Acta
Entomology and Zoology

E-ISSN: 2708-0021
P-ISSN: 2708-0013
www.actajournal.com
AEZ 2022; 3(1): 34-39
Received: 25-11-2021
Accepted: 27-12-2021

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Mating frequencies of sympatric red millipedes differ across substrate due to absolute abundances

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DOI: https://doi.org/10.33545/27080013.2022.v3.i1a.62

Abstract
Relative mating frequencies were assessed in sympatric red millipedes of the genus *Centrobolus* across the ground and tree substrata. There was a significant absolute difference between mating frequencies of *C. anulatus* and *C. inscriptus* (Z-score=1.65, n=2, 2, p<0.05). There was a significant relative difference between mating frequencies of *C. anulatus* and *C. inscriptus* (Z-score=1.65, n=2, 2, p<0.05) of these two species. There was a relative difference between mating frequencies on the ground (0.00; 0.04) compared with mating frequencies in the trees (0.03; 0.08) (Z-score=1.79, n=2, 2, p=0.04). Mating frequencies were correlated with absolute abundances (r=0.96, Z score=1.91, n=4, p=0.03). Male and female mating frequencies were positively related to absolute abundances (r=0.66, Z score=2.88, n=16, p<0.01).

Keywords: Absolute, abundance, ratio, size, species

1. Introduction

The millipede genus *Centrobolus* is found in the temperate South African subregion, its northern limits on the east coast of southern Africa being about -17° latitude South (S) and its southern limits being about -35° latitude S. It consists of taxonomically important species with 12 species considered threatened and includes nine vulnerable and three endangered species [18]. It occurs in all the forests of the coastal belt from the Cape Peninsula to Beira in Mocambique [17]. Common with worm-like millipedes is the mating frequency which is known to differ in several populations of the genus [6]. Mating frequencies are seasonal and probably determined by the sex ratio which in turn determines the optimal copulation durations for individuals of each species at any one time [7-9].

Mating frequencies are compared during the breeding season in two sympatric species in the pachybolid millipede genus *Centrobolus* Cook, 1897 [5, 10, 17]. The aim is to test the null hypotheses that (1) there is no difference in mating frequencies across species, and (2) there is no difference between mating frequencies on the ground compared to in the trees.

2. Materials and Methods

Two species (*C. anulatus* and *C. inscriptus*) were identified as belonging to the genus *Centrobolus* Cook, 1897 [5]. The mating frequencies on the ground and in the trees during the breeding season were obtained for *C. anulatus* (0.00, 0.03) and *C. inscriptus* (0.0372, 0.0828) [6]. The P-value Calculator was used to test the two null hypotheses (https://www.gigacalculator.com/calculators/p-value-significance-calculator.php).

3. Results

There was a significant absolute difference between mating frequencies of the two species (Fig. 1: Z-score=1.648850, n=2, 2, p=0.049589). There was a significant relative difference between mating frequencies of the two species (Fig. 2: Z-score=1.843398, n=2, 2, p=0.032635). There was a relative difference between mating frequencies on the ground (0.00; 0.0372) compared with mating frequencies in the trees (0.03; 0.0828) (Fig. 3: Z-score=1.786554, n=2, 2, p=0.037005). Mating frequencies were positively related to absolute abundances (Fig. 4: r=0.95738232, Z score=1.91354709, n=4, p=0.02783896). Mating frequencies were not related to sex ratios (r=0.80309117, Z score=1.10725847, n=4, p=0.13409114). Mating frequencies were not related to sexual size dimorphism (r=0.75904866, Z score=0.99396671, n=4, p=0.16011954).

