97	0	132	0	1105	2205	A
1105	5147	m	211	0	142	0	218	0	179	0	211	0	168	0	139	0	97	0	0	0	1105	2220	A
1105	5148	f	0	0	142	142	218	218	179	179	209	210	170	170	137	139	97	97	132	132	1105	2205	A
1105	5149	f	206	223	142	142	218	218	179	179	209	210	170	172	137	139	97	97	0	0	1105	2205	A
1105	5150	f	0	0	142	142	218	218	179	179	210	210	170	170	139	139	97	97	132	132	1105	2205	A
1105	5151	f	208	212	142	144	218	218	179	179	210	211	168	168	139	141	97	97	0	0	1105	2206	A
1105	5152	f	206	207	142	142	218	218	179	179	210	210	170	170	139	139	97	97	132	132	1105	2205	A
1105	5153	f	206	223	142	142	218	218	179	179	209	210	170	172	137	139	97	97	132	132	1105	2205	A
1105	5154	f	209	224	142	150	218	220	179	179	218	218	166	170	153	155	93	93	136	136	1105	1206	C
1106	5155	m	0	0	0	0	218	0	0	0	0	0	178	0	0	0	0	0	132	0	1106	2231	A
1107	5156	m	216	0	158	0	214	0	0	0	228	0	168	0	137	0	107	0	111	0	1107	107	B
1108	5157	m	208	0	142	0	218	0	179	0	210	0	168	0	139	0	97	0	0	0	1108	2209	A
1108	5158	m	210	0	142	0	218	0	179	0	209	0	180	0	139	0	97	0	0	0	1108	2201	A
1108	5159	m	205	0	0	0	218	0	179	0	210	0	168	0	139	0	97	0	98	0	1108	2201	A
1108	5160	f	209	214	142	142	218	218	179	179	209	210	168	168	137	139	97	97	0	0	1108	2229	A
1108	5161	f	209	214	142	142	218	218	179	179	209	210	168	168	137	139	97	97	0	0	1108	2229	A
1108	5162	f	210	210	142	142	218	218	179	179	210	210	180	180	139	139	97	97	0	0	1108	2201	A
1108	5163	f	205	210	142	142	218	218	179	179	209	210	168	180	139	139	97	97	132	132	1108	2201	A
1108	5164	f	209	214	142	142	218	218	179	179	210	210	168	168	139	139	97	97	136	136	1108	2229	A
1108	5165	f	205	210	142	142	218	218	179	179	210	210	168	180	139	139	97	97	132	132	1108	2201	A
1108	5166	f	210	210	142	142	218	218	179	179	209	209	180	180	139	139	97	97	98	98	1108	2201	A
1108	5167	f	205	210	142	142	218	218	179	179	210	210	168	180	139	139	97	97	98	98	1108	2201	A
1108	5168	f	205	210	142	142	218	218	179	179	210	210	168	180	139	139	97	97	0	0	1108	2201	A
1108	5169	f	205	210	142	142	218	218	179	179	209	210	168	180	139	139	97	97	98	98	1108	2201	A
1108	5170	f	210	210	142	142	218	218	179	179	210	210	180	180	139	139	97	97	98	132	1108	2201	A
1108	5171	f	205	210	142	142	218	218	179	179	209	210	168	180	139	139	97	97	98	98	1108	2201	A
1108	5172	f	205	210	142	142	218	218	179	179	210	210	168	180	139	139	97	97	98	132	1108	2201	A
1108	5173	f	205	210	142	142	218	218	179	179	209	210	168	180	139	139	97	97	98	132	1108	2201	A
1109	5174	m	209	0	142	0	218	0	179	0	210	0	169	0	137	0	99	0	134	0	1109	2202	A
1109	5175	m	209	0	142	0	218	0	179	0	210	0	168	0	137	0	97	0	98	0	1109	2224	A
1109	5176	m	211	0	150	0	214	0	201	0	220	0	168	0	159	0	95	0	170	0	1109	1216	C
1109	5177	f	210	226	150	150	212	214	201	203	222	224	168	176	153	155	95	95	111	111	1109	1201	C

1109	5178	f	209	231	142	142	218	218	179	179	209	209	168	174	139	139	97	97	134	140	1109	2214	A
