

Population size and growth rate, sex ratio and behaviour in the ant isopod, *Platyarthrus hoffmannseggii*

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(With figure in the text)

Female-biased sex ratios are often associated with small, isolated populations. These conditions are exhibited in populations of *Platyarthrus hoffmannseggii* (Brandt, 1833), a small, blind woodlouse which lives almost solely in ant nests. This study was undertaken to determine how sex ratio varies with population size in *P. hoffmannseggii* and how both of these factors affect population growth rate. To accomplish this, a total of 2155 of these isopods were collected from 20 nests of the ant *Lasius flavus* (Fabricius, 1781). The majority of the isopod populations were female-biased. The behaviour and survivorship of the isopods in their own and foreign ant colonies were compared and suggest that the free movement of *P. hoffmannseggii* individuals among ant colonies may be extremely limited. These studies also show how isopods are nutritionally linked to their hosts. Measurement of the woodlice revealed two distinct size/age classes in each population and allowed the change in sex ratio from one generation to the next to be estimated. Female-biased populations produce in future generations relatively more females and fewer males than populations of a similar size with a sex ratio of unity. There was no correlation between the degree of female bias and the rate of population growth. These findings are reviewed in the light of recent theoretical sex ratio models and the possible control of the isopods' sex allocation by unusual chromosomal mechanisms and intracellular parasites.

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Introduction

Strategies of reproductive sex allocation which determine population sex ratios have recently attracted much theoretical and empirical attention because relatively simple models can be used to make quantitative predictions about the fitness of individuals (Charnov, 1982; Bulmer, 1986). Sex

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ratios with large deviations from unity are most commonly found in populations that are very small or those with a geographical structure so that they consist of small subpopulations with low rates of immigration and emigration (Bulmer, 1986). A classic example are sex ratios resulting from local mate competition, in which individuals in small groups produce female-biased progeny to maximize their fitness by minimizing competition among their sons (Hamilton, 1967; Nunney, 1985).

Female-biased sex ratios are known in a wide variety of terrestrial isopods in a great diversity of habitats (Vandel, 1938; Legrand & Juchault, 1972; Johnson, 1977; Katakura, 1984). However, very little is known about the effective breeding population size in the vast majority of isopods (but see Linsenmair, 1985 and references therein). Apart from direct effects of population size and population structure, two other factors are believed to have a possible role in producing female-biased sex ratios in terrestrial isopods: (a) their unusually complicated chromosomal sex determination (Bull, 1983; Katakura, 1984); and (b) the presence of intracellular parasites (Juchault & Legrand, 1970, 1972; Legrand & Juchault, 1972; Johnson, 1977), similar to the son-killer parasites in *Drosophila* and *Nasonia* (see Williamson & Poulson, 1979 and Skinner, 1985; Werren, Skinner & Huger, 1986, respectively), that are inherited through female lines. In either case, the spatial structure of isopod populations is likely to be of crucial importance in preventing the extinction of female-biased populations, and any sex ratio controlling parasites they may support. Whether or not female-biased brood production is inherited in isopods genetically or via intracellular parasites, the consequences will be similar to those apparently caused by chromosomal anomalies in the African butterfly, *Acraea encedon*, which lead to strains of females that produce only female offspring. It appears that meiotic drive of the Y-chromosome in these butterflies results in a strain of females that produce only female offspring. If such strains become increasingly common, males will become so rare that in a random mating population extinction is likely to result. Models of these butterfly populations have shown that this sex ratio polymorphism can only be maintained if normal females have a higher mating success or the population is structured geographically such that subpopulations of mostly abnormal females periodically become extinct and are re-invaded by normal female migrants from more healthy colonies (Heuch, 1978; Heuch & Chanter, 1982; Bulmer, 1986). To determine what maintains female biases in populations of terrestrial isopods, information is therefore required on both the deme structure and effect of sex ratio on population growth rates. A prime candidate for such a study is the isopod *Platyarthrus hoffmannseggi* (Brandt, 1833) which is a guest of ant colonies. *Platyarthrus hoffmannseggi* is known to live almost exclusively in the nests of ants and to have female-biased sex ratios (Standen, 1912; Vandel, 1962; Bernard, 1968). The movement of such guests between ant colonies is often severely restricted because they take on the colony-specific odour of their hosts (Van der Meer & Wojcik, 1982).