Male and female mating frequencies were positively related to absolute abundances (Fig. 5: r=0.66272615, Z score=2.87600145, n=16, p=0.00201380). Male mating frequencies were positively related to absolute abundances (Fig. 6: r=0.68380795, Z score=1.86987087, n=8, p=0.03075081). Female mating frequencies were positively related to absolute abundances (Fig. 7: r=0.76447772, Z score=2.46639674, n=8, p=0.00682401). Mating frequencies at the end of the season were normal (D=0.2454, K=0.4907, n=4, p=0.4907). Mating frequencies at the beginning for the season were normal (D=0.1441, K=0.2882, n=4, p=0.9937). Mating frequencies on the ground were normal (D=0.3044, K=0.6088, n=4, p=0.2122) Mating frequencies in the trees were normal (D=0.2505, K=0.5009, n=4, p=0.5039).

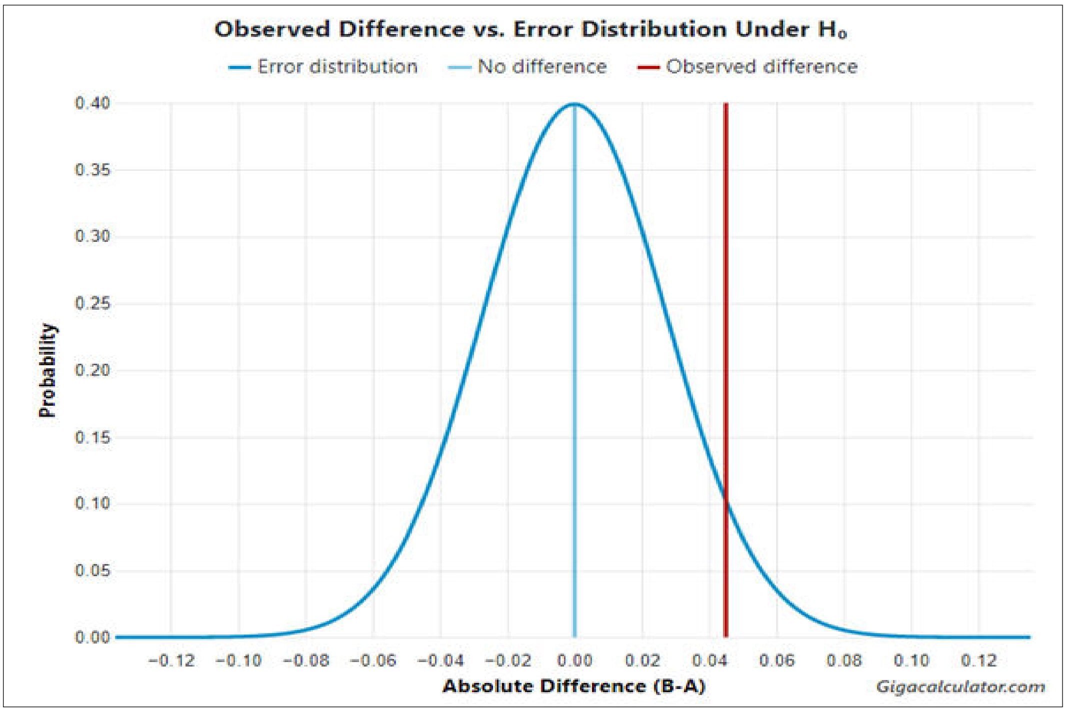

Fig 1: P-value showing a significant absolute difference (0.0450) between the mating frequencies of *Centrobolus anulatus* (0.0150) and *C. inscriptus* (0.06).