1109	5179	f	209	219	142	142	218	218	177	179	209	210	168	170	137	139	97	97	0	0	1109	2202	A
1109	5180	f	209	219	142	142	218	218	177	179	210	210	168	170	137	139	97	99	146	146	1109	2202	A
1109	5181	f	206	209	142	142	218	218	179	179	210	210	168	170	137	139	97	97	130	136	1109	2203	A
1109	5182	f	209	209	142	142	218	218	177	179	210	210	169	170	139	139	97	97	0	0	1109	2202	A
1109	5183	f	206	209	142	142	218	218	179	179	210	210	168	170	137	137	97	97	136	136	1109	2203	A
1109	5184	f	207	231	142	142	218	218	179	179	209	210	168	174	139	139	97	97	134	140	1109	2214	A
1109	5185	f	209	209	142	142	218	218	179	179	210	210	168	170	137	137	97	97	132	136	1109	2203	A
1109	5186	f	209	209	142	142	218	218	179	179	210	210	168	170	137	137	97	97	136	136	1109	2203	A
1109	5187	f	0	0	142	142	218	218	179	179	209	210	168	174	139	139	97	97	162	162	1109	2214	A
1109	5188	f	209	209	142	142	218	218	179	179	210	210	168	170	137	139	97	97	136	136	1109	2203	A
1109	5189	f	206	209	142	142	218	218	179	179	210	210	168	170	137	139	97	97	0	0	1109	2203	A
1109	5190	f	206	216	154	154	214	214	189	189	224	226	168	168	149	153	95	95	115	115	1109	119	B
1109	5191	f	207	231	142	142	218	218	179	179	209	209	168	174	139	139	97	97	0	0	1109	2214	A
1109	5192	f	207	231	142	142	218	218	179	179	209	209	168	174	139	139	97	97	0	0	1109	2214	A
1109	5193	f	210	210	150	150	214	214	203	203	219	224	168	176	153	159	95	95	136	136	1109	1201	C
1109	5194	f	214	216	152	154	214	214	0	0	221	232	164	168	137	151	97	103	111	115	1109	102	B
1109	5195	f	210	210	148	150	214	214	0	0	222	224	168	168	153	155	95	95	111	111	1109	1201	C
1110	5196	m	211	0	142	0	218	0	179	0	209	0	170	0	139	0	97	0	0	0	1110	2204	A
1110	5197	m	212	0	152	0	214	0	203	0	222	0	170	0	155	0	95	0	130	0	1110	1207	C
1110	5198	m	212	0	148	0	212	0	199	0	218	0	164	0	155	0	95	0	144	0	1110	1221	C
1110	5199	m	216	0	156	0	214	0	189	0	221	0	166	0	153	0	101	0	115	0	1110	101	B
1110	5200	f	214	214	142	142	218	218	181	181	209	209	168	168	139	141	97	97	0	0	1110	2216	A
1110	5201	f	209	214	142	142	218	218	179	179	205	209	172	174	139	139	97	97	132	132	1110	2204	A
1110	5202	f	209	211	142	142	218	218	179	179	205	209	170	174	139	139	97	97	132	132	1110	2204	A
1110	5203	f	212	216	154	156	214	214	189	193	221	221	166	166	153	153	101	101	115	115	1110	101	B
1110	5204	f	214	214	142	142	218	218	179	181	209	209	168	168	137	141	97	97	0	0	1110	2216	A
1110	5205	f	207	207	142	142	218	218	179	179	209	210	172	172	139	139	97	97	132	132	1110	2217	A
1110	5206	f	212	216	154	156	214	214	189	193	221	221	166	168	153	153	101	101	115	115	1110	101	B
1111	5207	m	222	0	154	0	214	0	199	0	226	0	168	0	155	0	101	0	113	0	1111	110	B
1111	5208	m	207	0	142	0	218	0	179	0	211	0	168	0	139	0	0	0	0	0	1111	2206	A
1111	5209	f	214	214	152	154	214	216	191	191	221	230	168	168	153	153	97	97	115	115	1111	121	B
