Room for Females Only? Exploring Strongly Female-Biased Sex Ratios in Ingolfiella (Crustacea: Peracarida: Ingolfiellida) in Relation to Ecological Condition

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Room for Females Only? Exploring Strongly Female-Biased Sex Ratios in *Ingolfiella* (Crustacea: Peracarida: Ingolfiellida) in Relation to Ecological Condition

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ABSTRACT

While in most species the adult sex ratio is around 1:1, it can be strongly skewed in some species; some of this can be explained by ecological conditions and limits to dispersal. We hypothesize that stronger isolation imposed by ecological conditions leads to more pronounced female-biased sex ratios in the groundwater peracarid genus *Ingolfiella* Hansen, 1903. About 75% of all adults are female, and female-biased sex ratios are present in 30/42 of species for which individuals have been sexed. Sex ratios were not correlated with sexual size dimorphism. The adult sex ratio varied little between species found in different habitats (caves, beach sand, and seabed) thus not supporting our hypothesis that ecological conditions shape adult sex ratios. It appears that sediment structure in most habitats restrict ingolfiellids in their movement. Limited dispersal abilities and small mating assemblages may favour strongly female-biased sex ratios.

KEY WORDS: beach and coral rubble interstitial, cave systems, Crustacea, seabed sediments, stygobionts

INTRODUCTION

Metazoan sex ratios may differ between species and between higher taxa; the most common sex ratio is 50:50, which occur when females invest equally in sons and daughters (Fisher, 1930; Trivers & Willard, 1973; Godfray & Werren 1996). There are nevertheless clear differences in adult sex ratios between some taxa, with birds and snakes showing an adult sex ratio skewed towards males, whereas in lizards, amphibians, and mammals it is skewed towards females (Donald, 2007; Pipoly et al., 2015). Accounting for the variation in adult sex ratios can be challenging as it requires detailed understanding of the biology of a species, including for instance information on sex-linked patterns of dispersal (the process that involves the movement of an individual or multiple individuals away from the population in which they were born to another location, or population, where they will settle and reproduce (Croteau, 2010)), levels of competition and cooperation, and sex and age specific mortality rates. The adult sex ratio should also vary with ecological and environmental conditions (Charnov et al., 1981; West & Sheldon, 2002), as these may for instance have an effect on dispersal abilities and rates of inbreeding.

The adult sex ratio of crustaceans can be strongly skewed towards females (Carpenter, 2021), and it has been postulated that this is due to a combination of greater predation on males as adults (Hirst et al., 2010), shorter lifespans of males, environmental sex determination and sex change (Gusmão et al., 2013), including sex change as a result of feminizing parasites (Ewers-Saucedo, 2019). For those crustaceans that only disperse short distances (i.e., in the order of tens of metres; Danielopol et al., 1999), for instance due to hydrogeological limitations in the groundwater landscapes (Steenken, 1998; Khaldoun, 2015) or by sequence of arrival (Capderrey, 2013), and/or those species that brood their offspring in aggregate in mating assemblages, brothers would compete directly for matings, whereas sisters do not (Dangerfield & Telford, 1994; Ewers-Saucedo, 2019). Thus, a mother's fitness increases in a linear fashion with the number of daughters she produces but not with the number of sons. Therefore, mothers should only produce enough sons to fertilize all females but they should maximize the number of daughters they produce (Hamilton, 1967).

Building upon this, Premate et al. (2021) tested for amphipod crustaceans of the European and Middle Eastern

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groundwater genus *Niphargus* Schiødte, 1847 whether species along a gradient of subterranean environments had female-biased adult sex ratios. Using data from 35 species, they tested the hypothesis that the adult sex ratios become more female-biased with increased isolation from the surface (i.e., with decreased opportunities for dispersal). In 27 species of these groundwater amphipods sex ratios were indeed female-biased, and it was weakly female-biased for species living at the surface-subterranean boundary and most strongly female-biased in underground caves.