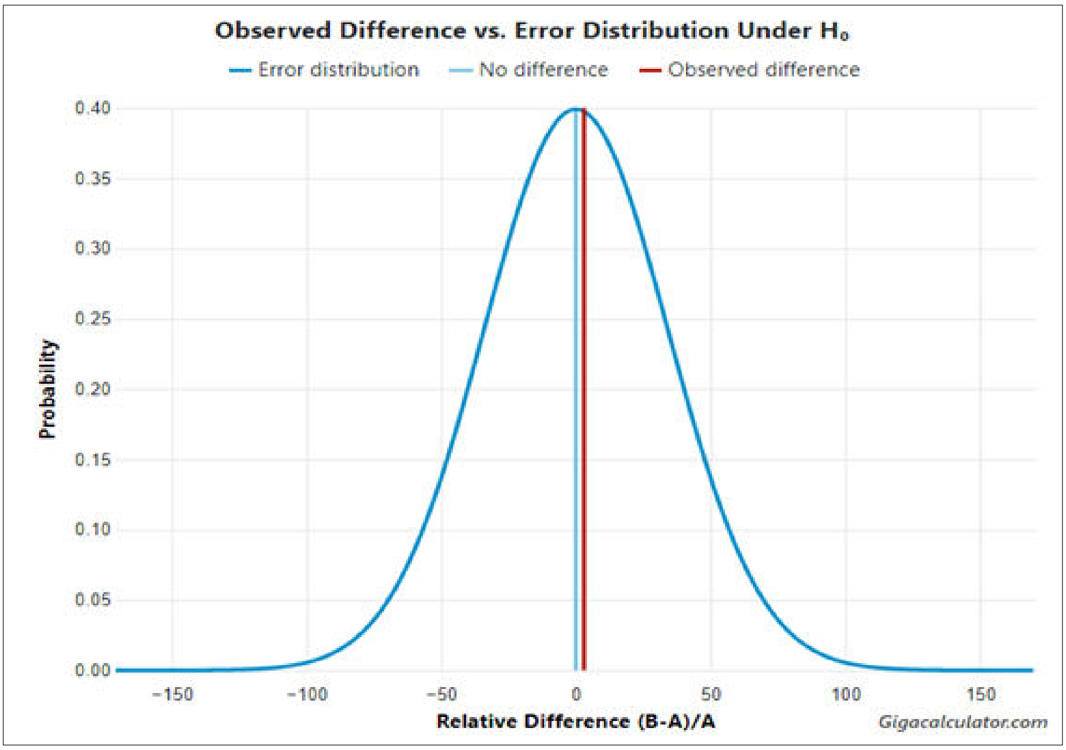

Fig 2: P-value showing a significant relative difference (3) between the mating frequencies of *Centrobolus anulatus* (0.0150) and *C. inscriptus* (0.06).

