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DETERMINANTS OF GRASSHOPPER DISPERSAL: AN EXPERIMENTAL APPROACH

Oluwafisayo Hazeizat Adeniran

748940

Submitted in partial fulfilment of the requirements for the degree of Master of Sciences in
Environmental Biology: Conservation and Resource Management of Swansea University,
Wales

September 2014

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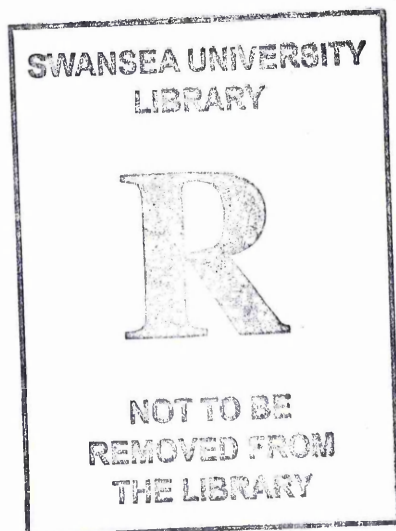


TABLE OF CONTENTS

	Page
LIST OF FIGURES	ii
LIST OF TABLES	iii
ACKNOWLEDGEMENT	iv
1. INTRODUCTION.....	1
1.1. Movement of Grasshoppers	1
2. METHODS.....	5
2.1. The Study Site.....	5
2.2. Experimental Design.....	7
2.3. Study Species.....	7
2.3.1. <i>Chorthippus dorsatus</i> : Gomophocerinae.....	7
2.3.2. <i>Euchorthippus elegantulus</i> : Gomophocerinae.....	8
2.3.3. <i>Pezotettix giornae</i> : Catantopinae.....	8
2.4. Vegetation Survey.....	9
2.5. Cutting Treatment	10
2.6. Grasshopper Survey	11
2.7. Predator Survey.....	13
2.8. Mark-Release-Resight Experiment	14
2.8.1. Marking the Grasshoppers	14
2.8.2. Spatial Reference System	15
2.8.3. Release of Marked Individuals	17
2.8.4. Daily Resighting and Recording.....	17
2.9. Data Management and Statistical Analysis	18
2.9.1. Statistical Tests	18
2.10. Movement Data Analysis.....	19
3. RESULTS	22
3.1. Vegetation Survey:.....	22
3.1.1. Vegetation Cover	22
3.1.2. Legumes.....	23
3.1.3. Forbs	24

3.1.4. Distribution of Vegetation Height	25
3.2. Grasshopper Survey (Pre-Cut and Post-Cut)	26
3.2.1. <i>Euchorthippus elegantulus</i>	26
3.2.2. <i>PezotettixGgiornae</i>	30
3.2.3. <i>Chorthippus Dorsatus</i>	34
3.3. Predator Survey.....	37
3.4. Linking Dispersal and Favourable Habitats.....	39
3.5. Mark and Re-sight Studies.....	40
3.6. Resighting	42
3.7. Settled Individuals	47
3.8. Individuals Yet to Settle.....	45
3.9. Distance Covered by “Settled” and “Yet to Settle” Individuals	47
3.10. Interaction of Average Distance Covered by Settled Population and Average Body Size	50
4. DISCUSSION	58
4.1. What are the Rate and Scales of Dispersal of the Three most Widespread and Dominant Grasshopper Species	58
4.2. Are Differences in Body Size and Movement Capacity (winged/wingless) Related to Interspecific Differences in Dispersal?.....	60
4.3. Does Dispersal Increase in Areas with Less Favourable Habitats?.....	62
4.3.1. Linking Dispersal with Vegetation Cover	63
4.3.2. Linking Dispersal with Vegetation Structure	64
4.3.3. Linking Dispersal with Predator Density.....	65
4.4. Do Sex Differences explain Individual Differences in Dispersal and is this in accordance or Opposite to Sex Differences in Body Size?.....	65
4.5. Are there Consistent Personality Differences which Relate to Differences in Dispersal?.....	67
4.6. Limitations	69
4.6.1. Use of the Box Sampler for Grasshopper Survey	69
4.6.2. Temperature in the Mesocosm.....	69
4.6.3. Marking.....	70
4.6.4. Resighting Exercise	73
5. CONCLUSION.....	74

REFERENCES73

APPENDICES82

APPENDIX I -	VEGETATION PROFILE WITHIN THE 144 QUADRATS & HERVBIVORY DATA
APPENDIX II-	INDIVIDUAL ATTRIBUTES
APPENDIX III-	RESPONSE TO HANDLING
APPENDIX IV -	RESIGHT FREQUENCY
APPENDIX V -	INDIVIDUALS THAT SETTLED
APPENDIX VI -	INDIVIDUALS YET TO SETTLE
APPENDIXVII-	INTERACTION OF RESIGHT FREQUENCY WITH RESPONSE TO HANDLING, SPECIES AND SEX
APPENDIXVIII-	RELATION SHIP WITH VEGETATION COVER
APPENDIX IX-	POISSON REGRESSION ANALYSIS OUTPUT

LIST OF FIGURES

Figure	Pages
1. Aerial View of the Mesocosm	6
2. 2m x 2m Quadrats	6
3. Layout and Dimensions of the Experimental Facility	7
4. Vegetation Dominance Map	10
5. Quadrats Selected for Cutting Treatment	13
6. Arrangement of the Four Dots on the Pronotum	14
7. Assignment of X and Y Coordinates to all Points in the Mesocosm.....	16
8. Layout Showing Release Points and Possible Orientation of Movement	17
9. Percentage Grass Cover for 144 Quadrats in the Mesocosm.....	23
10. Percentage Legume Cover for 144 Quadrats in the Mesocosm.....	24
11. Percentage Forb Cover for 144 Quadrats in the Mesocosm	25
12. Density of Male <i>E.elegantulus</i> within the four Blocks Pre-Cut	28
13 Density of Male <i>E.elegantulus</i> within the four Blocks Post-Cut.....	29
14. Density of Female <i>E.elegantulus</i> within the Four Blocks Pre-Cut.....	29
15. Density of Female <i>E.elegantulus</i> within the Four Blocks Post-Cut	30
16. Density of Male <i>P giornoae</i> in the 144 Quadrats (Pre-Cut)	31
17. Density of Male <i>P giornoae</i> in the 144 Quadrats (Post-Cut).....	32
18. Density of Female <i>P giornoae</i> in the 144 Quadrats (Pre-Cut).....	33
19. Density of Female <i>P giornoae</i> in the 144 Quadrats (Post-Cut).....	33
20. Density of Male <i>C.dorsatus</i> within the 144 Quadrats (Pre-Cut)	35
21. Density of Male <i>C dorsatus</i> within the 144 Quadrats (Post-Cut).....	35
22. Density of Female <i>C dorsatus</i> within the 144 Quadrats (Pre-Cut)	36
23. Density of Female <i>C dorsatus</i> within the 144 Quadrats (Post-Cut)	36
24. Predator Density within the 144 Quadrats (Pre-Cut).....	38
25. Predator Density within the 144 Quadrats (Post-Cut)	38
26. Distribution of Temperament for Marked Individuals.....	41
27. Frequency of Re-Sighting	43
28. Distribution of Distance Moved By Settlers.....	47
29. Distribution of Expected Distance to Be Travelled after 14 Days.....	48

30. Distribution of Average Distance covered by Females in relation to average body size of the three species	50
31. Distribution of Average Distance By Males Covered In Relation to Average Body Size of the Three Species.....	51
32. Net Square Displacement of Marked Individuals.....	52
33. Net Displacement Curve of <i>C.dorsatus</i> Individuals	53
34. Net Displacement Curve of <i>E.Elegantulus</i> Individuals	54
35. Net Displacement Curve of <i>P.Giornae</i> Individuals.....	55
36. Average Net Squared Displacement of the Three Study Species	56
37. Pattern of Redistribution from the Release Points.....	57

LIST OF TABLES

Table	Page
1. Grasshopper Density in the Mesocosm Pre-Cut	26
2. Grasshopper Density in the Mesocosm Post-Cut.....	26
3. <i>E.elegantulus</i> distribution at Block level Pre-Cut	27
4. <i>E. elegantulus</i> distribution at block level Post-Cut.....	27
5. Block density of <i>P.giornae</i> (Pre-Cut)	30
6. Block density of <i>P.giornae</i> (Post-Cut).....	31
7. Block density of <i>C. dorsatus</i> (Pre-Cut).....	34
8. Block density of <i>C. dorsatus</i> (Post-Cut).....	34
9. Predator densities in the four Blocks (Pre-cut)	37
10. Predator densities in the four blocks (Post-Cut)	37
11. Marked Males and Females	40
12. Distribution of active females amongst the three study species	40
13. Shows the number of active and calm males for the three study species	41
14. Summary of re-sight success in relation to temperament	42
15. Settled Individuals	44
16. Response to handling by Settled Individuals	44
17. Number of individuals that settled in each block.....	45
18. Individuals yet to settle	46
19. Response to handling by individuals yet to settle.....	46
20. Average distance covered by Settled Individuals	49
21. Expected distance after 14 days	50
22. Expected Distance after 21 days	50

ACKNOWLEDGEMENTS

This dissertation is dedicated to God Almighty for is matchless grace and His tender mercies

I would like to express my deep gratitude to Dr Luca Borger, my research supervisor for his patience, attentiveness and most importantly assistance at every step of this research.

I also express my deep appreciation to Dr Isabelle Badenhauer and Dr Nicholas Gross for their contribution to this study.

To all my lecturers and the entire Administrative staff of Department of Biosciences, I extend my profound gratitude.

To my love, my heart, my pride and my joy, Mr Ademola Aderemi Adisa Adeniran. I thank you for your unflinching support.

To my mothers, Mrs Abimbola Banjoko and Mrs Olayinka Adeniran, you are truly rare gems.

To Dr. Ezekiel Adelere Adeniran my father and mentor, words cannot describe how grateful I am for your contributions and consistent vote of confidence in me.

To my siblings Mr Abayomi Banjoko and Mr Kayode Banjoko , thank you and I love you so much

ABSTRACT

Understanding and predicting animal movements is of crucial importance for the conservation and management of natural resources. Grasshoppers are ecological indicator species used to monitor the spatio-temporal changes, to help reduce further loss of biodiversity on open grasslands. However, their current decline on European landscapes as a consequence of intense agricultural practices has elicited the need to understand all aspects of their ecology especially their movement on these highly fragmented landscapes.

With the use of a mesocosm, a mark and re-sight study was conducted in the Poitou Charentes Region of Western France, to investigate the movement dynamics of three widespread species in that area. With emphasis placed on the determinants of their rate and scale of movement in addition to the influence of individual behavioural trait variations on dispersal plasticity.

Net square displacement and mean squared displacement was used to quantify rate and pattern of movement. Two sub populations were identified and classified as settled and yet to settle sub-population. Poisson regression analysis and generalized linear models were used to test significance of interactions between grasshopper species and microhabitat constituents

Average distance travelled by re-sighted individuals ranged from 3.50metres to 18.66 metres. However the variation in average distance estimated for each of the species, arose from species specific interactions with micro habitat conditions especially vegetation functional class found within the quadrat.

Inter specific differences due to the possession of morphological correlates with dispersal; large body size and wing development, explained variation in magnitude of dispersal especially between *C.dorsatus* and *P.giornae*. However the rate of displacement exhibited by *E.elegantulus* suggest that possession of these traits in relation to proximity to food resources influences dispersal kernel.

The study was conducted during grasshopper breeding season when sex specific reproductive traits were likely to be more apparent. As a result of this, average distance travelled by male individuals exceeded that of females, but then these differences were not statistically significant.

1. INTRODUCTION

1.1. MOVEMENT DYNAMICS OF GRASSHOPPERS

Movement is fundamental to the life of all organisms (Darwin, 1859), for example the movement of organisms links habitats and ecosystems and mediates coexistence in communities (Turchin, 1998), and an important field of ecological research, called Movement Ecology, is aimed at understanding and predicting why, when, and where animals move (Nathan et al. 2008). Seminal studies have shown that adaptations for achieving movement, e.g. to disperse to new habitats, are of great importance even in stable and uniform environments (Comins, Hamilton & May 1980) but the capacity to move becomes even more important under environmental variation, especially for reacting to the current rapid and widespread human-induced changes (Tesson & Edelaar 2013). Furthermore, whilst traditional ecological models have been based on the simplifying assumption of random movements of identical individuals, research over the last decades has shown the need to better understand, quantify, and predict the large variation in movement behaviour between and within species that is commonly observed in natural populations (e.g. Morales et al. 2010; Rasmussen & Belk, 2012).

The unhindered exchange of resources among habitat patches is particularly essential to spatially structured populations like most orthopteran assemblages (Hein, 2004), because connectivity supports exchange of individuals and resources between patches, ensuring colonization (recolonization of new patches), reducing the likelihood of extinction (Burgess, Tremil & Marshall, 2012). Although several studies have correlated grasshopper species diversity and abundance with spatial configuration of landscapes (Quinn, Mark & Walgenbach, 1990; Bridle, Baird & Butlin, 2001; Guido & Gianelle 2001; Steck et al, 2007; Gardiner Haines, 2008; Badenhausser & Cordeau, 2012; Humbert et al, 2012) an emerging aspect of their ecology emphasizes the need to gain a full understanding of the biological processes that control and influence movement and redistribution patterns of grasshoppers (Penone et al. 2012; Schindler et al., 2013) to effectively manage and conserve populations occurring on intensively managed and heavily fragmented landscapes (Nathan et al., 2008; Badenhausser, 2012).

The movement of grasshoppers like most organisms is greatly influenced by interactions occurring between biotic (e.g. vegetation composition, height and topography)

and abiotic (e.g. temperature, wind direction, polarized light) components of the environment (Gardiner & Hill, 2004). Due to the importance of dispersal to most organisms, anthropogenic induced threats like habitat fragmentation and climate change in addition to density dependent factors (crowding, food resource availability, competition and predation) stimulate the evolution of heritable local adaptive traits (polymorphism) especially within meta-populations (Lutsccher, 2007; Bonte, Hovestadt & Poethke, 2009; Hawkes, 2009; Gueijrman et al, 2013). Individual phenotypic trait variations in terms of morphology, physiology and behaviour are bound to have an effect on disposition towards dispersal and habitat selection (Bowler & Benton, 2005; Cote et al 2010).

Whitman (2008) in his review of the significance of body size for orthopterans revealed that wing development and ability to fly in some grasshopper species is based on the attainment of a threshold body size. Here individual variations within population can be explained by body size and food resources available to the individual during developmental stages. Sexual dimorphism in most grasshopper species can also explain variability in dispersal capabilities, females are usually larger than males, with the exception of about 0.4% and 13% of Caelifera and Ensifera species, respectively (Hochkerch & Groning, 2008). Due to their larger body size, it is likely that female members of the same species of grasshoppers will move faster than males (Whitman, 2008). However, heterogeneity associated with reproductive needs, especially during breeding season, influences propensity to disperse in males, which is vital to maximize rate of fertilization, promoting fecundity of the population (Hochkerch & Groning, 2008; Colbert et al 2009). Besides from between sex differences, some orthopteran species exhibit within sex variation in terms of their dispersal abilities (Innocent et al, 2010). The females of *Gryllus firmus* and *Gryllus rubens* have been reported to exhibit variation in cellular respiration in relation to wing development—large females with long wings are dispersers with higher metabolic rate while smaller females with short wings have a lower metabolic rate and are sedentary (Roff, 1986; Zera & Mole 1994). According to Zera & Denno (1997), wing polymorphism within species is determined by the concentration of juvenile hormones and ecdysone present in the individuals; the concentration of these hormones is however influenced by density dependent (crowding) and environmental factors (temperature, duration of light exposure) the individual was exposed to during its life cycle. The authors further highlight that wing polymorphism within grasshopper species can be correlated not only with dispersal plasticity but also with the fertility of the individuals—winged individuals are usually less fecund than brachypterous individuals (Roff, 1986).

Habitat selection can also vary within species; most grasshopper species use crypsis to avoid predation, therefore polymorphism within the population in terms of pigmentation affects survival and preferred habitat choice by individuals (Wennersten, Karpestam & Forsman, 2012). This was tested by Gillis (1982) by manipulating the pigmentation of individual *Circotettix rabula rabula*; it was revealed that these grasshoppers selected microhabitats by colour matching.

Behavioural differences resulting from random evolutionary processes or natural selection of traits that increase fitness, have been shown to have cascading effects on dispersal ability and habitat selection of individuals within the same population (Hawkes, 2009; Brodin & Drotz, 2014). The decision of an individual to leave their natal patch to colonize a novel patch can be correlated with boldness, sociability and aggression of that individual (Cote et al, 2010). Bold individuals within *Gasterosteus aculeatus* populations have been documented to show more propensity to explore new habitats (Dubois & Giraldeau, 2014) while aggressiveness has been positively correlated with settlement success within populations of *Sialia mexicana* and *Pacifastacus linnusculus* (Hudina, Hock & Zganec, 2014). Social individuals within *Marmota flaviventris* are usually sedentary unlike the asocial individuals within the population that exhibit more tendencies to disperse (Cote et al, 2004).

Personality variations within population have far reaching ecological and evolutionary consequences (Wolf & Weissing, 2012). Studies on distinctive behavioural traits exhibited within grasshopper population in relation to dispersal patterns and propensity are however lacking. Most studies on personality variations within insect populations have been concentrated on other taxa. For example, Tremelle & Muller (2013) showed that food quality did not only influence growth rate but also the display of boldness in individual mustard beetles *Phaedon cochleariae*, while Muller, Grossmann & Chitka (2010) revealed that most individuals within the population of *Bombus terrestris* exhibited “episodic personality traits” in response to changes in flower colour. Here, I address this using a newly developed large outdoor experimental facility to study determinants of grasshopper dispersal and the effects of behavioural traits towards dispersal plasticity. Unlike many caged experiments which are small and restrict movement, this caged experiment is distinctive because the experimental facility (mesocosm) used is built on natural open grassland with a dimension of 30m² x 30m² - making it large enough in relation to known scales of grasshopper movement (Badenhausser, 2009). Additionally, three trophic levels of interactions exist within the mesocosm, i.e, the plant community (primary producers), grasshoppers (herbivores) while spiders, mantis and

crickets (*Conocephalus spp*) represent predators. Furthermore for this mark and re-sighting study, I used natural densities of the three most abundant species naturally living in the grassland (out of a total of seven identified species of grasshoppers existing within the enclosure), to address the following questions: (i) What is the rate and scales of dispersal of the three most widespread and dominant grasshopper species in temperate grasslands?; (ii) Are differences in body size and movement capacity (winged/wingless) related to interspecific differences in dispersal?; (iii) Does dispersal increase in areas with less favourable habitat?; iv) Do sex differences explain individual differences in dispersal and is this in accordance or opposite to sex differences in body size? (v) Are there consistent personality differences which relate to differences in dispersal?

This study was carried out in parallel to a study on trait based grasshopper habitat use and community structure, to which I also substantially contributed. The results of this parallel study will be mentioned within the main text or within the Appendices as appropriate

2. METHODS

2.1. THE STUDY SITE

The study area was located in the Chize Centre for Biological Studies, within a long term ecological research site (LTER “Zone Atelier Plaine et Val de Sèvre”, 450 km² extent), in central-western France (46° 11' N, 0° 28' W). The area contains intensively managed agricultural plains and a large forest reserve, the latter adjacent to the experimental mesocosm facility (see below). The agricultural plains are mostly dedicated to cereal crop production, with interspersed grasslands covering around 12% of the study area, the latter comprising both typical species rich calcareous grasslands as well as cultivated alfalfa grasslands. The grasslands harbour a rich community of grasshoppers (Caelifera, 30 species recorded; Badenhauer 2012).

2.1.1. THE MECOSOM EXPERIMENTAL FACILITY

The study was conducted in a 30m x 30m mesocosm erected on an old extensively managed grassland field (cutting once per year, no fertilizer applications) within the research facility, adjacent to the forest reserve. As shown in the Figure 1 which shows an aerial view of the facility.

The grassland contained a natural community of grasshoppers, which continued to live and reproduce in the mesocosm also after the closure of the insect proof nets in 2012 (Badenhauer, personal communication). The mesocosm was covered with transparent insect proof nets (PE 22.30,920 x 920µ, Diatex France). The interior of the mesocosm contained no barriers, allowing the grasshoppers to freely move within the entire area. The grassland within the mesocosm was subdivided into four blocks, separated by a pathway with shortly cut grass. Within each block a 2m x2m grid was established by marking one corner of each quadrat with three coloured wooden sticks. Please see Figure 2

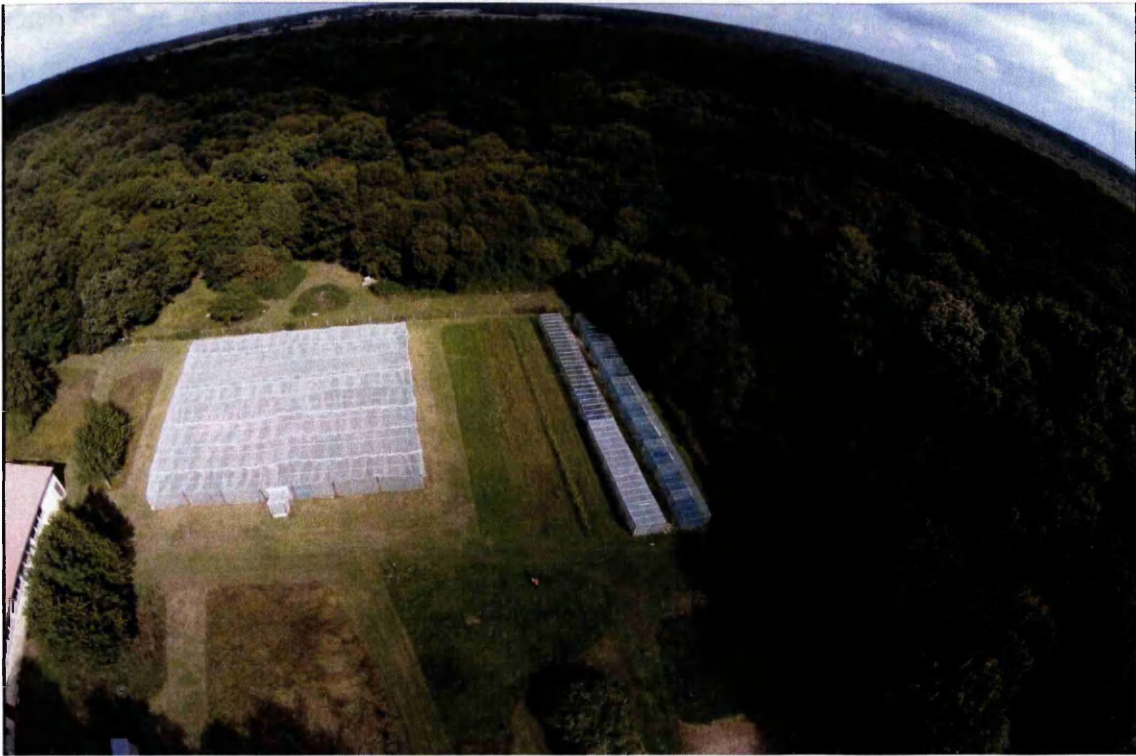


Fig. 1. Aerial View of the Mesocosm (Badenhasser, 2014)



Fig. 2. 2metre x 2metre quadrats (Borger, 2014)

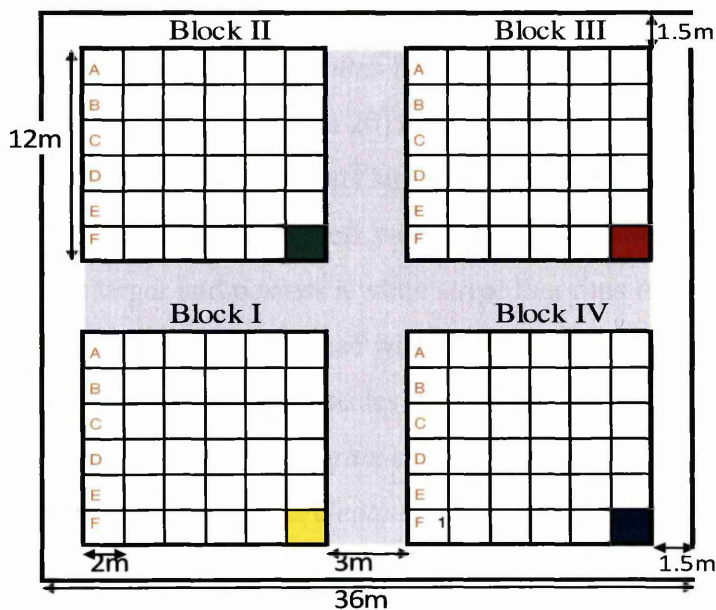
, for a total of 144 quadrats (Figure 3) is divided into four blocks which are 3 metres apart and 12 metres long. For ease of identification these blocks have been assigned colour codes. Block I is yellow, Block II is the green while Blocks III and IV are red and blue respectively.

Each of these blocks is further subdivided into 36 rows of 2metres x 2metres squares (Figure 1). The total number of 2metres x 2 metres squares in the enclosure is 144 replicates.

The study began on the 21st of July 2014 and was concluded on the 27th of August 2014.

2.2. EXPERIMENTAL DESIGN

Figure 3. Layout and dimensions of the experimental facility



Importantly, the mesocosm was erected two years ago and the plant and insect communities within the quadrats continued to naturally persist in the enclosure since then. Previous to the construction of the experiment the field was a natural open grassland with no artificial modification (cutting or fertilizer application) previously applied.

2.3. STUDY SPECIES

2.3.1. *Chorthippus dorsatus*: Gomphocerinae

These are dimorphic green or light brown grasshoppers, usually found on nutrient rich extensively managed grasslands or wet meadows (Wagner, 2005). They are also one of the

dominant species found within the study area (Badenhausser et al, 2009). *C. dorsatus* are medium sized winged grasshoppers that predominantly feed on grass (*e.g. Arrhenatherum eliatum, Dactylis glomerata*), although it has been documented by Deraison et al (*in review*) that they forage on some forbs (*e.g. Plantago lanceolata, Salvia pratensis, Achillea millefolium*). The adults of *C. dorsatus* usually appears from July to early November. Even though they possess wings and are capable of flight (Reinhardt et al 2005), these short horned grasshoppers prefer walking as a mode of dispersal in between preferred habitat patches especially in an east west direction (Picaud & Petit, 2007).

2.3.2. *Euchorthippus elegantulus*: Gomophocerinae

They are commonly referred to as Jersey grasshoppers. These grasshoppers are very widespread in hot areas especially places in close proximity to the sea, and natural grasslands (Sutton, 2008). *Euchorthippus elegantulus* have also been reported to use road verges as alternative habitats (Badenhausser et al 2012) and has been identified as one of the 13 most dominant species found around the study site since 2004 (Badenhausser 2009). These are brownish or straw coloured grasshoppers with slender body structure especially males, females are usually larger and possess a white stripe that runs from their thorax to the abdomen. They also possess a large head with body size ranging from 10 – 22 mm and feed on grasses, especially slow growing species with high leaf dry matter content (*e.g. Bromus erectus, Elytrigia repens, Arrhenatherum eliatum, Dactylis glomerata*) (Badenhausser, 2014; Deraison et al, *in review*). Adult *E. elegantulus* start appearing from July to October (Sutton, 2008). *E. elegantulus* preferred mode of dispersal is by flight.

2.3.3. *Pezotettix giornae*: Catantopinae

These are brachypterous species of grasshoppers (Bretagnolle et al, 2011) usually found on dry steppes in moist microhabitats especially in Mediterranean areas (Gangwere & Agacino, 1970). They are small grey or dark brown grasshoppers with a body size ranging from 11-15mm for males and 12-18mm for females (Badenhausser, 2014). Their diet comprises of mainly legumes (*e.g. Trifolium partense, Trifolium repens, Ononis repens*) and forbs (*e.g. Centaurea jacea, Convolvulus arvensis, Plantago lanceolata*) (Deraison et al, *in review*). Adults of these species emerge from of June to October (Wagner, 2005) Due to the morphology of their wings which makes them incapable of flight, their preferred mode of movement is jumping .

2.4. VEGETATION SURVEY

The survey was conducted from the 21st of July 2014 to the 28th of July 2014. We conducted this survey to determine the floristic composition and quantify the resources available for grasshopper assemblages within the mesocosm. The materials used for this exercise include:

- a. 1 metre x 1 metre sampling quadrat subdivided into four 0.25metre x 0.25metre squares
- b. Measuring tape

Methodology

The 1m² quadrat was placed in each 2metre x 2 metres square four times to visually estimate total percentage vegetation cover of legumes, forbs and grass for each quadrat. We assessed vegetation canopy height during the survey (Badenhausser & Cordeau, 2012) using a collapsible measuring tape to determine the height that is representative of the canopy in each of the 0.25metre x 0.25metres square. Due to the subdivision of the 1m² sampling quadrat into four squares of 0.25metres x 0.25metres, 16 observations were recorded for each quadrat within each block. The total observations made for the 144 quadrats were 2304. These observations were recorded in field forms. The recorded data were then transferred into Microsoft excel spreadsheet, where average percentage cover of all the vegetation types (legumes, forbs and grass) in the enclosure was calculated. The average vegetation height was also determined. The information generated from the survey was used for different analysis and for the production of a vegetation dominance map (Please see figure 4.) which was very useful to all aspects of our study.

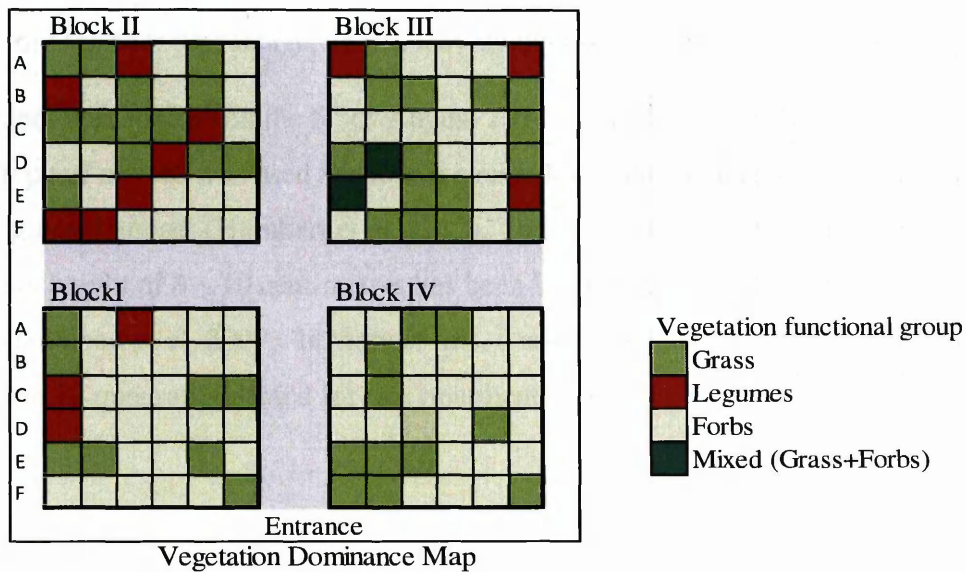


Fig 4. Vegetation Dominance Map.

Each quadrat is classified according to the dominant vegetation type (plus a mixed category for grass and forbs were the median cover was very similar)

2.5. CUTTING TREATMENT

The vegetation inside the enclosure was modified by applying cutting treatment to 72 quadrats (18 quadrats / block) and all the walk paths within the mesocosm. (As illustrated in Figure 5.) The cutting treatment was applied to understand how change in micro habitat characteristics affects the population dynamics of grasshopper assemblages in the mesocosm. This was crucial to our experiment as several studies have indicated that grassland invertebrates especially grasshoppers are affected by intensive cutting practices directly (responsible for 65- 85% mortality) and indirectly (habitat loss and fragmentation) (Guido & Gianelle, 2001; Stotata et al, 2009; Humbert et al 2009; Badenhausser & Cordeau, 2012; Humbert et al, 2012).

We used data from the vegetation survey to randomly select the quadrats that were mowed. This was achieved by analysing the data recorded for all the three vegetation cover types (legumes, forbs and grass) in all the 144 quadrats in R statistical environment. Percentage

vegetation cover of each of the vegetation types/ block was grouped into four quantile classes (0-25%, 25-50%, 50-75% and 75- 100%). This was followed by randomly selecting at least three blocks from the four percentage classes leaving out outliers.

Cutting treatment was applied on the 5th of August 2014, using a hand pushed motor bar mower. This type of mower was used because it causes less damage in terms of invertebrate mortality and ground impact (Humbert et al, 2012). To further reduce the direct impact of mowing, cutting height of 8 – 10 centimetres has been suggested for biodiversity conservation (Humbert et al, 2009). In view of this, a cutting height of 8.8 centimetres was applied to all the 72 quadrats selected for this treatment.

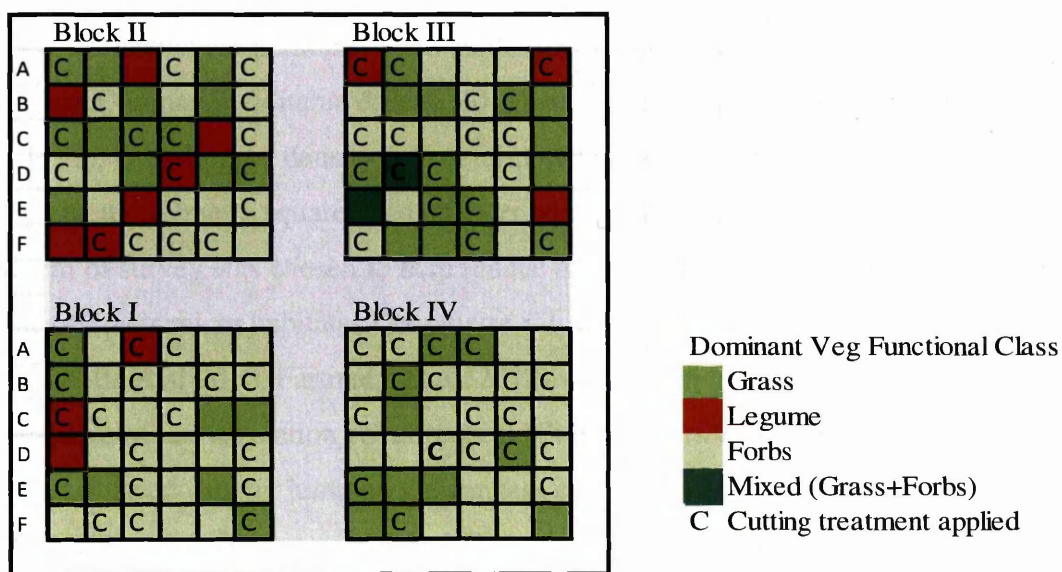


Fig 5. Quadrats selected for cutting treatment

2.6. GRASSHOPPER SURVEY

We conducted two surveys to estimate the distribution and relative abundance of the difference in grasshopper species with the mesocosm, before and after the cutting treatment. The first survey started on the 29th of July 2014 and was concluded on the 4th of August 2014. The second survey started on the 14th of 2014 August to 16th of August 2014. The timing at the end of July assured that most individuals had reached the adult stage for both surveys

(Badenhausser et al, 2009). Each survey was done by the same two observers, following the method developed by (Badenhausser et al 2009):

- 0.7m high 1metre x 1 metre box sampler with sides covered with opaque green canvass.