1112	5210	m	215	0	148	0	220	0	201	0	219	0	166	0	153	0	93	0	142	0	1112	1223	C
1112	5211	m	226	0	150	0	212	0	199	0	217	0	162	0	155	0	95	0	130	0	1112	1215	C
1112	5212	f	212	214	148	156	220	220	199	201	219	222	166	166	153	153	93	95	164	164	1112	1208	C
1112	5213	f	212	214	148	156	220	220	197	201	219	222	166	166	153	153	93	95	164	164	1112	1208	C
1112	5214	f	207	209	142	142	218	218	179	181	209	209	172	176	139	141	97	97	0	0	1112	2222	A
1112	5215	f	214	220	148	148	212	220	197	201	219	223	166	166	153	153	93	95	142	164	1112	1208	C
1112	5216	f	207	209	142	142	218	218	179	181	209	209	172	176	139	141	93	97	140	140	1112	2222	A
1112	5217	f	207	212	142	142	218	218	179	181	209	209	168	172	139	141	93	97	140	140	1112	2222	A
1112	5218	f	207	212	142	142	218	218	179	181	209	209	168	172	139	141	93	97	140	140	1112	2222	A
1112	5219	f	207	212	142	142	218	218	179	181	209	209	168	172	139	141	93	97	140	140	1112	2222	A
1112	5220	f	207	212	142	142	218	218	179	181	209	209	168	172	139	141	93	97	115	115	1112	2222	A
1113	5221	m	209	0	144	0	218	0	179	0	210	0	168	0	137	0	97	0	0	0	1113	2224	A
1113	5222	m	212	0	156	0	214	0	191	0	221	0	168	0	153	0	95	0	113	0	1113	120	B
1113	5223	f	207	213	142	144	218	218	177	179	209	210	166	170	137	139	97	97	0	0	1113	2207	A
1113	5224	f	215	228	142	142	218	218	179	179	209	210	170	176	139	139	97	97	0	0	1113	2223	A
1113	5225	f	207	213	142	142	218	218	177	179	209	210	166	170	137	139	97	97	132	132	1113	2207	A
1114	5226	m	243	0	148	0	212	0	201	0	226	0	168	0	153	0	95	0	146	0	1114	1202	C
1114	5227	m	207	0	142	0	218	0	179	0	209	0	170	0	139	0	97	0	132	0	1114	2205	A
1114	5228	f	208	208	142	142	218	218	179	179	210	210	172	172	139	139	97	97	0	0	1114	2209	A
1114	5229	f	208	208	142	142	218	218	179	179	210	210	172	172	139	139	97	97	136	136	1114	2209	A
1114	5230	f	208	216	154	156	214	216	197	199	221	221	168	169	155	155	97	101	115	115	1114	111	B
1114	5231	f	238	243	148	148	214	214	197	201	208	226	168	170	153	155	93	95	0	0	1114	1202	C
1115	5232	m	213	0	142	0	218	0	179	0	209	0	168	0	139	0	97	0	0	0	1115	2227	A
1115	5233	f	222	222	148	150	212	218	199	201	218	221	168	168	153	153	0	0	140	140	1115	1205	C
1116	5234	m	209	0	142	0	218	0	179	0	209	0	174	0	139	0	97	0	132	0	1116	2101	A
1116	5235	m	214	0	154	0	214	0	191	0	221	0	168	0	137	0	103	0	115	0	1116	108	B
1116	5236	m	228	0	148	0	214	0	201	0	222	0	174	0	153	0	95	0	0	0	1116	1117	C
1116	5237	f	214	214	154	156	214	216	191	193	221	224	168	168	137	137	103	105	113	115	1116	105	B
1116	5238	f	206	222	142	142	218	218	179	179	209	210	170	180	137	139	97	97	134	134	1116	2134	A
1116	5239	f	208	227	142	142	218	218	179	179	209	209	170	172	139	139	97	97	132	132	1116	2106	A
1116	5240	f	208	227	142	142	218	218	179	179	210	210	170	172	139	139	97	97	132	132	1116	2111	A