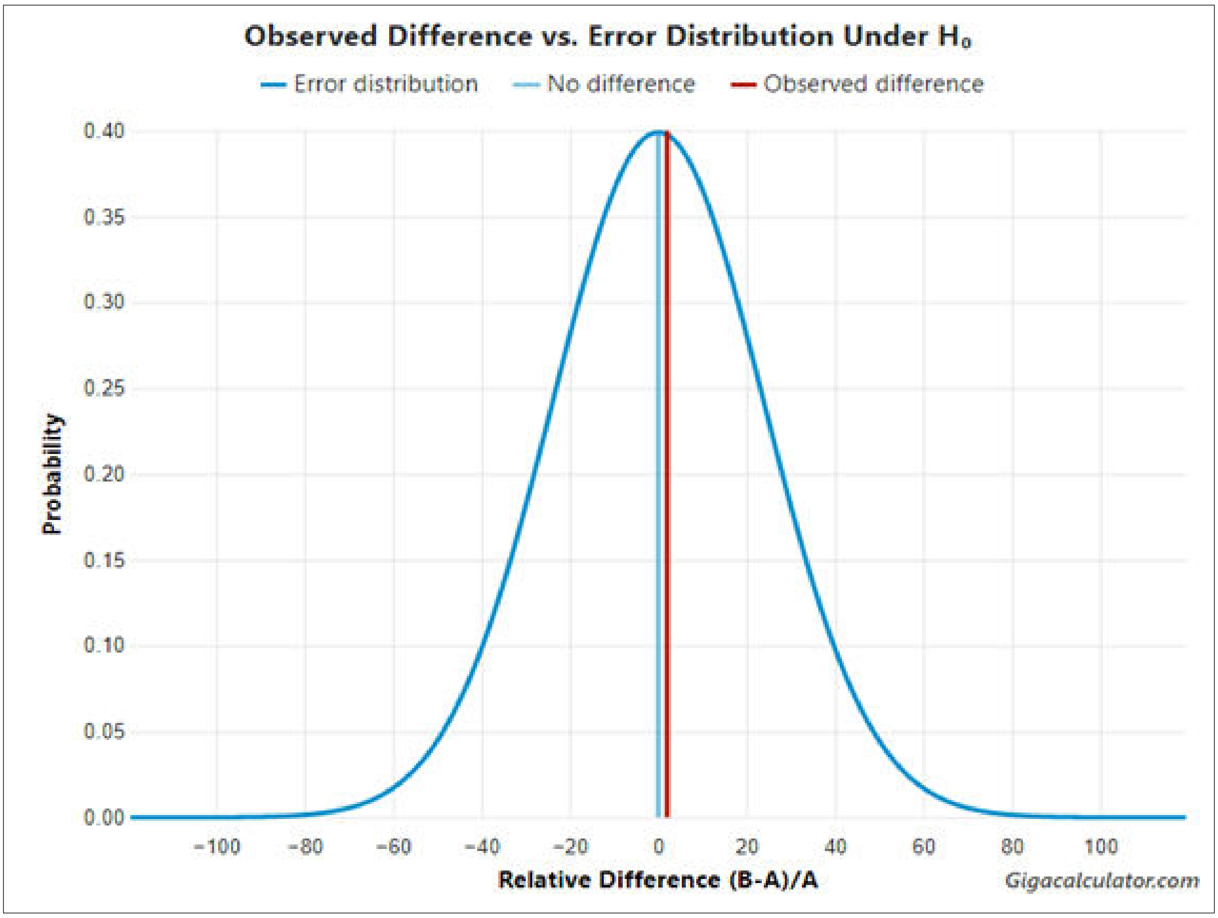

Fig 3: The P-value shows a relative difference (2.032258) between mating frequencies on the ground (0.0186) compared with mating frequencies in the trees (0.0564).