- A Small sweep net

- A Transparent container with four holes covered with wire mesh and other

- Small plastic containers

- 1metre x 1metre microcosm (as used by Deraison et al, in review) covered with transparent insect prove netting (PE 22.30,920 x 920 μ , Diatex France)

- CNRS Grasshopper Species Identification Key by Defaut(1992)

The surveys were conducted twice in a day, in the morning before 0800hrs and in the evening starting at 1800hrs as outside temperatures were cooler and grasshoppers less active (Guendouz-Benrima, Doumandji-Mitchie & Petit, 2011) and hence less “agitation dispersal” (*sensu* Turchin 1998). Grasshopper density was determined in each of the 4 blocks by surveying all the 2meter x 2metre squares in a checker board pattern (A₁, A₃, A₅) See Figure 5 . Also this pattern of survey was chosen to help reduce movement activity of grasshoppers due to disturbance of their micro habitats. The 1metre x 1 metre box sampler (Badenhausser et al, 2009; Bretagnolle et al 2010; Fartmann et al, 2012) was placed in the quadrat at a position representative of the vegetation cover present. Grasshoppers within the area where the box sampler was placed usually jump on the canvass covering the sides of the sampler. We also used the handle of the sweep net (especially areas with dense and tall vegetation cover) to gently disturb the vegetation inside the sampler, this encouraged the grasshoppers to jump on the canvass covering. This method of sampling was chosen, because the design of the box sampler decreased the incidence of grasshoppers jumping in and out from the quadrat being surveyed or other quadrats in close proximity (Gardiner, Hill & Chismore, 2005). Grasshoppers were then carefully removed from the sides of the sampler with small plastic containers (Badenhausser et al, 2009). Removal of grasshoppers from the quadrats was done to accurately identify species present in the mesocosm (Gardiner et al, 2005) and also to avoid recounts. Species identification and classification (gender and developmental stage) was done using the CNRS Grasshopper Species identification Key by (Defaut 1992). The adults of the most dominant species *Euchorthippus elegantulus*, *Pezotettix giornae* and

Chorthippus dorsatus were then transferred into separate 1 metre x 1 metre microcosms (Deraison et al, in review) placed at the centre of the mesocosm with the aid of transparent containers with four holes covered with wire mesh. Other species found, but not in high densities included *Chorthippus albomarginatus*, *Chorthippus bigatullus*, *Omocetus rufipes*, *Gomophocerippus rufus*. These were kept in transparent containers and later released back at the end of the survey.

2.7. PREDATOR SURVEY

We conducted a predator survey on the 4th of August 2014 to determine the distribution and identity of predatory species present in the mesocosm. The materials used for the survey include:

- A Small Sweep net and
- Small plastic containers to store the specimens for identification

Each 2m² quadrat was surveyed by slowly walking through the vegetation, spending 5 minutes in each quadrat. All predatory species seen were captured and placed in small plastic containers for identification. The specimens were taken to the entomology laboratory on site for species identification. Most of the predators in the mesocosm were ambush predators, with high densities in quadrats characterized with tall vegetation cover. Dominant predatory species found were members of the Araneidae (e.g. *Agriope bruennichi*, *Araniella cucurbitina*), Tettigoniidae (e.g. *Conocephalus spp*, *Ruspolia nitidula*) and Mantidae (*M. religiosa*) families. The data derived from the survey was used to produce a predator distribution map. (Deraison et al, in review). However there were several non – predatory invertebrate species present, these include butterflies (e.g. *Papilio machaon*, *Polyommatus icarus*, *Heodes virgaureae*), moths (e.g. *Euplagia quadripunctaria*, *Macroglossum stellatarum*), shield bugs (e.g. *Staria lunata*, *Lygaeus equestris*, *Graphosoma lineatum*), Gryllidae (*Nemobius sylvestris*), hornets (*Vespidae spp*), lady bugs (*Coccinellidae*) hover flies (*Syrphidae*), horse flies (*Tabanidae spp*), soldier beetles (*Cantharidae spp*), harvestman spiders (*Opiliones*) and molluscs (*Gastropoda*). Due to their non-predatory nature we did not conduct a survey to determine their density.

2.8. MARK- RELEASE – RESIGHT EXPERIMENT

2.8.1. MARKING THE GRASSHOPPERS

Climatic and habitat factors greatly affect the population and movement dynamics of most grasshopper species (Gardiner & Hill, 2004). Due to the important role of dispersal in ensuring the continued existence of organisms, the quantification of the individual and phenotypic variations in terms of dispersal behaviour is necessary for effective management and conservation (Borger & Fryxell, 2012).

Mark and recapture techniques has been used by numerous studies for the quantification and analysis of movement behaviour of mobile organisms (vertebrates and invertebrates) (Nakumura et al, 1964; Schneider, 2003). Due to their “intermediate” dispersal capabilities, several studies on temperate grasshopper assemblages’ movement ecology and dispersal patterns (Narisu et al 1999; Gardiner & Hill 2004; Walters et al 2010) have also adopted this method. In our study we used an adaptation of this process, which is the Mark – resight technique (Minta & Mangel 1989; Keller, 2012) to gain insights concerning individual phenotypic variations and how it affect dispersal and redistribution patterns (Lettinik & Armstrong, 2003). This method was adapted to reduce the incidence of stress induced mortality from handling and the interference of normal dispersal patterns of marked individuals which usually occurs in the recapture phase (Mallet et al, 1987; Turchin, 1998). The marking of all the grasshoppers used for our study was conducted in the mesocosm on the 5th of August 2014 to the 6th of August 2014. Grasshoppers were uniquely marked with four dots on their pronotum (illustrated in figure 6) using the flat end of a pin and Humbrol™ enamel paint, following the method of (Richards & Waldoff, 1954).

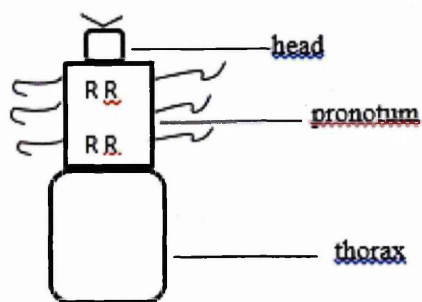


Fig. 6. Arrangement of the four dots on the pronotum

Marking was done by the same two individuals (plus a helper to keep record of the colour code used for each individual) and it took an average of two minutes to mark each grasshopper. One person held the grasshopper to mark by gently clasping the hind legs to the sides of the abdomen, preventing the grasshoppers from jumping while the other person applied paint with utmost care on the pronotum to avoid the paint going on the wings, eyes or other parts of the insect. Unique colour codes were generated from the five colours (Red-Satin 174, Green-Gloss 38, Yellow-Gloss 69, Blue- Ment 52 & White- Matt 34) for 100 individuals of *Euchorthippus elegantulus*, 102 *Chorthippus dorsatus* and 101 *Pezotettix giornae*. (Please see AppendixII). During the marking process, we made a note of each individual grasshopper's reaction towards being handled, if the individual was trying to resist and escape being manipulated or if it did freeze and not move. This was done to determine if there is a relationship between temperament displayed and dispersal propensity as there is increasing evidence that the behaviour during capturing operations provides a very good correlate of "boldness" of individuals (e.g. Reale et al, 2000). We used 1 to describe active (bold) individuals while 0 was used to index calm grasshoppers. Marked individuals of different species were kept in separate 1metre x 1 metre microcosms at the centre of the enclosure prior to their release.

2.8.2. SPATIAL REFERENCE SYSTEM

We chose a resolution of 2metres to record movements of the released grasshoppers by recording the identification of the quadrat, a marked individual was resighted and by assigning a location to the centre point of each quadrat. To achieve this we set up a spatial reference system. Two dimensional Cartesian coordinates were assigned to all the quadrats and walk paths in the enclosure as shown Fig 7. In addition, the two dimensional Cartesian coordinates system was used (X, Y) to quantify the rate and pattern of dispersal from the time of release for each individual, using the Pythagorean theorem to calculate Euclidian distance between re-sighted locations

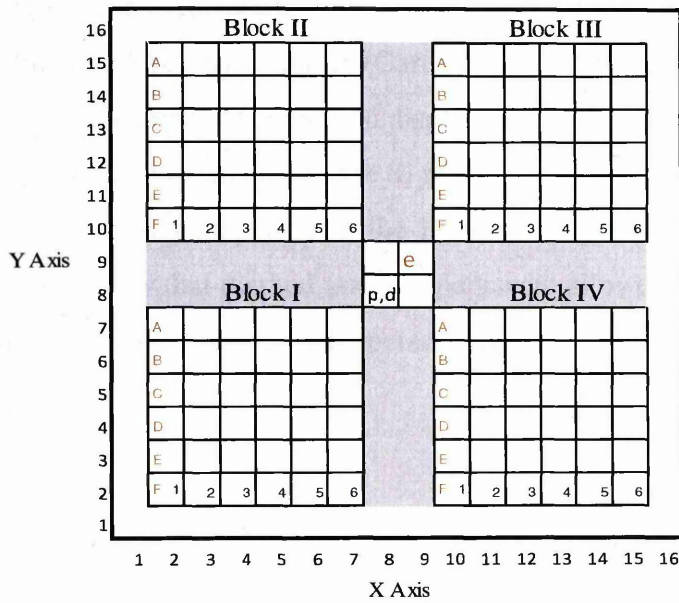


Fig.7. Assignment of X and Y coordinates to all quadrats in the mesocosm Each unit corresponds to a 2metres distance. P and D refers to the point of release for *C.dorsatus* and *P.giornae* while e is the release point of *E.elegantulus*

The box in the centre represents the release points of the marked individuals.100 marked *Euchorthippus elegantulus* were released at position (9,9) on the top right while 101 and 102 marked *Pezotettix giornae* and *Chorthippus dorastus* were released in(8,8) which is the bottom left

The Euclidian distance is derived by taking the square root of the summed squared differences between the assigned X and Y coordinates (Barret, 2005).

$$dxy = \sqrt{(x1 - y1)^2 + (x2 + y 2)^2} \quad \text{(Equation 1)}$$

where dxy = Euclidian distance

X₁ = X coordinate of the origin

X₂= X coordinate of the end point

Y₁ = Y coordinate of the origin

Y₂= Y coordinate of the end point

2.8.3. RELEASE OF MARKED INDIVIDUALS

The marked grasshoppers were released on the evening (21:00 GMT -1) of 6th of August 2014. We chose to release the grasshoppers in the evening because they are less active at night due to reduced temperature (Gardiner et al, 2005;Guendouz-Benrima et al, 2011), limiting the incidence of “agitation dispersal”(Turchin,1998). The point of release was at the centre of the mesocosm (see figure 8) and this was done by slowly removing the transparent insect proof netting used to cover the 1metre x 1metre microcosms marked individuals where kept. Importantly that marked grasshoppers were allowed to initiate movement naturally without any encouragement to disperse from the point of release.

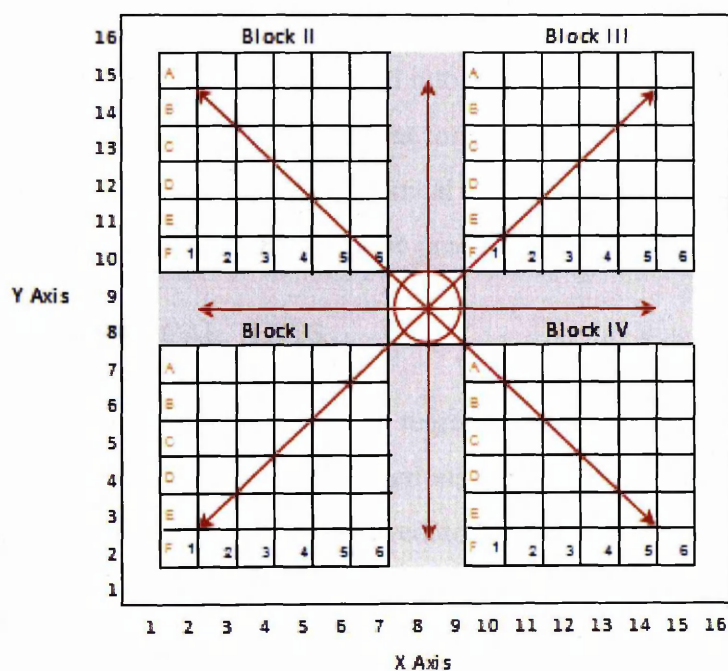


Fig. 8. Layout showing release points and possible orientation of movement

2.8.4. DAILY RESIGHTING AND RECORDING

Post release re-sighting was carried out on daily between 7th of August 2014 till the 27th of August 2014. This was done twice in a day, in the morning at 0900hrs and in the evening at 1800hrs surveying half of the mesocosm each time.

These sessions were designed to avoid temporal and spatial bias regarding re-sighting probabilities (Lettink & Armstrong 2003). Two blocks were surveyed per session, Block I and II in the morning then Block III and IV in the evening and vice versa on the next day. In each session also all the walk paths between the blocks were surveyed. An equal amount of time was spent in each quadrat with double the time spent in uncut quadrats as compared to cut quadrats, given the lower detectability in the former.

Re-sighting survey data was recorded in a field form with columns that included: date, time, block, assigned X and Y coordinates of point where the marked individual was re-sighted, species, sex and unique colour code. This was used to quantify the displacement and mean rate of dispersal of each marked individual by modelling distance covered as a function of time since release.

2.9. DATA MANAGEMENT AND STATISTICAL ANALYSIS

All field data recorded were entered into Microsoft excel spreadsheets and saved as c.s.v files for further analysis in R environment for statistical computing (R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.)

2.9.1. STATISTICAL TESTS

Linear regression analysis, Poisson regression analysis and generalized linear models were used to test relationships and interactions between different vegetation cover classes and grasshopper abundance, effect of predator density on grasshopper abundance and also the effect of temperament or response to handling, species and sex to on frequency of re-sighting. Two tail sample T test for unequalled variances was used to test the significance of distance estimates for the three different species between sexes and amongst the species. Also Population proportion test was also used to obtain determine the significance of the ratio between sexes, temperament exhibited by individuals within settled and yet to settle sub-population.

2.10. MOVEMENT DATA ANALYSIS

Movement data analyses

We used the squared displacement approach of Börger & Fryxell (2012) to identify the movement mode of the released individuals – sedentary individuals, i.e. individuals which remained within the release site without dispersing, dispersers, i.e. individuals which moved away from the release site but then settled into a new area, and non-settled dispersers, i.e. individuals which moved away from the release site and had not stabilized into a new area within the 21 days of the experiment– and estimate the movement parameters, timing and distance of dispersal. The approach is based on the squared displacement statistic, a fundamental statistic in movement analysis (Turchin 1998; Nouvellet et al, 2009) – the square of the Euclidian distance between the first point in the movement path (here, the release point) and each of the successive locations. The Borger & Fryxell approach (2012) is based on the observation that the shape of the squared displacement curve over time can be predicted from theory, for organisms moving with contrasting strategies. If an organisms moves without ever settling into a certain area, it can be predicted from theory that the squared displacement from the starting location will continuously increase over time, on average. Hence, the most appropriate model for the squared displacement values over time will be a linear model:

$$MSD = 4Dt \quad (\text{Equation 2})$$

where MSD is the squared displacement value, D is the diffusion constant (multiplied by 4 for two-dimensional movements) and t is the time since start; or, more generally, a power relationship:

$$MSD = Dt^\alpha \quad (\text{Equation 3})$$

which reduces to equation 2 for a linear model. If an animal remains within the same area over a given time interval, often this is called the home range (here, it would apply to individuals which remain within the surroundings of the release area), it can be shown that the squared displacement values will initially increase over time and then stabilize around a constant value: Thus, the change over time of the squared displacement values can be modelled using:

$$MSD = \phi_1 [1 - \exp(-\phi_2 t)] \quad (\text{Equation 4})$$

where ϕ_1 is the asymptote and ϕ_2 is a rate constant. If an organism disperses away from the release point, moves through the landscape but then settles down into a certain area, the squared displacement pattern will show a sigmoid pattern (Borger & Fryxell 2012; see also Bowler & Benton 2005 and Clobert et al. 2009 regarding the three-phasic nature of dispersal) and can be modelled using:

$$MSD = \frac{\phi_3}{1 + \exp\left[\frac{(\phi_4 - t)}{\phi_5}\right]} \quad (\text{Equation.5})$$

where ϕ_3 is the dispersal distance; ϕ_4 is a parameter for the inflexion point, in units of time since start (t), and thus models the timing of the transience phase; ϕ_5 is a scale parameter on the time axis governing the shape of the curve. Also, 95% of the dispersal distance will be reached at the following settlement time:

$$t_{settle} = \phi_4 + 3\phi_5. \quad (\text{Equation 6})$$

Thus, t_{settle} can be taken as a rational approximation of the start of the settlement phase (similarly for the start of the transience phase). Hence, this equation can provide an estimate of both the distance and timing of the dispersal phases. Importantly, these are continuous time models and hence can accommodate unequal time intervals between locations, contrary to many other approaches. Following Borger & Fryxell (2012), nonlinear mixed models, using the nlme package in R (R Core Team, 2013) were used to fit the models to the displacement data of each grasshopper and the fit was assessed using the Correspondence criterion (see Borger & Fryxell 2012 and references therein). The model that was best supported by the data was chosen to classify the individuals into settled and non-settled dispersers (note, no released individual remained close to the release site) and the estimated individual parameters were used to provide a measure of dispersal distance (after 21 days) and timing of dispersal (for the settled individuals only). These values were then used to test for the hypothesized drivers of individual differences in dispersal.

3. RESULTS

3.1. VEGETATION SURVEY

3.1.1. GRASS COVER

The average grass cover within the quadrats in the mesocosm accounted for 46.8% of the total vegetation cover within the mesocosm. Dominant grass species identified within the mesocosm were: *Arrhetherum elatius L.*, *Bromus erectus Huds.*, *Dactylis glomerata L.*, *Festuca rubra*, *Festuca arundinacea*, *Poa angustifolia*. At the block level, Block IV had the highest grass cover of 55.46%, while blocks III, II and I, had grass cover of 46.26%, 43.15% and 42.29% respectively. The variation in grass cover was more apparent between the 2m x 2m squares within each of the blocks (Fig 9) In Block I the percentage of grass cover ranged from 32.5% to 60.63%. Median cover of grass for the entire block was 39.69%.

In Block II the percentage grass cover ranged from 26.25 % to 69.38%. Median percentage grass cover is 42.50%.

Grass cover within Block III ranged from 25.00% to 70.63% found in A4 and F3 respectively. Median grass cover for within this block is 45.94%. Within Block IV the percentage grass cover ranged from 28.94% to 78.75%. The median percentage cover of grass in Block IV was 53.59 %

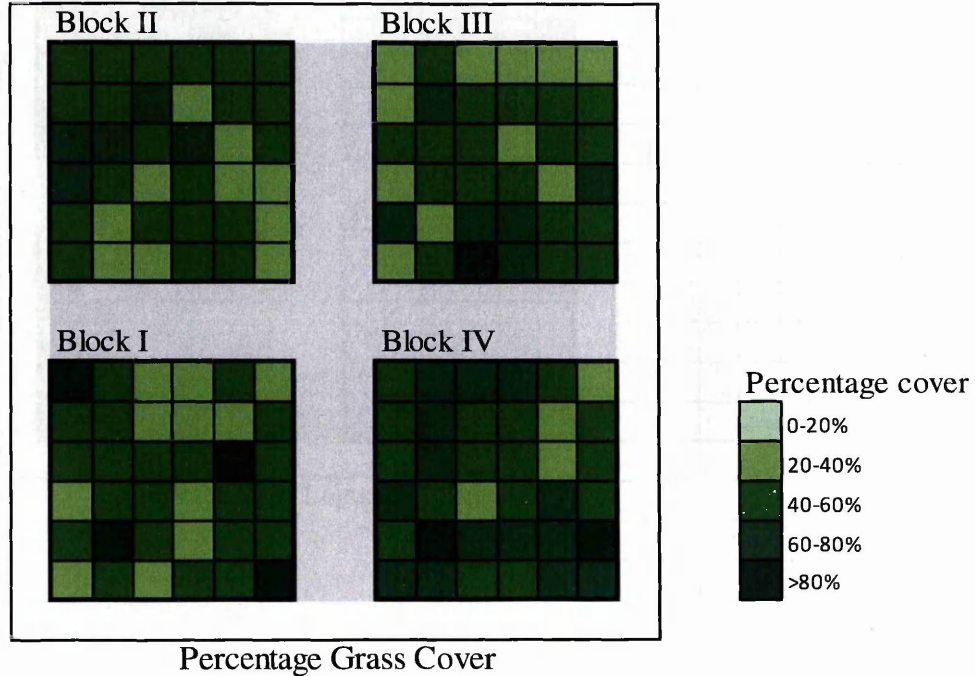


Fig 9. Percentage Grass Cover for 144 Quadrats in the mesocosm

3.1.2 LEGUMES

Cover by legumes was on average 16.4%. Legumes in the mesocosm displayed a sparsely distributed clustered growth pattern which is very apparent within the blocks. Frequently occurring species include, *Trifolium partense*, *Trifolium repens*, *Medicago Arabica*, *Ononis repens*.

Block II had the highest percentage of legume cover, with a block average of 24.29%, Block I with 18.61% while Blocks III and IV had block averages of 16.50% and 6.02% respectively.

For Block I, the percentage cover of legumes ranged from 0% to 61.88%. (Figure 10).

Median legume cover is 14.06%.

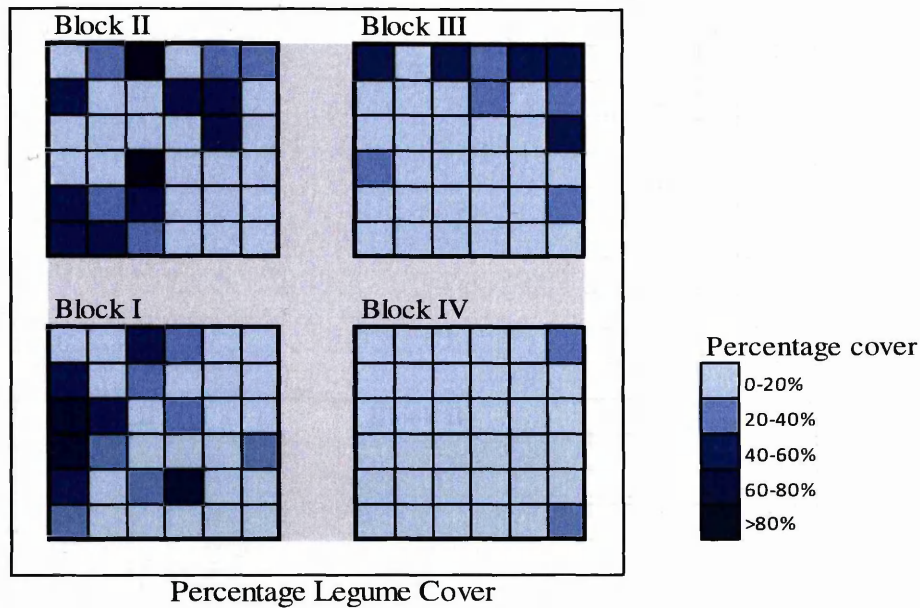


Fig. 10. Percentage Legume Cover for 144 Quadrats in the mesocosm

Within Block II the average legume cover ranged from 0.63% to 73.125% . The median percentage legume cover was 16.41%. Percentage legume cover in Block III ranged from 0% to 47.50%. The median legume cover is 12.5%. Block IV, highest legume cover within this block is 37.5% The median legume cover for this block is 0.63%.

3.1.3. FORBS

These herbaceous plants accounted for 54.0% of the total plant cover in the mesocosm. The predominant species included: *Daucus carota*, *Picris hieracioides*, *Centaurea jacea*, *Convolvulus arvensis* and *Plantago lanceolata*. Block IV has the highest percentage cover of forbs with 63.19%, Block I with 54.55% while III and II have block averages of 52.55 % and 45.75%. Within Block I the percentage cover of forbs ranged from 33.13% to 76.25% as shown in Figure 11 below. The median percentage forb cover is 53.75%. The percentage cover within Block II percentage forb cover ranged from 21.56% to 77.50%. Median forb cover is 44.06%. For Block III, the forb cover percentages ranged from 34.68% to 81.25%.

The median percentage forb cover for this block is 49.38%. Block IV forb cover ranged 37.50% to 90.00%. Median percentage forb cover is 65.63%.

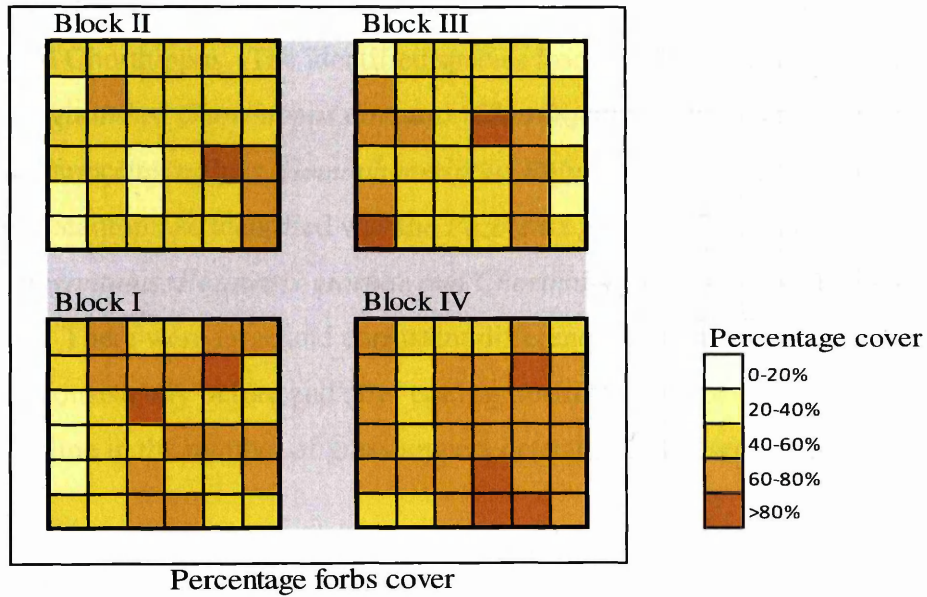


Fig 11. Percentage forb Cover for 144 Quadrats in the mesocosm

3.1.4. DISTRIBUTION OF VEGETATION HEIGHT.

The average canopy height within the mesocosm is 24cm. At Block level the average canopy height for Block I is 23cm while Blocks II, Block III and IV have average canopy height of 23cm, 24cm, and 24.57cm respectively. Height distribution within the blocks is described as follows

Block I, height values ranged from 13cm to 37cm. The median height distribution is 22cm.

The height distribution within Block II, ranged from 17cm to 39cm the median canopy height is 21cm. The distribution of the vegetation canopy height in Block III that ranging from 18cm to 37cm. Median canopy height is 22.81cm. For Block IV, height values ranged from 18 cm and 37cm. Median canopy height is 23.94cm.

3.2. GRASSHOPPER SURVEY (PRE CUT AND POST CUT).

Seven grasshopper species were recorded in the mesocosm, all from the Gomophocerinae and Catantopinae family. Six out of the seven species were grass feeders from the genera *Euchorthippus* and *Chorthippus*. The identified species from these genera were the, *Euchorthippus elegantulus*, *Chorthippus dorsatus*, *Chorthippus bigatulus*, *Chorthippus albomarginatus*, *Omocetus rufipes*, *Gomophocerippus Rufus*. The only legume /forb feeder from the Family Catantopinae identified was the *Pezotettix giornae*. Our study species *Euchorthippus elegantulus*, *Pezotettix giornae* and *Chorthippus dorsatus* were the three dominant species. There were large and consistent differences in total grasshopper counts between blocks, consistently before and after cutting treatment and for both sexes, albeit overall 43.6% decline in the number of grasshoppers detected for the second survey. (Table 1 and 2)

Table 1. Grasshopper Density in the Mesocosm Pre-Cut

BLOCK	MALE	FEMALE	TOTAL DENSITY WITHIN BLOCK
I	104	137	241
II	57	67	124
III	76	98	174
IV	121	131	252
Total density	358	433	791

Table 2. Grasshopper Density in the Mesocosm Post Cut

BLOCK	MALE	FEMALE	TOTAL DENSITY
I	41	63	104
II	45	50	95
III	60	47	107
IV	60	80	140
Total density	206	240	446

3.2.1. *Euchorthippus elegantulus*

This is the most dominant species within the mesocosm. Before the application of cutting treatment 422 were counted during the survey (180 males and 242 females), after the cutting

treatment 231 individuals were counted (92 males and 139 females), thus a 45.30% decline. There were also large differences between the blocks in numbers of *E. elegantulus* counted and these differences remained consistent before and after the cutting treatment (Table 4 and 3).

Table. 3. *E.elegantulus* distribution at Block level Pre-Cut

BLOCK	MALE	FEMALE	TOTAL BLOCK DENSITY
I	64	76	140
II	21	24	45
III	22	44	66
IV	73	98	171

Table. 4. *E. elegantulus* distribution at block level Post – Cut.

BLOCK	MALE	FEMALE	TOTAL BLOCK DENSITY
I	23	42	65
II	15	18	33
III	20	24	44
IV	34	55	89

The variation in the distribution of *E. elegantulus* was more apparent within the 2m x 2m quadrats. Figures 12 and 13 are heat maps showing the relative abundance of male and female *E. elegantulus* within the 144 quadrats before and after the application of cutting treatment.

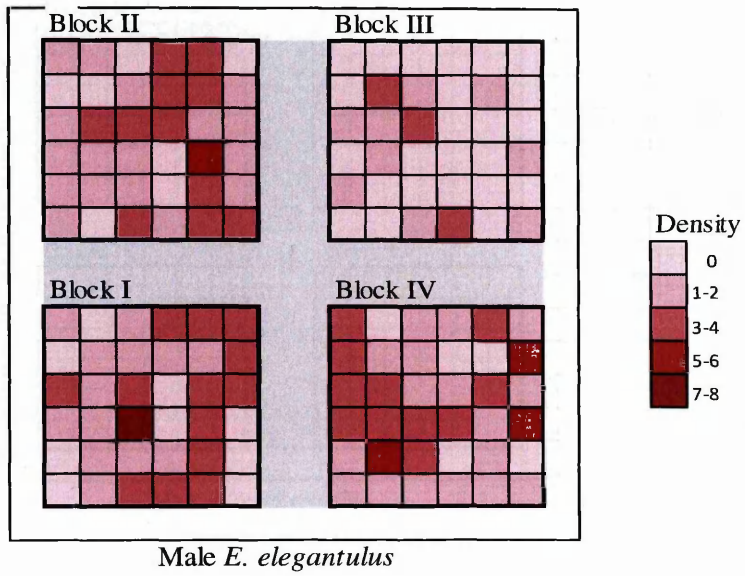


Fig 12. Density of Male *E. elegantulus* within the four blocks Pre -cut

At the quadrat level, the number of individuals recorded for *E. elegantulus* ranged between 0 – 8 individuals (average density 1 individual per quadrat) pre-cutting and 0-4 post-cut.

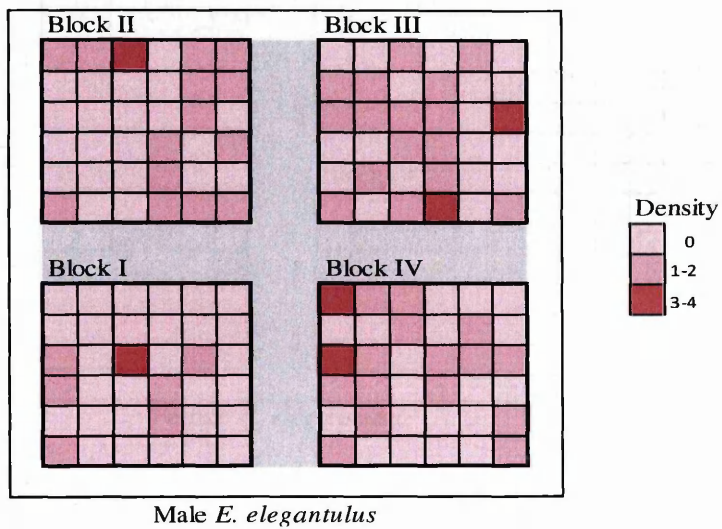


Fig.13. Density of Male *E.elegantulus* within the four blocks Post –cut

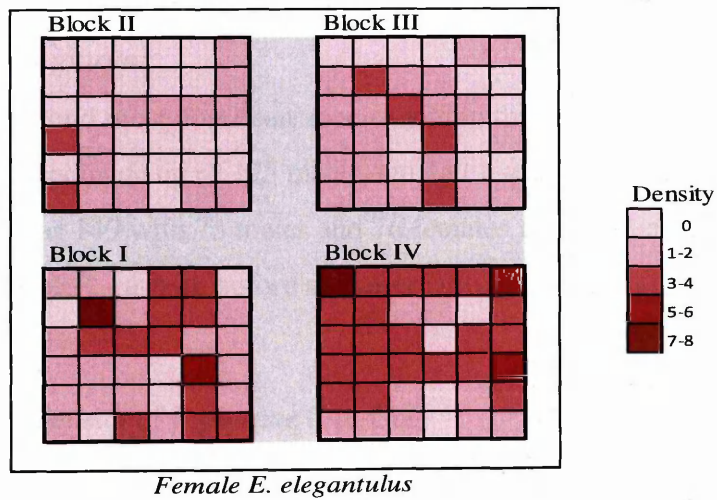


Fig. 14 Density of Female *E.elegantulus* within the four blocks Pre Cut.

Pre-cut density of females with quadrats ranged from 0-8 individuals.. Average density of females per quadrat was 2 individuals per quadrat.

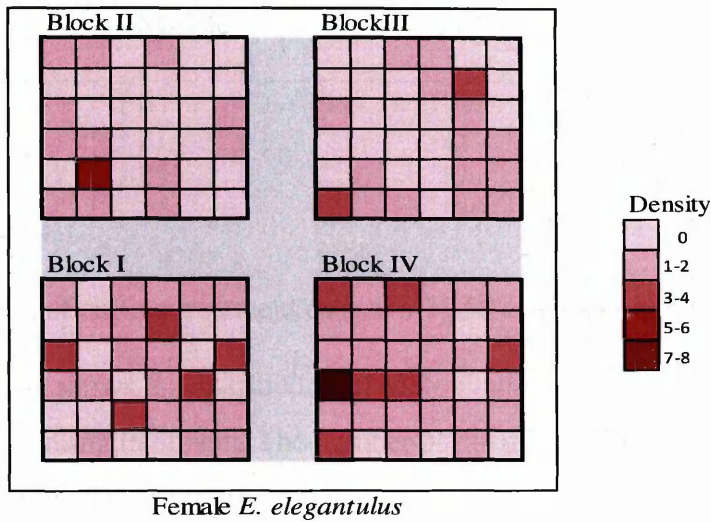


Fig. 15 .Density of Female *E.elegantulus* within the four blocks Post Cut.

Post -cut density ranges from 0-7 individuals per quadrat. Average density of female *E.elegantulus* reduced to 1 individual per quadrat.

3.2.2. *Pezotettix giornae*

This was the second most dominant species within the mesocosm with a total relative density of 272 individuals made up of 125 males and 147 females. Post cut density of *P. giornae* in the enclosure was 149 with 73 males and 76 females representing a 45.22% decline. The block densities of *P. giornae* before and after cutting treatment is detailed below in Tables 5 and 6 respectively.

Table 5. Block density of *P.giornae* (Pre-Cut)

BLOCK	MALE	FEMALE	TOTAL BLOCK DENSITY
I	35	51	86
II	27	37	64
III	30	38	68
IV	33	21	54

Table 6. Block density of *P. giornae* Post- Cut.