1116	5241	f	207	209	142	142	218	218	179	179	211	211	168	174	139	139	97	97	134	134	1116	2115	A
1116	5242	f	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93	93	146	146	1116	1199	C
1117	5243	m	0	0	142	0	218	0	179	0	209	0	174	0	0	0	97	0	134	0	1117	2123	A
1117	5244	m	216	0	150	0	216	0	209	0	224	0	168	0	153	0	95	0	0	0	1117	1103	C
1117	5245	m	229	0	152	0	218	0	199	0	220	0	166	0	151	0	93	0	138	0	1117	1104	C
1117	5246	m	225	0	142	0	218	0	179	0	210	0	170	0	139	0	97	0	0	0	1117	2120	A
1117	5247	f	209	209	142	142	218	218	179	179	209	209	168	170	139	143	97	97	132	132	1117	2118	A
1117	5248	f	214	225	142	142	218	218	179	179	209	209	170	176	137	139	97	97	132	132	1117	2129	A
1117	5249	f	210	228	152	152	212	218	199	199	220	227	166	174	151	155	93	93	138	142	1117	1104	C
1118	5251	m	215	0	142	0	218	0	179	0	211	0	174	0	139	0	97	0	132	0	1118	2101	A
1118	5252	m	224	0	148	0	216	0	199	0	221	0	172	0	0	0	95	0	132	0	1118	1101	C
1118	5253	m	223	0	142	0	218	0	179	0	208	0	176	0	145	0	97	0	0	0	1118	2128	A
1118	5254	m	207	0	142	0	218	0	0	0	210	0	170	0	139	0	99	0	132	0	1118	2109	A
1118	5255	m	0	0	142	0	218	0	179	0	209	0	170	0	139	0	97	0	132	0	1118	2106	A
1118	5256	m	208	0	142	0	218	0	179	0	209	0	174	0	139	0	99	0	132	0	1118	2108	A
1118	5257	m	209	0	142	0	218	0	179	0	209	0	170	0	145	0	97	0	132	0	1118	2101	A
1118	5258	m	222	0	142	0	218	0	179	0	210	0	170	0	139	0	97	0	0	0	1118	2107	A
1118	5259	f	222	222	142	142	218	218	179	179	210	210	170	170	139	139	97	97	132	136	1118	2107	A
1118	5260	f	222	222	142	142	218	218	179	179	210	210	170	170	139	139	97	97	132	132	1118	2107	A
1118	5261	f	228	228	142	142	218	218	179	179	209	209	168	168	143	143	95	97	142	142	1118	2136	A
1118	5262	f	209	209	142	142	218	218	179	179	208	208	170	174	137	137	97	99	0	0	1118	2113	A
1118	5263	f	208	208	142	142	218	218	179	179	208	209	174	174	137	139	99	99	0	0	1118	2108	A
1118	5264	f	217	217	142	142	218	218	179	179	209	210	170	172	139	139	97	97	0	0	1118	2119	A
1118	5265	f	208	208	142	142	218	218	179	179	209	209	174	174	137	139	99	99	0	0	1118	2108	A
1118	5266	f	222	222	142	142	218	218	179	179	210	210	170	170	139	139	97	97	132	132	1118	2107	A
1118	5267	f	214	214	152	152	214	214	189	189	221	230	168	168	155	165	97	99	113	115	1118	103	B
1118	5268	f	228	228	142	142	218	218	179	179	209	209	168	168	143	143	95	97	142	142	1118	2136	A
1118	5269	f	208	215	142	142	218	218	179	179	209	210	169	170	139	145	97	97	132	132	1118	2101	A
1118	5270	f	208	209	142	142	218	218	179	179	210	211	169	174	139	139	97	97	132	132	1118	2101	A
1118	5271	f	207	217	142	142	218	218	179	179	209	210	170	172	139	139	97	99	132	132	1118	2109	A
1118	5273	f	207	217	142	142	218	218	179	179	209	210	170	172	139	139	97	99	0	0	1118	2109	A
1118	5274	f	222	222	142	142	218	218	179	179	209	210	170	170	139	139	97	97	130	130	1118	2130	A