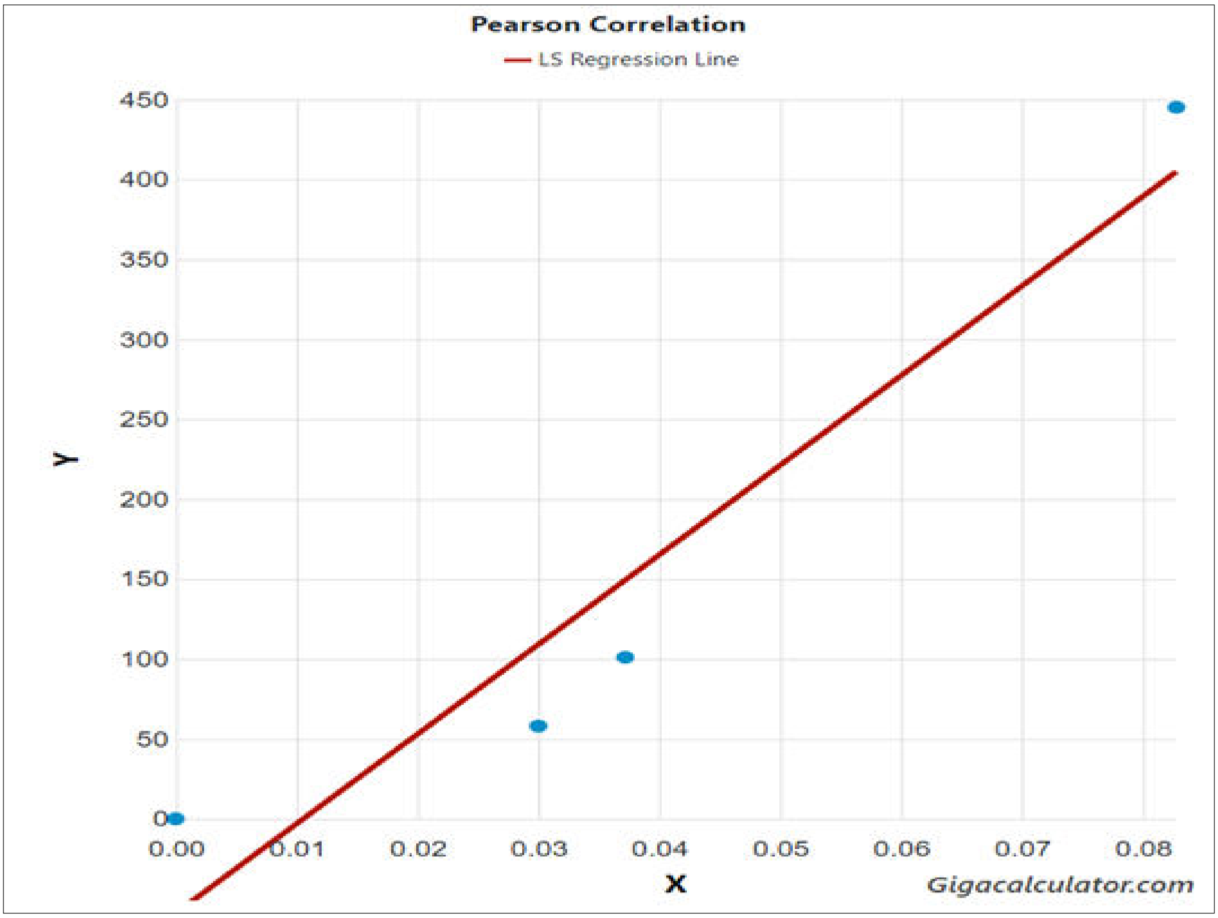

Fig 4: The positive relationship between mating frequency (x) and absolute abundance (y) in *Centrobolus*.