BLOCK	MALE	FEMALE	TOTAL BLOCK DENSITY
I	6	15	21
II	21	25	46
III	25	19	44
IV	21	17	38

The application of cutting treatment caused a 75.58% reduction in the density of this species

Figure 16 below shows the distribution of Male *P. giornae* within the quadrats before the application of cutting treatment. The number of the male individuals found per block ranges from 0-5. Average density of males before cutting treatment was 1 male *P. giornae* / quadrat

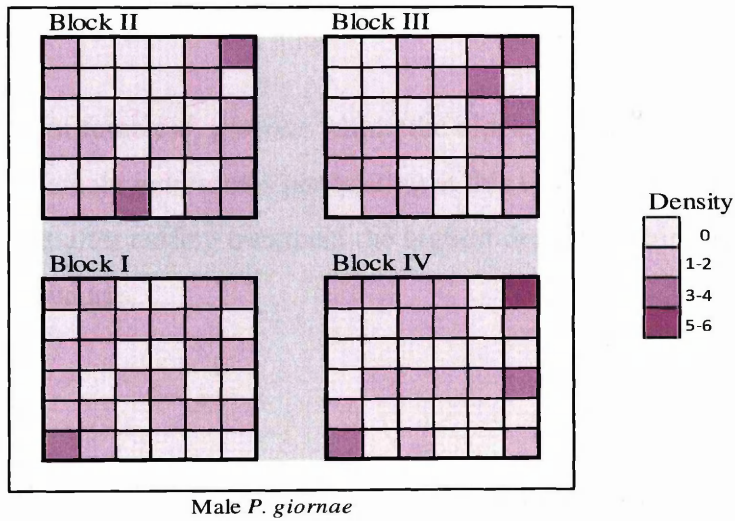


Fig 16. Density of Male *P. giornae* within the 144 quadrats (Pre- Cut)

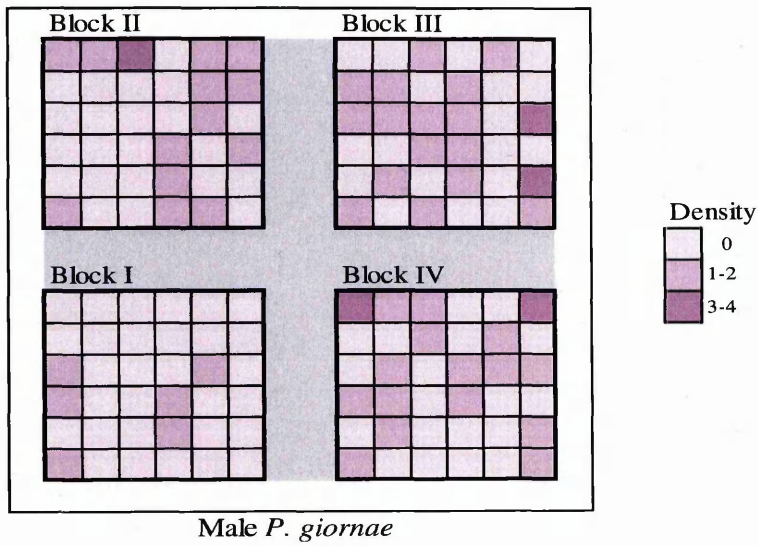


Fig. 17 Density of Male *P. giornae* within the 144 quadrats (Post – Cut)

The distribution of female *P. giornae* within the blocks ranged from 0 – 8 individuals per block. Average female individuals per quadrat at this time was 1 per quadrat. Figure 19 also below shows that after cutting treatment the highest density within the quadrats declined to 3 individuals per quadrat.

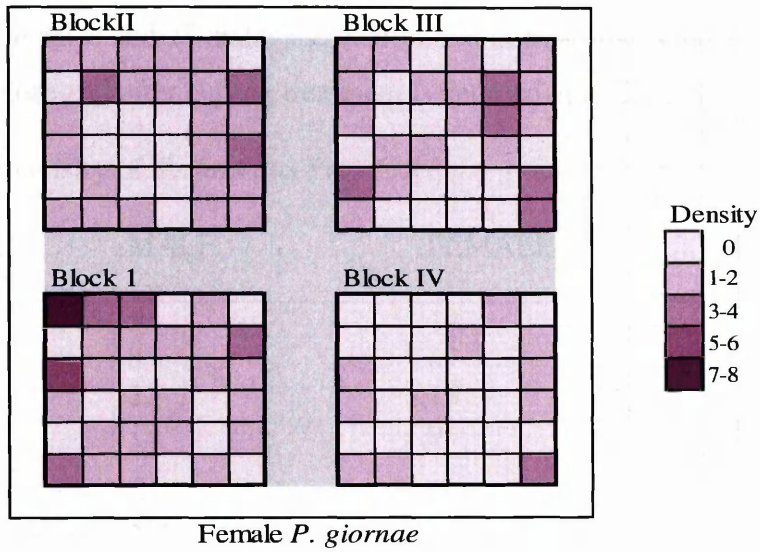


Fig. 18 Density of Female *P. giornae* in the 144 quadrats (Pre - Cut)

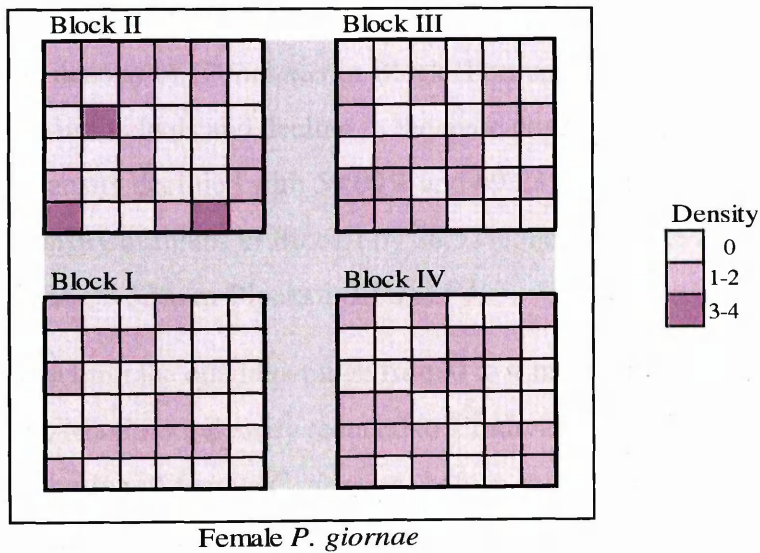


Fig. 19 Density of Female *P. giornae* in the 144 quadrats (Post - Cut)

3.2.3 *Chorthippus dorsatus*

These species had a density of 89 individuals within the mesocosm this was made up of 48 males and 41 females. However after the application of cutting treatment the density reduced to 50 with 23 females and 27 males the distribution of male and female *C.dorsatus* at the block level before and after cutting treatment is detailed in tables 7 and 8 below.

Table 7. Block density of *C. dorsatus* Pre - Cut

BLOCK	MALE	FEMALE	TOTAL BLOCK DENSITY
I	5	10	15
II	8	6	14
III	22	16	38
IV	13	9	22

Table 8. Block density of *C. dorsatus* Post Cut

BLOCK	MALE	FEMALE	TOTAL BLOCK DENSITY
I	7	6	13
II	7	7	14
III	9	4	13
IV	4	6	10

Cutting treatment reduced the density in Blocks I, III and IV by 13.33%, 65.79% and 54.55% respectively. The density of *C dorsatus* in Block II remained the same with an increase in the density of female individuals and decline in the male population within that block. In blocks III and IV male density declined with 59.09% and 69.23% respectively. We recorded an increase in the density of males in Block I by 28.57%. Female individuals decreased by 40.00%, 62.5% and 33.33% in Blocks I, III and IV.

Male *C.dorsatus* within the quadrats range from 0 to 4 individuals per quadrat. (Please see figure 20 and 21). Maximum density reduced to 2 individuals per quadrat .Figures 22 and 23 outlines the distribution of female *C. dorsatus* before and after cutting treatment. We recorded a very sparse density of females at the end of the grasshopper surveys, maximum density in quadrats with *C. dorsatus* was 2 female individuals.

Fig. 20. Density of Male *C. dorsatus* within the 144 Quadrats (Pre Cut)

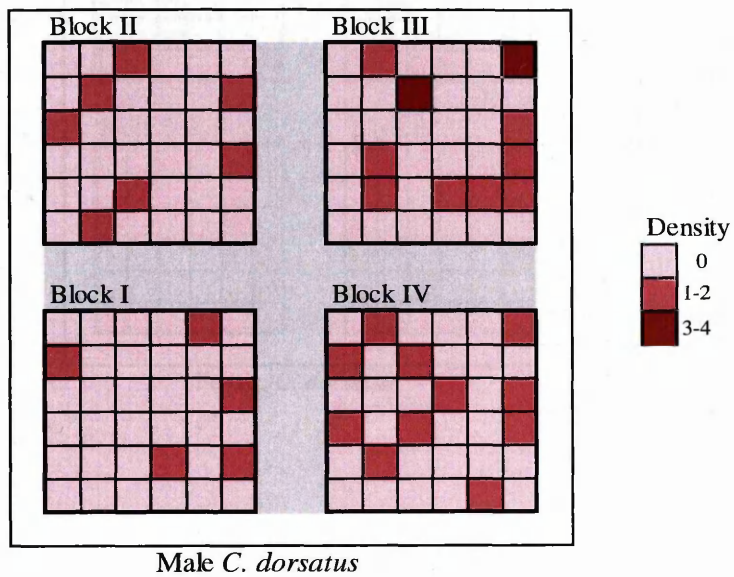
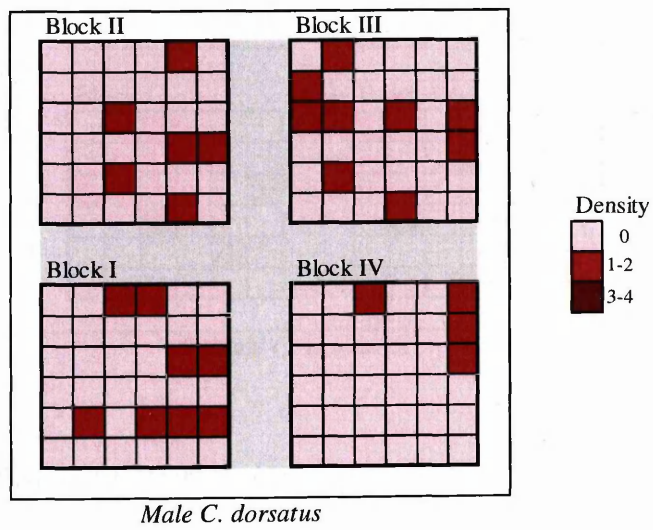


Fig. 21 Density of Male *C. dorsatus* within the 144 Quadrats (Post -Cut)



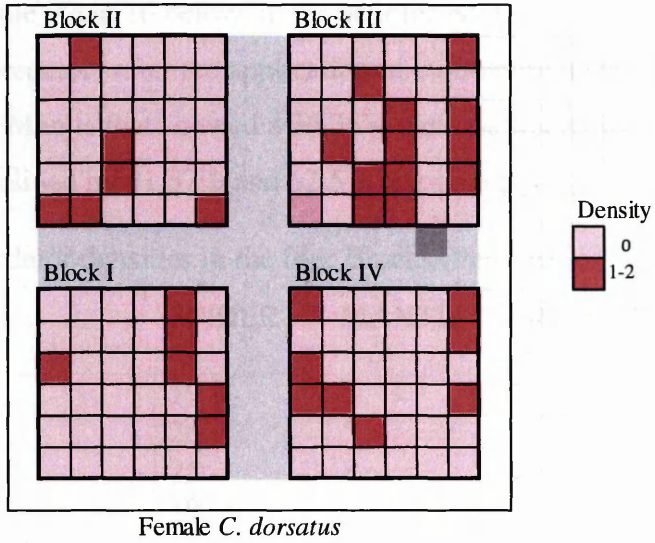


Fig. 22. Density of Female *C. dorsatus* within the 144 Quadrats (Pre -Cut)

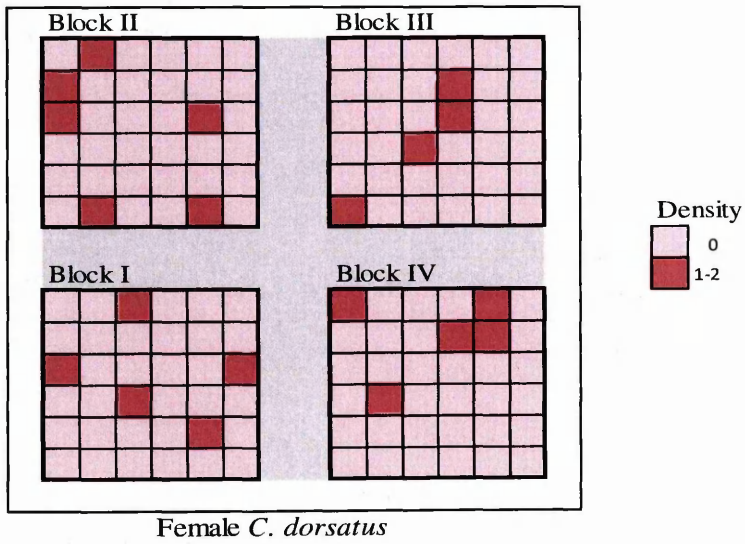


Fig. 23. Density of Female *C. dorsatus* within the 144 Quadrats (Post -Cut)

3.3. PREDATOR SURVEY

From the table 9 and 10 below, it can be inferred that there was a 37.01% decrease in total density of predators after the application of cutting treatment within the mesocosm. However asides from Mantis that showed a 36.36% increase in density post cut, spiders and cricket numbers declined by 41.57% and 62.5% respectively

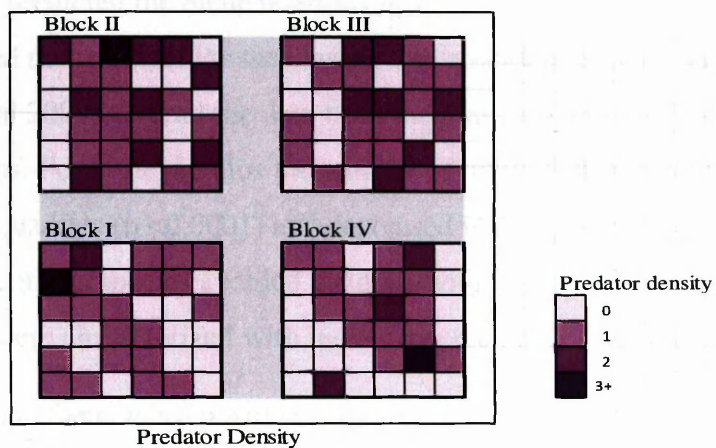
Table 9 .Predator densities in the four Blocks (Pre-cut)

BLOCK	SPIDER	MANTIS	CRICKET	TOTAL BLOCK DENSITY
I	19	2	4	25
II	26	5	5	36
III	25	3	4	32
IV	19	1	3	23
TOTAL DENSITY	89	11	16	116

Table10. Predator densities in the four blocks (Post Cut)

BLOCK	SPIDER	MANTIS	CRICKET	TOTAL BLOCK DENSITY
I	6	4	3	13
II	15	7	0	22
III	21	2	1	24
IV	10	2	2	14
TOTAL DENSITY	52	15	6	73

Fig 24. Predator Density within the 144 quadrats (Pre- Cut)



Maximum number within quadrats was 3

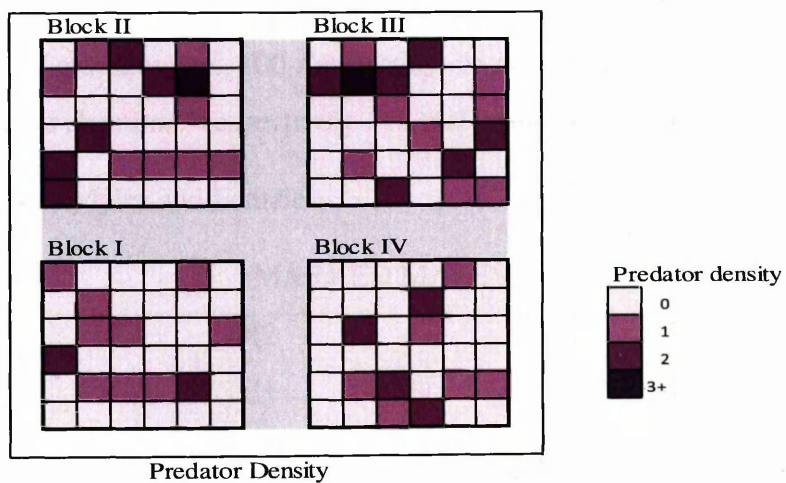


Fig 25. Predator Density within the 144 quadrats (Post - Cut).

After cutting treatment, maximum numbers of predators decreased to 2

3.4. LINKING DISPERSAL AND FAVORABLE HABITATS.

Grasshopper niche relationships.

I tested the predicted the niche relationships of Deraison et al (in revision) using generalized linear mixed models with Poisson family and a random term to account for over dispersion (Bolker et al 2009) Overall the data from the grasshoppers surveys confirmed the predicted relationships. For *E. elegantulus* the number of individuals sighted increased with grass cover within the quadrats ($p < 0.0001$) and decreased with legume cover ($p < 0.0001$). Furthermore individuals of this species avoided quadrats with more predators ($p < 0.0001$), especially if these also were characterized with higher legume cover ($p < 0.0001$).

For *P. giornae* there was a positive response to legume cover ($p < 0.05$) and a negative response to predator density ($p < 0.01$) whereas for *C. dorsatus* there was a positive response albeit not significant (0.05) to grass cover. A positive and significant response to legume cover ($p < 0.01$)

3.5. MARK AND RESIGHT STUDIES

We marked 303 grasshoppers, 100 *Euchorthippus elegantulus*, 101 *Pezotettix giornae* and 102 *Chorthippus dorsatus*. respectively 142 males and 161 females. (Table 11)

Table 11. Marked Males and Females

SPECIES	MARKED MALES	MARKED FEMALE
<i>E. elegantulus</i>	42	58
<i>P. giornae</i>	31	70
<i>C. dorsatus</i>	69	33

The sex ratio of the captured and marked grasshoppers was markedly and significantly female biased for *P. giornae* ($p < 0.0001$, $\chi^2 = 14.3$, 95% CI 0.22 – 0.40, two-tailed proportion test), male biased for *C. dorsatus* ($p < 0.0001$, $\chi^2 = 12.0$, 95% CI 0.58 – 0.76, two-tailed proportion test) whereas the sex ration was more even and not significantly different from an equal ration for *E. elegantulus* ($p > 0.05$, $\chi^2 = 2.25$, 95% CI 0.32 – 0.52, two-tailed proportion test).

Most of the grasshoppers actively resisted being manipulated during the marking operations (204 vs. 79 individuals; data not available for 20 individuals;

Table 12. Distribution of Active Females amongst the three study species

SPECIES	ACTIVE INDIVIDUALS	CALM INDIVIDUALS
<i>E. elegantulus</i>	23	19
<i>P. giornae</i>	52	18
<i>C. dorsatus</i>	28	5

Interestingly, whilst there was no strong significant difference in the proportion active and calm individuals *E. elegantulus* females ($P > 0.05$; two sided proportion test). For *P. giornae* and *C. dorsatus* females there were more than twice as many active (“bold”) individuals than calm ones ($p < 0.0001$), two sided proportion test

Table 13 shows the number of active and calm males for the three study species

SPECIES	ACTIVE INDIVIDUALS	CALM INDIVIDUALS
<i>E. elegantulus</i>	20	18
<i>P. giornae</i>	23	8
<i>C. Dorsatus</i>	58	11

A similar pattern was observed for males a nearly equal proportion of active to calm individuals for *E. elegantulus* and a large preponderance of more active individuals during the marking operations for *P. giornae* ($p < 0.05$) and *C. dorstus* ($p < 0.0001$) however Fig 26 shows difference between sexes remained consistent also combining the data from both sexes

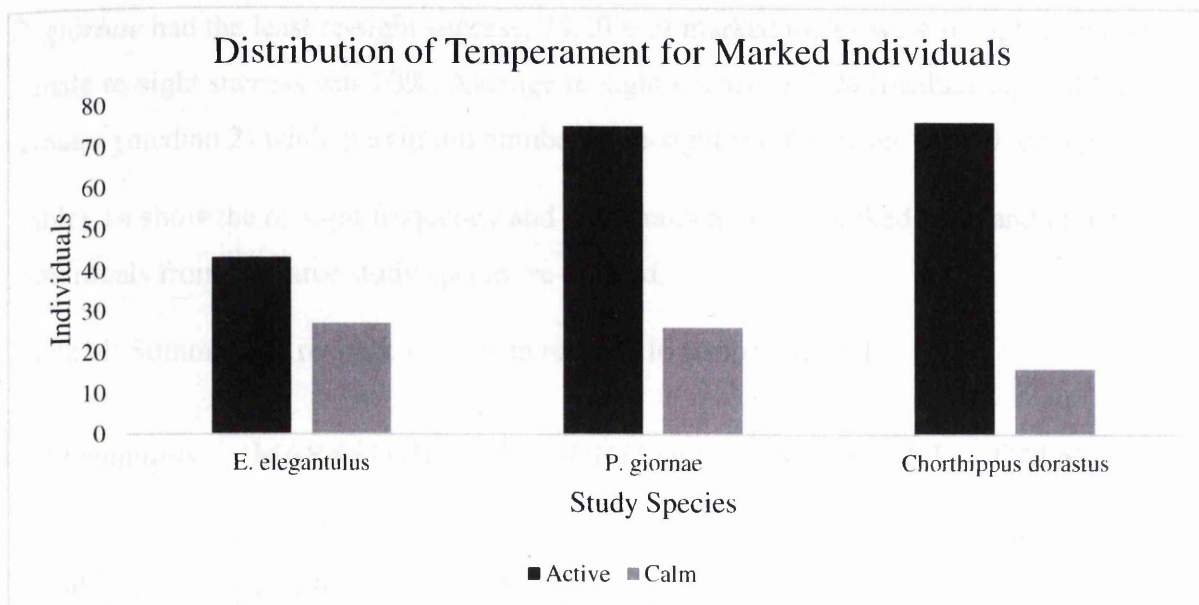


Fig 26 . Distribution of Temperament amongst the three study species

3.6. RESIGHTING

Resight success for our mark and recapture studies was 85.81%. 43 individuals (29 *P. giornae*, 9 *E. elegantulus* and 5 *C. dorsatus*) out of 303 marked individuals were not seen throughout the exercise . Female *C. dorsatus* had 100% re-sight success because we saw all marked individuals at least once, males recorded 92.7% success. The average rate of re-sight is 4.78 (median of 5) for males while females have a re-sight rate of 7.76 (median is 8). The maximum number of re-sight for male and female *C.dorstus* is 13 times.

E. elegantulus had the second highest re-sight success amongst the species with 93.10% and 88.10% re sight success for female and male individuals respectively. Average re sight rate for males and females is 2.9523(median 3) and 5.35(median 6) respectively. Maximum resight frequency for individuals from this specie is 8 for males and 14 times for females.

P. giornae had the least re-sight success, 74.20% of marked males were re-sighted while female re-sight success was 70%. Average re-sight success is 1.94 (median 2), 2.12 for females (median 2) while maximum number of re-sight is 6 for males and 10 for females

Tables 14 show the re-sight frequency and temperament of all marked male and female individuals from the three study species re-sighted.

Table 14. Summary of re-sight success in relation to temperament

<i>E. Elegantulus</i>	MARKED (%)	RESIGHTED(%)	RESISTANT (%)	CALM (%)
Male	42 (42)	83.33 (35)	*54.29(19)	*37.14(13)
Female	58(58)	87.93 (52)	*38.46 (20)	*32.69(17)
<i>P. giornae</i>				
Male	30.69(31)	64.52(20)	75(15)	25 (5)
Female	69.31(70)	68.57(48)	68.75(33)	31.25(15)
<i>C. dorsatus</i>				
Male	67.65(69)	91.30(63)	66.66 (42)	16.67 (7)
Female	32.35(33)	100(33)	84.85%(28)	15.15(5)

*A note of the temperament displayed during handling for 18 individuals from the *E.elegantulus* marked population (15 females and 3 males) re-sighted was not made at the time of marking.

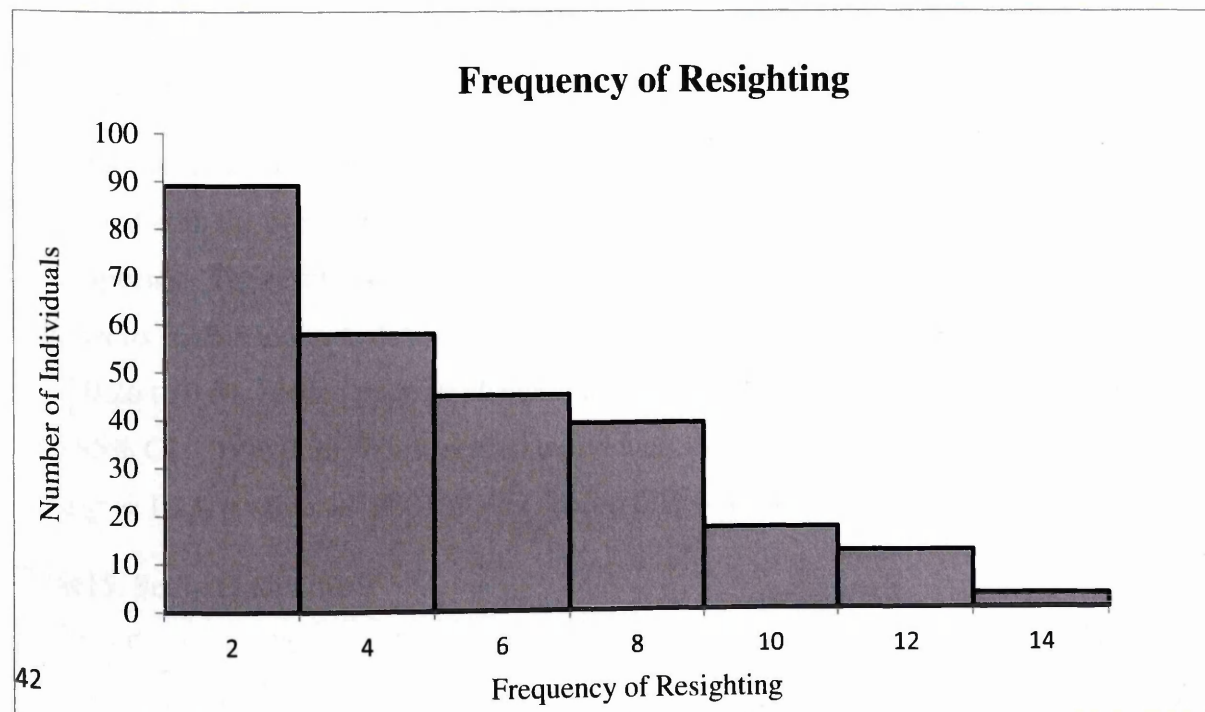


Fig 27. The histogram shows the frequency of re-sighting success. Most of the re-sighted marked individuals were sighted at least twice while only 3 individuals were sighted 14 times

Using Poisson GLMM I tested if the re-sighting rate was related to the boldness (during marking) of the individuals, to the sex, and / species. The differences in re-sighting rate were highly significant between species ($p < 0.0001$) and the re-sighting rate was also consistently lower for males across all species ($p < 0.0001$), The boldness instead was not related to probability to be re-sighted for all species

What is the rate and scales of dispersal of the three most widespread and dominant grasshopper species?

Results from this displacement analysis revealed that 144 individuals visited a total of 1140 locations within the enclosure. 98 individuals have dispersed and settled into a quadrat while 52 individuals were yet to settle.

3.7. SETTLED INDIVIDUALS

Table 15 below shows the distribution of settled individuals amongst the 3 study species. Please see appendix for full list of settled individuals for each of the study species.

I used a two-tailed population proportion test to determine the significance of the variation associated with the proportion of males to females within this population for each of the study species. The results were as follows: Chi square value of the proportion of settled *C.dorsatus* female individuals to their male counterparts is $\chi^2 = 1.97$, p value > 0.0001 , 95% CI of 0.26 to 0.54. Settled male *E. elegantulus* to females has a $\chi^2 = 10.62$, p value < 0.0001 with 95% CI 0.09 to 0.38. While settled individuals of *P.giornae* male to female proportion has a $\chi^2 = 1.23$, p value > 0.0001 95% CI from 0.10 to 0.61

Table 15. Settled Individuals

SPECIES	MALE	FEMALE	TOTAL
<i>C.dorsatus</i>	31	20	51
<i>E.elegantulus</i>	7	27	34
<i>P.giornae</i>	9	4	13

Table 16 below shows the proportion of settled individuals with respect to their response to handling during the marking process. 10 individuals from the settled *E. elegantulus* population did not have a note of their disposition towards handling documented.

Table. 16. Response to Handling by Settled Individuals

SPECIES	RESISTANT	CALM
Female <i>C.dorsatus</i>	19	1
Male <i>C. dorsatus</i>	28	3
*Female <i>E. elegantulus</i>	9	9
*Male <i>E. elegantulus</i>	4	2
Female <i>P. giornae</i>	4	5
Male <i>P.giornae</i>	2	2

*Out of the 27 female *E elegantulus* that settled 9 of them did not have a temperament profile while just one male out of the settled *E.elegantulus* did not have this data documented.

Results from the proportion of population two tail test revealed a $\chi^2=14.45$, p value <0.0001 with 95% CI of 0.26 to 0.54 for calm settled females *C.dorsatus* to resistant females within the population. Male *C. dorsatus* test of calm to resistant individuals had($\chi^2= 18.58$, p value <0.0001 95% CI 0.25 to 0.27)Within the settled population of *C.dorsatus*($\chi^2= 34.58$, p-value < 0.0001 95 % CI 0.03 to 0.20.)

Distribution of calm to resistant individuals in female *E elegantulus* has ($\chi^2 = 0$ p value >1 with 95% CI, 0.29 to 0.71). For males the proportion of calm to individuals to those that resisted handling has ($\chi^2 = 0.17$, p value >0.0001 with 95% CI 0.06 to 0.8.) Within the settled population of *E elegantulus* male and female inclusive($\chi^2 = 0.04$ p value > 0.0001, 95% CI 0.26 to 0.67.) $\chi^2 = 0$ p value > 0.0001 1 with 95% confidence interval was derived for the ratio of calm to resistant females of settled individuals of *P. giornae*. While for their male counterparts the test revealed a ($\chi^2= 0$ p > 1 with 95% CI of 0.15 to 0.85.) Entire

proportion of cam to resistant *P.giornae* individuals ($\chi^2=0$, p-value > 0.0001, 95% CI 0.20 to 0.74)

Table 17 below shows the number of individuals that settled in the four blocks with regards to the three study species

Table 17. Number of individuals that settled in each Block

SPECIES	BLOCK I	BLOCK II	BLOCK III	BLOCK IV
<i>E.elegantulus</i>	0	8 (23.5%)	10 (29.41%)	12(35.29%)
<i>C. dorsatus</i>	13(25.4%)	20 (39.21%)	12 (23.53%)	3(5.88%)
<i>P.giornae</i>	5(38.46%)	4(30.77%)	1(7.92%)	3(23.08%)

Within the settled population four *E.elegantulus* individuals remained at the release point including three individuals within the *C.dorstus* population. Amongst the population that settled *C.dorsatus* individuals visited an average of 5 quadrats before settling while *P.giornae* and *E.elegantulus* individuals visited an average of 4 quadrats each before settling.

3.8. INDIVIDUALS YET TO SETTLE

Distribution of individuals yet to settle is enumerated in the Table 18 below, however full list of yet to settle individuals is provided in the Appendix VI

Table 18. Individuals yet to settle

SPECIES	MALE	FEMALE	TOTAL
<i>C.dorsatus</i>	13	7	20
<i>E.elegantulus</i>	7	11	18
<i>P.giornae</i>	2	5	7

The population proportion test was also applied to determine the significance of the proportion of males and females yet to settle.

C dorsatus ratio of males to females as tested by this two tail test, had ($\chi^2=1.25$, p value >0.0001 with 95 % CI 0.16 to 0.59). *E elegantulus*: ($\chi^2=0.5$, p value > 0.0001 with 95% CI 0.18 to 0.64). *P. giornae*: ($\chi^2=0.5714$, p value > 0.0001 95% CI from 0.51 to 0.69.)

Table 19. Shows the distribution of the temperament displayed by these individuals, asides from two females of *E elegantulus* that did not have their disposition to handling documented during the exercise.

Table 19. Response to Handling by Individuals yet to Settle

SPECIES	RESISTANT	CALM
Female <i>C. dorsatus</i>	5	2
Male <i>C. dorsatus</i>	10	3
Female <i>E. elegantulus</i>	4	5
Male <i>E. elegantulus</i>	4	3
Female <i>P. giornae</i>	4	1
Male <i>P. giornae</i>	2	0

Test of proportions of resistant to calm yet to settle individuals within the population of male and females are as follows: Within Female *C. dorsatus* ($\chi^2 = 0.57$, p value > 0.0001 95% CI of 0.05 to 0.69). Male *C. dorsatus*, ($\chi^2 = 2.77$, p value > 0.0001, 95% of CI 0.62 to 0.54). For the entire population as a whole ($\chi^2 = 4.05$, p-value =>0.0001 95% CI: 0.01 to 0.49)

Within the Female *E. elegantulus* population test of the proportion of resistant to calm individuals has ($\chi^2 = 0$, p value >0.0001, 95% CI of 0.15 to 0.77.) For the male population the ($\chi^2 = 0$ p value >0.0001, with 95% CI 0.12 to 0.80). For the entire population. ($\chi^2 = 0$, p-value > 0.0001 95% CI: 0.28 to 0.72). Within the female population of *P. giornae* individuals yet to settle, the test of proportion of temperament amongst this group has ($\chi^2 = 0.8$, p value >0.0001 with 95% CI 0.01 to 0.70) No test was done for the male population because the 2 individuals yet to settle were both resistant.