In this paper, we examine growth rate and change in sex ratio in 20 populations of *P. hoffmannseggi* in the discrete nest mounds of the ant *Lasius flavus*. The yellow meadow ant *Lasius flavus* is well known for its habit of building conspicuous, regularly-spaced, nest mounds. Such mounds often contain 100 or more litres of soil and persist for decades (King, 1981). Ants in neighbouring mounds are mutually hostile and maintain underground feeding territories (Waloff & Blackith, 1962; Pontin, 1963). We analyse the behaviour and survivorship of *P. hoffmannseggi* to determine whether they can move freely between host nests and we also elucidate the nutritional link between these ant-guests and their hosts. In addition, we report the first observations of mating and fighting behaviour in this isopod.

Materials and methods

Twenty discrete populations of *P. hoffmannseggi* were sampled from individual *Lasius flavus* nest-mounds in Black Rock Drove, Cheddar Gorge, Somerset, between 14 October 1984 and 13 March 1985. Each *L. flavus* nest-mound was completely excavated and all the *P. hoffmannseggi* were removed in the laboratory from the finely sifted soil. The head capsule of every isopod was measured at its widest point to an accuracy of 0.025 mm as a reliable measure of body size (Sutton, 1980) and its sex determined by examination of the exopodites and endopodites of the 1st and 2nd pleopods. Only isopods with obvious external genitalia were included in the data. The frequency of isopods that were excluded because their sex could not be easily determined was less than 1 in 100. In addition, in 13 of the 20 nests sampled, the smallest individuals were clearly male, so that our census did not overestimate the number of females by assigning small, sexually ambiguous individuals to the female category. When used in behavioural studies or experiments, the isopods were not sexed and measured until the end of the study.

A culturing method was developed which permitted close observation of the isopods and the ants in artificial soil-free nests. The nests were constructed of a 2-mm thick cardboard floor placed on a glass sheet of the same size. Walls and central dividers were made of card and held in position with masking tape; the card was kept moist by cellulose wicks leading from the nest to a dish of water. A roof of large microscope slides supported by the nest dividers allowed access to all parts of the nest. A plastic tube 40 mm long, internal diameter 3.5 mm, connected the inside of the nest with a foraging arena in which egg- and honey-based ant food (Bhatkar & Whitcomb, 1970) was always available. The nest could be observed through a binocular microscope mounted on a free-moving platform. All light was excluded save for an optical fibre ring, mounted round the objective lens of the microscope, linked to a cold light source giving dim white light which did not appear to disturb either ants or isopods.

On the basis of a series of 1 h observation bouts, ethograms were constructed for *P. hoffmannseggi* with their own ants and with ants from unrelated *L. flavus* nests to which they were introduced (the former will be termed 'established' isopods, the latter 'introduced'). The isopods that had been introduced to unfamiliar ants were observed at intervals over an 8-day period. Introduced and established isopods received equal handling. A large nest 300 mm by 300 mm was used for introduced *P. hoffmannseggi* because the colony was quite large (2000 ants), whereas a smaller nest 120 mm by 150 mm containing approximately 300 ants housed 8 established isopods. In neither nest did the isopods appear to be restricted by the density of ants. Queenless ant colonies with all stages of brood were used. At the beginning of each observation bout a single isopod was selected at random and continually observed for an hour. Each behavioural act exhibited by this focal animal (Altmann, 1974) was recorded. A behaviour was defined as a single logical unit such as grooming. A total of 20 h of such observation were made for both introduced and established isopods. During the course of these observations the vital dye, neutral red, was introduced to the ants' food in the foraging arenas. The isopods had no direct access to this food.

To determine the effect of host familiarity on isopod survival, 44 isopods were reintroduced to their own colony in an artificial nest following the usual sifting of nest soil and separation of ants and isopods. At the same time, 40 isopods were removed from their own ant colony and introduced to a culture with a similar density of *L. flavus* workers from an unfamiliar colony. After 40 days the number of surviving isopods in these different cultures were counted.