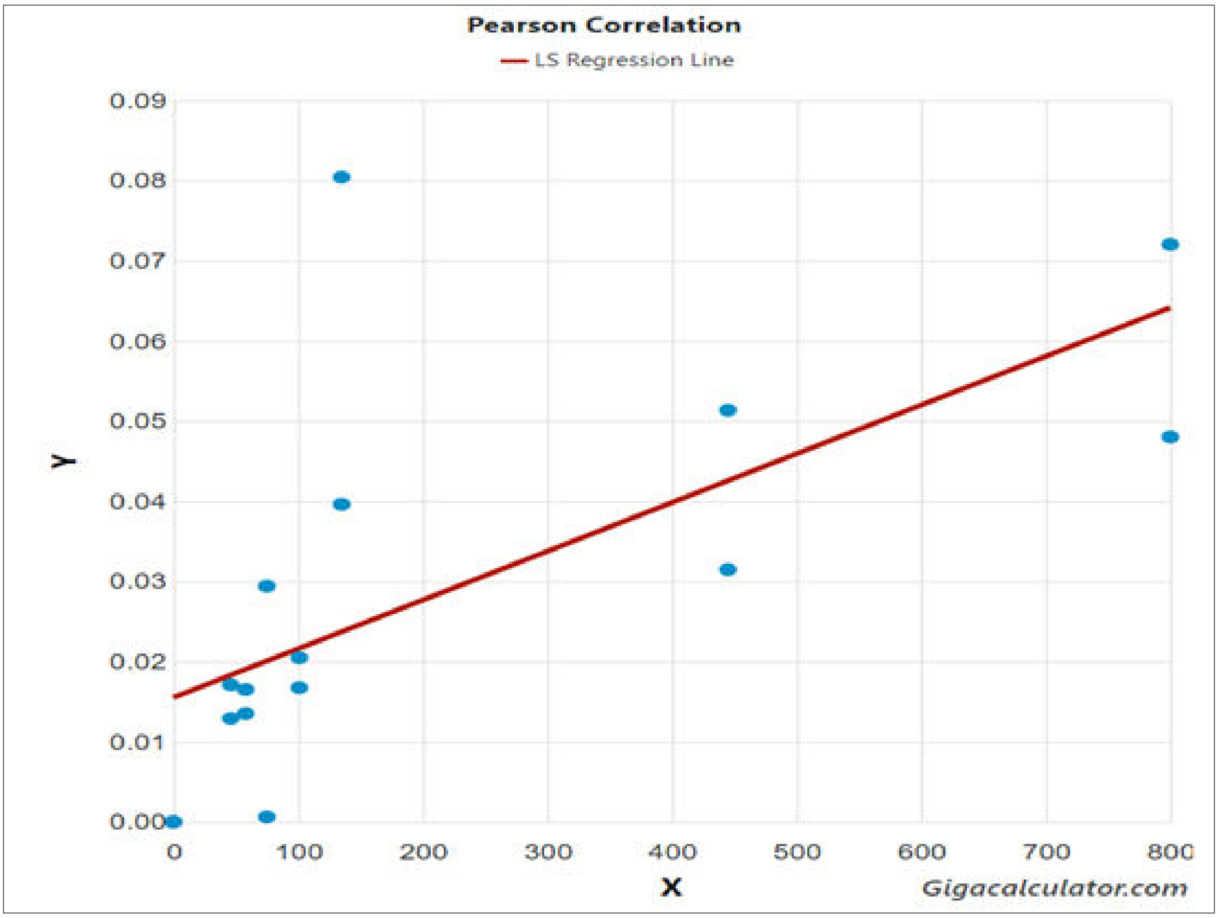

Fig 5: The positive relationship between mating frequencies of males and females (x) and absolute abundance (y) in *Centrobolus*.