3.9. DISTANCE COVERED BY "SETTLED" AND "YET TO SETTLE" INDIVIDUALS

The box plot below summarizes the range of values for distance travelled by the 98 individuals that have settled within certain quadrats in the mesocosm:

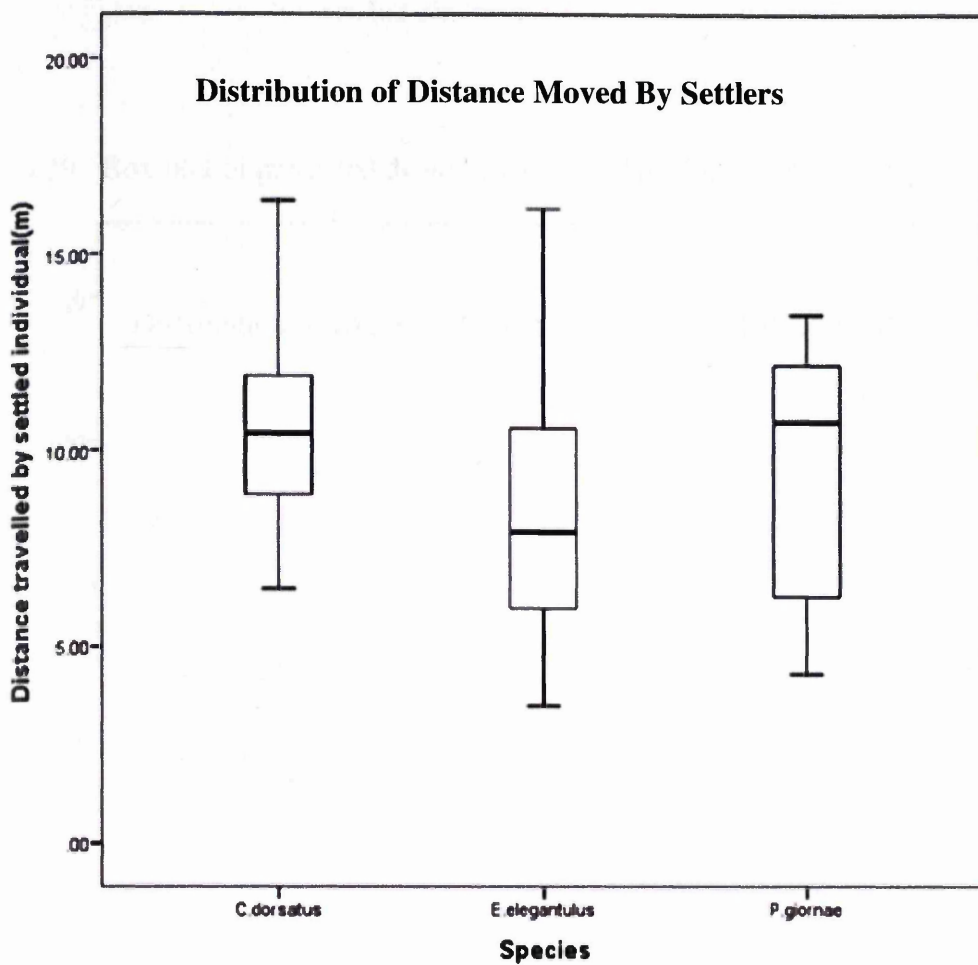
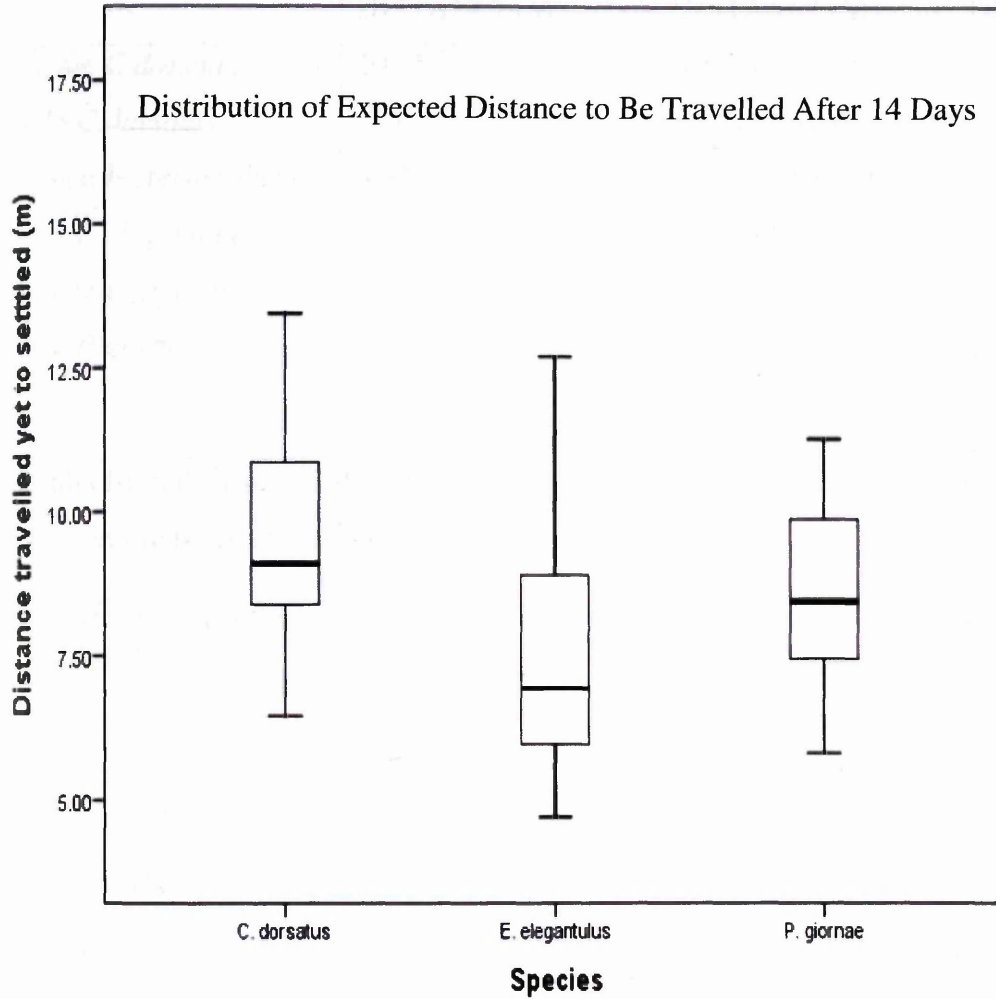


Fig 28. Box plot showing the distribution of the distance moved by settlers from the three study species

From the plot it is clear that *E.elegantulus* has the widest range of values although they are not as high as distance values estimated for *C.dorsatus* and *P. giornae*. The median distance of 7.91 metres for *E elegantulus* is represented in the lower quartile of the distance data set. Minimum distance travelled by individuals that have settled from this species is 3.50m while maximum distance is 8.45m. *C. dorastus* has a more compact data in terms of the distant travelled by settled population. The values of distant estimates range from 6.84 to 18.66metres with a median value of 10.43metres which is representative of about 50% of the data set for distance travelled by settled *C.dorsatus*. Mean distance covered by this species is 10.43metres. The median distance of 10.73metres is represented in the upper quartile of the distant values for settled *P.giornae*. Because *P.giornae* has the lowest number of individuals that settled so the upper and lower whiskers of the box plot is shortest with a minimum distance of 4.32m while maximum distance travelled is 13.46m. Average distance covered by this species is 10.01metres. Below is a box plot showing the distribution of predicted expected distance to be covered 14 days after the last re-sighting exercise for individuals that were yet to sett

Fig 29. Box plot of predicted distance After 14 days for individuals yet to settle



The predicted median distance after 14 days for *E. elegantulus* is 6.94m with a mean of 7.50m, the range of expected distance to be covered by yet to settle individuals from this species, lies between 4.70m to 12.70m. However for *C. dorsatus* the average predicted distance is 10.01m with a median of 9.10m which is represented in the lower quartile (within 25% of data range). Expected distance after 14 days for this species ranges from 6.46m to 13.44m (with the exception of 16.77m predicted for one individual). Extrapolated distance for 14 days for *P. giornae* individuals yet to settle range from 5.82m to 12.51m with a median of 8.19m and mean = 8.61m

Are there significant sex differences regarding the rate of movement?

The table 20 below shows the average distance covered by settled individuals, minimum and maximum distance covered by individuals including their unique colour codes for both sexes of the study species

Table 20. Average distance covered by settled individuals

SPECIES	AVERAGE DISTANCE(M)	MINIMUM DISTANCE(M)	MAXIMUN DISTANCE(M)
Female <i>C.dorsatus</i>	10.35	6.85 (WYWW)	17.21 (YRRY)
Male <i>C.dorsatus</i>	11.01	6.46 (YYWY)	18.66 (RWR Y)
Female <i>E.elegantulus</i>	8.33	3.50 (GRRG)	16.16 (RGGY)
Male <i>E.elegantulus</i>	8.90	4.93 (YRRG)	12.60 (YWWY)
Female <i>P.giornae</i>	9.30	4.32 (WGGG)	13.32 (YRRW)
Male <i>P.giornae</i>	10.24	5.86 (GYYG)	13.46 (GWGW)

Results from the two tailed sample T test used for the comparison of distance covered by males and females are as follows :

For *C dorsatus* p value > 0.0001, while *E elegantulus* p value > 0.0001 ,*P.giornae* p value >0.0001.

Table 21 below enumerates the averages , minimum and maximun expected distance to be covered by males and females at the end of 14 days.

Table 21. Expected distance after 14 days

SPECIES	AVERAGE DISTANCE(M)	MINIMUM DISTANCE(M)	MAXIMUN DISTANCE(M)
Female <i>C.dorsatus</i>	10.12	7.53 (GWGG)	13.44 (RGGG)
Male <i>C.dorsatus</i>	9.94	6.46 (RWWW)	16.77 (GGGR)
Female <i>E.elegantulus</i>	6.91	4.70 (GYYY)	9.41 (YYYG)
Male <i>E.elegantulus</i>	8.43	5.51 (YRGG)	12.70 (YGGY)
Female <i>P.giornae</i>	8.19	5.82 (YWYW)	11.28 (WWYY)
MALE <i>P.giornae</i>	9.65	8.50 (RGRY)	10.84 (WYRR)

Results from the two tailed sample to test the significance of the difference between expected distance to be covered in 14 days by male and females yet to settle are as follows:

C.dorsatus p value >0.0001 , *E.elegantulus* p value >0.0001 , *P.giornae* p value >0.0001

Table 22 Extrapolated Distance after 21 days

SPECIES	AVERAGE DISTANCE(M)	MINIMUM DISTANCE(M)	MAXIMUN DISTANCE(M)
Female <i>C.dorsatus</i>	12.59	9.22 (GWGG)	16.45 (RGGG)
Male <i>C.dorsatus</i>	12.42	7.92 (RWWW)	19.48(GGGR)
Female <i>E.elegantulus</i>	8.55	5.76 (GYYY)	15.56 (YYYG)
Male <i>E.elegantulus</i>	10.54	6.74 (YRGG)	11.52 (YGGY)
Female <i>P.giornae</i>	10.58	7.13 (YWYW)	13.81 (WWYY)
MALE <i>P.giornae</i>	12.51	8.45(RGRY)	10.84 (WYRR)

3.10. INTERACTION OF AVERAGE DISTANCE COVERED BY SETTLED POPULATION AND AVERAGE BODY SIZE

C. dorsatus females have the largest body size amongst the species with an average distance travelled of 10.35 metres while *E.elegantulus* with the second largest body size travelled the least distance with 8.33metres . *P.giornae* has the smallest average body size and it covered an average of 9.30metres. As shown in the Figure 30 below

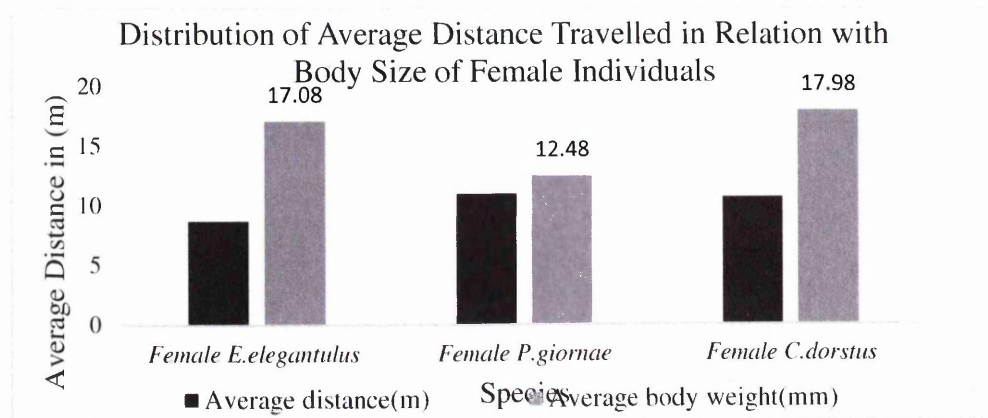


Fig. 30 . Distribution of Average Distance covered by Females in relation to average body size of the three species.

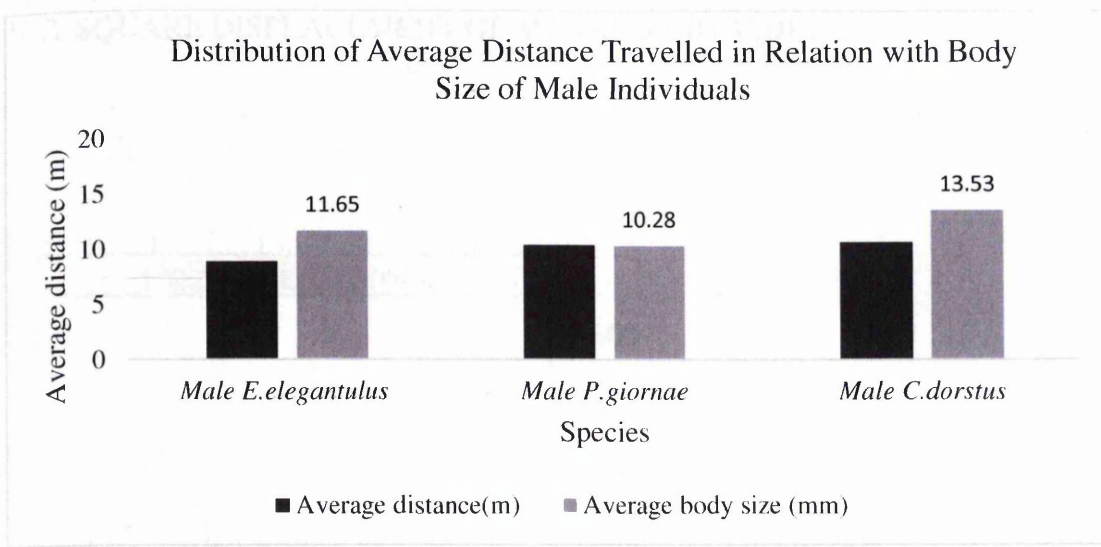


Fig 31. Distribution of Average Distance by Males covered in relation to average body size of the three species.

C. dorsatus males have the largest body size amongst the species with an average distance travelled of 11.01 metres while *E.elegantulus* with the second largest body size travelled the least distance with 8.90metres . *P.giornae* has the smallest average body size and it covered an average of 10.24metres

NET SQUARE DISPLACEMENT OF MARKED INDIVIDUALS

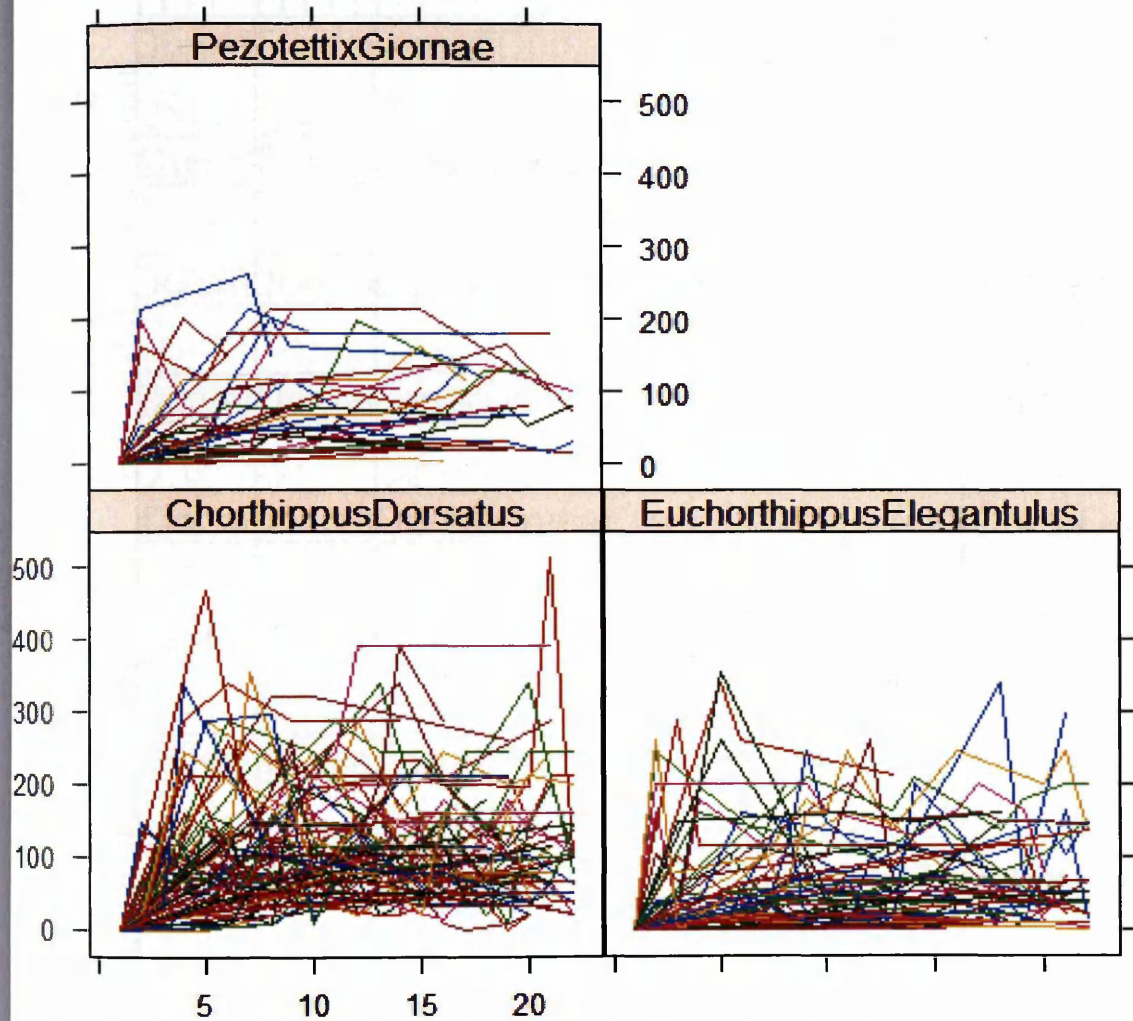


Fig.32. Net Square Displacement of the Three Study Species
Days

Illustrates the NSD of all marked individuals that have visited 4 or more locations including the release point. over the period of 21 days. NSD values range from 12.27metre to 348.17metres.

NET DISPLACEMENT CURVE OF *C.dorsatus* INDIVIDUALS

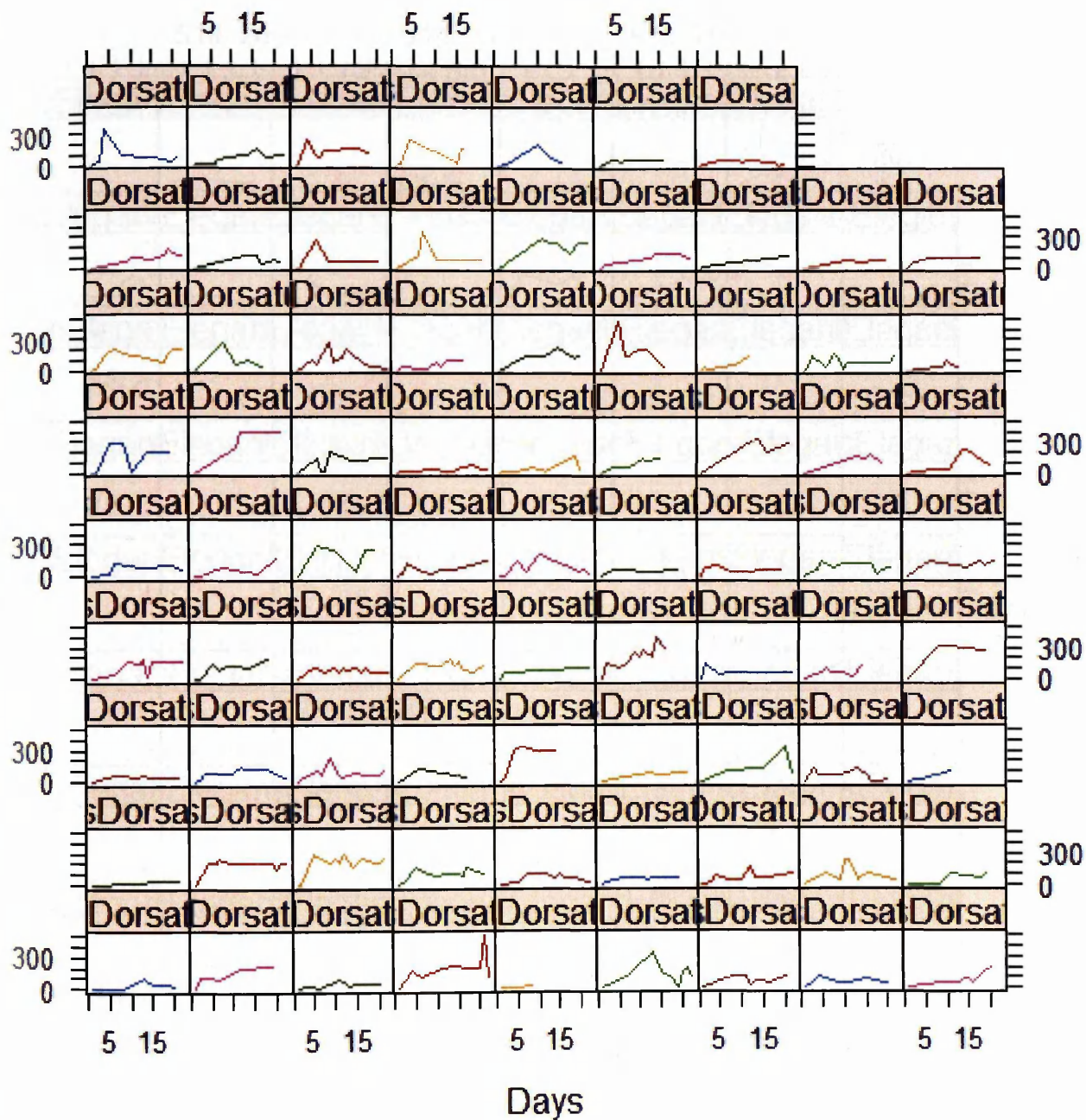


Fig 33. This illustrates the individual net displacement pattern of all *C. dorsatus* resighted at least four times including the release point, 51 individuals settled while 20 individuals were yet to settle at the end of our mark and re-sight studies

NET DISPLACEMENT CURVE OF *E.elegantulus* INDIVIDUALS

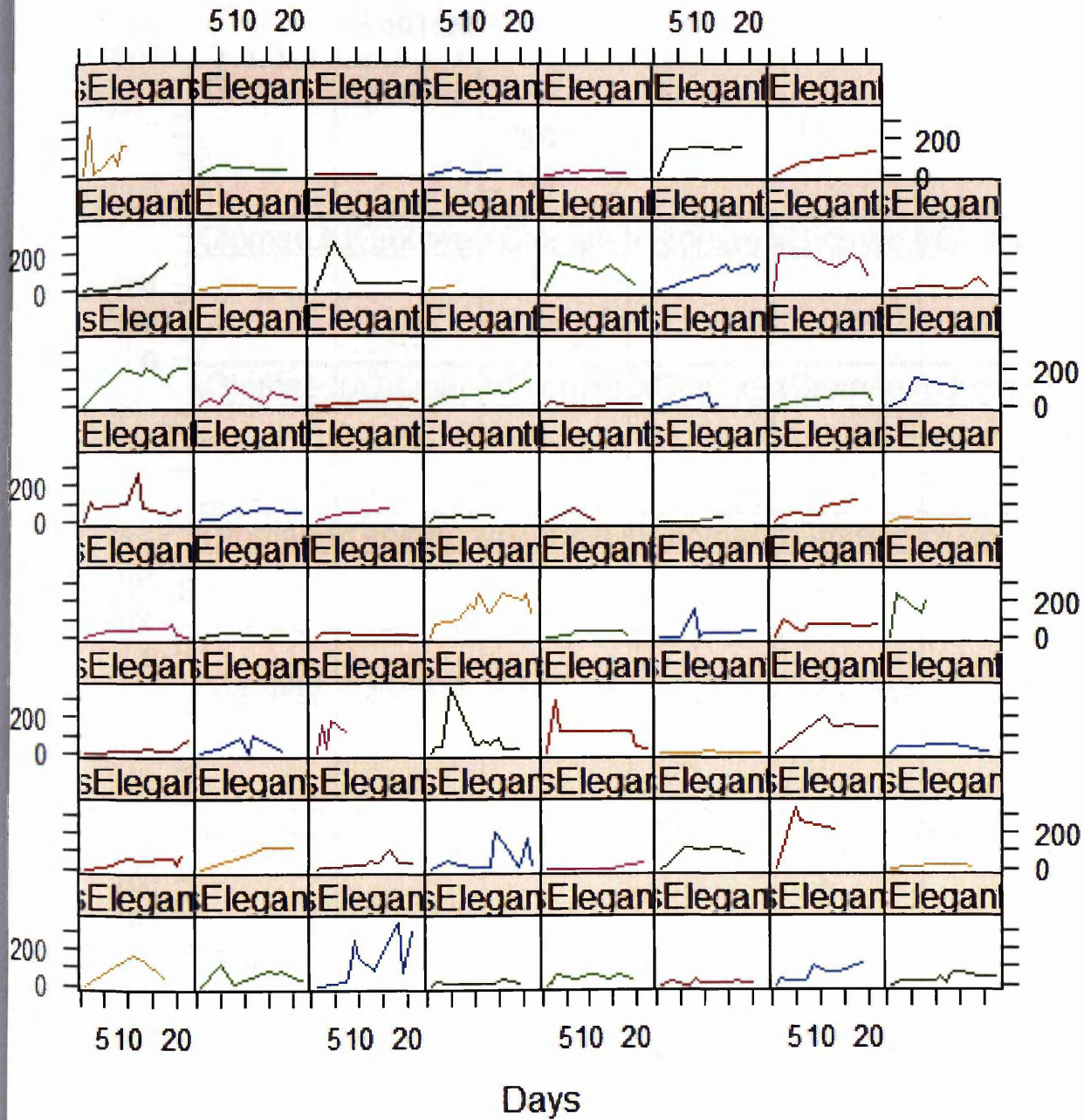


Fig 34. This illustrates the individual net displacement pattern of all *E.elegantulus* re-sighted at least four times including the release point , 34 individuals settled while 18 individuals were yet to settle at the end of our mark and re-sight studies

NET DISPLACEMENT CURVE OF *P.giornae* INDIVIDUALS

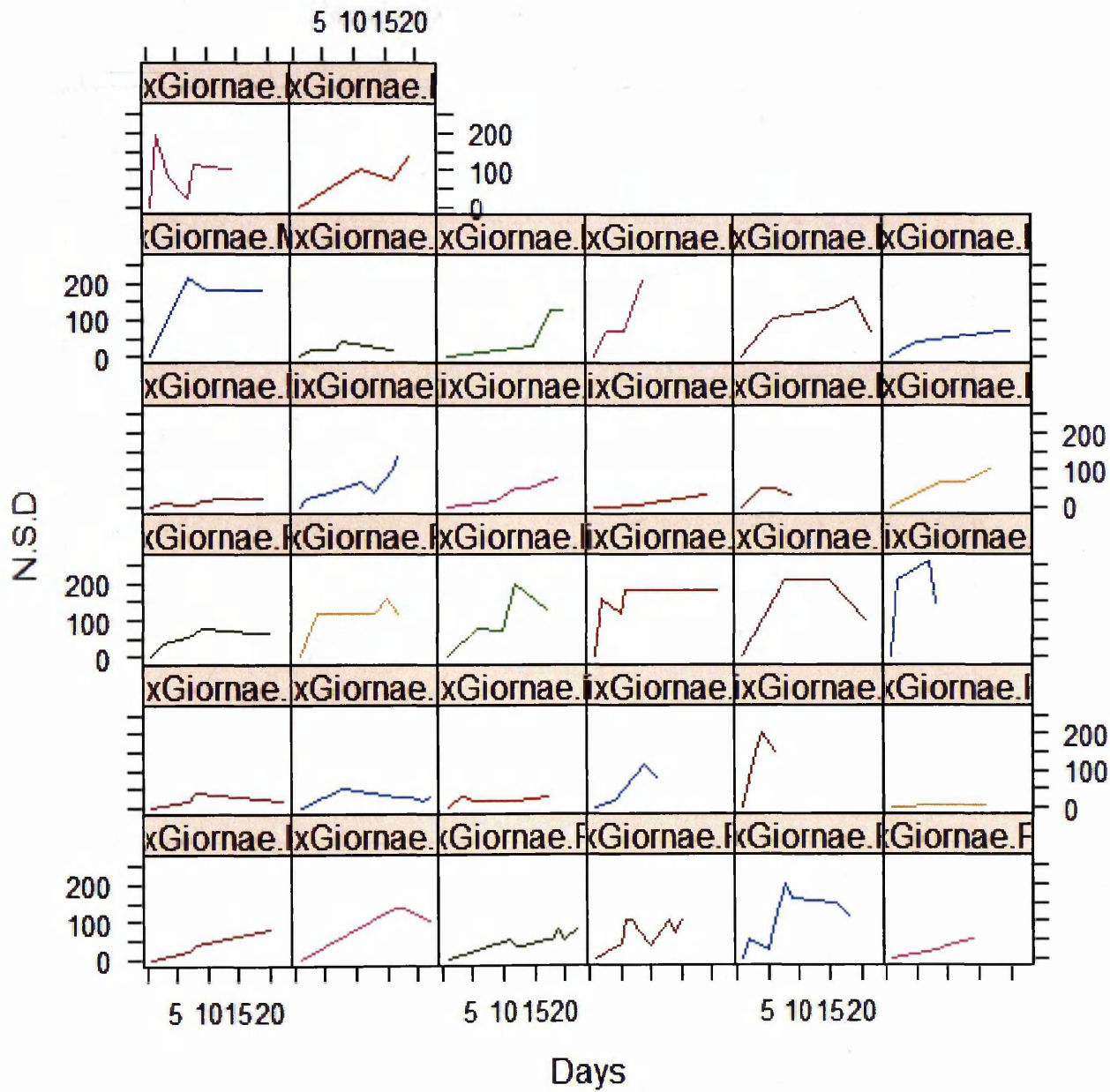


Fig 35 This illustrates the individual net displacement pattern of all *P.giornae* resighted at least four times including the release point , 13 individuals settled while 8 individuals were yet to settle at the end of our mark and re-sight studies

AVERAGE NET SQUARED DISPLACEMENT OF THE THREE STUDY SPECIES

ChorthippusDorsatus ◊
EuchorthippusElegantulus ◊
PezotettixGiornae ◊

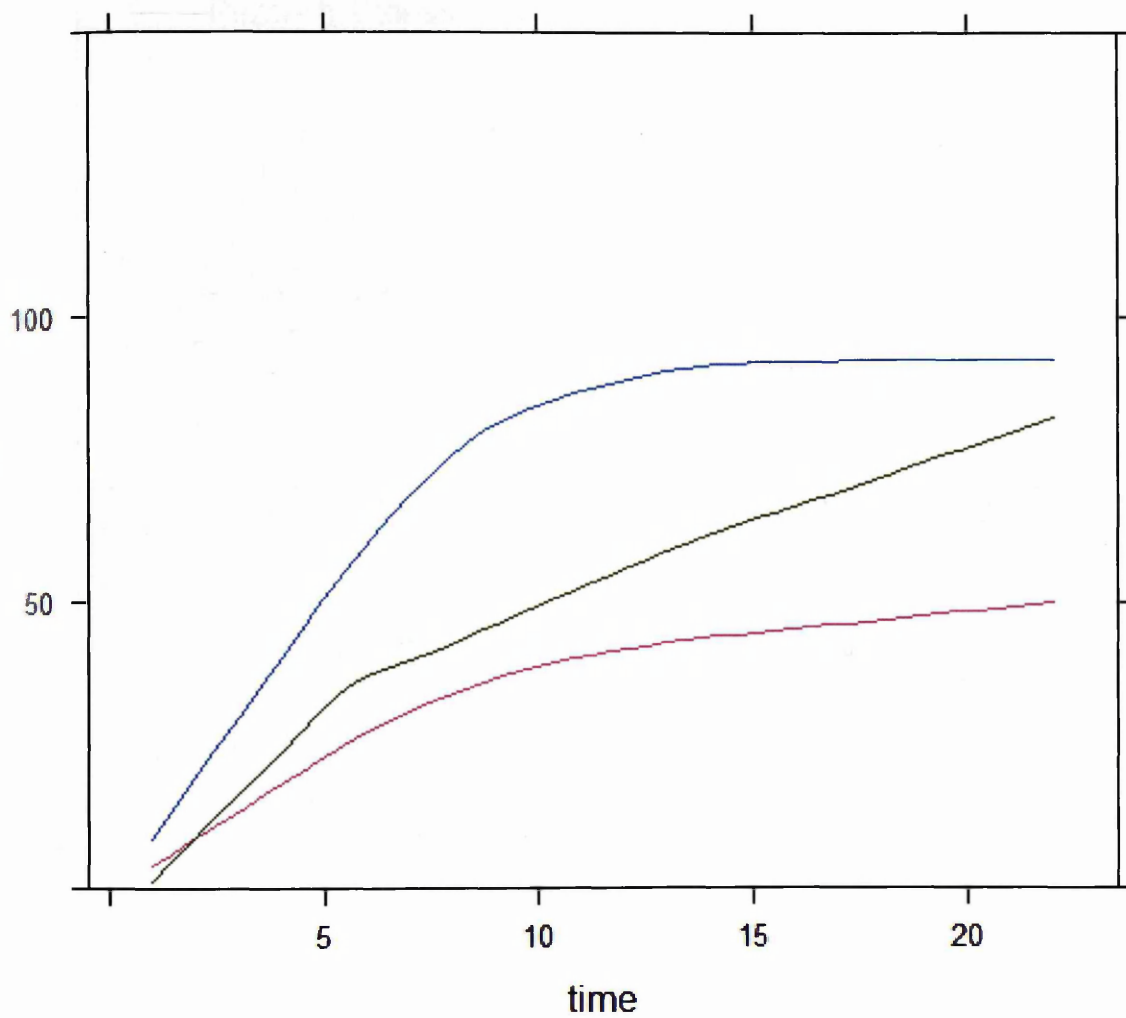


Fig 36. Average Net Squared Displacement of the three study species

This shows the average Net Square Displacement for our study species for the period of 21 days. *C.dorstus* average net displacement is 122.85metres, *E.elegantulus* 82.70metres while *P.giornae* 101.32metres

MOVEMENT PATTERN FROM RELEASE POINT OF RESIGHTED INDIVIDUALS

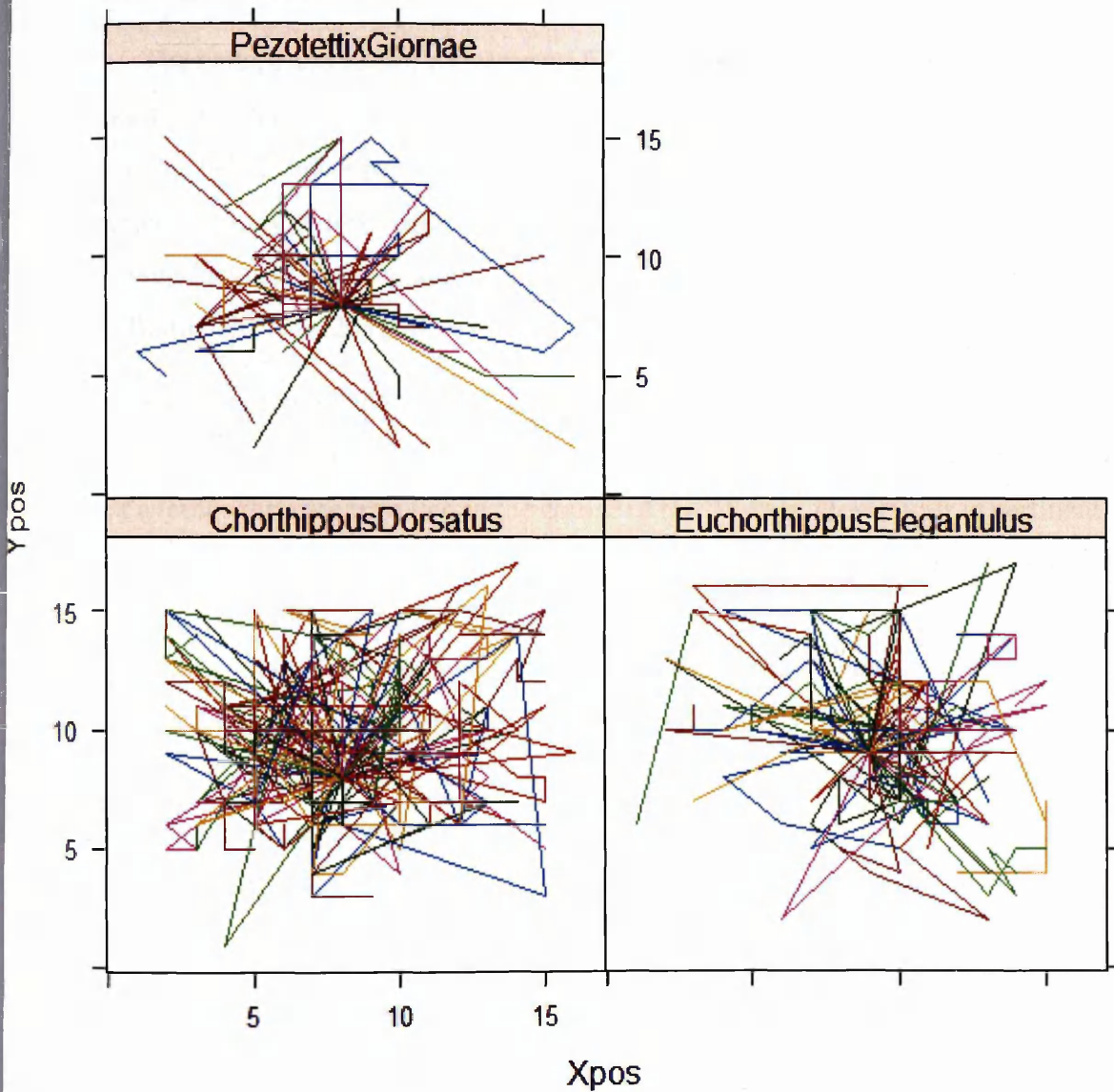


Fig 37. Pattern of Redistribution from the release Points

This figure displays the movement patterns of all the re-sighted marked individuals sighted in more than 4 locations including the point of release. Values on the X axis represents the assigned Cartesian X coordinates with 16 points taking account all the paths within the mesocosm while the Y axis of the graph shows the assigned Y Cartesian coordinates from 1-16. The X, Y coordinates for the release point of *E. elegantulus* was (9, 9) while *P. giornae* and *C. dorstus* was (8,9)

4. DISCUSSION

4.1. What are the rate and scales of dispersal of the three most widespread and dominant grasshopper species.

The pattern and rate of movement of grasshoppers have been described as being leptokurtic which is characteristic to most organisms that exhibit correlated random movements like grasshoppers (Walters et al, 2006). However studies on the quantification of movement ecology of most organisms have reiterated the need to fully understand the underlying factors that cause this leptokurtic distribution of movement. (Kareiva & Shigesada 1983; Bunnefeld et al, 2011; Borger& Fryxell, 2012)

Estimation of the distance travelled by all individuals from the three study species showed that *E. elegantulus* individuals within the settled and yet to settle population had lowest average distance travelled in the course of the 21 days. However it is pertinent to mention that within the population of the *E. elegantulus* some individuals displayed variability in comparison to the average distance travelled by the entire population, for example individual with the colour code RGGY (Red-Green-Green-Yellow) travelled a total distance of 16.16metres although average distance covered by the population of settled individuals was 8.45metres. *C. dorsatus* individuals were the most mobile species, within population, individual marked with RWRY (Red-White-Red-Yellow) travelled the highest distance of 18.66m while population average was 10.75metres. While the brachypterous *P. giornae* population travelled with an average distance 9.59metres although maximum distance covered by an individual GWGW (Green-White-Green-White) within the population is 13.46metres before settling into a quadrat. This heterogeneity within the population has very important ecological and evolutionary consequences in terms ensuring the persistence of meta-population. Individuals that are regarded as settlers ensure the persistence of the source population while those with the propensity to travel long distances within the population ensure spatial spread of the population on the landscape ensuring persistence of the meta-population (Santini et al, 2013).