1118	5275	f	208	208	142	142	218	218	0	0	209	210	169	170	139	145	97	97	132	132	1118	2101	A
1118	5276	f	217	217	142	142	218	218	179	179	209	210	170	172	139	139	97	97	0	0	1118	2119	A
1118	5277	f	208	215	142	142	218	218	179	179	210	211	169	174	139	139	97	97	132	132	1118	2101	A
1118	5278	f	222	222	142	142	218	218	179	179	210	210	170	170	139	139	97	97	132	132	1118	2107	A
1119	5279	m	216	0	148	0	212	0	199	0	218	0	166	0	151	0	95	0	144	0	1119	1121	C
1119	5280	m	209	0	142	0	218	0	179	0	210	0	168	0	143	0	97	0	130	0	1119	2126	A
1119	5281	m	209	0	142	0	218	0	179	0	211	0	174	0	139	0	97	0	0	0	1119	2101	A
1119	5282	m	236	0	148	0	212	0	201	0	219	0	176	0	153	0	93	0	138	0	1119	1113	C
1119	5283	m	209	0	142	0	218	0	179	0	210	0	168	0	143	0	97	0	130	0	1119	2126	A
1119	5284	f	227	227	142	142	218	218	179	179	209	209	170	172	139	139	97	97	132	132	1119	2106	A
1119	5285	f	208	227	142	142	218	218	179	179	209	209	170	172	139	139	97	97	132	132	1119	2106	A
1119	5286	f	209	209	142	142	218	218	179	179	210	210	174	174	143	143	97	97	140	140	1119	2140	A
1119	5287	f	211	235	142	142	218	218	179	179	209	209	170	174	139	141	97	97	138	138	1119	2124	A
1119	5288	f	206	209	142	142	218	218	179	179	211	211	168	174	139	139	97	97	134	134	1119	2115	A
1119	5289	f	230	234	148	150	212	218	199	199	218	225	166	168	153	153	93	97	136	136	1119	1111	C
1119	5290	f	208	227	142	142	218	218	179	179	209	210	170	172	139	139	97	97	136	136	1119	2106	A
1119	5291	f	227	227	142	142	218	218	179	179	209	209	170	172	139	139	97	97	0	0	1119	2106	A
1119	5292	f	209	209	142	142	218	218	179	179	210	210	174	174	143	143	97	97	113	113	1119	2140	A
1120	5293	m	209	0	142	0	218	0	179	0	209	0	168	0	139	0	97	0	0	0	1120	2135	A
1120	5294	m	228	0	148	0	218	0	199	0	223	0	172	0	153	0	95	0	132	0	1120	1101	C
1120	5295	m	218	0	148	0	216	0	201	0	227	0	166	0	153	0	95	0	136	0	1120	1119	C
1120	5296	m	214	0	156	0	214	0	193	0	221	0	168	0	0	0	97	0	111	0	1120	104	B
1120	5297	m	222	0	142	0	218	0	179	0	211	0	172	0	143	0	97	0	132	0	1120	2131	A
1120	5298	f	208	220	142	142	218	218	179	179	209	209	168	170	139	139	97	97	136	136	1120	2104	A
1120	5299	f	207	207	142	142	218	218	179	179	209	211	168	172	139	139	97	97	128	128	1120	2117	A
1120	5300	f	207	220	142	142	218	218	179	179	208	210	168	170	137	139	97	97	134	140	1120	2110	A
1120	5301	f	207	220	142	142	218	218	179	179	208	209	168	170	139	139	97	97	136	136	1120	2104	A
1120	5302	f	216	216	154	156	214	214	193	193	226	230	164	164	171	171	99	99	111	115	1120	115	B
1120	5303	f	220	228	148	148	212	216	199	199	219	224	166	168	153	155	95	95	126	152	1120	1103	C
1120	5304	f	220	220	142	142	218	218	179	179	208	209	168	176	139	139	97	97	136	140	1120	2104	A
1120	5305	f	207	207	142	142	218	218	179	179	209	211	168	168	139	139	97	97	130	132	1120	2117	A

1121	5306	m	223	0	142	0	218	0	179	0	209	0	170	0	141	0	97	0	115	0	1121	2112	A