Results

Sex ratios

The populations of *P. hoffmannseggi* contained from 20 to 495 individuals ($\bar{x} = 108$, S.D. = 117) and these were found to have sex ratios, expressed as proportion of female, of between 0.45 and 0.76 (Table I). Female-biased sex ratios were seen in 14 out of the 20 nests, although only six of

TABLE I
Population data for *Platyarthus hoffmannseggi* from 20 nests of *Lasius flavus*

Nest	Population size	Estimated number of each sex in each age class				Overall proportion female	Growth rate ¹
		M ₁	F ₁	M ₂	F ₂		
A	57	13.5	11	17.5	15	0.45	1.33
B	96	18	26	20	32	0.60*	1.18
C	25	3	8.5	3	10.5	0.76**	1.17
D	123	17.5	17	35.5	53	0.57	2.56
E	98	21.5	26	26.5	24	0.51	1.06
F	143	11	71	23	48	0.76**	0.87
G	21	1	5	9	6	0.52	2.50
H	80	15	15	19	31	0.57	1.67
	20	0	2	10	8	0.50	9.00
J	193	43.5	47.5	38.5	63.5	0.57**	1.12
K	100	24.5	26	29.5	20	0.46	0.98
L	319	83	63	85	88	0.47	1.18
M	42	11	8.5	11	11.5	0.48	1.15
N	72	21	13	15	23	0.50	1.12
O	29	5	10	6	8	0.62	0.93
P	30	6	8	5	11	0.63	1.14
Q	39	12	18.5	1	7.5	0.67**	0.28
R	151	38	31	34	48	0.52	1.19
S	22	4	3	4	11	0.64	2.14
T	495	89	104	99	203	0.62**	1.56

¹ Growth rate estimated as number of young (new age class) individuals divided by the number of older age class individuals

* χ^2 : $P < 0.05$

** $P < 0.01$

these deviations from unity were significant (χ^2 tests, $P < 0.05$). There were no significantly male-biased sex ratios. The overall sex ratio of the 2155 isopods collected was 0.57 ($\chi^2 = 40.93$, $P < 0.01$).

Size-frequency histograms are distinctly bimodal for each sex in each population (see Fig. 1). These modal groups will be assumed to be equivalent to annual age classes. Each age class was approximately normally distributed and the division between one class and the next was made at the lowest point of overlap between each normal distribution for each sex. For example in Fig. 1 (t), female age classes separated at 0.725 mm and male age classes separated at 0.575 mm. Half of the number of isopods in the category at the dividing point were added to each age class. The dividing point did not change more than 0.25 mm among all the nest populations.

Multiple linear regressions (Snedecor & Cochran, 1980) of the number of young males (M₂) or young females (F₂) on the number of old females (F₁) and old males (M₁) show that the number of female offspring in a population is equally dependent on the number of females and males in the previous year (Table II), whereas the number of male offspring is far more dependent on the number of males in the previous year than the number of females in that year (Table III). These relationships between the numbers of each sex in each generation are best described by: (a) $F_2 = -4.8 + 0.886 F_1 + 0.828 M_1$ ($r_2 = 0.86$, $P < 0.001$: both regression coefficients are significant