These distance estimates could be described as intriguing because considering the phenotypic properties of *E. elegantulus* in terms of body size and wing development, it is logical to classify it as the most mobile out of the three study species while *P. giornae* will be designated as the sedentary species due to its small size and brachypterous nature. However

as rightly pointed out by Walz and Syrbe (2013), the rate and scale of movement during the process of dispersal is directly related to the availability of suitable habitat that optimally supports life process especially in terms of dietary and reproductive needs. This statement of fact makes mobility a subjective trait that is highly dependent on the species habitat requirement and its spatial configuration on the landscape (Marini et al 2010). This is especially true for most grasshoppers because they exhibit species specific herbivory in terms of functional traits expressed by plants (Stam & Yang 1996). Aikman & Godfrey (1972) in their study on the rate and form of dispersal in grasshoppers reported that within the population of *Melanoplus mexicanus*, cumulative distance covered by individuals from these species is directly proportional to the proximity of preferred food plant.

Plant nutritional quality and biomass are two major factors responsible for the heterogeneity in space and in time at different spatial scales of insect herbivores in the plant community (Oedekoven & Joern et al 2000). The vegetation survey conducted at the inception of this study revealed the spatial configuration of the three plant functional groups within the mesocosm. The most widespread grass species within the mesocosm were more suited to the diet of *E elegantulus* which has been documented by (Deraison et al in review)to have 55.51% herbivory impact on grass species similar to those found in the mesocosm . Consequently due to the patchy distribution of habitats that favour the dietary requirements of the two other species, this argument could also be a factor to justify the scale of the mean displacement estimated for *C.dorstus P. giornae* because due to their dietary needs, individuals from these populations had to visit several quadrats to find suitable habitats. Data from the re-sighting exercise revealed that most individuals from the *E.elegantulus* population were frequently re-sighted in blocks III and IV while *C.dorsatus* individuals were re-sighted in all the blocks. *P.giornae* was mostly re-sighted in legume patches existing in the four blocks.

4.2. Are differences in body size and movement capacity (winged/wingless) related to interspecific differences in dispersal?

Body size for many organisms has been linked with fitness because it has an effect on all life processes that ensure survival of the organisms (Woodward et al 2005). Size of an organism has been described by Hillbrand & Azovsky 2001 as an important factor that determines dispersal ability, which has cascading effects on regional and local species richness. Rate and scale of dispersal of most organisms has often been positively correlated

with their body size (Sutherland et al 2000). However, as rightly pointed out by Whitman (2008) small organisms especially in grasshopper exhibit more agility. The positive correlation of body size and dispersal ability, stems from the larger strides moved by large organisms, which allows them to cover long distances in shorter time (Yang, 2000). In addition larger individuals within a population are often viewed as superior hence the propensity to disperse from their natal patch increases with competition from other large individuals within the population (Bowler & Benton, 2005). In small seed dispersing ants, the larger worker ants within the population disperse better and further than the smaller individuals (Ness et al 2004). This “allometric scaling” of body size and movement capacity has also been related to the ability of migratory species like the *Tropidacris spp* a large grasshopper which weighs up to 30 grammes and disperse effectively over long distances (Whitman, 2008). Results from the estimation of dispersal rates of the three study species partly supports this hypothesis because the largest species *C.dorsatus* amongst the three study species had the highest average dispersal distance, on the other hand, individuals from the second largest species *E. elegantulus* travelled the least distance when compared with the cumulative average distance covered by the smallest specie *P.giornae* during the course of 21 days.

The pattern and scale of movement displayed by *E.elegantulus* individuals as highlighted earlier could be related to the widespread distribution of grass cover within the mesocosm. In support of this argument, Mayer et al (2002) in their response to Sutherland et al, (2000) suggested that dispersal distance should not only be scaled with body size for mammals because the distribution of food resources on a landscape has simultaneous effects on the rate and scale of movement. This applies not only to mammalian species the simultaneous effects of habitat heterogeneity and body size have been documented for different insect species in relation to their body size. Yang (2000) reported that at different stages of the life cycle of the Spined soldier bug *Podiscus maculiventris* movement capacity is a factor of body size and structure of their preferred food plants *S rugosa*, *S.altissima* and *S.junceae*. Landscape effects have also been reported to greatly influence the movement ability of *Metrioptera bicolor* (Kindervall, 1999).

Similarly the presence of wings has been positively correlated with dispersal distance and plasticity, however the average distance recorded for *E.elegantulus*; a grasshopper often described as a readily flying specie suggest otherwise. Several studies on traits that correlate with dispersal and wing polymorphism have attributed the development of wings and its

persistence within a population as a means of escaping from unfavourable habitats or density dependent factors (Zera & Mole, 1994). Due to the energetic cost of flight most insects that have wings will prefer to walk or hop in between favourable habitat patches rather than flying (Roff, 1986). The presence of predators has been reported by Kunert & Weisser (2003) to cause pea aphids (*Acyrtosiphon pisum*.Harris) to develop morphs with wings to ease dispersal into new habitats. While in some Homoptera and Gerridae, the number of wingless morphs within a population is a function of habitat stability (Roff, 1986). This is because most insect herbivores tend to spend longer periods in habitats with their preferred food plants (Underwood, 2004). The outcome from these investigations supports the observations made in this current study, because between the two winged species there was a marked difference in dispersal distance which could be explained by the presence of suitable habitat conditions for *E.elegantulus* while *C.dorsatus* individuals had the highest mean dispersal distance and highest re-sight rate due to the search for a suitable habitat within the enclosure. However interspecific differences in terms of wing development is corroborated by the variation in the dispersal distance travelled by *P.giornae* in comparison to that of *C.dorsatus* despite the fact this difference was not statistically significant (p value = 0.24) , the presence of wings adequately explains the peculiarity in their dispersal kernel.

Larger body size and presence of wings are traits that positively correlate with successful dispersal in most grasshoppers; however they cannot be viewed in isolation as determinants that set species apart in terms of dispersal plasticity. Results from this study suggest that spatial configuration of habitat that supports life process in this case dietary needs has a multiplier effect on rate and scale of movement. Several studies on the effect of habitat disturbance on grasshopper assemblages have pointed out that habitat loss is more detrimental to winged species because of the energy cost associated with flying , to locate another suitable patch while the negative effects of habitat fragmentation impact wingless species more significantly due to inter-patch related movements which increase with fragmentation (Marini et al 2010).

4.3. Does dispersal increase in areas with less favourable habitats?

Grasshopper dispersal is influenced by a plethora of factors which could be climatic or habitat related (Gardiner & Hill, 2004). Due to their strong interaction with abiotic and biotic factors prevailing in their immediate environment, grasshoppers are expected to stay longer in habitats that optimally support their life processes or disperse effectively away from unfavourable patches (Debinski & Holt, 2000). The ecological factors that promote habitat

suitability and influence movement dynamics of grasshoppers are vegetation composition and architecture, predator density, interspecific competition and microclimate (Lin & Batzil 2001)

4.3.1. Linking dispersal with vegetation cover

It has been suggested by Van der Plas, Anderson & Olf (1999) that the functional traits of plant species can influence the life processes of insect herbivore species that forage on them. As a result the composition of plant species within a habitat patch is a contributory factor that will inform the decision to stay or leave that patch (Colbert et al 2001). The redistribution patterns of grasshoppers used in this study is in agreement with this statement. A closer look at the pattern of distribution and movement of the 98 individuals that settled into quadrats reveals a dispersal pattern which is believed to be resource led. Within the settled population *E. elegantulus*, individuals stayed in quadrats with at least 25% grass cover in Blocks II, III and IV, these individuals visited an average of 3 quadrats before they settled. *C. dorsatus* individuals were spread out in the four blocks in quadrats with a fair representation of all three plant classes, before settling, *C. dorsatus* individuals visited an average of 5 quadrats. *P. giornae* individuals visited an average of 4 quadrats before settling in Blocks I, II and IV with only one individual settling in Block III. Also within the population that are yet to settle most of the quadrats visited by the individuals so far were within these blocks as enumerated above although the average number of quadrats visited varies. *C. dorsatus* individuals that were yet to settle had visited an average of 6 quadrats while *P. giornae* and *E. elegantulus* “yet to settle” population had been in an average of 4 and 5 quadrats respectively. Maximum number of quadrats visited by an individual is 11 for *C. dorsatus*, 8 for *P. giornae* and *E. elegantulus*. Linear and Poisson regression analysis was used to test the relationship between the three study species and vegetation cover type dominant within the blocks they settled in, the results revealed that a positive interaction exists between *E. elegantulus* and grass cover but a significant negative relationship with legumes, while *C. dorsatus* individuals had a weak non-significant positive interaction with legumes, grass and forbs. *P. giornae* due to its preference for legumes showed a significant positive relationship with legume cover and a positive relationship with grass which was not significant. The average number of blocks visited by each species and results from the regression analysis gives an insight that the rate and scale of movement of the three study species was determined by the spatial configuration of the three plant cover types. The

feeding niche selection of most grasshoppers could be restrictive, the sensitivity to some plant functional traits prevents them from foraging on plants that are not preferred food plants even though these are widespread in the habitat (Unsicker et al 2008). Although *C.dorsatus* is Gomophocerinae species it has been documented to by (Deraison et al in review) that they sometimes exhibit higher herbivory impact on some leguminous species(63.55%) than on some grass or forb species, this was attributed to their incisive strength and preference for grasses that have lower leaf dry matter content and Carbon : Nitrogen ratio. Therefore it is suggested that their dispersal kernel was influenced by the search for patchily distributed legumes within the mesocosm. In support of this argument Sutherland et al 2000 stated that the expected dispersal distance of some mammals and birds increases with declining food resources within their home range. This type of resource led movement behaviour has been documented for several butterfly species, which travel long distances to forage on preferred food plants (Bonte et al, 2009). It has also been reported by Bowler & Benton 2005 that emigration rates and propensity to disperse was reduced for juvenile *Acipter gentilis* by providing experimental food supplements. The pattern of redistribution answers the question that dispersal distance will increase in unfavourable habitats due to the huge influence foraging patterns have on most insect herbivore population (Behmer, 2009). As outlined above, other factors like vegetation structure and predator density act as contributory factors to the suitability of habitat. I will briefly discuss their effects on dispersal and redistribution patterns of the three study species

4.3.2. Linking dispersal with vegetation structure

Structure of vegetation is important to most orthopteran assemblages during different stages of their life cycle. This affects the micro climatic conditions (e.g temperature and humidity) prevailing on the habitat, which makes it an important factor to be considered for most temperate grasshoppers due to their thermophilic nature. As point out by Fartmann et al, (2012) bare ground provides optimum conditions for ovi-positioning while intermediate vegetation canopy height (< 30cm) provides resources necessary for nymphal development through to adulthood. Several orthopteran species like *Decticus verrucivorus* and *Aiolopus thalassinus* exhibit different preferences concerning vegetation canopy height, the former prefers tall vegetation while the latter is best suited to shorter vegetation (Batary et al, 2006).

Due to the exclusion of avian predation as a consequence of this being a caged experiment which might influence the micro habitat use differently, grasshopper densities were lowest in

quadrats that had a vegetation average canopy greater than 30centimetres. These quadrats were used as refuge areas, (Badenhausser &Cordeau, 2012) especially after the application of cutting treatment, to avoid been trampled on during grasshopper surveys and re-sighting exercise. Therefore altering their dispersal and redistribution patterns and increasing agitation dispersal (Guido& Gianelle, 2001). The avoidance of these quadrats is also an anti-predator approach by the grasshoppers to increase chances of survival due to the presence of ambush predators like *Argiope bruennichi*, *Mantis religiosa* and *Conocephalus spp.*

4.3.3. Linking dispersal with predator density

Predation and availability of food resources have been identified as two major factors that shape grasshopper communities (Belvosky &Slade 1993). The effects of predation could be direct due to increased mortality resulting in the decline in density, which was evidenced in this study, or indirect with emphasis placed on behavioural changes regarding duration and pattern of foraging; exacerbating energy budgets and reducing overall fitness (Danner & Joern, 2003). Schmitz et al (1997) reported that *M femurrubrum* exhibited 10% reduction in their food intake with a population decline of 20% under experimental conditions with *P. mira* spiders with glued mouthparts. In relation to predatory effects on dispersal, Baines, McCauley & Rowe (2014), used a mesocosm to study the interactive effects of competition and predatory risk in insects their results showed that increased emigration of *N undulata* was a consequence of increased predation risk. They went further to explain that the relationship was not linear but occurred in tandem with increased density of the insect. Consequently, the presence of predators have been reported by Kunert &Weisser (2003) to cause pea aphids(*Acyrtosiphon pisum*.Harris) to develop morphs with wings to ease dispersal into new habitats The density of predators in the mesocosm did not have a significant effect on our rate of re-sighting, their presence in some quadrats affected the redistribution patterns of the marked grasshoppers . Possion regression analysis was used to test the response of our three study species to predator density. *E.elegantulus* and *C.dorsatus* had a negative intercept value although this was not significant for *C.dorsatus*. *P. giornae* individuals had positive but not significant relationship with presence of predators

4.4. Do sex differences explain individual differences in dispersal and is this in accordance or opposite to sex differences in body size?

Sexual size dimorphism is a common phenomenon displayed by organisms, in vertebrates (birds and mammals) males are usually larger while in most invertebrates, size dimorphism is

usually female biased (Hockirch & Groning, 2008). This trend can be seen amongst population of the three study species. The average body size of *C.dorsatus* females is 17.98mm while male average body size is 13.53mm. *E.elegantulus* average body size for both sexes is 17.08mm for females and 11.65mm for males. *P.giornae* females have an average body size of 12.48mm and males 10.28mm. Due to the larger body size of females, it is simpler to categorise them as the better dispersers than their male counterparts (Whitman, 2008). However results from this study suggests that, between sexes, the propensity to disperse is controlled by a number of factors which goes beyond just their body size. This is assumption is evidenced in large gravid female *Metrioptera roeseli*, dispersal propensity is reduced due to increased body mass (Poniatowski & Fartmann, 2011).

Amongst the three study species, the number of females marked was higher in two species *E.elegantulus* and *P.giornae*. Although in *E.elegantulus* the proportion of males to females was not significant, the female biased marking of *P.giornae* was significant. *C.dorstus* marked population was also significantly male biased. It is however pertinent to mention that bias marking of females or males within the population was not premeditated. All the grasshoppers used for the study were captured in-situ with the exception of 2% of the *C.dorstaus* population. Hence the proportion of males and females marked could be representative of the actual population proportions in the mesocosm.

Sex ratio has been identified as a catalyst that influences the decision of an organism to leave its habitat. This reaction to gender proportions was noticed in an experiment regarding the effects of sex ratio on population dynamics of *Proctolaelaps kirmsei*, it was noticed that males were dispersing from population with high male sex ratio to female dominated ones. (Bowler & Benton 2005). This reaction to gender ratio was not apparent in this study because natural densities were used, in addition size and design of the experimental facility allowed free movement reducing the effects of crowding.

Estimation of the dispersal distance of the sub- populations that settled and those yet to settle revealed that males were more mobile than females for all the three species. The number of females in the settled population is 51 while males were 47, for the “yet to settle population” males were 22 and females 23. Though the differences in the distance travelled was not statistically significant. This same trend was recorded by Poniatowski & Fartmann (2011) when *Metrioptera roeselii* males had a daily movement distance of 9.0 metres while for females it was 7.8metres. They went further to describe this trend as a “common

phenomenon” in orthopteran assemblages, which is attributed to the sex specific behaviour in terms of reproductive ecology. The reproductive ecology of male and female grasshoppers could be very divergent. Males due to their smaller size are more agile (Whitman, 2008) and increase their fecundity by being highly mobile during breeding season, while females especially those with wings exhibit philopatric movements by staying close to ovipositioning sites once they have been fertilized (Poniatowski & Fartmann, 2011). The energy budget expended on flight has been linked to reduction of fecundity in females. The trade-off is exhibited in the female morphs of *Gryllus rubens* and *Gryllus firmus*, short winged flightless morphs are more fertile than long winged morphs (Zera & Mole, 1994)., however the reverse is the case for certain species like *Locust migratoria* and *Schistocerca gregaria* Because increased mobility has been reported to stimulate fertility (Mcanelly & Rankin, 1986) in the females of these species. Reproductive needs could be a plausible explanation for the increased mobility displayed by male individuals, because the mark and recapture study was conducted during the breeding season of the three grasshoppers species.

It has been stated by Samietz & Kohler (2012), that dispersal differences between sexes is based on the interaction of body size, foraging pattern, predator escape strategies and individual personality traits with sex specific traits for reproduction. The effects of body size could be used to explain interspecific differences in dispersal kernel, which is quite apparent between maximum distances travelled by individuals of different sexes from *C.dorstus* and *P. giornae*. It cannot be viewed in isolation as a major factor in the variation displayed by male and female members of the same species, in this case it is clear that differences in reproductive needs could have informed the distances recorded for the different sexes.

4.5. Are there consistent personality differences which relate to differences in dispersal?

Personality traits refer to the constant display certain behavioural responses by individuals within a population (Wolf & Wessing 2002). This unique response of these individuals to external stimuli could have a strong influence on the fitness and persistence of that population. Personality variation within a population could be heritable traits passed from parent to offspring for example the habitat matching trait displayed by *Dissotichus mawsoni* to increase fitness in extreme weather conditions or resulting from experiences during developmental stage as exhibited in *Phaedon cochleariae*, (Tremmel & Muller, 2012; Bolnick & Otto 2013). In the context of dispersal, personality traits like boldness, aggressiveness and sociability have been correlated with dispersal plasticity (Cote et al 2010)

however it is still not clear how these traits are developed especially in grasshoppers (Dubois & Giraldeau 2014).

Handling of insects during marking exercise has been described as a stress inducing exercise for most insects, this causes them to react in a “flight or fight” response similar to reaction to predators, inducing the release of stress hormones octopamine (Mallet et al, 1986; Adamo, 2010). However during the marking exercise I noticed a variation in the temperament displayed by the grasshoppers. The individual’s disposition to handling was noted to test if handling will have an effect on the dispersal plasticity and overall movement behaviour of the individual. Stress from handling was observed to have short term effects on the movement dynamics of *Heliconius* butterflies (Mallet et al, 1986). This was also observed for the three study species because the first three days of the re-sighting exercise most of the grasshoppers were still concentrated close to the release points.

Within the *C.dorsatus* population 86 individuals were resistant to handling while 16 were calm, *E. elegantulus* 43 resistant and 37 calm while *P. giornae* had 75 resistant and 26 calm. In the sub population of those that settled 92.16% of the *C dorsatus* were resistant to handling while 7.84% were calm. 54.16% of settled *E.elegantulus* showed resistance during marking while 45.83% were calm. However for *P.giornae* 53.84% were calm during marking while 46.15% showed resistance. For population yet to settle 75% of the *C.dorsatus* were resistant while 25% calm, *E.elegantulus* proportion of resistant to calm individuals is equal while *P.giornae* is 85% for resistant grasshoppers and 14.28% for calm individuals. A test of proportion was conducted to test the significance of the proportion that settled regarding temperament displayed by each individual, this revealed that a significant number of resistant individuals settled for *C.dorsatus* while in *P giornae* and *E.elegantulus* although the resistant individuals numbers were higher it was not significant. In the yet to settle population *C.dorstus* and *P.giornae* resistant individuals were significantly higher, while *E.elegantulus* individuals proportion of resistant to calm in the subpopulation was not significantly higher. Overall re-sight success was higher for resistant individuals. Poisson regression analysis was used to test the significance of temperament on rate of re-sight for the study species, results from the analysis showed that temperament did not have a significant effect on re-sighting frequency. It is however clear that the results presented above do not give a clear indication if disposition towards handling had an effect on the rate and scale of movement of the three species or can be classified as personality or episodic traits. Even though the most re-sighted females *E.elegantulus* and *P.giornae* were both calm, the least travelled male *C.dorsatus* was

resistant during marking. . Personality traits are consistent behavioural differences displayed by individuals within a population (Cote et al 2010). For example *Rivulus hartii* rate of dispersal is positively correlated with boldness (Rasmussen & Belk, 2012), winged female morphs of *Gryllus taxensis* are usually less aggressive (Cote et al, 2010) the effects of starvation have been documented to increase death feigning behaviour in *Cylas formicarius* (Tremmel & Muller, 2012). Episodic traits however are not consistent and they can vary with time, this kind of behavioural traits has been reported for *Bombus terrestris* and *Octopus tetricus* in response to novel visual stimuli placed in their habitat (Muller et al 2010).It is however clear that within the population of the grasshoppers used for this study there were variations within the population; settled and yet to settle. However due to the inconsistencies in temperament of individuals within these sub-populations which could be a consequence of the unequal proportions of resistant to calm individuals, I cannot prove beyond reasonable doubt if behavioural traits had an effect on the redistribution pattern and rate of dispersal. To adequately determine the effects of personality on dispersal , it is however important to study the individuals at different stages of their development to determine the factors that stimulate individual behavioural variations within the population in terms of the development of personalities , rather than taking “snap shots “ of their personality as aptly described by Muller et al (2010). This opens up an opportunity for further research as it is easily to assume ephemeral responses to stimuli as personality traits. It is however necessary to fully investigate the how behavioural traits are developed in grasshopper species and to understand if they are consistent enough to be correlated with their dispersal behaviour.

4.6. LIMITATIONS

4.6.1. USE OF THE BOX SAMPLER FOR GRASSHOPPER SURVEY

Though this method was very effective, but due its size and weight the sampler left impressions on the vegetation cover mimicking the effects of trampling and caused agitation dispersal away from the quadrat being sampled. It is believed that this could have had an effect on density of grasshoppers being surveyed per quadrat and movement of marked individuals.

4.6.2. TEMPERATURE IN THE MESOCOSM

The temperature in the mesocosm also was distinctively warmer within the enclosure, although this augments the development and activity of grasshoppers,it however shortened

time spent on making observations especially on days with exceptionally high temperatures which had an effect on re sighting exercise.

4.6.3. MARKING

According to Hagler& Jackson (2001) a good marker should be lightweight fast drying, non-toxic, and persistent .The enamel paint used to mark the grasshoppers did not have any toxic effect on the grasshoppers, however at the end of two weeks into the re-sighting exercise it was noticed that the paint markings had begun to come off which prevented the identification of the individual during the exercise which had an effect on the frequency of re-sighting for such individuals.

4.6.4. RESIGHTING EXERCISE

According to Narisu et al 1999, the four stages that are common to all mark and recapture studies alter animal behaviour. We opted for an adaptation of the recapture phase which is re-sighting, to reduce the incidence of “fight and flight” reaction which often occurs during the recapture phase. However the layout of the experimental facility increased the incidence of agitation dispersal, because to gain access into the quadrats located at the centre of the each block especially during the re-sighting exercise we needed to walk into the blocks thereby causing agitation dispersal into other quadrats altering their movement pattern and re-sighting frequency.

5. CONCLUSION

The process of dispersal is very fundamental to the persistence of organisms that exist as meta-populations (Cote et al, 2010). Due to the importance of movement to population dynamics of organisms, recent studies (Bowler & Benton 2005; Tremmel & Muller, 2013) emphasize the need to understand individual variations that affect the dispersal plasticity within these spatially structured assemblages.

Most mark and re-sight studies on insect dispersal have used mass marking techniques, with results that make general assumptions about the population movement dynamics excluding the probability of individual variations within assemblages. This recently completed study went a step ahead by taking into consideration the individual differences that might be inherent especially regarding behavioural trait variations which is certain to have an effect on the individual's life processes. The generation of unique colour codes for 303 individuals allowed the mapping of spatial and temporal movement of individuals re-sighted at least more than once for the duration of 21 days. In lieu of this, conclusions were drawn on important factors that influence individual and interspecific variation concerning propensity or plasticity towards dispersal.

The rate and scale of movement of grasshoppers is significantly influenced by the spatial configuration of their preferred food plants. In relation to variances in movement dynamics within or between species, the effects of conditions prevailing in the habitat, body size, presence/absence of wings, and sex specific reproductive prerequisites become more apparent.

Study species had contrasting traits in terms of body size (*C.dorsatus* and *E.elegantulus* vs *P.giornae*), feeding niche preferences (*E.elegantulus* vs *C.dorsatus* vs *P.giornae*) and movement capacity (*C.dorsatus* and *E.elegantulus* vs *P.giornae*). Distance estimates confirmed that spatial and temporal variation in movement was determined by differences dietary requirements and movement capacity. Interspecific differences regarding body size and wing development influence on dispersal, was more apparent between *C.dorsatus* and *P.giornae*. Habitat selection was influenced by vegetation cover type, average canopy height and predator density. Effects of predator density was however negligible due to constant removal after release of marked individuals.

Comparisons made between average distance travelled by male and females revealed that there was no significant difference between the sexes however, individual distance estimates suggest that males were more mobile than females. Sex specific reproductive responsibilities seems plausible to explain this variation because the mark and re-sight studies was conducted during grasshopper breeding season.

Response to handling was documented during marking exercise to investigate if variations exhibited amongst individuals are consistent enough to be classified as personality traits which might have an influence dispersal behaviour exhibited. However inconsistencies in the temperament exhibited by individuals within settled and yet to settle population suggest that these might just be episodic traits.

In closing, I suggest that to adequately identify individual behavioural correlates to dispersal within grasshopper assemblages, it is necessary to study sample population at different stages of their life cycle to know 1)if grasshoppers can develop consistent personality traits, if they can, 2) do these traits occur solely from environmental interactions or they are heritable adaptive traits. This information is lacking for mostly Gomophocerinae and Catantopinae species which are quite widespread on European grasslands. In addition, I suggest that subsequent mesocosm experiments should be conducted in parallel with open area experiments investigating the same relationships, although this might be intensive and time consuming, it will provide robust inferences by taking into account stochastic effects often times excluded from caged experiments.

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APPENDICES

- APPENDIX I - VEGETATION PROFILE WITHIN THE 144 QUADRATS & HERBIVORY DATA
- APPENDIX II- INDIVIDUAL ATTRIBUTES
- APPENDIX III- RESPONSE TO HANDLING
- APPENDIX IV - RESIGHT FREQUENCY
- APPENDIX V - INDIVIDUALS THAT SETTLED
- APPENDIX VI - INDIVIDUALS YET TO SETTLE
- APPENDIX VII- INTERACTION OF RESIGHT FREQUENCY WITH RESPONSE TO HANDLING, SPECIES AND SEX
- APPENDIX VIII- RELATIONSHIP WITH VEGETATION COVER
- APPENDIX IX- POISSON REGRESSION ANALYSIS OUTPUT



DEPARTMENT OF BIOSCIENCES

STUDENT PROJECT LOG

Name of Student (print)	ADENIRAN OLUNAFISAYO H.
Student Number (print)	748940
Degree Scheme	MSc ENVIRONMENTAL BIOLOGY.
Title of Project	DETERMINANTS OF GRASSHOPPERS! AN EXPERIMENTAL APPROACH.

ACTIVITY	DATE	STUDENT SIGNATURE	SUPERVISOR SIGNATURE
Discuss project + Logistics	18/02/14	hu.	<i>Luca Börger</i>
Literature review	23/05/14	hu.	<i>Luca Börger</i>
Experimental design + Methods	23/06/14	hu.	<i>Luca Börger</i>
Grasshopper washing	04/08/14	hu.	<i>Luca Börger</i>
Data analysis	24/08/14	hu.	<i>Luca Börger</i>
Thesis write-up	01/09/14	hu.	<i>Luca Börger</i>

We sign that the above is a true record of our meetings in relation to the project.

Name	Signature
LUCA BÖRGER	<i>Luca Börger</i>
ADENIRAN OLUNAFISAYO	hu.

Terrestrial Fieldwork Risk Assessment 2014

Hazard	Risk/Consequence	Persons exposed	Controls	Risk
weed, wild ip, other bers of the ceae	Burns, skin irritation, scars	All	Awareness when working in long grass, long sleeved tops to reduce contact with the plant	Moderate
ling faecal rial	Disease transmission	All	Wear gloves when handling faecal material Use alcohol based hand wash after handling	Moderate
and endo- ites	Disease transmission	All	Awareness of potential risks explained, inform GP immediately if any symptoms occur post field work	Low
thorn, bramble, plants with s / thorns	Eye injury, lacerations, septic wounds, puncture wounds	All	Avoid walking through scrub, appropriate clothing and footwear (stout trousers, wellies etc), do not look down or kneel in scrub	Moderate
ation/poor s	Other risks are enhanced from this hazard	All	Ensure that someone knows the location where you are working and when you are due to return. Buddy system to be used at all times. Protocol to contact emergency services after a predominated time has expired	High
tigating dens and ws	Risk of injury from cornered animal	All	Do not put hands etc into dens and burrows prior to checking the entrance using a torch/stick	Low
rsing uneven id	Injury	All	Extreme care required, sturdy boots with ankle support, use of torch	Moderate
ealed burrows, sing burrows	Falls, sprained ankle, other injury	All	Where rabbits/other burrowing species are present walk at slow pace maintaining good balance. Wear footwear with good ankle support. First aid kit and mobile phone to be carried	Moderate
t/sunny er	Heat exhaustion/sunstroke/sun burn	All	During hot/sunny weather maintain water intake, wear a hat and high factor sun cream	High
t bites	Allergic reaction	All	Wear insect repellent, carry antihistamine, make colleagues aware of previous allergic relations to bites	Moderate
chill	Hypothermia	All	Be aware of the risk, wear appropriate clothing including headgear and gloves	Low/moderate
	Bites, <i>Toxicara</i>	All	If threatened back off but do not turn back, do not handle dog faeces without gloves, seek immediate medical attention if bitten	Low

en glass, needles	Infections/cuts/lacerations	All	Vigilance required before sitting, parting vegetation. Wear gloves/stout clothing in high risk areas	Moderate
r / water body	Drowning, hypothermia	All	Take care when walking on the river path, avoid working close to the edge of the river bank, do not access the river	Moderate
posure at trail s / river gorges	Fall, severe injury and drowning	All	Correct footwear, extreme caution, sensible behaviour, use assigned paths, follow ALL instructions from staff	High

* refers to HIGH risk categories – extra care must be taken with these risks

Following rules apply to all workers:

Mobile phones should be carried at all times.
Workers are permitted to work alone.

Read the risk assessment and agree to follow the guidelines stipulated:

Participant: ABENIRAN OLUWAFEMIWA HAZERAT [748940] Lu.

Supervisor: Lina Boyer

Name ADENIRAN OLUNAFISAVO H Signature AD date 24/09/14

Supervisor* LUCA BORGER Signature Luca Borger date 24/09/14

Activity title Grasshopper survey + marking Base location (room no.) France
 (* the supervisor for all HEFCW funded academic and non-academic staff is the HOC)

University Activity Serial # (enter Employee No. or STUREC No.)

Start date of activity (cannot predate signature dates)

End date of activity (or 'on going')

Level of worker (delete as applicable) PG

UG PG research assistant, technician, administration, academic staff, other (state)

Approval obtained for Gene Manipulation Safety Assessment by SU ? Yes/not applicable
 Licence(s) obtained under "Animals (Scientific Procedures) Act (1986)" ? Yes/not applicable
 Approval obtained for use of radioisotopes by COS ? Yes/not applicable

Record of specialist training undertaken

Course	date
<u>NA</u>	<u>/</u>

Summary of protocols used; protocol sheets to be appended plus COSHH details for chemicals of category A or B with high or medium exposure

Protocol Details					Protocol Details						
#	Assessment				#	Assessment					
	1st date	Frequency of re-assessment	Hazard category	Secondary containment level	Exposure potential		1st date	Frequency of re-assessment	Hazard category	Secondary containment level	Exposure potential
1	<u>NA</u>	<u>/</u>	<u>/</u>	<u>/</u>	<u>/</u>	11	<u>NA</u>	<u>/</u>	<u>/</u>	<u>/</u>	<u>/</u>
2						12					
3						13					
4						14					
5						15					
6						16					
7						17					
8						18					
9						19					
10						20					

See notes in handbook for help in filling in form (Continue on another sheet if necessary)

Protocol # /	Title: NA
Associated Protocols # /	Description: /

Location: /

circle which Bioscience and Geography Local Rules apply –

Boat Field Genetic-Manipulation Laboratory Office/Facility Radioisotope

Identify here risks and control measures for work in this environment, additional to Local Rules

Chemicals	Quantity	Hazards	Category (A,B,C,D)*	Exp. Score
/	/	/	/	/

Hazard Category (known or potential) A (e.g. carcinogen/teratogen/mutagen) B (e.g. v.toxic/toxic/explosive/pyrophoric) C (e.g. harmful/irritant/corrosive/high flammable/oxidising) D (e.g. non classified)	Exposure Potential Circle the highest Exposure Score above. Use this to calculate the exposure potential for the <u>entire</u> protocol (see handbook). Indicate this value below.		
	<input checked="" type="radio"/> Low	<input type="radio"/> Medium	<input type="radio"/> High

Primary containment (of product) sealed flask/bottle/glass/plastic/other (state) :- /

Storage conditions and maximum duration :- /

Secondary containment (of protocol) open bench/fume hood/special (state) :- /

Disposal e.g. autoclaving of biohazard, SU chemical disposal /

Identify other control measures (circle or delete) - latex/nitrile/heavy gloves; screens; full face mask; dust mask; protective shoes; spillage tray; ear-defenders; other (state) /

Justification and controls for any work outside normal hours /

Emergency procedures (e.g. spillage clearance; communication methods) /

Supervision/training for worker (circle)

None required Already trained Training required Supervised always

Declaration I declare that I have assessed the hazards and risks associated with my work and will take appropriate measures to decrease these risks, as far as possible eliminating them, and will monitor the effectiveness of these risk control measures.

Name & signature of worker AD ENIQA PESAY O / M. Date 24/09/14.

Name & counter-signature of supervisor LUCA BORGER / Luca Borger Date 24/09/14.

Date of first reassessment _____ Frequency of reassessments _____

Note – you are strongly advised to complete electronic versions of this form, enabling you to readily expand and contract sections as required to ensure clarity and adequate documentation. Do **not** delete any sections! Instead, mark inappropriate sections with NA (not applicable) and contract the section to save space on the final printed form.

Protocol - any self-contained procedure. This could be any activities undertaken, be they lab-work, use of equipment, fieldwork or office work. Your complete research/teaching/administration **activity** (e.g. undergraduate project, PhD study, research grant, other) is therefore made up from separate **protocols**. If the protocol is mainly of low hazard, but with one or more hazardous components, consider making the manipulation of the latter a separate protocol and tie them together by completing the “*Associated Protocol*” box. This is because the entire protocol must be conducted under conditions required for the handling of the most hazardous component.

Title/Description - give sufficient detail to make it obvious what the protocol involves.

Location – identify which local rules apply. More than one rule may apply. Then add any additional risks and control measures peculiar to this protocol (e.g. site-specific fieldwork information; use of autoclaves, sonicators; mechanical, electrical hazards). You may also wish to stress any particularly important risks and controls even if indicated in local rules.

Chemicals etc. - give name, maximum quantity used, list hazards, hazard category (see Table 1) and calculate the **Exposure Score** (see Table 2) for **every** chemical used. Expand the area in the table as required.