We herein use a comparable data set for a group of amphipod related, stygobiont crustaceans, the Ingolfiellida Lowry & Myers, 2017, to test whether these also show a female-biased sex ratio, and if isolation imposed by ecological conditions leads to a more pronounced female-biased sex ratio. Similar to Premate et al. (2021) we tested for three different habitats (caves, beach sand, and seabed) representing an ecological gradient in terms of available habitat (small to large) and dispersal abilities (most to least restrictive). Most species within the order Ingolfiellida reside in the genus *Ingolfiella*, which are strictly subterranean (interstitial) in a wide variety of aquatic habitats, from the ocean floor to shallow marine interstitial sand habitats, through to caves and brackish and fresh continental groundwater (Stock, 1977; Vonk & Schram, 2003, Rodriguez et al., 2017). Despite that many species are known from just one or a few locations, the genus has a panglobal distribution. Ingolfiellids have no free-swimming larvae in the water column and species appear to have a low egg production (Siewing, 1963). Their capacity for long distance dispersal is supposedly limited, and while tracing data are lacking, we suspect that in many cases dispersal during lifespan has to be measured in a few tens of meters rather than kilometres, with recurring assemblage patterns (Danielopol et al., 1999). Geographically separated populations show subtle but fixed morphological differences and, in the absence of molecular phylogenetic comparisons, they are typically considered to represent different species.

MATERIALS AND METHODS

We followed the taxonomic classification of Lowry & Myers (2017), and we recognise 42 species (Horton et al., 2022) within *Ingolfiella* (Fig. 1). For 13 species we used data from Vonk & Nijman (2006) on the male:female sex ratios, and maximum body size for males and females. We obtained data from an additional 29 species from the literature, including species that were described after 2006 (Iannilli et al., 2008; Iannilli & Vonk, 2013; Ohtsuka et al., 2006; Rodriguez et al., 2017; Rubal & Larson, 2013; Vonk & Jaume, 2013, 2014a, b). The sampling sites were grouped into the three main habitat types recognised by Siewing (1958, 1963), i.e., caves, man-made wells connecting with underground rivers or a groundwater saturation zone, freshwater riverbed sediments and springs ('caves'), interstitial spaces in marine littoral and shallow sublittoral sands and coral rubble and anchialine pools ('beach'), and deep-sea mud and detritus, including seamounts, at depths between 10 and 3500 m ('sea'). For each species we obtained the body size, measured from the tip of the head (rostrum) to the posterior margin of the abdomen, including the telson, which is streamlined with the last urosomite and does not extend beyond the downward sloping abdomen. The largest male and the largest female were selected allowing us to calculate sexual dimorphism in body size. We test against an equal sex ratio, and we accept significance when $P < 0.05$ in a two-tailed test. Numbers were log-transformed prior to analysis to approach a normal distribution more closely. We present means ± SEM throughout.

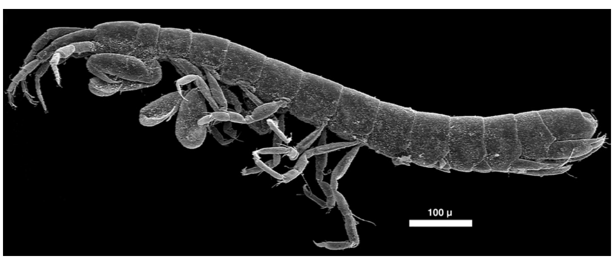

Figure 1. An example of the general form of ingolfiellids, *Ingolfiella ischitana* Schiecke, 1976 (SEM photo from Vonk & Schram, 2003 –).

RESULTS

There is clear evidence for a female-biased adult sex ratio in ingolfiellids. Of all sexed individuals combined, irrespective of species, 75.2% are female, and when we give equal weight to all 42 species, 72.9% of individuals are female. Focussing only on the ten best studied species (with sample sizes between 11–120 sexed individuals), these percentages are 78.5% and 76.6%, respectively. Equally, for those species that are known from just one single individual, it was a female in 81.8% of the cases.

For four species there was a male-biased adult sex ratio, there was an equal sex ratio in eight, and there was a female-biased adult sex ratio (binominal test, $P = 0.00002$) (Table 1) in 30. A statistically significant female-biased adult sex ratio was found in eight species (two freshwater, three beach, marine marine) and there were no species in which the adult sex ratio was significantly male-biased (Table 1).