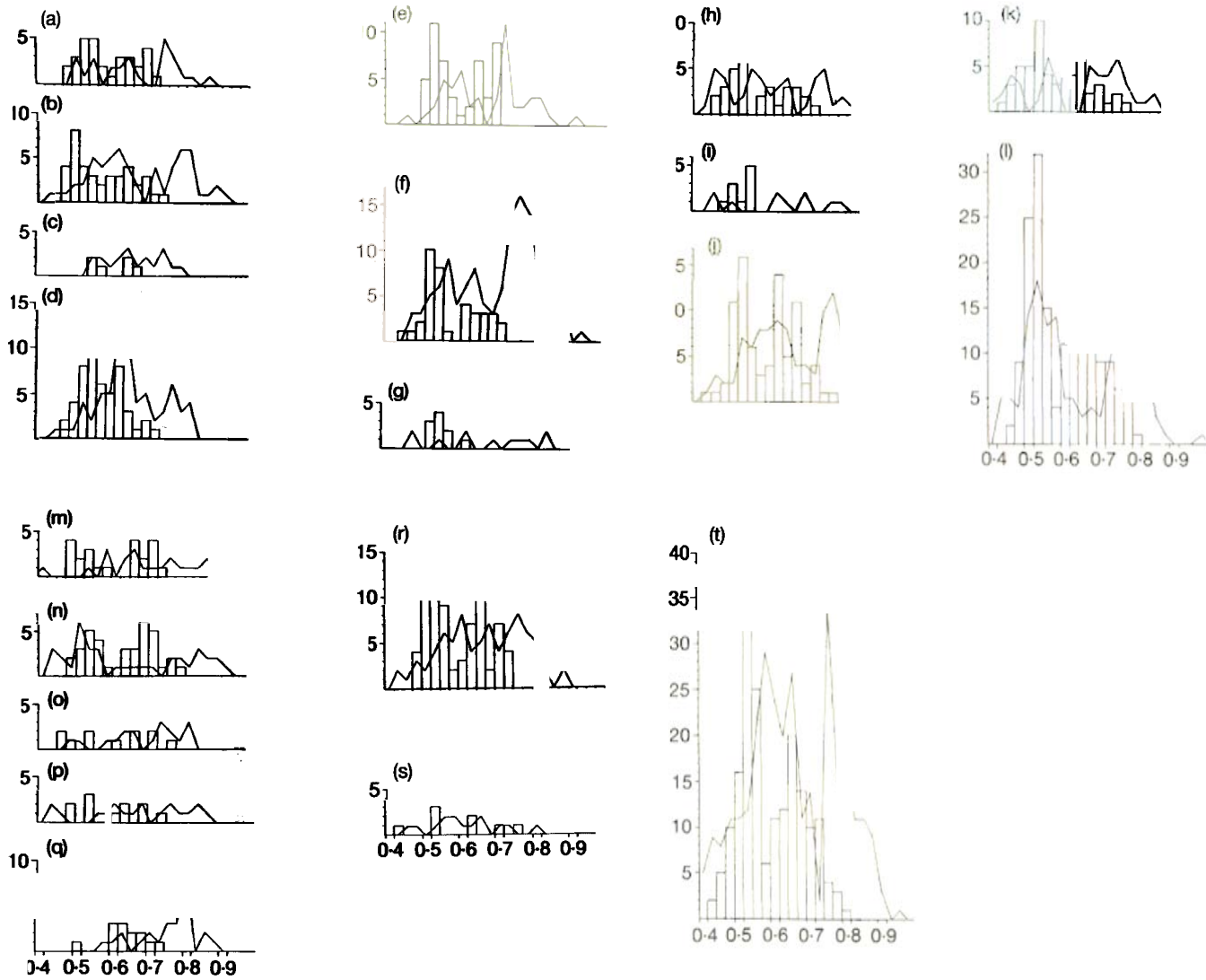


FIG. 1. Size frequency data for 20 populations of *Platyarthrus hoffmannseggii* (see Table I). Males are indicated by histograms, females by continuous lines. The scale of the abscissae is the same in all cases and represents head width in mm.

TABLE II

Regression of the number of young females in each population (F_2) on the older females (F_1) and older males (M_1): $F_2 = -4.8 + 0.886(F_1) + 0.828(M_1)$ ($r^2 = 0.86$)

Analysis of variance				
Source of variation	<i>d.f.</i>	Sums of squares	Mean square	<i>F</i>
Regression	2	33607	16804	55.5**
Error	17	5151	303	
TOTAL	19	38758		

Sequential			
Source	<i>d.f.</i>	sums of squares	<i>F</i>
Females (1)	1	31138	12.6**
Males (1)	1	2470	
Error	17		
Males (1)	1	30351	0.3*
Females (1)	1	3256	
Error	17		

** $P < 0.005$

* $P < 0.01$

at $P < 0.01$ see Table II); and (b) $M_2 = 1.50 + 0.169 F_1 + 0.857 M_1$ ($r^2 = 0.94$, $P < 0.001$: the F_1 regression coefficient is significantly different from zero $P < 0.01$ but the M_1 coefficient is not significant $P > 0.05$, see Table III). No significant correlations were found between sex ratio and the ratio of younger to older individuals in each population (see Table I). This ratio of the total number of young individuals ($M_2 + F_2$) divided by the total number of old individuals ($M_1 + F_1$) is an index of *per capita* fecundity and population growth rate if mortality rates are approximately constant in the different populations. This last assumption is probably justified given the stability and comparative safety of the ant-nest environment. The relationship between this *per capita* population growth rate and the parental sex ratio is best described by:

$$(M_2 + F_2 / M_1 + F_1) = 1.39 - 0.127 (F_1 / (M_1 + F_1))$$

($r^2 = 0.01$, $P > 0.1$, $n = 19$: population I was excluded because its growth rate was four standard deviations from the mean).