Exposure Potential (see Table 3) - complete this section for the chemical which has the **highest** exposure score in your chemical list as this defines the highest risk factor.

Primary containment/Storage - detail how and where, and for how long, the resultant product from the protocol will be stored. The product must be labelled with the date of synthesis, and disposed of (see below) before the maximum duration time has elapsed.

Secondary containment - detail where the protocol will be performed (refer to Table 4).

Disposal - detail how you will dispose of surplus reagents and the product of the protocol. Final disposal must be undertaken within the period noted in the ‘maximum duration’ under ‘Storage’ (above).

Identify other control measures – typically these refer to special protective clothing etc.

Justification and controls for any work outside normal hours – out of hours working is only allowed under special conditions (e.g. 24h sampling, sampling related to tides etc.); convenience is not an acceptable reason.

Emergency procedures - detail how spillages etc. would be handled, including clearance of the laboratory etc. as required. For field work indicate emergency communication and first-aid coverage.

Supervision/training - detail here what special supervision and training is required by the worker named at the bottom of the form. Note that all undergraduates are always considered as research incompetent. First-year PhD students and MSc students are not to be used to supervise the activities of others.

Declaration - both the worker and the supervisor must sign this on the date entered here.

Reassessment - the first reassessment must be undertaken as soon as possible after the first time the protocol has been undertaken in order to identify any unforeseen hazards. After this first reassessment, the protocol should be reassessed every 6-12m, depending on the nature of the chemicals, to take account of changing knowledge concerning the hazardous nature of chemicals. The protocol must be reassessed immediately if new knowledge on the chemical hazards becomes available.

NOTE - standard protocols can be produced for each environment **BUT** each worker must have their own personalised version, signed by them and their supervisor, and dated. These completed personalised protocols must then be appended to the SU risk assessment form for the Teaching/Research activity belonging to the individual.

Hazards, Risks and Containment - Definition of terms

Hazard	potential for doing harm, <i>e.g.</i> toxic, flammable, carcinogenic <i>etc</i>
Exposure potential	the risk to the user depends very much on the exposure, which depends on the physical properties of the material, the quantity used and for how long.

$$\text{Risk} = \text{"Hazard"} \times \text{"Exposure Potential"}$$

The risk is decreased to a safe level by:

- a) Containment
- b) Personal Protection
- c) Good Laboratory Practice (GLP)

Levels of containment

The containment required for a given activity is of two basic kinds: the primary (or intrinsic) containment provided by the apparatus or equipment in which the substances are handled and the additional (or secondary) containment needed to ensure appropriate control of exposure.

HAZARD CATEGORY

TABLE 1- General Guidelines for determining hazard categories

A	EXTREME HAZARD	Substances of known or suspected exceptional toxicity (e.g. carcinogen, teratogen, potential mutagen)
B	HIGH HAZARD	All substances whose toxicity exceeds that of the medium hazard category, except for those known or believed to be so highly toxic as to merit special precautions (i.e. those in the "extreme" category)
C	MEDIUM HAZARD	Substances meeting criteria for CPL* classification as "Harmful" or 'Irritant'
D	LOW HAZARD	Substances not matching criteria for CPL* classification as "Harmful" or "Irritant"

CPL = the Classification, Packaging and Labelling Regulations 1984.

NOTE:

1. The toxicity considered should be that of the substance or mixture handled, including any impurities.
2. Substances may have other properties (*e.g.* flammability) which may call for additional precautions.
3. The above general guidance may need to be supplemented by developing additional criteria with the help of expert toxicological advice. (Additional criteria may be developed using, for example, data given in HSE Guidance Notes such as EH40).
4. Time factors, such as frequency and duration of activity should also be considered. Short duration tasks, involving a few seconds exposure at infrequent intervals, should not affect the initial estimate, whereas continuous operations on a daily basis would probably raise the estimate to the next highest category.

TABLE 2 - exposure score to be calculated for all chemicals used in a protocol

EXPOSURE SCORE				
Calculation Value		1	2	3
(i)	Quantity	<1g	1-100g	>100g
(ii)	Properties	Dense solid Non- volatile liquid No skin absorption	Dusty solids Lyophilised solids Volatile liquids (b.p.>80°C)	Gases, Aerosols Highly volatile liquids (b.p.<80° C) Solutions promoting skin absorption
(iii)	Pressure	Normal	Low/Vacuum	>1 atmosphere
(iv)	Temperature	Room temperature	25°C - 100°C	>100°C

Exposure Score calculation = (i) x (ii) x (iii) x (iv)

The Exposure Potential

TABLE 3 - Rough calculation of exposure potential

EXPOSURE SCORE (FROM TABLE 2)			
Total score	<10	10-54	>54
Exposure Potential	L (low)	M (medium)	H (high)

Secondary containment level calculation

Table 4 - use to determine secondary containment

SECONDARY CONTAINMENT LEVEL					
Hazard Category		A	B	C	D
Exposure potential (from table 3)	H	SA	SA	FH	FH
	M	SA	FH	FH	OB
	L	FH	FH	OB	OB

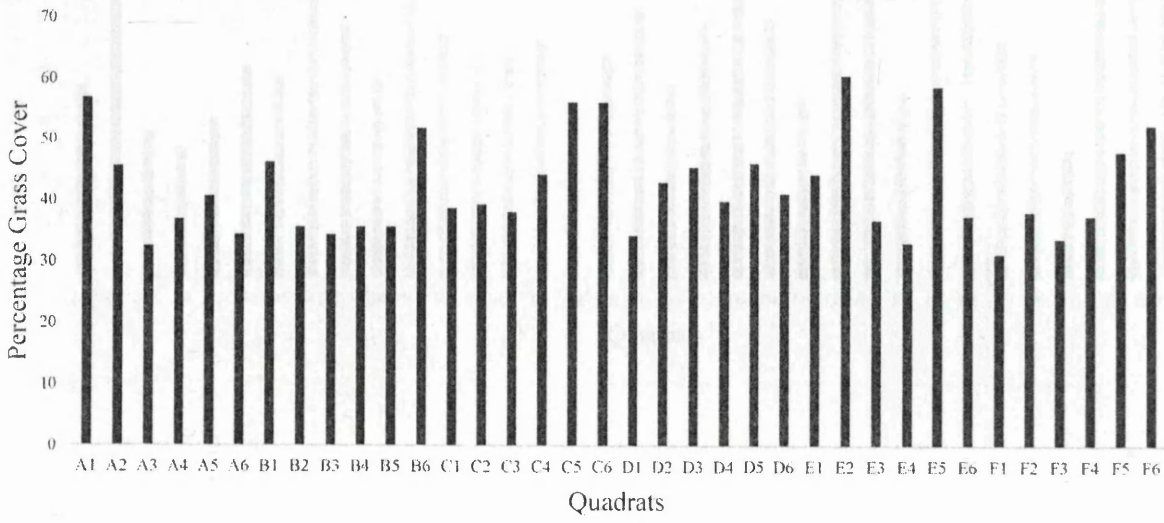
OB = Open Bench; FH = Fume Hood; SA = Special Attention (see supervisor)

Percentage of cover for each species

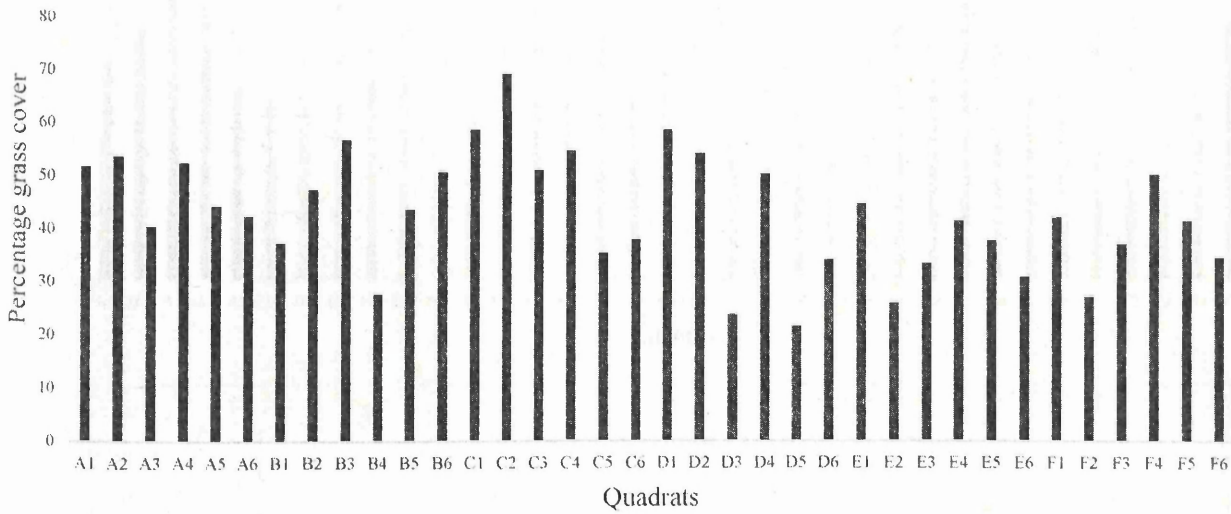
APPENDIX I - VEGETATION PROFILE WITHIN THE 144 QUADRATS & HERBIVORY DATA

VEGETATION COVER DISTRIBUTION

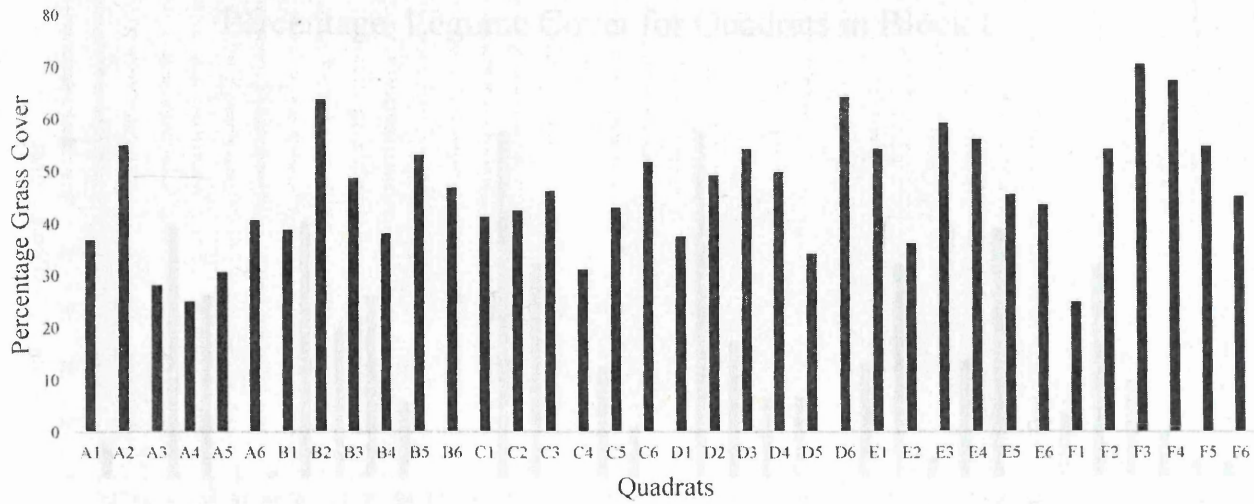
Percentage Grass Cover for Quadrats in Block I



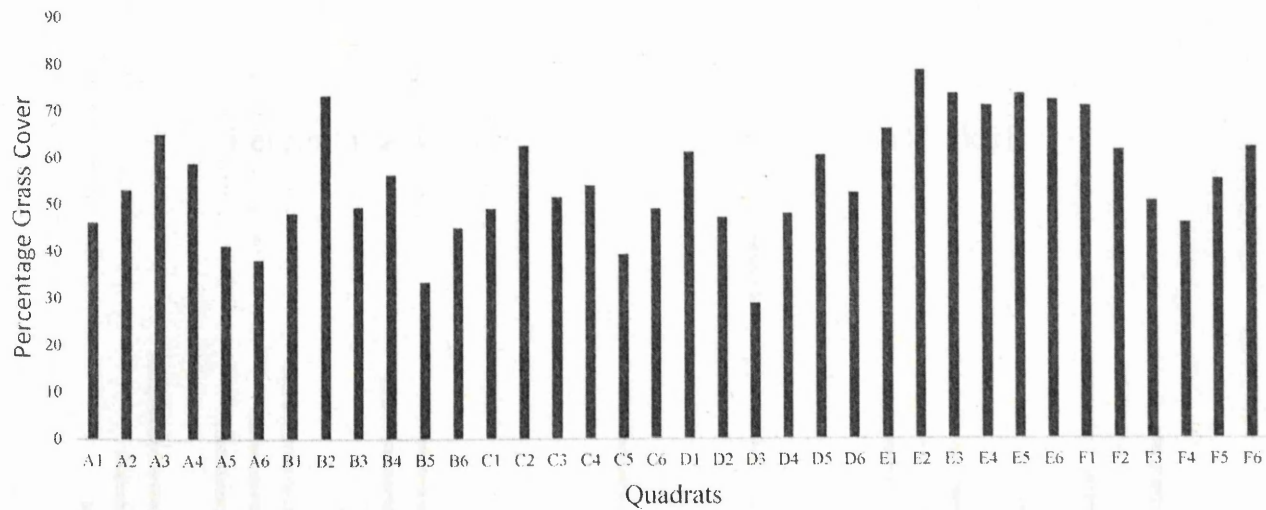
Percentage Grass Cover for Quadrats in Block II



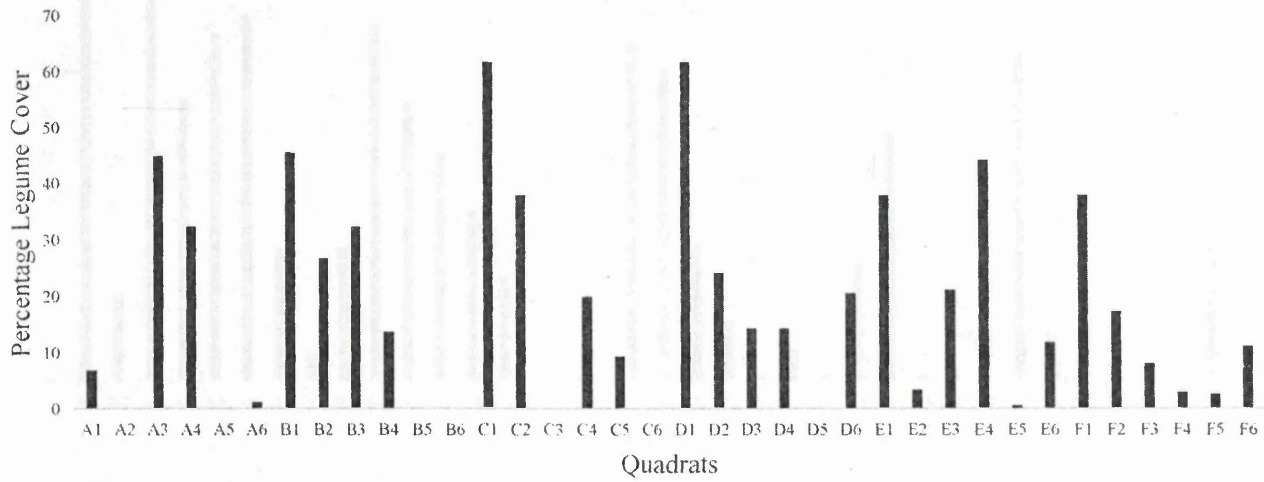
Percentage Grass Cover for Quadrats in Block III



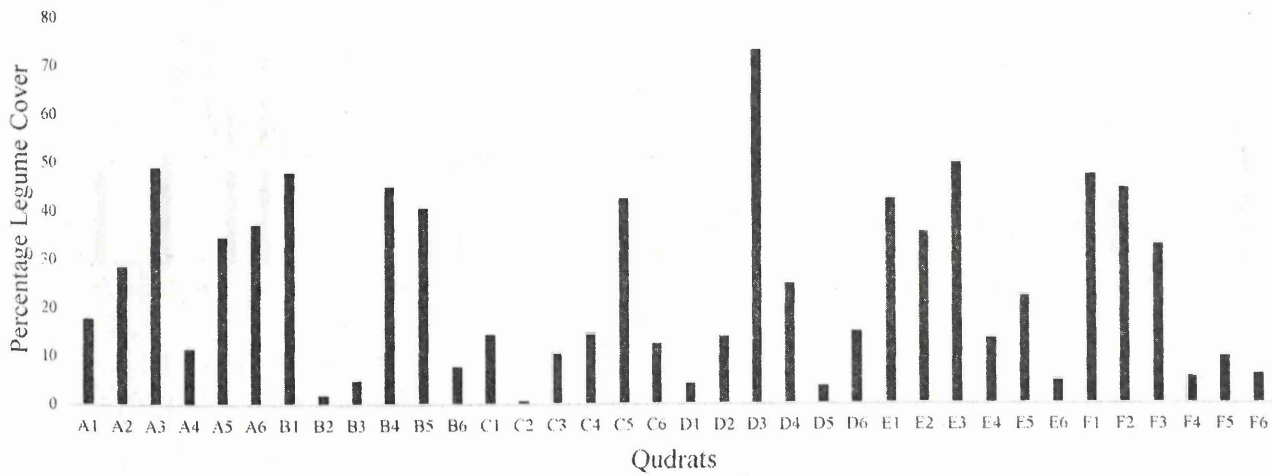
Percentage Grass Cover for Quadrats in Block IV



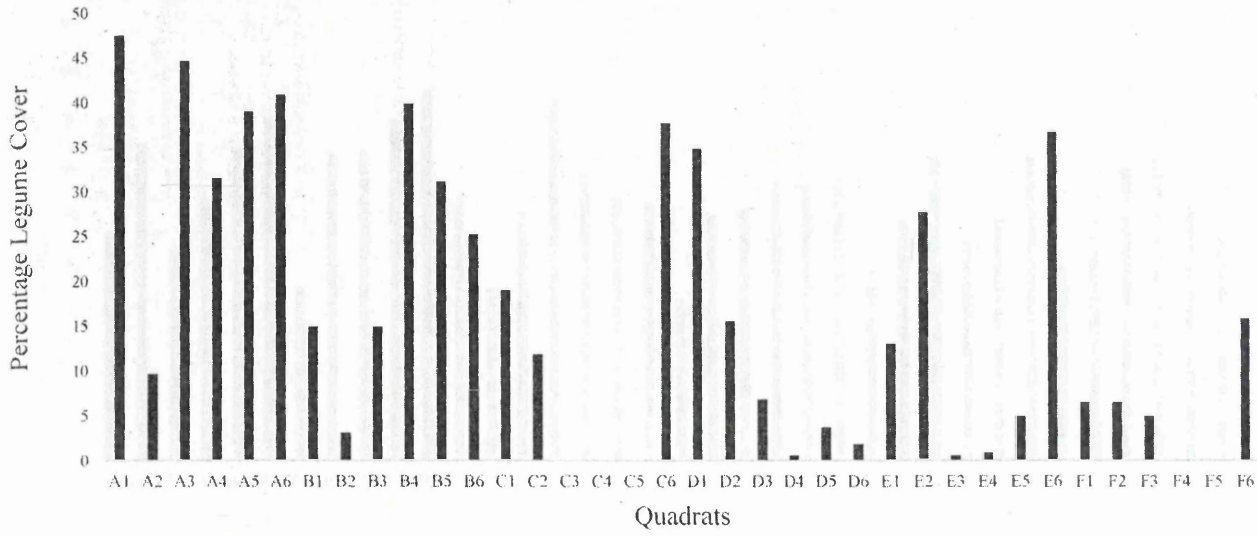
Percentage Legume Cover for Quadrats in Block I



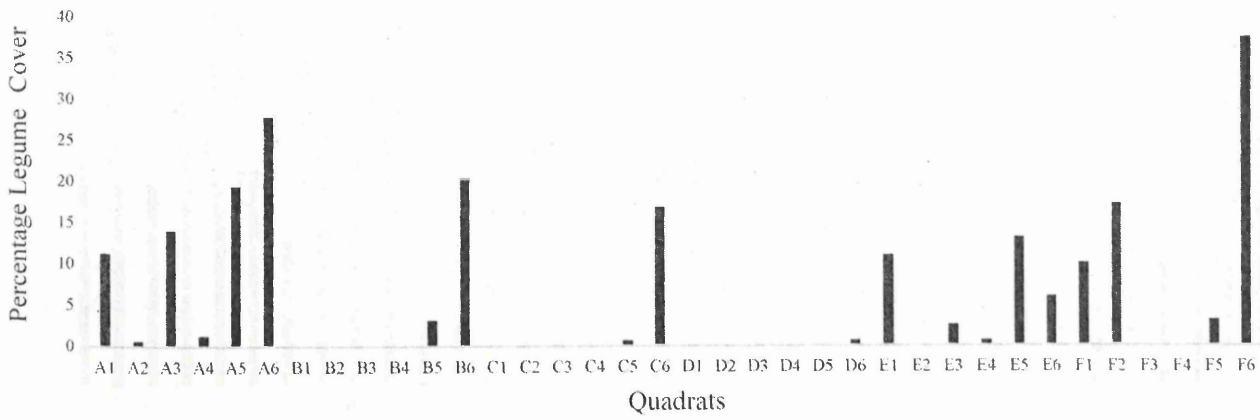
Percentage Legume Cover for Quadrats in Block II



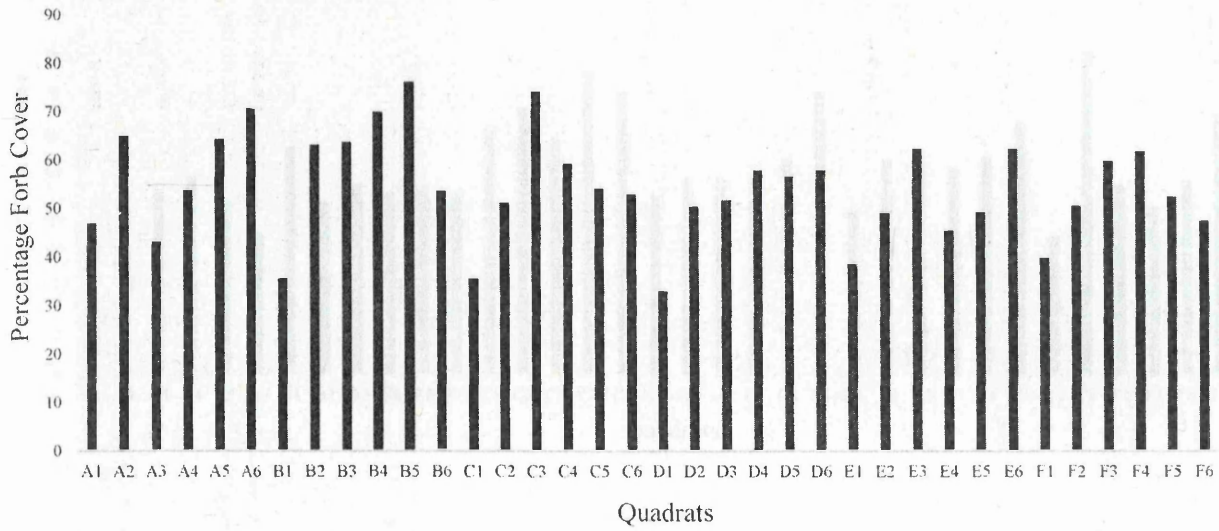
Percentage Legume Cover for Quadrats in Block III



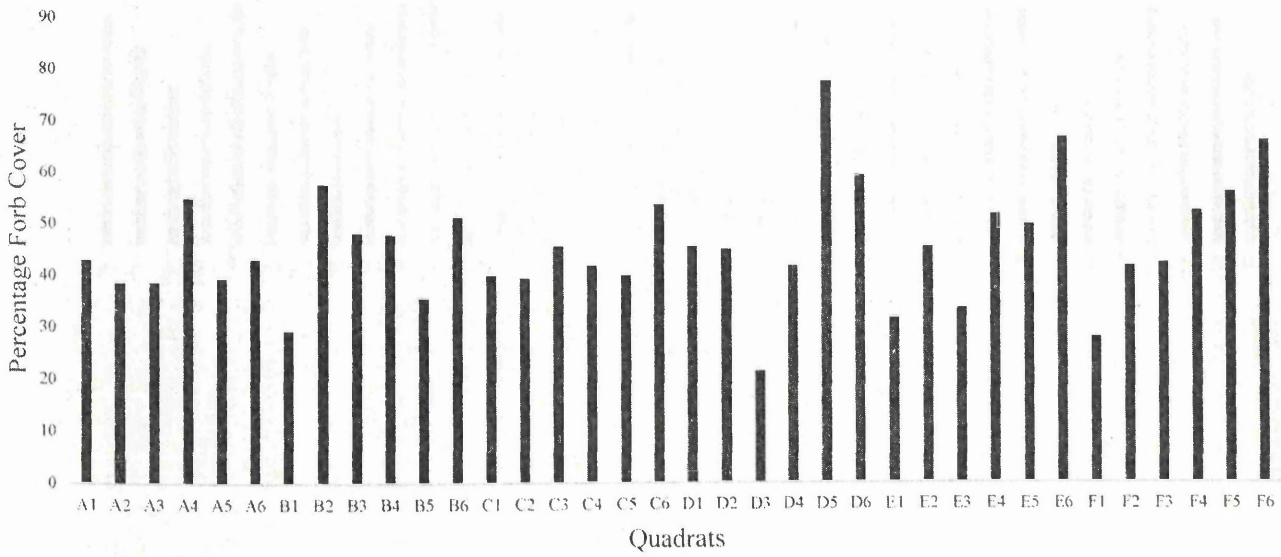
Percentage Legume Cover for Quadrats in Block IV



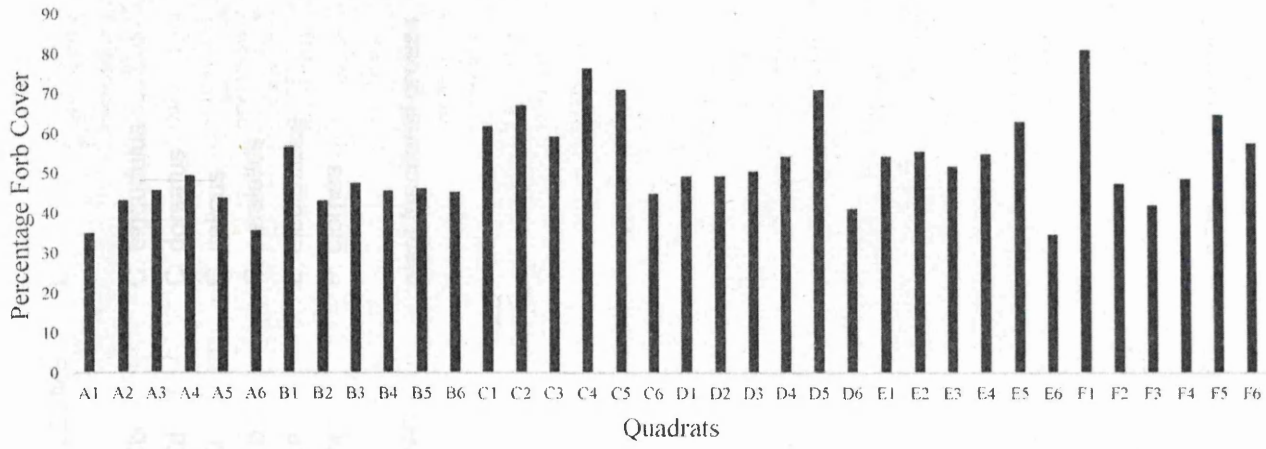
Percentage Forb Cover for Quadrats in Block I



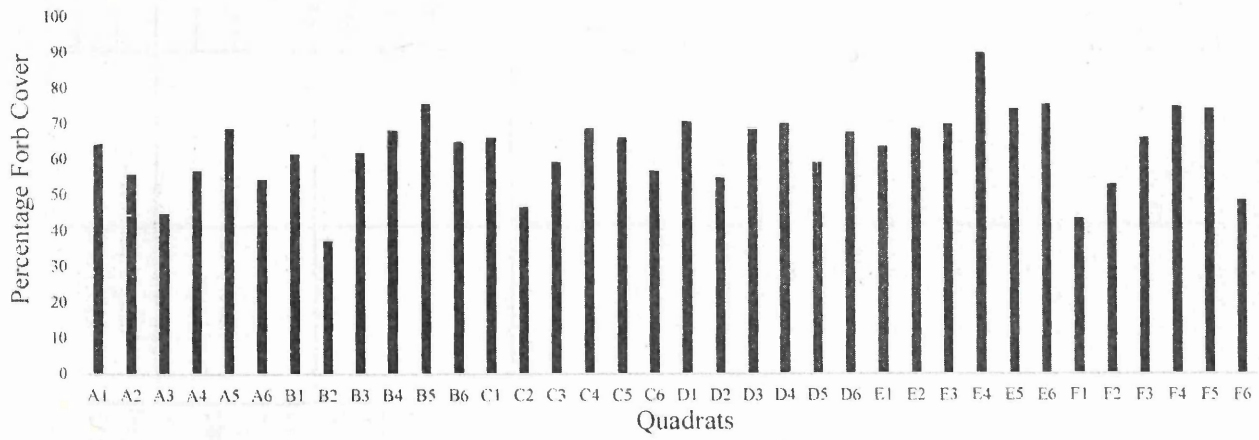
Percentage Forb Cover for Quadrats in Block II



Percentage Forb Cover of Quadrats in Block III



Percentage Forb Cover for Quadrats in Block IV



Species code	Sex	Body size	Incisive strength
Cbig	F	16.4145602	0.095444864
Cbig	M	12.9637922	0.080012578
Cd	F	17.9825669	0.133032536
Cd	M	13.5330566	0.063427312
Cit	F	22.2265022	0.069805437
Cit	M	14.2799805	0.057464755
Cp	F	15.9709629	0.105287203
Cp	M	13.0472496	0.055318099
Ee	F	17.0833674	0.101440055
Ee	M	11.6499916	0.114483605
Pg	F	12.4817561	0.057491223
Pg	M	10.2828667	0.051357501

Species code	Sex	Body size	Incisive strength
Cbig	F	16.4145602	0.095444864
Cbig	M	12.9637922	0.080012578
Cd	F	17.9825669	0.133032536
Cd	M	13.5330566	0.063427312
Cit	F	22.2265022	0.069805437
Cit	M	14.2799805	0.057464755
Cp	F	15.9709629	0.105287203
Cp	M	13.0472496	0.055318099
Ee	F	17.0833674	0.101440055
Ee	M	11.6499916	0.114483605
Pg	F	12.4817561	0.057491223
Pg	M	10.2828667	0.051357501

EuchoorthippusElegantulus	M	RRWW	0
EuchoorthippusElegantulus	F	WWRR	1
EuchoorthippusElegantulus	F	RRRW	0
EuchoorthippusElegantulus	F	WWWR	1
EuchoorthippusElegantulus	F	WRWW	1
EuchoorthippusElegantulus	F	RWRR	1
EuchoorthippusElegantulus	F	RRWR	0
EuchoorthippusElegantulus	F	WWRW	0
EuchoorthippusElegantulus	F	WRRW	1
EuchoorthippusElegantulus	F	RWWR	1
EuchoorthippusElegantulus	F	RRGY	0
EuchoorthippusElegantulus	F	RRYG	1
EuchoorthippusElegantulus	F	GGRY	1
EuchoorthippusElegantulus	F	GGYR	1
EuchoorthippusElegantulus	M	YYRG	0
EuchoorthippusElegantulus	M	YYGR	0
EuchoorthippusElegantulus	F	YGRY	1
EuchoorthippusElegantulus	M	YRGY	1
EuchoorthippusElegantulus	F	RGYR	1
EuchoorthippusElegantulus	M	RYGR	0
EuchoorthippusElegantulus	F	GYRG	0
EuchoorthippusElegantulus	M	GRYG	0
EuchoorthippusElegantulus	F	GRRY	1
EuchoorthippusElegantulus	M	YRRG	0
EuchoorthippusElegantulus	F	RGGY	0
EuchoorthippusElegantulus	M	YGGR	0
EuchoorthippusElegantulus	F	RYYG	0
EuchoorthippusElegantulus	M	GYR	0
EuchoorthippusElegantulus	F	RGY	0
EuchoorthippusElegantulus	M	GRY	0
EuchoorthippusElegantulus	F	YRGG	1
EuchoorthippusElegantulus	M	RYGG	1
EuchoorthippusElegantulus	M	GYRR	0

EuchoorthippusElegantulus	M	YGRR	0
EuchoorthippusElegantulus	M	WWRG	1
EuchoorthippusElegantulus	F	WWGR	0
EuchoorthippusElegantulus	M	WWBB	1
EuchoorthippusElegantulus	M	WGWR	1
EuchoorthippusElegantulus	M	WRWG	0
EuchoorthippusElegantulus	M	WRGW	1
EuchoorthippusElegantulus	F	WGRR	1
EuchoorthippusElegantulus	M	RGWW	0
EuchoorthippusElegantulus	M	GRWW	1
EuchoorthippusElegantulus	M	GRWW	1
EuchoorthippusElegantulus	M	GWWR	0
EuchoorthippusElegantulus	F	RWWG	1
EuchoorthippusElegantulus	F	GWRW	1
EuchoorthippusElegantulus	F	RWWG	0
EuchoorthippusElegantulus	M	RRWG	1
EuchoorthippusElegantulus	M	RRWG	1
EuchoorthippusElegantulus	M	RRGW	1
EuchoorthippusElegantulus	M	RRGW	1
EuchoorthippusElegantulus	M	GWRR	1
EuchoorthippusElegantulus	M	WGRR	1
EuchoorthippusElegantulus	M	GRRW	0
EuchoorthippusElegantulus	M	GRRW	1
EuchoorthippusElegantulus	M	WRRG	1
EuchoorthippusElegantulus	M	RGWR	1
EuchoorthippusElegantulus	M	RWGR	0
EuchoorthippusElegantulus	M	RWGR	1
EuchoorthippusElegantulus	M	RWRG	1
EuchoorthippusElegantulus	M	RGRW	1
EuchoorthippusElegantulus	M	WRGR	1
EuchoorthippusElegantulus	M	GRWR	1
EuchoorthippusElegantulus	M	GGWR	1
EuchoorthippusElegantulus	F	GGRW	0
EuchoorthippusElegantulus	F	RWGG	0
EuchoorthippusElegantulus	F	WRGG	1
EuchoorthippusElegantulus	F	WGGR	0
EuchoorthippusElegantulus	F	RGGW	1
EuchoorthippusElegantulus	F	GRWG	0

EuchothrippusElegantulus	F	GWRG		1
EuchothrippusElegantulus	F	WRGY		1
PezotettixGiornae	F	PRRRR		0
PezotettixGiornae	F	pgGGG		1
PezotettixGiornae	F	pwwwww		1
PezotettixGiornae	F	pYYYY		0
PezotettixGiornae	M	pRRRW		1
PezotettixGiornae	F	pWRRR		1
PezotettixGiornae	M	pRWRR		1
PezotettixGiornae	F	pRRWR		1
PezotettixGiornae	F	pRRRY		1
PezotettixGiornae	F	pYRRR		1
PezotettixGiornae	F	RYRR		1
PezotettixGiornae	F	RRYR		1
PezotettixGiornae	M	RRRG		0
PezotettixGiornae	F	GRRR		1
PezotettixGiornae	M	RRGR		0
PezotettixGiornae	F	RGRR		1
PezotettixGiornae	F	YYG		1
PezotettixGiornae	F	GYYY		0
PezotettixGiornae	F	YGY		1
PezotettixGiornae	F	YYGY		1
PezotettixGiornae	F	YVWV		1
PezotettixGiornae	F	WYYY		0
PezotettixGiornae	M	VWVY		0
PezotettixGiornae	F	YVWY		1
PezotettixGiornae	F	RYYY		1
PezotettixGiornae	F	YVYR		1
PezotettixGiornae	F	YVRY		0
PezotettixGiornae	F	YVRY		1
PezotettixGiornae	M	GGGR		1
PezotettixGiornae	F	RGGG		1
PezotettixGiornae	M	GRGG		0