The sample sizes that were available for analysis varied greatly between species, with only one specimen available in 12 species and up to 120 specimens in other species, but there was no effect of sample size on the calculated adult sex ratio (Pearson's R = 0.0412, $R^2 = 0.0017$, $N = 42$, $P = 0.7956$).

For the 24 species where we had body sizes for males and females, females were more likely to be larger than males (17/5 binomial test, $P = 0.0085$); in five species males were larger than females (mean 16.1 ± SE 4.7%), and in 17 species females were larger (mean 10.0 ± SE 2.4%). There was no statistically significant relationship between body size dimorphism and adult sex ratio (R = 0.0022, $R^2 = 0$, $N = 24$, $P = 0.9921$), and body size dimorphism did not differ between habitats ($F_{2,20} = 0.3682$, $P = 0.6966$) (Fig. 2).

The adult sex ratio varied between habitats but not in the predicted ratio (males in caves 38.4 ± 9.2%, beach 20.9 ± 5.5%, sea 25.5 ± 8.4%), and these differences were not statistically significant ($F_{2,40} = 0.3682$, $P = 0.6966$). Excluding the 12 species for which only a single specimen had been collected, the observed pattern was not changed (males in caves 37.4 ± 6.7%, beach 26.7 ± 6.3%, sea 30.6 ± 9.9%) ($F_{2,28} = 0.4776$, $P = 0.6254$).

Table 1. Sexual dimorphism (size of females relative to males) and adult sex ratio for those species of *Ingolfiella* that show a significant deviation from a 1:1 adult sex ratio. Habitat: 1, caves; 2, beach; 3, sea (see text for more detailed descriptions). *P*-values are based on binominal tests under the assumption of a 1:1 sex ratio.

Species	Habitat	Body-size dimorphism	Proportion of males (*N*)	*P*-value
I. alba Iannilli, Berera & Cottarelli, 2008	2	0.973	0.143 (14)	0.0065
I. britanica Spooner, 1960	3	0.900	0.176 (17)	0.0064
I. canariensis Vonk & Sánchez, 1991	2	0.947	0.082 (49)	0.0000
I. fuscina Dojiri & Sieg, 1987	3	0.739	0.147 (34)	0.0009
I. maldivensis Vonk & Jaume, 2014	3	n.a.	0.000 (6)	0.0157
I. manni Noodt, 1961	1	0.871	0.250 (120)	0.0000
I. quokka Gallego-Martinez & Poore, 2003	2	0.812	0.125 (16)	0.0021
I. vandeli Bou, 1970	1	0.909	0.261 (23)	0.0173

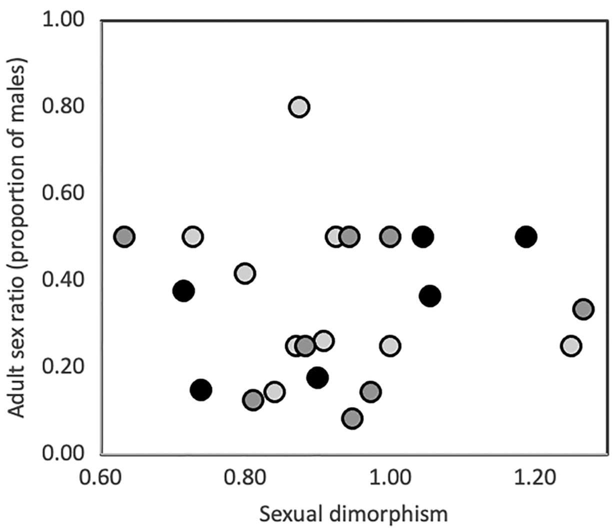

Figure 2. Relationship between sexual size dimorphism and adult sex ratio in 42 species of *Ingolfiella* sampled from three habitats: caves (light grey), beach (dark grey) and sea (black).