Behaviour and nutrition

A total of 31 types of behaviour were seen in *P. hoffmannseggii* (see the Appendix for a brief description of each behaviour). The frequency of each behaviour in 20 hours of observation for established and introduced isopods is listed in Table IV. Introduced isopods showed a marked aversion to association with the ants, and significantly higher frequencies of quick and random movement and 'clamping-down' in response to a higher frequency of ant investigative behaviour. Established isopods were more aggressive to one another and also showed a closer association with the ants such as climbing upon and licking these hosts (see Table IV).

TABLE III

Regression of the number of young males in each population (M_2) on the older females (F_1) and older males (M_1): $M_2 = 1.50 + 0.169(F_1) + 0.857(M_1)$ ($r^2 = 0.94$)

Analysis of variance				
Source of variation	<i>df.</i>	Sums of squares	Mean square	<i>F</i>
Regression	2	11871	5935	133**
Error	17	758	44	
TOTAL	19	12629		
Sequential				
Source of variation	<i>df.</i>	sums of squares		<i>F</i>
Females (1)	1	9229		3.5*
Males (1)	1	2642		
Error	17			
Males (1)	1	11753		99.8**
Females (1)	1	118		
Error	17			

** $P < 0.005$

* $P > 0.05$

The guts of both established and introduced isopods appeared red within 3 days of the ant diet being dyed with neutral red. As the isopods had no direct access to this food, their ability to take up the dye shows the nutritional link between the guests and their hosts. Processed food could have been available either from the ants' faeces or from the ants' regurgitated infra-buccal pellets, although isopods were only definitely observed feeding on the latter.

Survival

Nineteen of the 44 established isopods were still surviving with their familiar hosts after 40 days; only eight of the 40 isopods introduced to unfamiliar hosts were still alive after 40 days. Survival of the established isopods was significantly greater (χ^2 corrected for 1 *df.*) = 4.15, $P < 0.05$, Table V).

Discussion

We have demonstrated the nutritional link between the isopod *Platyarthrus hoffmannseggi* and the waste products of its host *Lasius flavus* and have also observed the woodlice eating a wide range of foods commonly found in the ants' nests, including wood, soil and their own faeces. This confirms the speculative remarks of Donisthorpe (1927), Vandel (1962), Bernard (1968) and Sutton (1980). *Platyarthrus hoffmannseggi* does not seem to be highly integrated into the social structure of its host colonies or to be of any vital importance or benefit to the ants. From our detailed observations, we believe *P. hoffmannseggi* to be a simple scavenger which is usually merely tolerated by the ants. Nevertheless, the quantitative behavioural studies have shown that there are marked differences in the frequency of interactions between the isopods and their familiar and

TABLE IV
Frequencies of behaviour acts seen in 20h of observation on established and introduced P. hoffmannseggi

Description of behaviour	Frequency of observations		
	Established isopods	Introduced isopods	
Rest on wall: with ants	32	1	***
with <i>Platyarthus</i>	22	14	
by self	18	80	
with midden	37	14	
Rest on floor: with ants	51	6	
with <i>Platyarthus</i>	8	2	
by self	17	45	
with midden	22	23	
Move: quickly and randomly	0	13	
up/down	89	78	
forward	131	85	
Rushes away: upon meeting ant	7	18	
upon meeting <i>Platyarthus</i>	8	1	
Stop upon meeting ant	28	18	
Turn 180°	57	79	
Receive attack: from ant	4	2	
from <i>Platyarthus</i>	33	11	***
Attacks <i>Platyarthus</i>	39	18	*
Clamp down	5	57	***
Raise uropods	28	30	
Investigated: by ants	16	46	
by <i>Platyarthus</i>	14	7	
Groom: mouthparts	6	34	
antennae	99	72	
legs	22	15	
telson/back	11	3	
Flex uropods/telson	29	31	
Feeds: on midden	19	12	
on other	19	0	***
Climbs on ant	65	0	***
Chews at ant	8	0	*
Defecates	13	0	***

* $P < 0.05$; *** $P < 0.001$; χ^2 Tests

unfamiliar hosts. Once they have become established, the safe and predictable habitat of ant nests provides the isopods with the benefit of a reliable food supply in a situation in which it will suffer very little predation. This special environment has resulted in *P. hoffmannseggi* evolving as the most K-selected of all British isopods: it produces relatively larger and many fewer offspring than other northern temperate woodlice (Sutton *et al.*, 1984).