PezotettixGiornae	F	GGRG	0
PezotettixGiornae	F	GGGY	1
PezotettixGiornae	F	YGGG	0
PezotettixGiornae	M	GGYG	1
PezotettixGiornae	F	GYGG	1
PezotettixGiornae	F	GGGW	1
PezotettixGiornae	F	WGGG	0
PezotettixGiornae	F	GWGG	1
PezotettixGiornae	M	GGWG	1
PezotettixGiornae	F	WGGW	0
PezotettixGiornae	F	GGWW	1
PezotettixGiornae	F	GGWW	1
PezotettixGiornae	F	WWGG	0
PezotettixGiornae	M	GWGW	0
PezotettixGiornae	F	WGWG	1
PezotettixGiornae	M	RRWW	1
PezotettixGiornae	M	WWRR	1
PezotettixGiornae	F	WRRW	1
PezotettixGiornae	F	RWWR	1
PezotettixGiornae	F	RWRW	1
PezotettixGiornae	F	WRWR	1
PezotettixGiornae	F	YGGY	1
PezotettixGiornae	M	GYYG	1
PezotettixGiornae	M	GGYY	1
PezotettixGiornae	M	YYGG	1
PezotettixGiornae	F	GYGY	1
PezotettixGiornae	F	YGYG	0
PezotettixGiornae	F	RGGR	1
PezotettixGiornae	M	GRRG	0
PezotettixGiornae	M	GGRR	1
PezotettixGiornae	F	RRGG	1
PezotettixGiornae	F	GRGR	1
PezotettixGiornae	F	RGRG	1

PezotettixGiornae	F	YRRY	0
PezotettixGiornae	F	RYR	1
PezotettixGiornae	M	RRY	1
PezotettixGiornae	M	YRR	0
PezotettixGiornae	F	YRR	1
PezotettixGiornae	F	RYR	0
PezotettixGiornae	F	YMWY	1
PezotettixGiornae	M	WYWW	1
PezotettixGiornae	M	YWW	1
PezotettixGiornae	M	WYWW	1
PezotettixGiornae	F	WYWW	1
PezotettixGiornae	F	YMWY	1
PezotettixGiornae	F	YRRW	0
PezotettixGiornae	F	RYWR	1
PezotettixGiornae	F	WRRY	1
PezotettixGiornae	M	RWYR	1
PezotettixGiornae	F	RRWY	0
PezotettixGiornae	F	RRYW	1
PezotettixGiornae	F	YVRR	1
PezotettixGiornae	M	WYRR	1
PezotettixGiornae	M	WRYR	1
PezotettixGiornae	F	YRWR	1
PezotettixGiornae	F	RWRY	1
PezotettixGiornae	M	RYRW	1
PezotettixGiornae	F	YRRG	0
PezotettixGiornae	F	GRRY	0
PezotettixGiornae	M	RYGR	1
PezotettixGiornae	M	RGYR	1
PezotettixGiornae	F	RRGY	1
PezotettixGiornae	F	RRYG	1
PezotettixGiornae	F	YGRR	1
PezotettixGiornae	M	GYRR	1
PezotettixGiornae	M	YRGR	1

PezotettixGiornae	F	GRYR	1
PezotettixGiornae	M	RGRY	1
PezotettixGiornae	F	PYRG	0
PezotettixGiornae	F	GRRW	1
ChorthippusDorsatus	M	RRRR	0
ChorthippusDorsatus	F	WWWWW	1
ChorthippusDorsatus	F	YYYY	0
ChorthippusDorsatus	F	RRRW	1
ChorthippusDorsatus	F	RRRW	1
ChorthippusDorsatus	F	WRRR	1
ChorthippusDorsatus	M	RWRR	0
ChorthippusDorsatus	F	RRWR	0
ChorthippusDorsatus	F	RRYR	1
ChorthippusDorsatus	F	RYRR	0
ChorthippusDorsatus	M	YRRR	1
ChorthippusDorsatus	M	GGGG	0
ChorthippusDorsatus	M	RRRY	1
ChorthippusDorsatus	M	WWWWR	1
ChorthippusDorsatus	M	RWWW	1
ChorthippusDorsatus	M	WWWRW	1
ChorthippusDorsatus	F	WRWW	1
ChorthippusDorsatus	F	WWWY	1
ChorthippusDorsatus	M	YWWWW	0
ChorthippusDorsatus	M	WWYVW	1
ChorthippusDorsatus	F	WYVWW	1
ChorthippusDorsatus	F	YYR	1
ChorthippusDorsatus	F	GGGW	1
ChorthippusDorsatus	M	WGGG	1
ChorthippusDorsatus	F	RYRY	1
ChorthippusDorsatus	F	GWGG	0
ChorthippusDorsatus	M	YRY	1
ChorthippusDorsatus	M	YRY	1
ChorthippusDorsatus	F	YYYY	1
ChorthippusDorsatus	M	WYYY	1

ChorthippusDorsatus	M	YYWY	1
ChorthippusDorsatus	M	YWVY	1
ChorthippusDorsatus	M	YWWW	1
ChorthippusDorsatus	F	WYVW	1
ChorthippusDorsatus	F	GGWG	1
ChorthippusDorsatus	F	YGYG	1
ChorthippusDorsatus	M	WVVY	1
ChorthippusDorsatus	M	GGRG	1
ChorthippusDorsatus	M	YVWW	1
ChorthippusDorsatus	M	WYVY	0
ChorthippusDorsatus	M	YVYW	0
ChorthippusDorsatus	M	RWWR	0
ChorthippusDorsatus	M	WRRW	1
ChorthippusDorsatus	M	RWRW	1
ChorthippusDorsatus	M	WVRR	1
ChorthippusDorsatus	M	GRGG	1
ChorthippusDorsatus	M	RRWW	1
ChorthippusDorsatus	F	YRRY	1
ChorthippusDorsatus	F	RYVR	1
ChorthippusDorsatus	F	RYRY	1
ChorthippusDorsatus	F	RYRY	1
ChorthippusDorsatus	F	YRYR	1
ChorthippusDorsatus	F	RGGG	1
ChorthippusDorsatus	M	RRYY	1
ChorthippusDorsatus	M	GGGR	1
ChorthippusDorsatus	M	YVRR	1
ChorthippusDorsatus	M	GGYG	1
ChorthippusDorsatus	M	YRRW	0
ChorthippusDorsatus	M	WRRY	1
ChorthippusDorsatus	M	GYGG	1
ChorthippusDorsatus	M	RWYR	1
ChorthippusDorsatus	M	RYWR	1
ChorthippusDorsatus	M	YGGG	1
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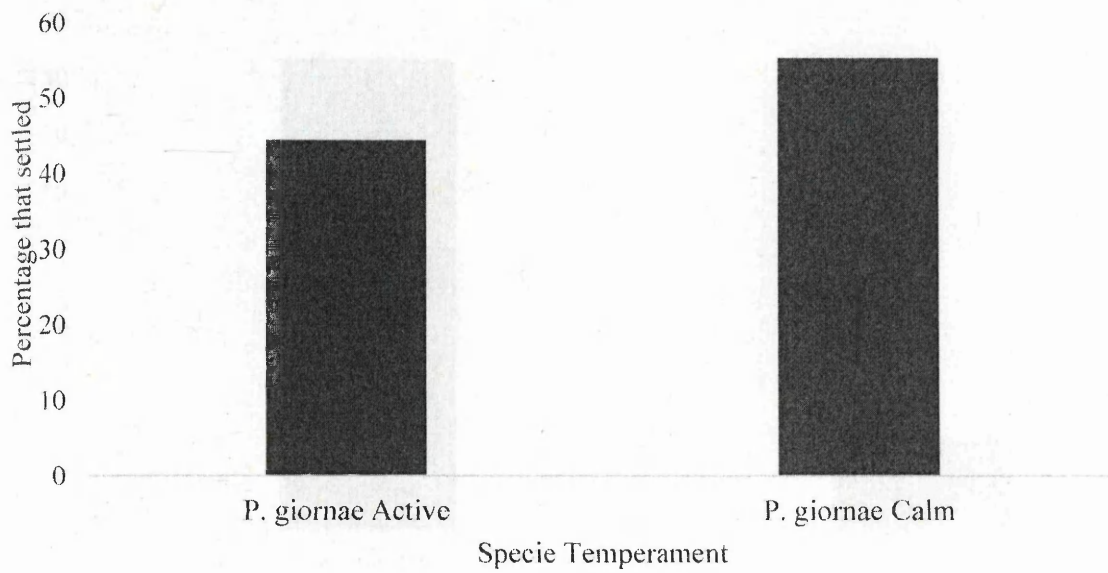
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ChorthippusDorsatus	M	GGYY	1
ChorthippusDorsatus	M	RRWY	1
ChorthippusDorsatus	M	YYGG	1
ChorthippusDorsatus	M	GYGY	1
ChorthippusDorsatus	M	RGGR	1
ChorthippusDorsatus	M	WYRR	1
ChorthippusDorsatus	M	GRRG	1
ChorthippusDorsatus	M	YWRR	1
ChorthippusDorsatus	M	GGRR	1
ChorthippusDorsatus	F	YRWR	0
ChorthippusDorsatus	F	WRYR	1
ChorthippusDorsatus	M	RWRY	1
ChorthippusDorsatus	M	RRGG	1
ChorthippusDorsatus	M	RYRW	1
ChorthippusDorsatus	F	RYYW	1
ChorthippusDorsatus	F	WVYR	1
ChorthippusDorsatus	M	YWRY	1
ChorthippusDorsatus	M	RGGR	1
ChorthippusDorsatus	M	GRGR	1
ChorthippusDorsatus	F	YRWY	1
ChorthippusDorsatus	F	YYWR	1
ChorthippusDorsatus	M	YYRW	1
ChorthippusDorsatus	M	WGGW	1
ChorthippusDorsatus	F	RWYY	1
ChorthippusDorsatus	M	WRYY	1
ChorthippusDorsatus	M	RYWY	1
ChorthippusDorsatus	F	WYRY	1
ChorthippusDorsatus	M	YWYR	0
ChorthippusDorsatus	M	RYBY	0
ChorthippusDorsatus	M	YRYW	1

ChorthippusDorsatus	F	YWWR	1
ChorthippusDorsatus	M	RWWY	1
ChorthippusDorsatus	M	WVRRW	1
ChorthippusDorsatus	M	WRYW	1
ChorthippusDorsatus	M	WWRY	1
ChorthippusDorsatus	M	WWYR	0
ChorthippusDorsatus	M	GWVG	1

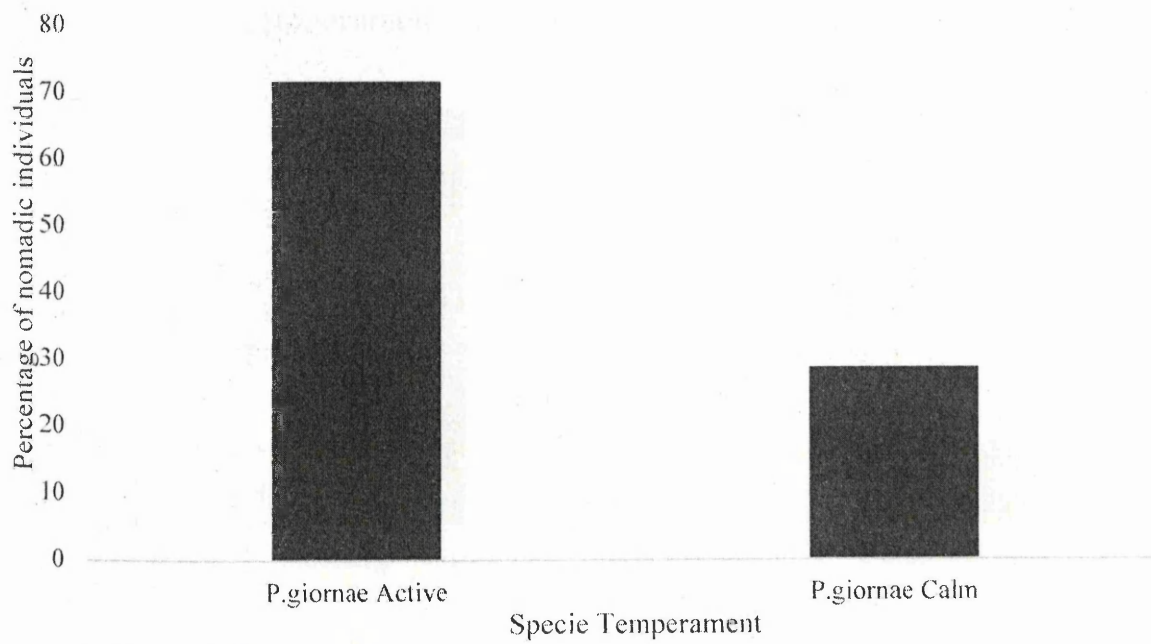
APENDIX III-

RESPONSE TO HANDLING

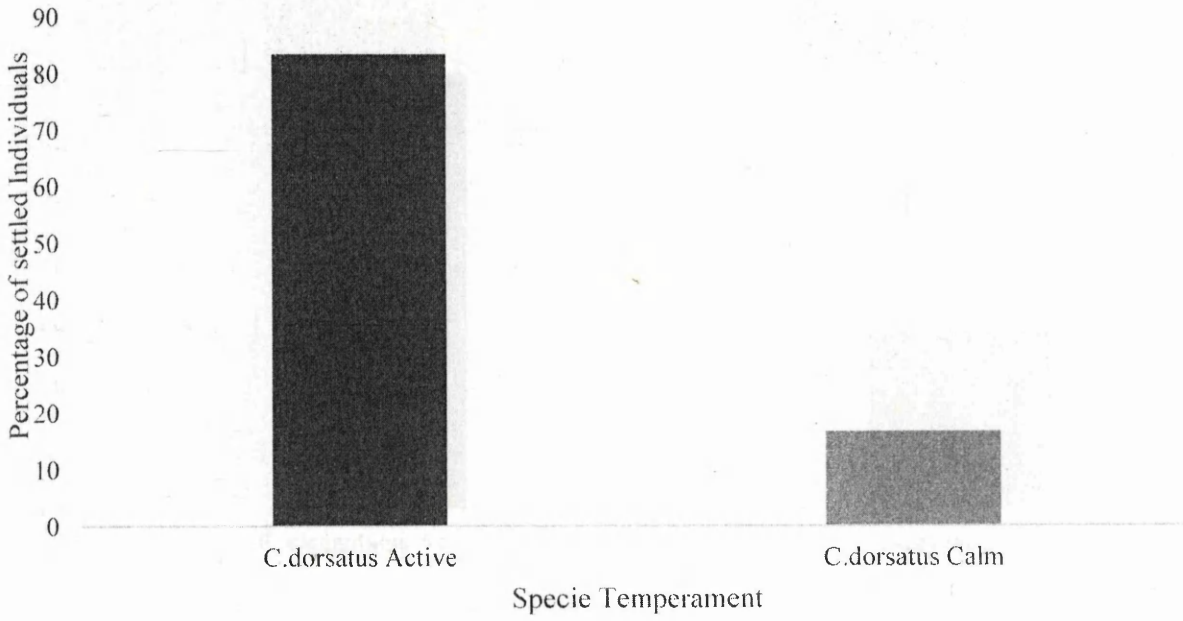
Temperament of Settled *P. giornae* Individuals



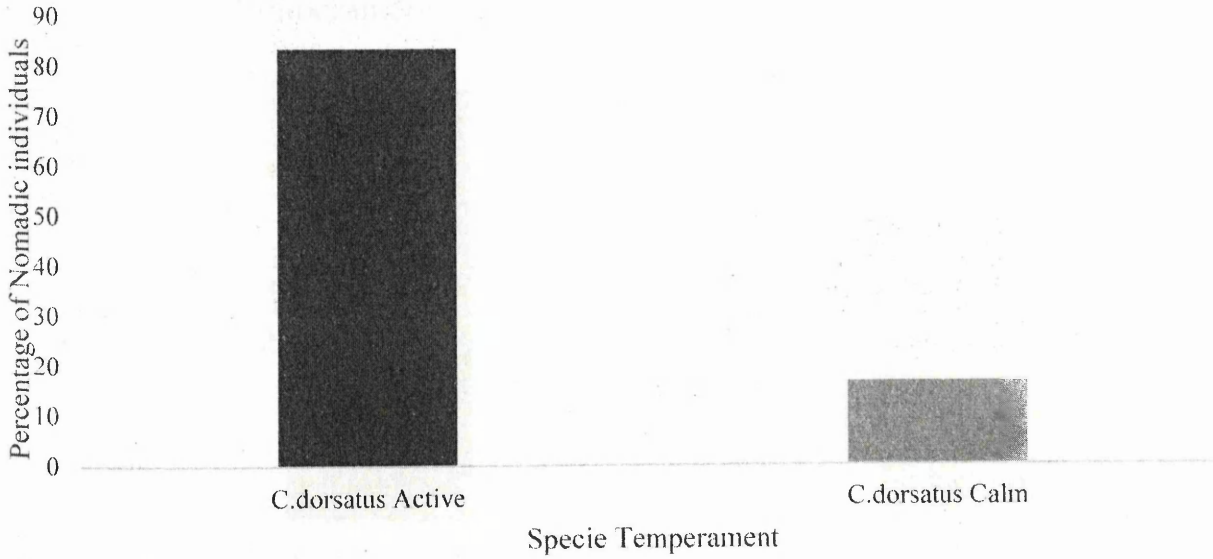
Temperament of Nomadic *P. giornae* Individuals



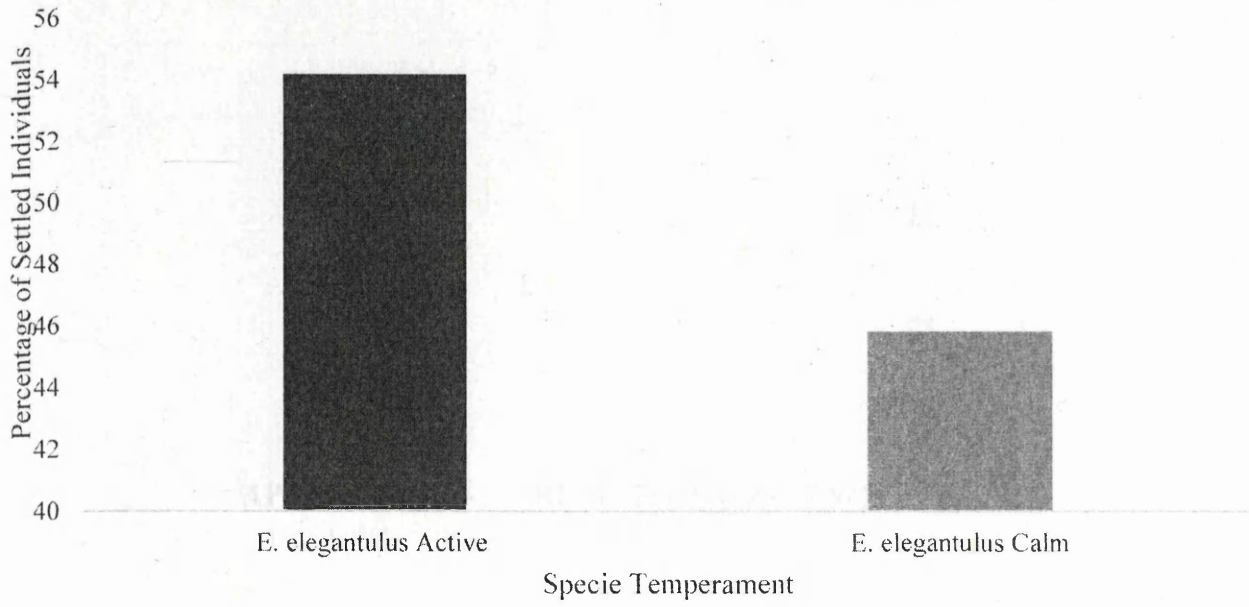
Temperament of Settled *C.dorstus* Individuals



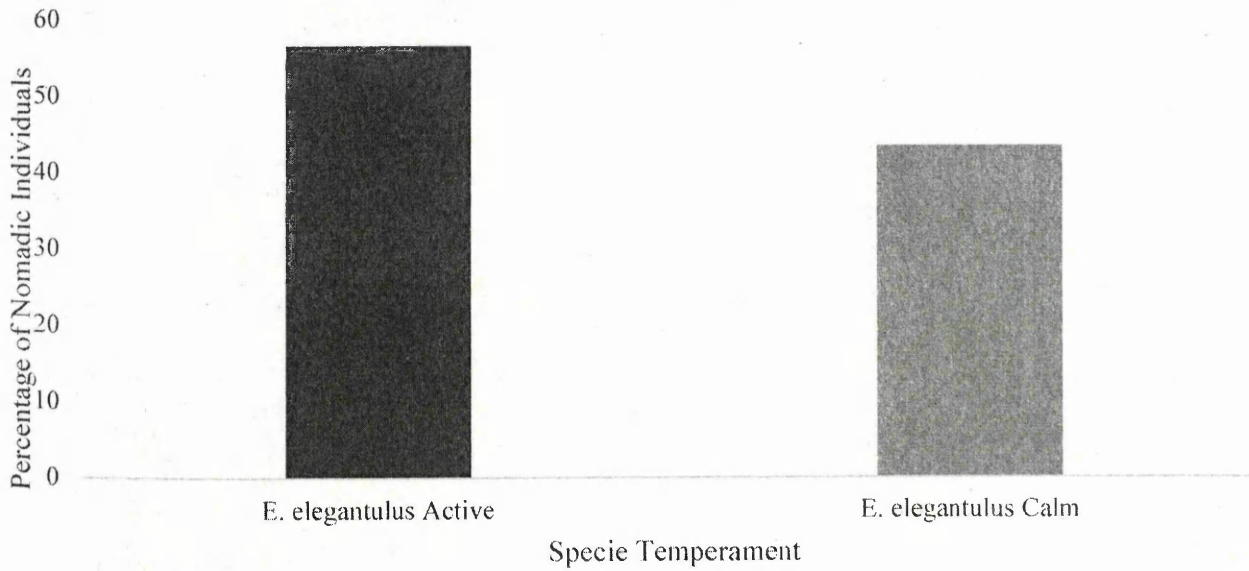
Temperament of Nomadic *C.dorastus* Individuals



Temperament of Settled *E. elegantulus* Individuals



Temperament of Nomadic *E. elegantulus* Individuals



Resight success of all marked Individuals

E. elegantulus females re sighted at least once

Unique colour code	Re-sighting Frequency	Temperament
1. GGGB	3	n/a
2. YWWW	3	n/a
3. WYWY	2	n/a
4. GGGY	2	0
5. GGY Y	2	1
6. YYGY	2	1
7. WRRR	1	0
8. WRWW	2	1
9. RRYG	2	1
10. GGYR	2	1
11. YGRY	1	1
12. WWGR	3	0
13. WGRW	2	1
14. GWRW	2	1
15. WRGY	1	1

E. elegantulus females re sighted at least 4 times

Unique colour code	Re-sighting Frequency	Temperament
1. WWWW	6	n/a
2. RRGG	6	n/a
3. RRGR	5	n/a
4. YYWY	4	0
5. GYYY	6	0
6. RRRW	6	0
7. WWWR	5	1
8. RRWR	6	0
9. RRGY	4	0
10. RGYR	4	1
11. RGGY	4	0
12. RWWG	6	1
13. RWGW	5	0
14. RWGG	6	0

Resighted Female *E. elegantulus* at least 7 times

Unique Colour Code	Re-sighting Frequency	Temperament
1. YYYY	7	n/a

2. RRRR	11	n/a
3. GRRR	8	n/a
4. GGRR	8	n/a
5. GGGR	7	n/a
6. GRGR	8	n/a
7. GRRG	12	n/a
8. YYYW	11	n/a
9. GYYG	10	1
10. YYYG	7	1
11. WWRR	7	1
12. RWRR	8	1
13. WWRW	11	0
14. WRRW	7	1
15. RWWR	11	1
16. GYRG	8	0
17. RYYG	10	0
18. GRYY	7	0
19. WRGG	7	1
20. GRWG	14	0
21. GWRG	7	1
22. GGRY	8	1

Resighted Male *E. elegantulus* at least once

Unique colour code	Resight Frequency	Temperament
RGGR	2	n/a
WWYY	2	n/a
YWYW	3	0
GGYG	1	1
YYGR	1	0
RYGR	1	0
GYYR	1	0
RYGG	2	1
GYRR	3	0
YGRR	3	0
RGWW	2	0
GRWW	3	1
GWWR	3	0
RRWG	2	1
RRGW	3	1
WGRR	1	1
RWGR	1	0
RWRG	3	1
RGRW	2	1

WRGR	1	1
GRWR	2	1
GGWR	1	1

E. elegantulus males re sighted at least 4 times

Unique colour code	Re-sight Frequency	Temperament
YWWY	4	n/a
RRWW	5	0
YRRG	5	0
YRGG	6	1
WGWR	5	1
GWRR	6	1
GRRW	6	0
WRRG	4	1
RGWR	6	1

Resighted Male *E. elegantulus* at least 7 times

Unique colour code	Re-sight Frequency	Temperament
YGGY	7	0
WWRG	8	1
WWBB	8	1
YRGG	6	1

Female *P. giornae* sighted at least once

Unique colour code	Resight Frequency	Temperament
WWWW	1	1
YYYY	1	0
WRRR	2	1
RRWR	3	1
RYRR	3	1
RRYR	3	1
YYYG	3	1
YYYW	2	1
YYWY	2	1
RGGG	3	1

GGRG	3	0
YGGG	2	0
GYGG	1	1
GGGW	3	1
WGGW	1	0
RWRW	1	1
YGGY	1	1
GYGY	1	1
GRGR	2	1
YRRY	3	0
RYYR	2	1
RYRY	2	0
YWWY	2	1
WRRY	2	1
RRWY	1	0
YWRR	2	1
RWRY	1	1
YRRG	2	0
GRRY	1	0
RRGY	2	1
RRYG	1	1
GRYR	1	1
RYRG	2	0
GRRW	2	1

. Female *P. giornaе* sighted at least 4 times

Unique colour code	Number of times sighted	Temperament
YYGY	6	1
YYRY	5	0
WGGG	4	0
WRWR	5	1
RGGR	5	1
RRGG	5	1
WWYY	4	1
YWYW	6	1
YRRW	4	0

Female *P. giornaе* sighted at least 7 times

Unique colour code	Resight Frequency	Temperament
RRRR	8	0
RRRY	8	1

GGWW	8	1
WWRR	7	1
YGYG	10	0

Male *P. giornae* sighted at least once

Unique colour code	Resight Frequency	Temperament
RRRW	2	1
RWRR	2	1
RRGR	1	0
GGGR	3	1
GRGG	3	0
GGYG	2	1
GGWG	1	1
GGYY	1	1
GRRG	1	0
GGRR	1	1
RRYY	2	1
WYYW	3	1
YYWW	1	1
WRYR	3	1
RYGR	2	1
RGYR	2	1
YRGR	2	1

Male *P. giornae* sighted at least 4 times

Unique colour code	Resight Frequency	Temperament
RRRG	4	0
GWGW	5	0
WYRR	6	1

Female *C. dorsatus* sighted at least once

Unique colour code	Resight Frequency	Temperament
RRRW	3	1
WRWW	1	1
YGYG	3	1
WRYR	1	1
YWWR	3	1

Female *C. dorsatus* sighted at least 4 times

Unique colour code	Resight Frequency	Temperament
RYRR	4	0
GGGW	6	1
GGWG	6	1
YRWR	4	0
YRWY	4	1

Female *C. dorsatus* sighted at least 7 times

Unique colour code	Resight Frequency	Temperament
WWWW	10	1
YYYY	8	0
WRRR	10	1
RRWR	10	0
RRYR	8	1
WWWY	7	1
WYWW	10	1
YYR	8	1
RYYY	11	1
GWGG	8	0
YYYW	13	1
WYYW	11	1
YRRY	7	1
RYYR	11	1
RYRY	11	1
YRYR	11	1
RGGG	10	1
RRYW	9	1
RYYW	10	1
WYYR	12	1
YYWR	11	1
RWYY	7	1
WYRY	8	1

Table 26. Male *C. dorsatus* sighted at least once

Unique colour code	Resight Frequency	Temperament
GGGG	3	0
WWYW	2	1
YYRY	1	1

YRY Y	2	1
GRGG	1	1
YRRW	3	0
GYGG	2	1
YGGY	2	1
GYYG	1	1
GGYY	1	1
YYGG	2	1
GYGY	2	1
YWRR	2	1
GGRR	1	1
RRGG	1	1
RYYR	2	1
GRGR	3	1
RYWY	3	1

Male *C. dorsatus* sighted at least 4 times

Unique colour code	Resight Frequency	Temperament
RWRR	5	0
RRRY	4	1
WWRW	6	1
WGGG	6	1
YWYY	6	1
GGRG	6	1
WYWY	4	0
WRRW	4	1
RWRW	6	1
WWRR	6	1
RRWW	5	1
RWYR	6	1
RYWR	5	1
GGGY	4	1
WYRR	6	1
GRRG	5	1
RWRY	4	1
YYRW	4	1
RYBY	4	0
YRYW	4	1
WYRW	4	1
WWRY	5	1
WWYR	5	0

GWVG	4	1
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Male *C. dorsatus* sighted at least 7 times

Unique colour code	Resight Frequency	Temperament
RRRR	7	0
YRRR	7	1
WWWR	13	1
RWWW	10	1
YWWW	8	0
WYYY	7	1
YYWY	9	1
WWYY	9	1
YYWW	7	1
YWYW	7	0
RWWR	7	0
RRYY	8	1
GGGR	10	1
WRRY	10	1
RGGR	7	1
YWRY	7	1
RGRG	9	1
WGGW	9	1
WRYY	8	1
YWYR	11	0
RWWY	8	1

APPENDIX V – INDIVIDUALS THAT SETTLED

IDcode	DispDist	DispXmid	DispScal	Dist travel	SettTime	Temp	Resight
PezotettixGiornae.F.pRRRR	79.66742	3.048897	0.4669916	8.925661	5	0	8
PezotettixGiornae.F.pRRRY	148.17413	5.364265	0.4669916	12.17268	7	1	8
PezotettixGiornae.F.RGGR	39.49866	2.194248	0.3744036	6.284796	4	1	5
PezotettixGiornae.F.RRGG	35.22254	2.194248	0.3744036	5.934858	4	1	5
PezotettixGiornae.F.WGGG	18.62552	2.194248	0.3744036	4.315729	4	0	4
PezotettixGiornae.F.WRWR	71.05475	2.966405	0.4669916	8.429398	5	0	4
PezotettixGiornae.F.WWRR	122.86833	2.919219	0.4669916	11.084599	5	1	7
PezotettixGiornae.F.YGYG	174.80122	2.19925	0.4669916	13.221241	4	0	10
PezotettixGiornae.F.YRRW	177.51991	3.313214	0.4669916	13.32366	5	0	4
PezotettixGiornae.M.GWGW	181.17925	3.319205	0.4669916	13.460284	5	0	5
PezotettixGiornae.M.GYVG	34.35226	2.194248	0.3744036	5.86108	4	1	4
PezotettixGiornae.M.RRRG	119.0188	3.160869	0.4669916	10.909574	5	0	4
PezotettixGiornae.M.RYRW	115.15557	3.157506	0.4669916	10.731056	5	1	5

4.769230769



IDcode	DispDist	DispXmid	DispScal	Dist travel	SettTime	Temp	Resight
EuchorthippusElegantulus.F.GGGR	65.35051	2.938508	0.4669916	8.083966		5 n/a	7
EuchorthippusElegantulus.F.GGRR	190.23198	7.603366	0.4669916	13.792461		10 n/a	8
EuchorthippusElegantulus.F.GRRR	47.54355	2.194248	0.3744036	6.895183		4 n/a	8
EuchorthippusElegantulus.F.GRRG	12.26883	2.194248	0.3744036	3.502689		4 n/a	12
EuchorthippusElegantulus.F.GWRG	107.87451	3.132106	0.4669916	10.386265		5	7
EuchorthippusElegantulus.F.RGGW	100.99057	2.970247	0.4669916	10.049406		5	5
EuchorthippusElegantulus.F.RGGY	261.08971	2.213917	0.2069569	16.158271		3	4
SEuchorthippusElegantulus.F.RGYR	23.01731	2.194248	0.3744036	4.797636		4	4
EuchorthippusElegantulus.F.RRGR	55.71929	2.902959	0.4669916	7.464535		5 n/a	5
EuchorthippusElegantulus.F.RRGY	126.93506	2.354359	0.4669916	11.266546		4	4
EuchorthippusElegantulus.F.RRRR	88.23847	2.824616	0.4669916	9.393533		5 n/a	11
EuchorthippusElegantulus.F.RRRW	111.55199	2.194248	0.3744036	10.561818		4	6
EuchorthippusElegantulus.F.RRW	13.00309	2.194248	0.3744036	3.605979		4	6
EuchorthippusElegantulus.F.RWG	154.01213	3.26129	0.4669916	12.410162		5	6
66 EuchorthippusElegantulus.F.RWGW	38.01531	2.194248	0.3744036	6.165656		4	5
EuchorthippusElegantulus.F.RWRR	39.6733	2.194248	0.3744036	6.298675		4	8
EuchorthippusElegantulus.F.RWWG	17.22885	2.194248	0.3744036	4.150764		4	6
EuchorthippusElegantulus.F.RWWR	16.88158	2.194248	0.3744036	4.10872		4	11
EuchorthippusElegantulus.F.RYVG	179.82275	2.213917	0.2858686	13.4098		4	10
EuchorthippusElegantulus.F.WGGR	35.95109	2.194248	0.3744036	5.995923		4	6
EuchorthippusElegantulus.F.WRGG	48.84475	2.87017	0.4669916	6.988902		5	7
EuchorthippusElegantulus.F.WRRW	65.67192	2.194248	0.3744036	8.103821		4	7
EuchorthippusElegantulus.F.WWRR	106.30676	2.397158	0.4669916	10.310517		4	7
EuchorthippusElegantulus.F.WWRW	59.7924	3.893751	0.4669916	7.732555		6	11
EuchorthippusElegantulus.F.WWWW	35.67534	2.194248	0.3744036	5.972884		4 n/a	6
EuchorthippusElegantulus.F.YYVW	15.4371	2.194248	0.3744036	3.929007		4 n/a	11
EuchorthippusElegantulus.F.YYVY	181.40359	3.321492	0.4669916	13.468615		5 n/a	7
EuchorthippusElegantulus.M.GRRW	55.95734	2.924681	0.4669916	7.480464		5	6
EuchorthippusElegantulus.M.WGWR	87.1491	2.194248	0.3744036	9.335368		4	5
EuchorthippusElegantulus.M.WRRG	108.7017	2.194248	0.3744036	10.426011		4	4
EuchorthippusElegantulus.M.WWRG	158.81519	2.194248	0.3744036	12.60219		4	8
EuchorthippusElegantulus.M.YRGY	27.27749	2.194248	0.3744036	5.222786		4	4
EuchorthippusElegantulus.M.YRRG	24.27353	2.194248	0.3744036	4.926818		4	5
EuchorthippusElegantulus.M.YVWVY	151.0104	2.213917	0.3323742	12.288629		4 n/a	4