DISCUSSION

While in some taxa a more than 75% female-biased adult sex ratio is very rare. Pipoly et al. (2015), for instance, presented data on 344 species of tetrapods and found that only 10 species, all mammals, fell into this category, but it is very common in other taxa such as eusocial insects (Mehdiabadi et al., 2003; Kobayashi et al., 2013). Crustaceans are somewhat intermediate in this respect (Wenner, 1972). *Ingolfiella* show an extreme female-biased adult sex ratio with some 75% to 80 % of all individuals being female. Unlike Premate et al. (2021), studying a groundwater amphipod, we did not find differences (Fig. 3) in female-biased adult sex ratio in three habitats differing in their dispersal potential (cf. Siewing 1958, 1963). The overall female-biased adult sex ratio in *Niphargus* was considerably lower (58.3% of all individuals, 60.9% when equal weight is given to the different species), than what we found in *Ingolfiella*. The lowest mean female-biased adult sex ratio we found in ingolfillids living in beaches was similar to the highest mean found in cave-dwelling species of *Niphargus* (Premate et al. 2021).

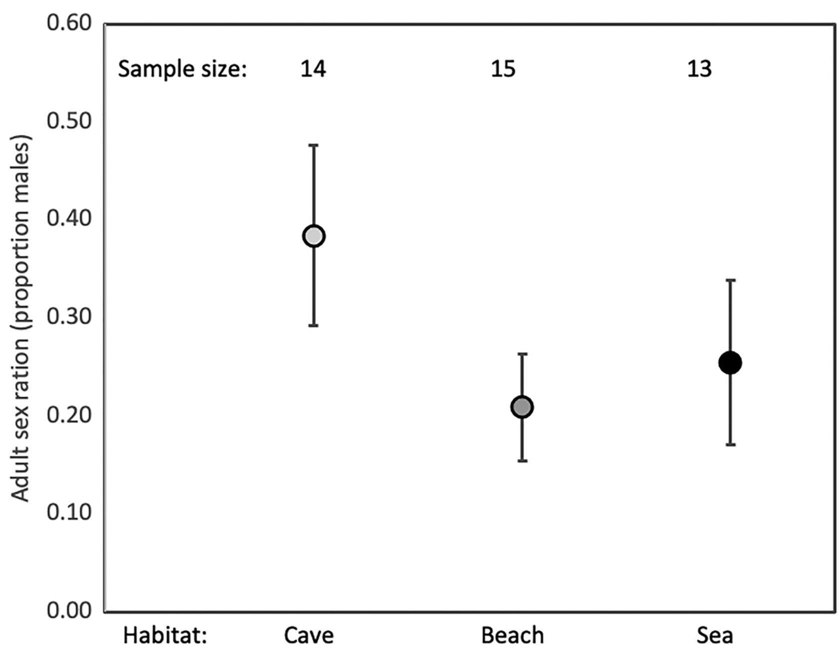

Figure 3. Relationship between adult sex ratio (mean ± SE) and habitat along a gradient of dispersal opportunities in 42 species of *Ingolfiella*.

There is no evidence to suggest that ingolfiellids change sex as males and females have been observed at all size classes (if there was, we would expect many more males in the smaller size classes) and there is only a limited amount of sexual dimorphism. There is no evidence to suggest that either sex has any life history trade that makes it less or more likely for researchers to collect one or the other sex more frequently. Importantly, the methods of collecting these small crustaceans, using probing tubes during SCUBA diving, groundwater handpumps and hand nets, with sex identification done under the microscope afterwards, does not allow for researchers to introduce a bias into collecting either males or females.

Other than the strong female-biased sex ratio, it is also evident that many species are known from a limited number of individuals. Senna & Serejo (2005) noted that 11 of 41 species are known only from females and a further three are only know from males; since then, six more species have been described based on only males or females. It is evident that there are many more undiscovered species of ingolfellids in many more localities than are currently known. Only a small number of individuals co-occur at a much smaller geographical and ecologically relevant scale, possibly hinting at small mating assemblages (Ewers-Saucedo, 2019).

Based on the above, we agree with Ewers-Saucedo (2019) that ingolfiellids may indeed fit the pattern whereby local mate competition has been an evolutionary driver of a strongly female-biased adult sex ratio. While these species occur in a wide range of habitats, the sediments in which they live pose restrictions on dispersal distance. The generally small number of individuals that researchers were able to collect at sampling sites may suggest small mating assemblages. In these small, isolating mating assemblages brothers would directly compete for matings, and in evolutionary terms it is advantageous to produce not more males than is strictly necessary to fertilize all females (Hamilton, 1967; Ewers-Saucedo 2019), thus leading to the strongly female-biased adult sex ratios we report.

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