The behavioural data and those relating to survival indicate that the migration of *P. hoffmannseggi*, even between adjacent ant nests in the field, is almost certainly highly restricted,

TABLE V

Platyarthus hoffmannseggi survivorship after reintroduction to their own ant colony—established isopods with their familiar hosts—or after introduction to an unfamiliar host colony

	Survivorship after 40 days		Totals used in experiments
	Alive	Dead	
Established	19	25	44
Introduced	8	32	40

χ^2 corr = 4.15, $P < 0.05$

so that their populations are segregated into distinct spatial demes with very little emigration and immigration.

The bimodal form of the size frequency data for each sex of isopod in each nest makes it possible to investigate the change in sex ratio from one generation to the next and how sex ratio affects population growth rates. The assumption that size is related to age is supported by studies of many other isopod species (Sutton, 1980). All the *P. hoffmannseggi* analysed in this study had obvious external genitalia, which strongly suggests that all surviving individuals would be sexually mature at the next breeding season in May through July (Sutton *et al.*, 1984). We will also assume that the female-biased sex ratios are not the results of a lower survival of males. This is probably a reasonable assumption as both sexes share the same environment and post-parturition mortalities would, of course, bias populations towards males.

Most populations were found to grow very slowly; the ratio of young to old isopods varied between 0.28 and 2.56 (nest I had an estimated growth rate of nine but this was exceptional). The multiple linear regression analyses showed that the frequency of the two sexes in the youngest generation is correlated in a different way with the number and sex of mature isopods in the previous year-class. As discussed earlier, it is unlikely that this difference is attributable to high rates of emigration or immigration. This is also supported by the extremely strong correlation between the size and sex ratio of future generations and the size and sex ratio of earlier generations: 86% and 94% of the variation in numbers of young females and young males, respectively, is explained by the composition of the earlier generation in the same subpopulation.

The number of second generation females is not dependent on the parental sex ratio but male production is relatively reduced if there is a female bias in the earlier age class. For this reason, female bias in *P. hoffmannseggi* populations is self-reinforcing, at population sizes well above those considered by most theoretical models.

Female-biased sex ratios occur in *P. hoffmannseggi* populations that are more than 10 times the size at which Hamilton's (1967) theory of local mate competition suggests that they should have reverted to a 1:1 sex ratio. In such relatively large populations, females producing a female-biased brood might be expected to have a lower fitness within each group than a female employing the Fisher strategy of equal investment in the sexes, or even a female producing a male-biased brood, for in both cases males (being the minority sex) will have a selective advantage over their sisters (Fisher, 1930). However, Fisher's rule might not apply if these isolated populations of isopods are subject to a special form of group selection. For example, mutant females bearing an allele causing

the production of female-biased broods may enhance the productivity of their own group to such a large extent that the allele is able to increase in frequency in the global population, despite being selected against at the level of the individual. However, this explanation for female-biased sex ratios involving interdemical-selection (Colwell, 1981; Wilson & Colwell, 1981 see also Nunney, 1985) is unlikely to apply to *P. hoffmannseggi* because, even though populations are isolated, there is no evidence in our data that female-biased populations grow faster than unbiased ones (see Tables II and III). Therefore, differential trait-group productivity appears unlikely to play a major role in maintaining female-biased sex ratios in these populations. A closely related hypothesis is the 'haystack' model of Bulmer & Taylor (1980), in which patchy habitats periodically become available for the rapid growth of isolated subpopulations for a limited number of generations before dispersal is caused by the disappearance of the haystack. This might be a possibility for *Platyarthrus hoffmannseggi* in *Lasius flavus* colonies, because, though the mounds may persist for more than 100 years, each ant colony has only one queen and may survive only for her life-time of one or two decades, before the death of the colony and the forced dispersal of the isopods to the predictable food supply and relative safety of other ant colonies. Mounds without ants may then be re-invaded by new ant colonies followed by isopods and may therefore represent new 'haystacks'. Selection, either during the exponential growth of isopod populations in new ant colonies (see for example population C) or just prior to dispersal, may favour female-biased broods (see for example population T). However, in our data as a whole, female-biased populations do not appear to grow more quickly and, since there are likely to be many generations within a mound before dispersal, there is likely to be population regulation within each large colony. This should select for sex ratios of unity (Charnov, 1982). Therefore, notwithstanding their appeal from a population structure perspective, 'haystack' models do not seem to provide a complete explanation for the female-biased sex ratios in these isopods.

Sex ratio and group productivity in *P. hoffmannseggi* are therefore difficult to explain in terms of sex ratio models based purely on the adaptive response of the isopods to their own subpopulation size and sexual environment.