1121	5307	m	214	0	148	0	220	0	201	0	219	0	166	0	153	0	93	0	144	0	1121	1114	C
1121	5308	m	214	0	154	0	214	0	201	0	228	0	170	0	137	0	101	0	115	0	1121	116	B
1121	5309	m	213	0	142	0	218	0	179	0	209	0	168	0	141	0	97	0	132	0	1121	2116	A
1121	5310	m	223	0	142	0	218	0	179	0	209	0	170	0	139	0	97	0	136	0	1121	2112	A
1121	5311	m	227	0	142	0	218	0	179	0	210	0	168	0	139	0	97	0	138	0	1121	2141	A
1121	5312	m	213	0	142	0	218	0	179	0	209	0	168	0	141	0	97	0	132	0	1121	2116	A
1121	5313	m	207	0	142	0	218	0	179	0	209	0	176	0	139	0	97	0	136	0	1121	2104	A
1121	5314	m	232	0	142	0	218	0	181	0	209	0	172	0	139	0	97	0	136	0	1121	2143	A
1121	5315	m	211	0	142	0	218	0	179	0	209	0	170	0	139	0	97	0	136	0	1121	2107	A
1121	5316	f	214	216	148	154	212	220	199	199	219	223	166	168	153	155	93	93	144	144	1121	1114	C
1121	5317	f	213	234	142	142	218	218	179	179	209	211	168	170	139	141	97	97	132	132	1121	2116	A
1121	5318	f	210	212	150	152	212	216	197	199	222	227	162	166	153	153	95	97	134	140	1121	1120	C
1121	5319	f	210	212	152	152	212	216	197	199	222	227	162	166	153	153	95	97	134	144	1121	1120	C
1121	5320	f	211	222	142	142	218	218	179	179	209	210	168	170	139	139	97	97	132	132	1121	2107	A
1121	5321	f	213	213	142	142	218	218	179	179	209	211	168	168	139	141	97	97	132	132	1121	2116	A
1121	5322	f	213	234	142	142	218	218	179	179	209	211	168	170	139	141	97	97	132	132	1121	2116	A
1122	5323	m	210	0	150	0	220	0	201	0	222	0	166	0	157	0	0	0	0	0	1122	1109	C
1122	5324	m	209	0	142	0	218	0	179	0	209	0	170	0	139	0	97	0	136	0	1122	2112	A
1122	5325	m	218	0	150	0	212	0	199	0	224	0	166	0	157	0	95	0	140	0	1122	1118	C
1122	5326	m	234	0	148	0	212	0	201	0	222	0	166	0	155	0	93	0	0	0	1122	1114	C
1122	5327	m	226	0	150	0	212	0	199	0	224	0	166	0	153	0	0	0	140	0	1122	1118	C
1122	5328	f	209	227	142	142	218	218	179	179	210	210	170	172	139	139	97	97	132	140	1122	2111	A
1122	5329	f	206	209	142	142	218	218	179	179	209	209	168	170	139	139	97	97	132	142	1122	2118	A
1122	5330	f	209	210	142	142	218	218	179	179	209	209	170	170	139	141	97	97	115	134	1122	2112	A
1123	5331	m	213	0	142	0	218	0	179	0	209	0	170	0	139	0	97	0	134	0	1123	2127	A
1123	5332	m	221	0	144	0	218	0	179	0	209	0	172	0	137	0	97	0	134	0	1123	2103	A
1123	5333	f	215	218	150	150	212	214	199	201	219	225	166	168	153	153	93	103	134	142	1123	1106	C
1123	5334	f	226	226	142	144	218	218	179	179	208	209	176	176	137	137	97	97	134	140	1123	2103	A
1123	5335	f	221	226	142	144	218	218	179	179	208	209	172	176	137	137	97	97	132	132	1123	2103	A
1124	5336	m	228	0	142	0	218	0	179	0	210	0	168	0	139	0	97	0	132	0	1124	2136	A
1124	5337	m	207	0	142	0	218	0	179	0	211	0	172	0	139	0	95	0	132	0	1124	2102	A
1124	5338	f	214	224	148	152	216	218	199	199	221	229	168	168	153	153	95	95	0	0	1124	1101	C
1124	5339	f	207	207	142	144	218	218	179	179	209	211	172	172	139	139	97	97	132	132	1124	2102	A