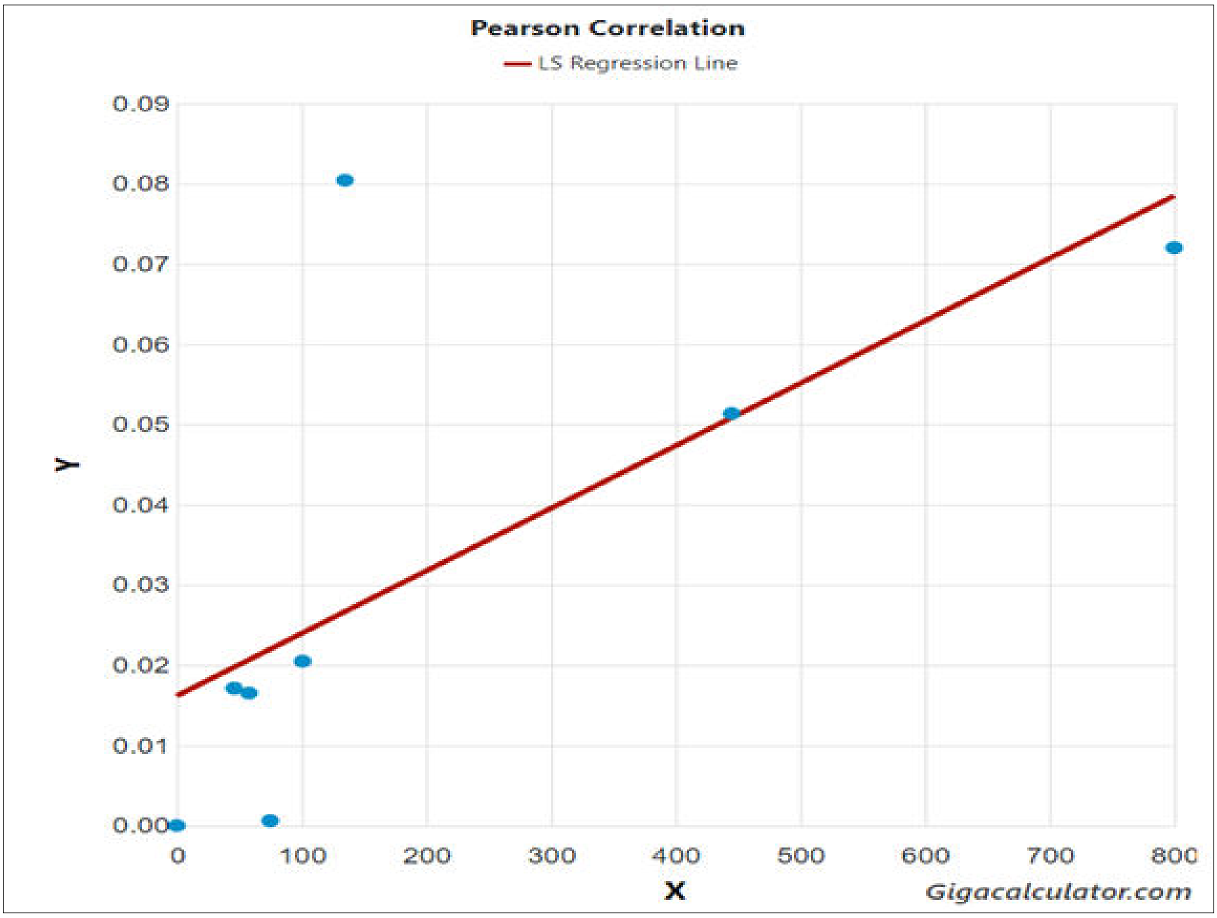

Fig 6: The positive relationship between male mating frequencies (x) and absolute abundance (y) in *Centrobolus*.