However, these data are entirely consistent with the expected results of the presence of a cytoplasmic parasite which causes female-biased broods and is inherited through female lines or unusual chromosomal sex determination. The presence of such parasites has been demonstrated by breeding and tissue implantation experiments with infected and uninfected isopods of *Armadillidium vulgare* (Juchault & Legrand, 1970, 1972; Legrand & Juchault, 1972). Females infected by an unidentified intracellular micro-organism are thelygenic, i.e. they produce female-biased broods, whereas uninfected females are amphogenic. The fact that the parasite is present in males as well as females suggested that the parasite caused the production of females by overriding the effects of their sex chromosomes rather than by controlling their segregation (Martin, Juchault & Legrand, 1973) (see Bull, 1983 for review). Johnson (1977) predicted the presence of such parasites in many terrestrial isopods. However, in addition to the effect of such parasites on the sexual composition of broods, certain isopods, including *Armadillidium*, also have unusual sex-determining mechanisms. Genetically, males are homozygous (ZZ) and females heterozygous (ZW), although homozygous (WW) females have been found to be both viable and functional (Howard, 1962; Katakura, 1984).

In a random population, alleles or intracellular parasites causing thelygeny will swiftly reach fixation, resulting in population extinction due to the absence of males. In a geographically structured set of population, some ant colonies will have only normal or uninfected *Platyarthrus* females and these will be a source for recolonization of new ant colonies or those whose abnormal

or infected isopods have become extinct. Some normal populations could become infected by abnormal females so that the long-term global coexistence of the two types of female would be possible only if a balance is struck between relative migration rates (and possibly greater mating success of normal females) and subpopulation extinction rates. Such coexistence of thelygenic strains in geographically structured populations occur in the African butterfly *Acraea encedon* (Heuch & Chanter, 1982; Bulmer, 1986).

Whether or not female biases in these isopods are caused by selection during colonization of new ant colonies, anomalies in their sex determination or the presence of intracellular parasites inherited through female lines—the persistence of thelygeny is likely to be a consequence of the unusual geographic structure of these isopod populations, which is a consequence of their symbiotic relationship with ants. Not only does *Platyarthrus hoffmannseggi* provide a special test case for sex ratio studies in terrestrial isopods, but its habit of associating with persistent ant colonies means that changes in sex ratio in its separate subpopulations can be tracked for several generations. Such long-term studies will be essential for testing the alternative hypotheses for sex allocation outlined in this paper.

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Appendix

A total of 32 behaviours were seen repeatedly in *Platyarthrus* (see Table IV). Here follows a brief description of each behaviour.

Resting—The isopods spent approximately two-thirds of their time resting. Resting was defined as inactivity for a minimum of 30 seconds. Isopods were often seen to associate with ants or each other when resting, although solitary resting was also common.

Move forward—Any forward movement from a creep to a quick walk.

Move up or down—Usually a change of position from wall to floor of nest or vice versa.

Move quickly and randomly—Only seen in introduced woodlice. The isopods rush forward frequently turning sharp angles. This would seem to be an escape reaction as it never lasted more than 30 seconds, after which shelter of some kind was discovered.

Turn 180°—An on-the-spot turn through an angle of approximately 180°. Sharp turning in *Platyarthrus* was suggested as an adaptation to life in narrow ant tunnels by Brooks (1942).

Stop upon meeting ant—the woodlouse immediately stops, ceases antennal movement and often lowers the body to the floor, although this was less exaggerated than clamping down.

Clamp down—One of the behaviours described by Gorvett & Taylor (1960), who said that following introduction to new ants, clamping down appeared to be induced even by “the light touch of the ants’ antennae”.

Raise uropods—also observed by Gorvett & Taylor (1960). The uropods have lobed tegumental glands which can release a viscous secretion. Upon attack by an ant, *Platyarthrus* clamps down after which the uropods are raised, and if the isopod is bitten the ant will quickly retreat wiping its mouthparts and head. The more severe the ant attack the greater was the degree of presentation of the expodites. At times, the back of the isopod became semicircular as it pushed up its telson. These glands are probably very important and effective in protecting *Platyarthrus* from its ant hosts, especially when entering a new nest.

Rushes away upon meeting ant or isopod—A panic reaction more commonly seen when meeting an ant. The woodlouse veers back and runs away, often without touching the ant but sensing its presence from half a body length away.