1124	5340	f	207	217	142	142	218	218	179	179	209	209	172	172	139	139	97	97	132	138	1124	2145	A
1124	5341	f	207	207	142	144	218	218	179	179	211	211	172	172	139	139	97	97	132	132	1124	2102	A
1124	5342	f	207	209	142	144	218	218	179	179	209	211	172	172	139	139	95	97	0	0	1124	2102	A
1124	5343	f	209	224	142	142	218	218	177	179	208	209	170	174	137	139	97	97	134	134	1124	2123	A
1124	5344	f	210	210	142	142	218	218	179	179	209	210	168	170	139	139	97	97	130	138	1124	2144	A
1124	5345	f	207	207	142	142	218	218	179	179	209	209	172	172	139	139	97	97	132	144	1124	2145	A
1125	5346	m	218	0	148	0	212	0	207	0	224	0	174	0	153	0	95	0	0	0	1125	1105	C
1126	5347	m	208	0	142	0	218	0	177	0	209	0	170	0	141	0	97	0	0	0	1126	2125	A
1126	5348	m	218	0	150	0	218	0	207	0	223	0	168	0	153	0	95	0	140	0	1126	1105	C
1126	5349	f	207	212	142	142	218	218	179	179	209	209	168	168	137	139	97	97	132	132	1126	2139	A
1127	5350	m	0	0	148	0	212	0	0	0	0	0	168	0	155	0	97	0	138	0	1127	1103	C
1127	5351	m	214	0	154	0	214	0	191	0	228	0	168	0	153	0	95	0	115	0	1127	108	B
1127	5352	m	211	0	150	0	220	0	199	0	225	0	168	0	155	0	97	0	136	0	1127	1112	C
1127	5353	m	209	0	142	0	218	0	179	0	209	0	172	0	139	0	97	0	0	0	1127	2123	A
1127	5354	m	224	0	152	0	218	0	201	0	223	0	168	0	153	0	95	0	0	0	1127	1101	C
1127	5355	f	208	226	142	142	218	218	179	179	209	211	168	170	139	141	97	97	132	132	1127	2125	A
1127	5356	f	216	216	148	148	214	220	199	199	225	225	168	168	153	155	95	95	136	140	1127	1112	C
1127	5357	f	209	221	142	142	218	218	179	179	209	209	168	172	139	139	97	97	134	140	1127	2114	A
1127	5358	f	216	216	148	148	214	220	199	199	225	225	168	168	153	155	95	95	140	140	1127	1112	C
1127	5359	f	209	221	142	142	218	218	179	179	209	209	168	172	139	139	97	97	136	136	1127	2114	A
1127	5360	f	220	220	148	150	212	212	197	199	226	226	168	168	155	157	93	93	130	130	1127	1110	C
1127	5361	f	217	217	142	142	218	218	179	179	209	210	170	178	139	143	97	97	134	144	1127	2119	A
1127	5362	f	216	216	148	148	214	220	199	199	225	225	168	168	153	155	95	95	140	140	1127	1112	C
1128	5363	m	209	0	142	0	218	0	179	0	209	0	170	0	139	0	97	0	0	0	1128	2127	A
1128	5364	m	216	0	150	0	218	0	179	0	224	0	166	0	153	0	101	0	0	0	1128	1115	C
1128	5365	m	216	0	156	0	214	0	193	0	221	0	170	0	157	0	99	0	115	0	1128	107	B
1128	5366	f	216	216	156	156	214	216	193	201	221	221	168	168	153	153	97	97	115	115	1128	106	B
1128	5367	f	209	217	140	142	218	218	179	179	209	209	168	170	137	139	97	97	132	136	1128	2122	A
1128	5368	f	209	217	140	142	218	218	179	179	209	209	168	170	137	139	97	97	132	136	1128	2122	A

1128	5369	f	218	218	148	148	218	218	199	199	218	225	166	166	153	161	95	95	142	142	1128	1111	C
1128	5370	f	209	217	140	142	218	218	179	179	209	209	168	170	137	139	97	97	128	132	1128	2122	A