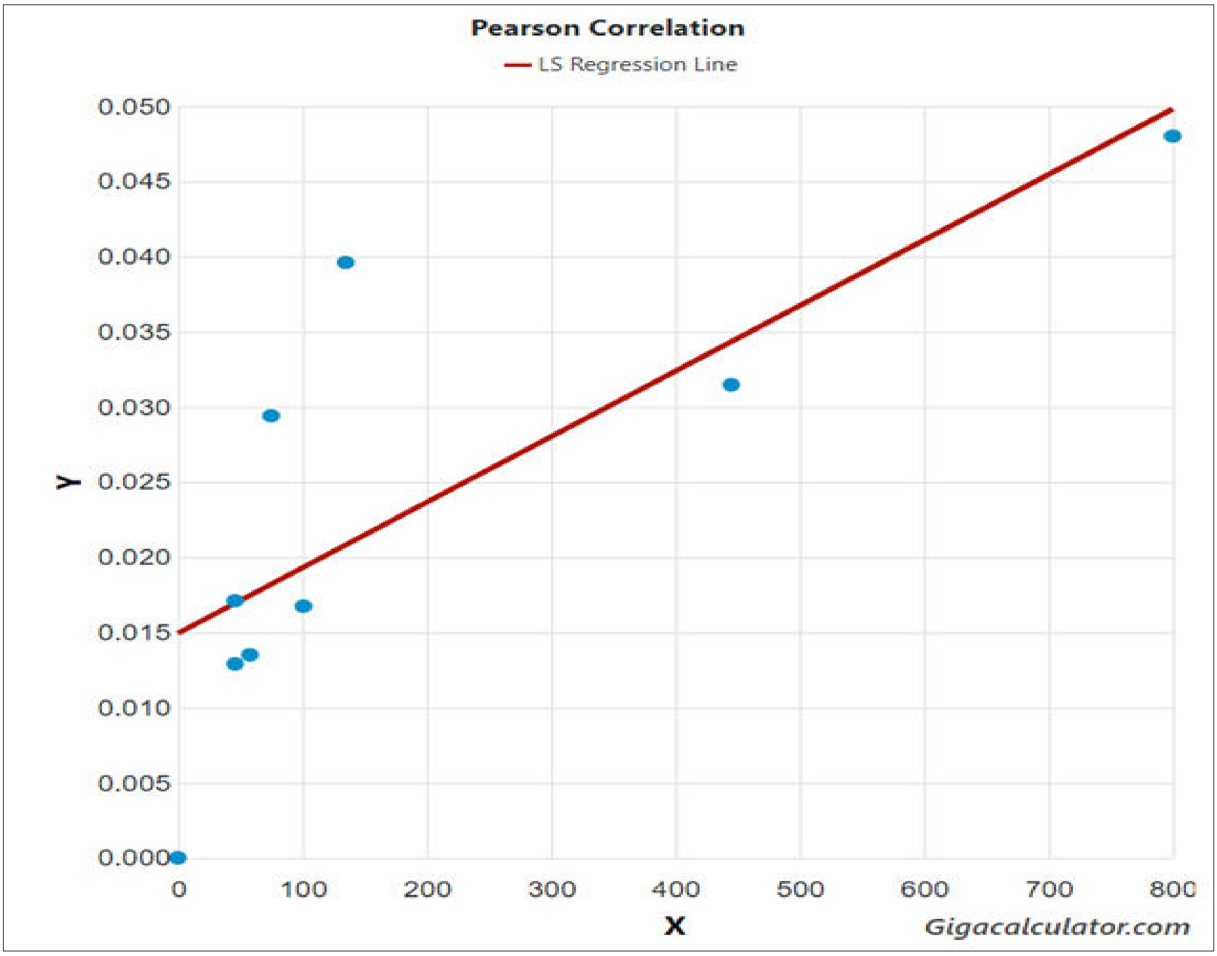

Fig 7: The positive relationship between female mating frequencies (x) and absolute abundance (y) in *Centrobolus*

4. Discussion

A difference (absolute and relative) was found between mating frequencies across sympatric *Centrobolus*. *C. anulatus* has the lower mating frequencies (0.00; 0.03) and *C. inscriptus* has the higher mating frequencies (0.0372; 0.0828). This study found mating frequencies recorded in the trees and on the ground in *C. anulatus* and *C. inscriptus* were also different. This study supports using mating frequency as a component of sexual selection in *Centrobolus* because there was an absolute and relative difference between species and a relative difference in mating frequencies across substrata. Mating frequencies are positively related to absolute abundance.

This is the first example of differences in mating frequencies between sympatric millipede species. Mating frequencies vary with the absolute abundances during seasonal activity patterns in species [1, 7, 8, 12-13]; and probably also during daily activity patterns [3, 11, 19]. Mating frequencies and bias of the sex ratio covary with SSD depending on the time and space in the season. Spatial changes in habitat preference are known in *C. fulgidus* and *C. richardii* [9]. These differences are likely due to the effects of differences in mating frequencies between the latter two species. Similarly, mating frequencies may be usefully investigated and compared with this study.

It is suggested there may be a benefit (direct or indirect) or cost for individuals mating in the tree substratum through dispersal. Mating frequency ultimately influences lifetime reproductive success and advantage through both sperm competition to males and fecundity advantage or disadvantage to females which is possible if they disperse into the trees [15]. Mating frequency was usefully investigated in potato tuber moth *Phthorimaea operculella* and Baluchistan Melon Fly *Myiopardalis pardalina* [4, 20]. Mating frequency in the female false codling moth *Thaumatotibia leucotreta* is a trade-off between fecundity and longevity [2]. In fungus-growing ants (*Attini*) mating frequency, colony size, polyethism, and sex ratio were related [21]. The mating frequency of the Papaya Fruit Fly *Toxotrypana curvicauda* was experimentally shown to depend on the availability of the host fruit [16]. In the Willow Leaf Beetle *Plagiodera versicolora* suboptimal mating frequency exacts a physiological cost that shortens the female life span and reduces fecundity [24]. Female mating frequency increases with temperature in two cricket species, *Gryllodes sigillatus* and *Acheta domesticus* [14]. Similarly, in *Centrobolus* habitat temperatures in the trees are probably higher than on the ground and rise from the forest floor upwards. Body size and shape affected mating frequency in the Brachypterous Grasshopper *Podisma sapporensis* but this was not so in *Centrobolus* [22].

Mating frequency is a useful indicator of mating success and also paternity success in the water strider *Aquarius remigis* [23]. Copulation duration is probably a misleading indicator of paternity success in polygynandrous mating systems such as millipedes and it is best to determine paternity from mating frequency and sperm precedence. Mating frequencies differ between males and females and are dependent on absolute abundance rather than sex ratio *per se*.

5. Conclusion

Mating frequencies varied systematically with species and substrata in two *Centrobolus* species. Variance in the mating frequencies occurs with higher frequencies of both species in the tree substrata.

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