Investigation by ant or isopod—Non-aggressive antennal contact ranging from brief encounter to prolonged investigation.

Receive attack from ant—Rapid aggressive movement; worker has open mandibles with which it tries to obtain a purchase on the back of the isopod. The reactions of the woodlice include rushing away, clamping down and raising uropods.

Aggression between isopods—Rapid antennal beating of the victim usually accompanied by a rearing up at the front, rapid leg and mouthpart movement. Biting of the opponent's antenna was also observed. The victor (usually the larger of the two) moves forward while the vanquished usually retreats rapidly, although the distance of retreat may be relatively short, hostilities ceasing when they are just half a body length apart. If an attack is made from the rear, the victim's uropods are immediately raised but with little effect. Such fighting may be associated with the acquisition or defence of good feeding sites or may be related to sexual competition.

Grooms mouthparts—The mouthparts and head are repeatedly rubbed with the first and occasionally second pair of legs.

Grooms antennae—Movement around or upon midden usually stimulates this behaviour. Each antenna is brushed in turn with one of the first pair of legs. After several such actions the leg itself is cleaned by passing it through the mouthparts.

Grooms legs—The more anterior legs are used to groom the legs immediately behind them and occasionally the isopods bent almost double and the 4th, 5th and 6th pairs of legs could be licked clean.

Groom telson/back—The underside of the telson is groomed by the 6th and 7th pairs of legs. This behaviour was on occasions seen after the uropod glands had secreted, or after defecation. Particles adhering to the pereion or pleon were removed by rubbing on the wall of the nest.

Flex uropods or telson—This behaviour was on only two occasions connected with anal drinking, but often seen after the uropod glands had secreted. The behaviour consisted of a combination of any of the following actions: the telson lowered and quickly raised, the exopodites separated laterally and brought together again, the exopodites brought tightly together and then relaxed, both exopodites moved to the left or right.

Feeding—In this study the woodlice have been observed eating particles of soil, their own faeces, infra-buccal pellets derived from the ant's diet, the cardboard of the nest, fragments of wood and fragments of the cellulose water wick also. When ants were supplied with diet dyed neutral red, the guts of the woodlice appeared red within 3 days, confirming the nutritional link between the ants and *Platyarthrus*.

Climbs on ant—This behaviour was only seen in the established isopods. The behaviour was usually accompanied by antennal movement and on two occasions the mandibles were opened wide, such as when regurgitating during trophallaxis. Climbing up on to the ants legs, gasters, etc. would seem to have perhaps just two possible causes. First, it may be done on the off-chance that it causes regurgitation, for when the woodlice made contact with the head of an ant, the head was pushed up and the isopod's mouthparts were seen to move quickly, possibly ready to receive the droplet of food. Secondly, climbing on the ants may be a way of maintaining colony odour.

Chews ant—This also was only seen in established *P. hoffmannseggii* and may either be related to attempts at trophallaxis with the ants, or to gaining a pheromone or nutritional particles adhering to the ants' cuticles.

Defecation—Quite why only established isopods were seen to defecate is difficult to answer. The introduced isopods spent much of the time nestling in midden and so the act of defecation may have been missed. Faecal pellets of *P. hoffmannseggi* are torpedo-shaped, approximately 0.075 mm long and littered the nest with the established isopods in large numbers. Established isopods were regularly seen to feed on such faecal pellets.

Mating—Mating was only seen on one occasion on 19 December 1984 and since it is normally carried out in complete darkness it is possible that the observed mating did not follow its usual course. The smaller male approached the front of the larger female and engaged in rapid antennal contact. After about 5 seconds he ran forward and up on to her back, turned through 180°, and within another 10 seconds moved into the first mating position (the right-hand stylets of his genitalia reaching her left genital opening). The male stayed in this position for some 35 seconds, after which he ran forward, nibbled at the top of the female's head (3 seconds) and dismounted over the front of her. He rested close to her for 5 minutes after which they were removed for closer examination and sexing. Post-coitally, the female did nothing except groom antennae and shift position slightly. The mating, from beginning to end took less than a minute. No attempt was made to mate with the right-hand side of the female. This differs from the mating of *Porcellio laevis* as described by Sutton (1980) in which the male licked the female's head for 5 minutes before copulation occurred. Sperm transfer lasted 5 minutes and was repeated on each side of the female. Therefore, it is possible that the *Platyarthrus* male found the female less receptive than he first believed, or that light disrupted the behaviour.