1129	5371	m	210	0	152	0	212	0	197	0	222	0	170	0	155	0	93	0	128	0	1129	1107	C
1129	5372	m	206	0	142	0	218	0	181	0	210	0	168	0	139	0	97	0	132	0	1129	2105	A
1129	5373	m	223	0	150	0	220	0	199	0	222	0	168	0	157	0	93	0	146	0	1129	1109	C
1129	5374	f	0	0	142	142	210	218	179	181	0	0	170	178	139	139	97	97	130	138	1129	2130	A
1129	5375	f	214	214	142	142	218	218	181	181	0	0	168	176	139	139	97	97	132	132	1129	2105	A
1129	5376	f	210	218	150	152	212	212	199	203	220	222	170	172	153	155	93	93	128	128	1129	1107	C
1129	5377	f	207	210	142	142	218	218	179	179	209	209	170	170	137	139	97	97	132	136	1129	2121	A
1130	5378	m	208	0	142	0	218	0	181	0	209	0	170	0	137	0	97	0	132	0	1130	2121	A

fig	species	male	female	total	constraint	unmated
1001	A	3	2	5	0	0
1004	A	1	0	1	0	0
1015	A	0	1	1	1	1
1021	A	0	1	1	1	1
1022	A	1	0	1	0	0
1023	A	1	0	1	0	0
1024	A	0	3	3	1	3
1031	A	0	2	2	1	2
1032	A	2	2	4	0	0
1037	A	2	5	7	0	0
1038	A	2	2	4	0	0
1040	A	0	1	1	1	1
1043	A	1	2	3	0	0
1101	A	1	0	1	0	0
1102	A	1	4	5	0	0
1105	A	3	6	9	0	0
1106	A	1	0	1	0	0
1108	A	3	14	17	0	0
1109	A	2	14	16	0	0
1110	A	1	5	6	0	0
1111	A	1	0	1	0	0
1113	A	1	3	4	0	0
1114	A	1	2	3	0	0
1115	A	1	0	1	0	0
1116	A	1	4	5	0	0
1117	A	2	2	4	0	0
1118	A	7	18	25	0	0
1119	A	3	8	11	0	0
1120	A	2	6	8	0	0
1121	A	8	4	12	0	0
1122	A	1	3	4	0	0
1123	A	2	2	4	0	0
1124	A	2	7	9	0	0
1126	A	1	1	2	0	0
1127	A	1	4	5	0	0
1128	A	1	3	4	0	0
1129	A	1	3	4	0	0
1130	A	1	0	1	0	0
1222	A	0	6	6	1	6
Totals		**62**	**140**	**202**	**6**	**14**

fig	species	male	female	total	constraint	unmated
1001	B	3	3	6	0	0
1003	B	3	2	5	0	0
1004	B	0	3	3	1	3
1005	B	2	8	10	0	0
1011	B	2	0	2	0	0
1016	B	1	1	2	0	0
1018	B	3	5	8	0	0
1019	B	1	2	3	0	0

1022	B	2	0	2	0	0
1031	B	0	1	1	1	1
1032	B	0	2	2	1	2
1033	B	1	2	3	0	0
1034	B	1	3	4	0	0
1037	B	4	1	5	0	0
1038	B	1	0	1	0	0
1048	B	1	4	5	0	0
1105	B	1	0	1	0	0
1107	B	1	0	1	0	0
1109	B	0	2	2	1	2
1110	B	1	2	3	0	0
1111	B	1	1	2	0	0
1113	B	1	0	1	0	0
1114	B	0	1	1	1	1
1116	B	1	1	2	0	0
1118	B	0	1	1	1	1
1120	B	1	1	2	0	0
1121	B	1	0	1	0	0
1127	B	1	0	1	0	0
1128	B	1	1	2	0	0
Totals		**35**	**47**	**82**	**6**	**10**

fig	**species**	**male**	**female**	**total**	**constraint**	**unmated**
1001	C	1	3	4	0	0
1003	C	1	2	3	0	0
1004	C	2	2	4	0	0
1005	C	2	5	7	0	0
1007	C	0	1	1	1	1
1010	C	1	1	2	0	0
1011	C	1	1	2	0	0
1015	C	1	0	1	0	0
1018	C	0	1	1	1	1
1019	C	2	1	3	0	0
1022	C	0	6	6	1	6
1030	C	2	0	2	0	0
1032	C	2	3	5	0	0
1033	C	2	1	3	0	0
1035	C	1	0	1	0	0
1037	C	1	3	4	0	0
1038	C	1	0	1	0	0
1046	C	1	0	1	0	0
1101	C	1	0	1	0	0
1105	C	0	1	1	1	1
1109	C	1	3	4	0	0
1110	C	2	0	2	0	0
1114	C	1	1	2	0	0
1115	C	0	1	1	1	1
1116	C	1	1	2	0	0
1117	C	2	1	3	0	0
1118	C	1	0	1	0	0
1119	C	2	1	3	0	0

1120	C	2	1	3	0	0
1121	C	1	3	4	0	0
1122	C	4	0	4	0	0
1123	C	0	1	1	1	1
1124	C	0	1	1	1	1
1125	C	1	0	1	0	0
1126	C	1	0	1	0	0
1127	C	3	4	7	0	0
1128	C	1	1	2	0	0
1129	C	2	1	3	0	0
1222	C	2	3	5	0	0
Totals		**49**	**54**	**103**	**7**	**12**