IDcode	DispDist	DispXmid	DispScaI	Dist travel	SettTime	Temp	Resight	
1	ChorthippusDorsatus.F.GGGW	51.55923	2.875803	0.4669916	7.180476	5	1	6
2	ChorthippusDorsatus.F.RRW	142.06092	3.078475	0.4669916	11.918931	5	1	10
3	ChorthippusDorsatus.F.RRYR	74.56166	3.001607	0.4669916	8.634909	5	1	8
4	ChorthippusDorsatus.F.RRYW	63.83574	2.194248	0.3744036	7.989727	4	1	9
5	ChorthippusDorsatus.F.RRYR	209.73351	2.213917	0.2501434	14.482179	3	1	11
6	ChorthippusDorsatus.F.RYYR	226.72089	3.239661	0.4669916	15.057254	5	1	10
7	ChorthippusDorsatus.F.RYYW	115.05344	2.846947	0.4669916	10.726296	5	1	10
8	ChorthippusDorsatus.F.RYYR	79.09871	3.055181	0.4669916	8.893746	5	1	11
9	ChorthippusDorsatus.F.WRRR	67.76425	2.893808	0.4669916	8.231904	5	1	10
10	ChorthippusDorsatus.F.WWWW	86.71577	3.27253	0.4669916	9.31213	5	1	10
11	ChorthippusDorsatus.F.WWWY	113.86979	3.153922	0.4669916	10.670979	5	1	7
12	ChorthippusDorsatus.F.WYWW	46.88892	2.194248	0.3744036	6.847548	4	1	10
13	ChorthippusDorsatus.F.WYYR	95.35377	2.816981	0.4669916	9.764925	5	1	12
14	ChorthippusDorsatus.F.WYVW	88.8343	2.933743	0.4669916	9.425195	5	1	11
15	ChorthippusDorsatus.F.YRRY	296.29465	2.929	0.4669916	17.213211	5	1	7
16	ChorthippusDorsatus.F.YRYR	59.96045	2.194248	0.3744036	7.743413	4	1	11
17	ChorthippusDorsatus.F.YVWR	140.74335	5.972582	0.4669916	11.86353	8	1	11
18	ChorthippusDorsatus.F.YVYR	118.38392	3.175908	0.4669916	10.880438	5	1	8
19	ChorthippusDorsatus.F.YVYV	85.71292	3.037079	0.4669916	9.258127	5	1	13
20	ChorthippusDorsatus.F.YVYV	119.53816	3.149339	0.4669916	10.933351	5	0	8
21	ChorthippusDorsatus.M.GGRG	75.6007	3.00821	0.4669916	8.694866	5	1	6
22	ChorthippusDorsatus.M.GRRG	78.28834	3.060401	0.4669916	8.84807	5	1	5
23	ChorthippusDorsatus.M.RGGR	211.49938	3.336236	0.4669916	14.543018	5	1	7
24	ChorthippusDorsatus.M.RRRR	84.36694	3.076004	0.4669916	9.185148	5	1	7
25	ChorthippusDorsatus.M.RRRY	62.01579	2.194248	0.3744036	7.87501	4	1	4
26	ChorthippusDorsatus.M.RRW	69.92543	2.194248	0.3744036	8.362143	4	1	5
27	ChorthippusDorsatus.M.RRY	88.08434	3.182253	0.4669916	9.385326	5	1	8
28	ChorthippusDorsatus.M.RWR	119.80466	3.166827	0.4669916	10.945531	5	0	5
29	ChorthippusDorsatus.M.RWR	199.65762	3.228277	0.4669916	14.130026	5	1	6
30	ChorthippusDorsatus.M.RWRY	348.16521	2.213917	0.161286	18.659186	3	1	4
31	ChorthippusDorsatus.M.RYBY	267.21113	3.464959	0.4669916	16.346594	5	0	4
32	ChorthippusDorsatus.M.RYWR	138.59035	3.222702	0.4669916	11.77244	5	1	5
33	ChorthippusDorsatus.M.WGGW	160.82252	3.094815	0.4669916	12.681582	5	1	9
34	ChorthippusDorsatus.M.WRRW	108.7181	3.134389	0.4669916	10.426797	5	1	4
35	ChorthippusDorsatus.M.WRRY	95.15544	3.08756	0.4669916	9.754765	5	1	10
36	ChorthippusDorsatus.M.WVRR	150.75311	3.253571	0.4669916	12.278156	5	1	6

37	ChorthippusDorsatus.M.WWRW	192.56201	2.213917	0.2693425	13.876671	4	1	6
38	ChorthippusDorsatus.M.WWWWR	89.66553	2.194248	0.3744036	9.469188	4	1	13
39	ChorthippusDorsatus.M.WYRR	82.73207	3.291855	0.4669916	9.095717	5	1	6
40	ChorthippusDorsatus.M.WVRRW	115.79255	3.206795	0.4669916	10.760695	5	1	4
41	ChorthippusDorsatus.M.WVWY	152.18152	3.258886	0.4669916	12.336187	5	0	4
42	ChorthippusDorsatus.M.WVYY	230.94996	3.410918	0.4669916	15.197038	5	1	7
43	ChorthippusDorsatus.M.YRRR	130.54938	2.810571	0.4669916	11.425821	5	1	7
44	ChorthippusDorsatus.M.YRVW	73.04555	2.994575	0.4669916	8.546669	5	1	4
45	ChorthippusDorsatus.M.YVRY	94.38748	2.899783	0.4669916	9.715322	5	1	7
46	ChorthippusDorsatus.M.YVWVW	104.17219	2.194248	0.3744036	10.206478	4	1	8
47	ChorthippusDorsatus.M.YVYVW	130.03044	2.213917	0.378096	11.403089	4	1	8
48	ChorthippusDorsatus.M.YVYY	122.8947	2.213917	0.3970535	11.085788	4	1	6
49	ChorthippusDorsatus.M.YVRW	109.65075	3.586638	0.4669916	10.471426	5	1	4
50	ChorthippusDorsatus.M.YVWW	53.85973	2.194248	0.3744036	7.338919	4	1	7
51	ChorthippusDorsatus.M.YVWY	41.7207	2.194248	0.3744036	6.459156	4	1	9

APPENDIX VI - INDIVIDUALS YET TO SETTLE

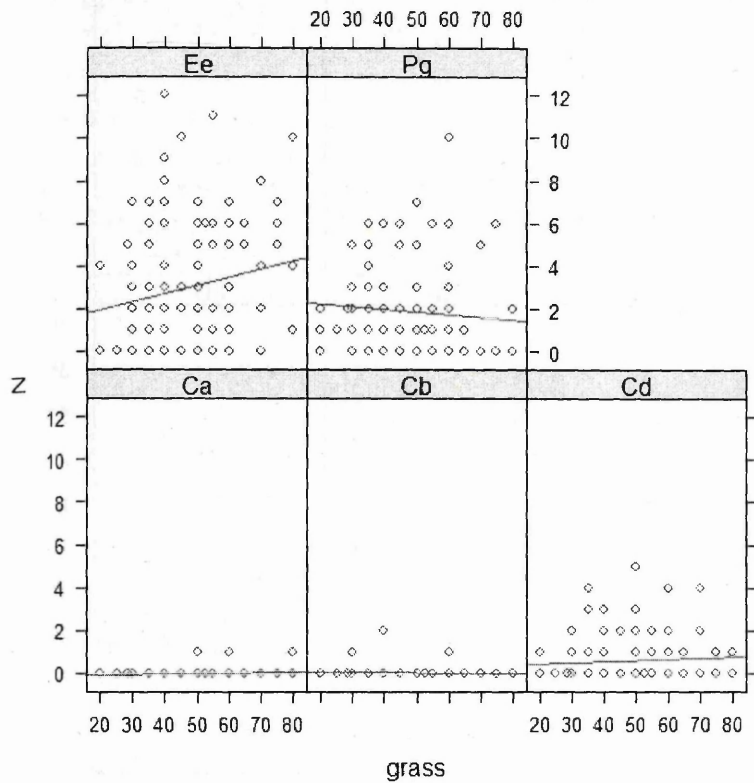
Species	NomD	NomExp	Expected dist 14day	Expected dis 21days	Temperament	Resight Frequency
ChorthippusDorsatus.F.GGWW	40.054005	0.5495453	13.069158	14.60941	1	6
ChorthippusDorsatus.F.GWGG	4.051204	1	7.53106	9.223627	0	8
ChorthippusDorsatus.F.RGGG	12.89967	1	13.438578	16.45883	1	10
ChorthippusDorsatus.F.RWYY	1	1.6648499	8.996334	12.608061	1	7
ChorthippusDorsatus.F.WWRY	1	1.5897403	8.147474	11.24586	1	8
ChorthippusDorsatus.F.YRWR	5.026464	1	8.388713	10.274033	0	4
ChorthippusDorsatus.F.YRWY	9.032488	1	11.245214	13.772518	1	4
ChorthippusDorsatus.M.GGGR	40.054005	0.7386591	16.773431	19.48308	1	10
ChorthippusDorsatus.M.GWWG	1	1.6115617	8.385482	11.625697	1	4
ChorthippusDorsatus.M.RGRG	5.925025	1	9.107709	11.154619	1	9
ChorthippusDorsatus.M.RWWR	8.508132	1	10.913929	13.366779	0	7
ChorthippusDorsatus.M.RWWW	2.98353	1	6.462926	7.915436	1	10
ChorthippusDorsatus.M.RWWY	1	1.5674283	7.911098	10.87031	1	8
ChorthippusDorsatus.M.RWYR	9.061883	1	11.263497	13.79491	1	6
ChorthippusDorsatus.M.WGGG	8.323166	1	10.794643	13.220684	1	6
ChorthippusDorsatus.M.WRYY	1	1.6693265	9.049633	12.694275	1	8
ChorthippusDorsatus.M.WWRY	8.183493	1	10.703686	13.109285	1	5
ChorthippusDorsatus.M.WWYR	5.910416	1	9.096474	11.140859	0	5
ChorthippusDorsatus.M.WWYY	6.85695	1	9.797821	11.999831	1	9
ChorthippusDorsatus.M.YWYR	5.876584	1	9.070401	11.108927	0	11

Species	NomD	NomExp	Expected dist 14days	Expected dis 21days	Temperame	Resight Frequency
PezotettixGiornae.F.GGWW	3.555142	1	7.054926	8.640485	1	8
PezotettixGiornae.F.WWYY	9.093897	1	11.283376	13.819256	1	4
PezotettixGiornae.F.YWYW	2.42199	1	5.823046	7.131746	1	6
PezotettixGiornae.F.YYGY	1	1.6604501	8.944256	12.5239	1	6
PezotettixGiornae.F.YYRY	1	1.5622364	7.857085	10.784737	0	5
PezotettixGiornae.M.RGRY	1	1.6180901	8.45803	11.741808	1	4
PezotettixGiornae.M.WYRR	8.400429	1	10.84463	13.281905	1	6

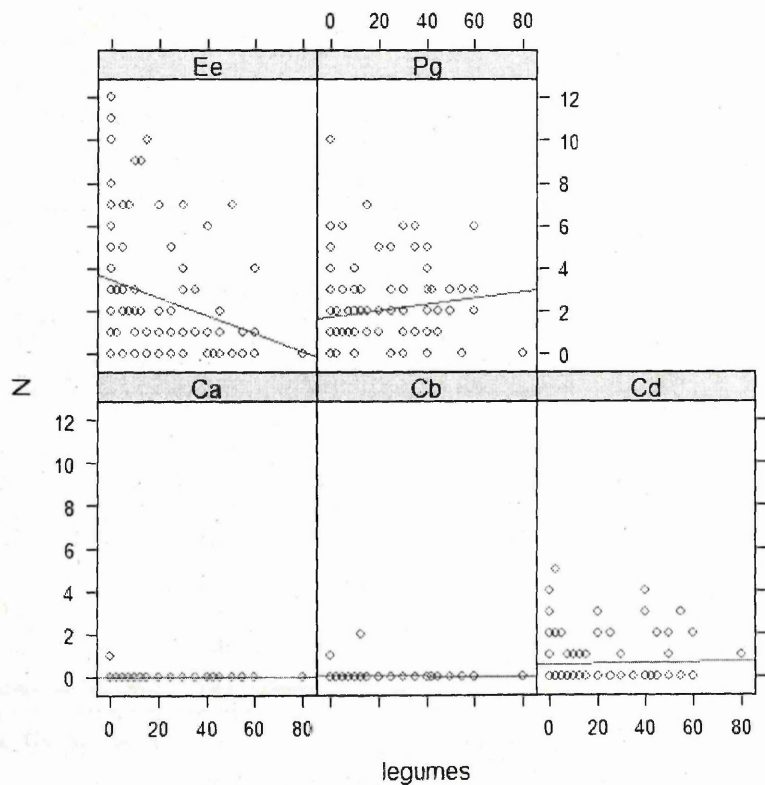
Species	NomD	NomExp	Expected dist 14days	Expected dis 21days	Temperament	Resight Frequency
EuchorhippusElegantulus.F.GGRY	1.845614	1	5.083168	6.225584	1	8
EuchorhippusElegantulus.F.GRRR	6.268887	1	9.368267	11.473737 n/a	0	8
EuchorhippusElegantulus.F.GRWG	2.954619	1	6.431537	7.876992	0	14
EuchorhippusElegantulus.F.GRYY	3.122722	1	6.611967	8.097973	0	7
EuchorhippusElegantulus.F.GYRG	2.998883	1	6.479534	7.935776	0	8
EuchorhippusElegantulus.F.GYYG	1	1.5271685	7.501797	10.224117	1	10
EuchorhippusElegantulus.F.GYYY	1.582539	1	4.706969	5.764836	0	6
EuchorhippusElegantulus.F.RRGG	1.867308	1	5.112955	6.262065 n/a	0	6
EuchorhippusElegantulus.F.WWWR	5.66368	1	8.904578	10.905837	1	5
EuchorhippusElegantulus.F.YYWY	2.936239	1	6.411501	7.852453	0	4
EuchorhippusElegantulus.F.YYGG	6.325867	1	9.410746	11.525762	1	7
EuchorhippusElegantulus.M.GWRR	5.665232	1	8.905798	10.907331	1	6
EuchorhippusElegantulus.M.RGWR	3.781804	1	7.276349	8.911671	1	6
EuchorhippusElegantulus.M.RRWW	1	1.6478846	8.797177	12.286619	0	5
EuchorhippusElegantulus.M.WWBB	6.933751	1	9.852539	12.066846	1	8
EuchorhippusElegantulus.M.YGGR	2.543441	1	5.967258	7.308369	0	4
EuchorhippusElegantulus.M.YGGY	11.528337	1	12.704201	15.559405	0	7
EuchorhippusElegantulus.M.YRGG	2.165202	1	5.505709	6.743089	1	6

APENDIXVII- INTERACTION OF RESIGHT FREQUENCY WITH RESPONSE TO HANDLING, SPECIES AND SEX

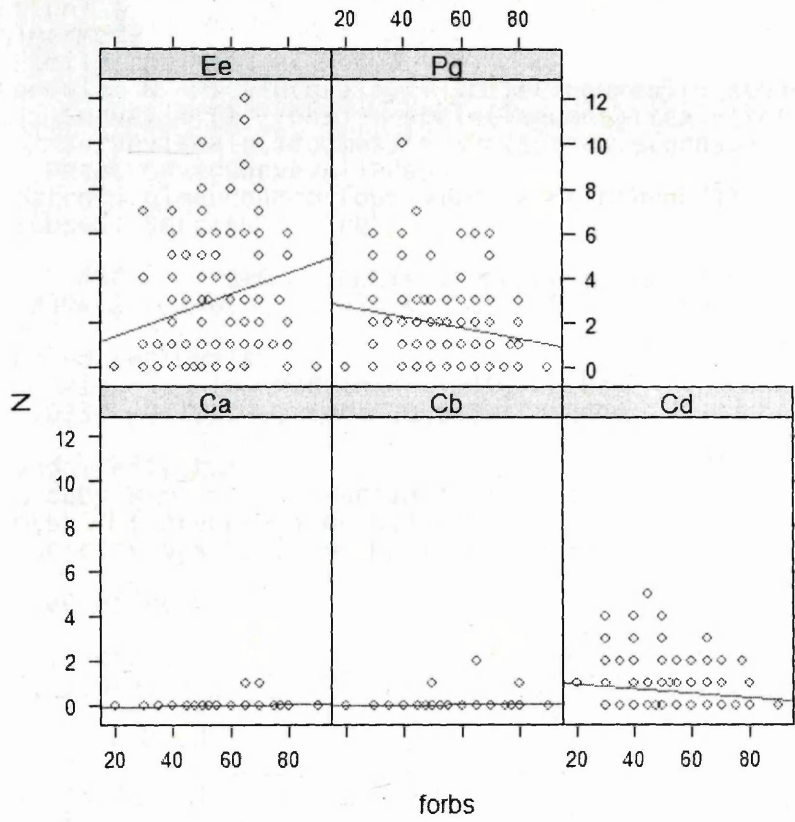
GRASSHOPPER RELATIONSHIP WITH GRASS COVER



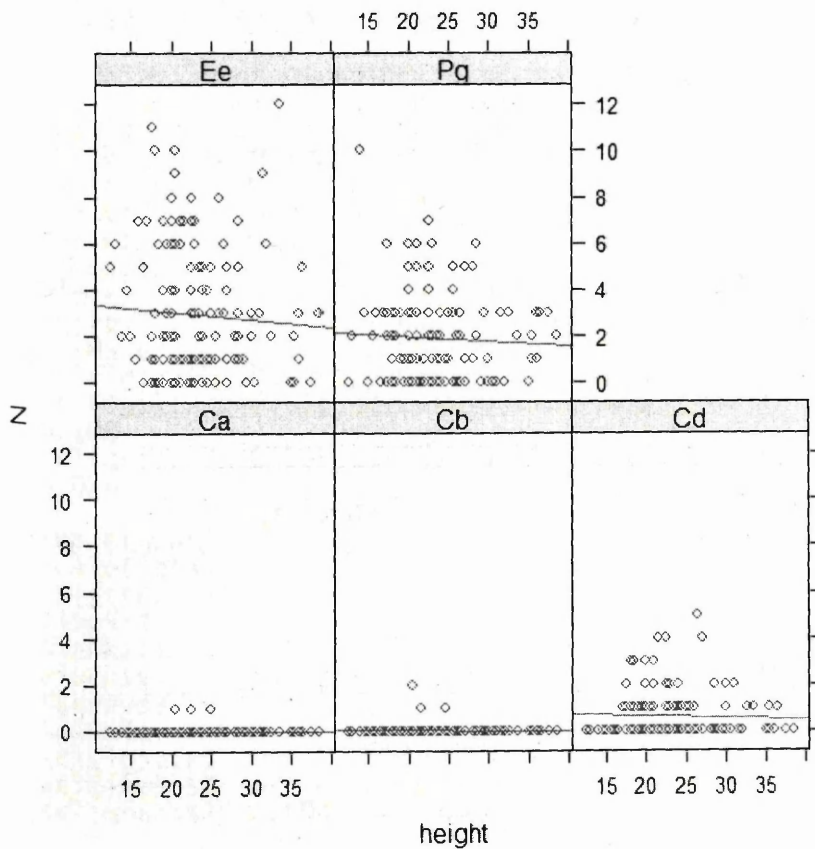
GRASSHOPPER RELATIONSHIP WITH LEGUME COVER



GRASSHOPPER RELATIONSHIP WITH FORB COVER



GRASSHOPPER RELATIONSHIP WITH VEGETATION HEIGHT



```
> summary(glmer1pg)
Generalized linear mixed model fit by maximum likelihood (Laplace Approxim
ation) [
glmerMod]
Family: poisson (log)
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +
Survey + (1 | obs) + scale(legumes):scale(totPreds) + Sex +
Survey:scale(legumes) + Survey:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
subset: Species == "Pg"
```

AIC	BIC	logLik	deviance	df.resid
1304.8	1361.4	-639.4	1278.8	559

```
scaled residuals:
Min      1Q  Median      3Q      Max
-1.0230 -0.7010 -0.5034  0.6429  3.1976
```

```
Random effects:
Groups Name      Variance Std.Dev.
obs (Intercept) 0.3014  0.549
Number of obs: 572, groups: obs, 572
```

```
Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)   -0.16870    0.14014  -1.204   0.2287
scale(grass)   -0.01928    0.08290  -0.233   0.8161
scale(legumes)  0.11444    0.07724   1.482   0.1385
scale(totPreds) -0.05822    0.06105  -0.954   0.3403
BlockII        0.01632    0.15786   0.103   0.9176
BlockIII       0.11170    0.15599   0.716   0.4740
BlockIV       -0.08949    0.17321  -0.517   0.6054
Surveys2      -0.66328    0.11881  -5.583 2.37e-08 ***
SexMale       -0.11267    0.11092  -1.016   0.3098
scale(legumes):scale(totPreds) 0.05585    0.04744   1.177   0.2391
scale(legumes):Surveys2      0.15781    0.12337   1.279   0.2008
scale(grass):Surveys2       0.30149    0.13077   2.305   0.0211 *
```

```
---
signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
Correlation of Fixed Effects:
(Intr) scl(g) scl(l) scl(P) BlckII BlcIII BlckIV srvs2 SexMal
```

```
s():(P
scale(grss)  0.122
scale(lgms) -0.072  0.405
scl(ttPrds) -0.021 -0.056 -0.013
BlockII     -0.551 -0.024 -0.028 -0.096
BlockIII    -0.585 -0.055  0.049 -0.083  0.502
BlockIV     -0.564 -0.203  0.114  0.062  0.443  0.495
Surveys2    -0.293 -0.024  0.054  0.194 -0.040 -0.034  0.000
SexMale     -0.370  0.006 -0.008  0.000 -0.004 -0.013 -0.026 -0.001
scl(lg):(P)  0.008  0.021 -0.188 -0.313 -0.061  0.015 -0.065 -0.091 -0.002
scl(lgm):S2  0.036 -0.264 -0.595 -0.115 -0.011  0.018 -0.011 -0.180  0.001
0.100
scl(grs):S2 -0.009 -0.595 -0.273 -0.090 -0.011  0.003 -0.023 -0.125  0.006
0.026
scl(l):S2
scale(grss)
scale(lgms)
scl(ttPrds)
BlockII
BlockIII
BlockIV
Surveys2
SexMale
scl(lg):(P)
scl(lgm):S2
scl(grs):S2  0.494
```

```
> summary(glmer2pg)
Generalized linear mixed model fit by maximum likelihood (Laplace Approxim
ation) [
glmerMod]
Family: poisson ( log )
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +
Survey + (1 | obs) + scale(legumes):scale(totPreds) + Sex +
Survey:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
Subset: Species == "Pg"
```

AIC	BIC	logLik	deviance	df.resid
1304.5	1356.6	-640.2	1280.5	560

```
Scaled residuals:
Min      1Q  Median      3Q      Max
-1.0755 -0.6835 -0.5302  0.6212  2.9651
```

```
Random effects:
Groups Name          Variance Std.Dev.
obs      (Intercept)  0.3085  0.5555
Number of obs: 572, groups: obs, 572
```

```
Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  -0.178670   0.140255  -1.274  0.20270
scale(grass)   0.008484   0.080459   0.105  0.91602
scale(legumes) 0.172709   0.062275   2.773  0.00555 **
scale(totPreds) -0.049368   0.060585  -0.815  0.41516
BlockII       0.018848   0.158161   0.119  0.90514
BlockIII     0.109238   0.156406   0.698  0.48491
BlockIV     -0.086839   0.173446  -0.501  0.61661
Surveys2    -0.638273   0.116882  -5.461 4.74e-08 ***
SexMale     -0.112765   0.111200  -1.014  0.31055
scale(legumes):scale(totPreds) 0.049799   0.047427   1.050  0.29371
scale(grass):Surveys2 0.220514   0.114146   1.932  0.05338 .
```

```
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
Correlation of Fixed Effects:
(Intr) scl(g) scl(l) scl(P) BlckII BlcIII BlckIV Srvys2 SexMal
s():P
scale(grss)  0.129
scale(lgms) -0.081  0.328
scl(ttPrds) -0.019 -0.089 -0.098
BlockII     -0.552 -0.029 -0.043 -0.093
BlockIII   -0.585 -0.053  0.074 -0.085  0.503
BlockIV    -0.563 -0.213  0.135  0.060  0.444  0.495
Surveys2   -0.290 -0.057 -0.023  0.179 -0.042 -0.033 -0.004
SexMale    -0.370  0.006 -0.010  0.001 -0.005 -0.013 -0.026 -0.001
scl(lg):(P) 0.001  0.048 -0.164 -0.297 -0.056  0.015 -0.063 -0.079 -0.002
scl(grs):s2 -0.034 -0.561  0.005 -0.040 -0.006 -0.004 -0.016 -0.042  0.006
-0.021
```

```
> summary(glmer3pg)
Generalized linear mixed model fit by maximum likelihood (Laplace Approxim
ation) [
glmerMod]
Family: poisson ( log )
```

```

Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +
Survey + (1 | obs) + scale(grass):scale(totPreds) + Sex +
Survey:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
Subset: Species == "Pg"

```

AIC	BIC	logLik	deviance	df.resid
1305.1	1357.3	-640.6	1281.1	560

scaled residuals:

Min	1Q	Median	3Q	Max
-1.0715	-0.6875	-0.5222	0.6149	3.0469

Random effects:

Groups Name	Variance	Std.Dev.
obs (Intercept)	0.3091	0.5559

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.180717	0.140540	-1.286	0.19849
scale(grass)	0.007658	0.080500	0.095	0.92421
scale(legumes)	0.178678	0.061628	2.899	0.00374 **
scale(totPreds)	-0.028481	0.058076	-0.490	0.62385
BlockII	0.023490	0.158053	0.149	0.88185
BlockIII	0.110075	0.156511	0.703	0.48187
BlockIV	-0.079921	0.173384	-0.461	0.64484
Surveys2	-0.624398	0.116749	-5.348	8.88e-08 ***
SexMale	-0.112921	0.111207	-1.015	0.30991
scale(grass):scale(totPreds)	-0.037761	0.056662	-0.666	0.50514
scale(grass):Surveys2	0.217597	0.114495	1.900	0.05737 .

signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	scl(g)	scl(l)	scl(p)	BlckII	BlckIII	BlckIV	Srvys2	SexMal
s():(P									
scale(grss)	0.130								
scale(lgms)	-0.082	0.331							
scl(ttPrds)	-0.018	-0.058	-0.135						
BlockII	-0.555	-0.030	-0.048	-0.118					
BlockIII	-0.585	-0.054	0.074	-0.089	0.504				
BlockIV	-0.563	-0.214	0.130	0.040	0.444	0.495			
Surveys2	-0.291	-0.049	-0.043	0.167	-0.045	-0.033	-0.011		
SexMale	-0.369	0.006	-0.009	0.000	-0.005	-0.013	-0.026	-0.002	
scl(gr):(P)	-0.001	-0.066	0.101	-0.070	0.046	-0.023	0.044	-0.060	0.005
scl(grs):S2	-0.035	-0.562	0.014	-0.057	-0.003	-0.001	-0.014	-0.048	0.006

0.080

```
> summary(glmer4pg)
```

```

Generalized linear mixed model fit by maximum likelihood (Laplace Approxim
ation) [
glmerMod]
Family: poisson ( log )
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +
Survey + (1 | obs) + Sex + Survey:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
Subset: Species == "Pg"

```

AIC	BIC	logLik	deviance	df.resid
1303.6	1351.4	-640.8	1281.6	561

scaled residuals:

Min	1Q	Median	3Q	Max
-1.0685	-0.6869	-0.5301	0.6400	3.0209

Random effects:

Groups Name	Variance	Std.Dev.
obs (Intercept)	0.3091	0.556

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.181839	0.140573	-1.294	0.19582
scale(grass)	0.003824	0.080452	0.048	0.96209
scale(legumes)	0.182768	0.061258	2.984	0.00285 **
scale(totPreds)	-0.031592	0.057853	-0.546	0.58501
BlockII	0.028439	0.157856	0.180	0.85703
BlockIII	0.107506	0.156522	0.687	0.49218
BlockIV	-0.075079	0.173204	-0.433	0.66467
Surveys2	-0.629310	0.116527	-5.401	6.64e-08 ***
SexMale	-0.112534	0.111200	-1.012	0.31154
scale(grass):Surveys2	0.223794	0.113796	1.967	0.04923 *

signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	scl(g)	scl(l)	scl(p)	BlckII	BlckIII	BlckIV	Srvys2	SexMal
scale(grss)	0.130								
scale(lgms)	-0.082	0.341							
scl(ttPrds)	-0.019	-0.076	-0.127						
BlockII	-0.556	-0.027	-0.052	-0.114					
BlockIII	-0.584	-0.056	0.078	-0.090	0.506				
BlockIV	-0.564	-0.212	0.128	0.044	0.443	0.498			
Surveys2	-0.292	-0.055	-0.038	0.164	-0.041	-0.035	-0.009		
SexMale	-0.369	0.007	-0.010	0.000	-0.005	-0.013	-0.026	-0.001	
scl(grs):s2	-0.035	-0.562	0.005	-0.055	-0.004	0.001	-0.015	-0.044	0.006

> summary(glmer5pg)

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]
 Family: poisson (log)
 Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block + Survey + (1 | obs) + Sex + Survey:scale(grass) + Sex:scale(grass)
 Data: GHVegSurveyAllPreds
 Control: glmerControl(optimizer = c("bobyqa"))
 Subset: Species == "Pg"

AIC	BIC	logLik	deviance	df.resid
1304.6	1356.8	-640.3	1280.6	560

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.0698	-0.6877	-0.5377	0.6152	2.9887

Random effects:

Groups Name	Variance	Std.Dev.
obs (Intercept)	0.304	0.5513

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.17927	0.14029	-1.278	0.20132
scale(grass)	0.05492	0.09625	0.571	0.56829
scale(legumes)	0.18257	0.06113	2.986	0.00282 **

```

scale(totPrds)      -0.03195      0.05776  -0.553  0.58022
BlockII             0.02720      0.15755   0.173  0.86294
BlockIII            0.10642      0.15622   0.681  0.49573
BlockIV            -0.07613      0.17292  -0.440  0.65975
Surveys2           -0.63014      0.11636  -5.416  6.11e-08 ***
SexMale            -0.11312      0.11111  -1.018  0.30864
scale(grass):Surveys2 0.22217      0.11361   1.956  0.05051 .
scale(grass):SexMale -0.10557      0.11082  -0.953  0.34080

```

```

---
signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Correlation of Fixed Effects:

```

(Intr) scl(g) scl(l) scl(P) BlckII BlckIII BlckIV Srvys2 SexMa1
s():s2
scale(grss) 0.102
scale(lgms) -0.083 0.282
scl(ttPrds) -0.018 -0.067 -0.126
BlockII     -0.556 -0.027 -0.052 -0.113
BlockIII    -0.584 -0.051 0.078 -0.090 0.506
BlockIV     -0.564 -0.182 0.128 0.044 0.443 0.497
Surveys2    -0.291 -0.051 -0.038 0.165 -0.041 -0.035 -0.008
SexMale     -0.369 0.020 -0.009 0.000 -0.005 -0.013 -0.026 -0.002
scl(grs):s2 -0.036 -0.476 0.005 -0.055 -0.004 0.001 -0.015 -0.043 0.009
scl(grs):SM -0.003 -0.551 0.006 0.007 0.008 0.008 0.009 0.009 0.007
0.014

```

```
> summary(glmer6pg)
```

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [

glmerMod]

Family: poisson (log)

Formula: N ~ scale(grass) + scale(legumes) + Block + Survey + (1 | obs) + Sex + Survey:scale(grass)

Data: GHVegSurveyAllPreds

Control: glmerControl(optimizer = c("bobyqa"))

Subset: Species == "Pg"

AIC	BIC	logLik	deviance	df.resid
1301.9	1345.3	-640.9	1281.9	562

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.0650	-0.6819	-0.5296	0.6334	3.0270

Random effects:

Groups Name	Variance	Std.Dev.
obs (Intercept)	0.3107	0.5574

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.1840073	0.1406125	-1.309	0.19067
scale(grass)	0.0003282	0.0802591	0.004	0.99674
scale(legumes)	0.1784881	0.0607747	2.937	0.00332 **
BlockII	0.0185786	0.1569440	0.118	0.90577
BlockIII	0.0997462	0.1559951	0.639	0.52255
BlockIV	-0.0708580	0.1731331	-0.409	0.68234
Surveys2	-0.6189363	0.1150045	-5.382	7.37e-08 ***
SexMale	-0.1125359	0.1112570	-1.011	0.31178
scale(grass):Surveys2	0.2204419	0.1136361	1.940	0.05239 .

```

---
signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Correlation of Fixed Effects:

	(Intr)	scl(g)	scl(l)	BlckII	BlcIII	BlckIV	Srvys2	SexMa1
scale(grss)	0.129							
scale(lgms)	-0.084	0.335						
BlockII	-0.562	-0.037	-0.069					
BlockIII	-0.589	-0.064	0.067	0.501				
BlockIV	-0.564	-0.210	0.135	0.451	0.505			
surveys2	-0.292	-0.043	-0.019	-0.023	-0.021	-0.016		
SexMale	-0.369	0.007	-0.010	-0.005	-0.013	-0.026	-0.001	
scl(grss):s2	-0.037	-0.569	-0.002	-0.009	-0.005	-0.013	-0.035	0.006

> summary(glmer1Ee)

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [

glmerMod]

Family: poisson (log)

Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block + Survey + (1 | obs) + scale(legumes):scale(totPreds) + Sex + Survey:scale(legumes) + Survey:scale(grass)

Data: GHVegSurveyAllPreds

Control: glmerControl(optimizer = c("bobyqa"))

Subset: Species == "Ee"

AIC	BIC	logLik	deviance	df.resid
1545.8	1602.4	-759.9	1519.8	559

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.3439	-0.7112	-0.2371	0.5080	3.6291

Random effects:

Groups	Name	Variance	Std.Dev.
obs	(Intercept)	0.2203	0.4693

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.66127	0.10438	6.335	2.37e-10 ***
scale(grass)	0.02632	0.06427	0.409	0.682183
scale(legumes)	-0.22820	0.07805	-2.924	0.003458 **
scale(totPreds)	-0.17617	0.05583	-3.156	0.001601 **
BlockII	-0.87302	0.14844	-5.881	4.07e-09 ***
BlockIII	-0.62346	0.13523	-4.610	4.02e-06 ***
BlockIV	0.11253	0.12215	0.921	0.356902
Surveys2	-0.63817	0.09808	-6.506	7.70e-11 ***
SexMale	-0.34260	0.09205	-3.722	0.000198 ***
scale(legumes):scale(totPreds)	-0.12677	0.06329	-2.003	0.045197 *
scale(legumes):Surveys2	0.06071	0.12225	0.497	0.619492
scale(grass):Surveys2	-0.04651	0.10123	-0.459	0.645878

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	scl(g)	scl(l)	scl(P)	BlckII	BlcIII	BlckIV	Srvys2	SexMa1
s():(P									
scale(grss)	0.093								
scale(lgms)	0.087	0.315							
scl(ttPrds)	0.025	-0.018	0.046						
BlockII	-0.445	-0.049	-0.046	-0.076					
BlockIII	-0.494	-0.095	0.041	-0.083	0.348				
BlockIV	-0.577	-0.239	0.130	0.049	0.378	0.459			
Surveys2	-0.352	0.023	-0.132	0.202	-0.004	-0.021	0.001		
SexMale	-0.381	-0.008	0.003	0.000	0.006	0.013	0.003	0.013	
scl(lg):(P)	0.048	0.023	0.014	0.217	-0.010	-0.001	-0.045	0.044	0.004

```

scl(lgm):s2 -0.085 -0.218 -0.622 0.003 0.025 -0.010 -0.009 0.188 0.000
0.189
scl(grs):s2 0.014 -0.592 -0.229 -0.092 0.024 0.024 -0.009 -0.036 0.004
0.043
scl(l):s2
scale(grss)
scale(lgms)
scl(ttPrds)
BlockII
BlockIII
BlockIV
Surveys2
SexMale
scl(lg):(P)
scl(lgm):s2
scl(grs):s2 0.389

```

```

> summary(glmer2Ee)
Generalized linear mixed model fit by maximum likelihood (Laplace Approxim
ation) [
glmerMod]
Family: poisson ( log )
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +
Survey + (1 | obs) + scale(legumes):scale(totPreds) + Sex +
Survey:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
Subset: Species == "Ee"

```

AIC	BIC	logLik	deviance	df.resid
1544.1	1596.3	-760.0	1520.1	560

```

Scaled residuals:
  Min      1Q  Median      3Q      Max
-1.3352 -0.7080 -0.2349  0.5117  3.6568

```

```

Random effects:
 Groups Name      Variance Std.Dev.
 obs      (Intercept) 0.2202  0.4693
Number of obs: 572, groups: obs, 572

```

```

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    0.66530   0.10398   6.399 1.57e-10 ***
scale(grass)    0.03326   0.06279   0.530 0.596305
scale(legumes) -0.20446   0.06118  -3.342 0.000833 ***
scale(totPreds) -0.17631   0.05589  -3.155 0.001606 **
BlockII        -0.87501   0.14839  -5.897 3.71e-09 ***
BlockIII       -0.62277   0.13524  -4.605 4.12e-06 ***
BlockIV        0.11307   0.12211   0.926 0.354487
Surveys2       -0.64755   0.09632  -6.723 1.78e-11 ***
SexMale        -0.34267   0.09204  -3.723 0.000197 ***
scale(legumes):scale(totPreds) -0.13279   0.06249  -2.125 0.033578 *
scale(grass):Surveys2 -0.06595   0.09335  -0.706 0.479905
---

```

```

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

```

Correlation of Fixed Effects:
      (Intr) scl(g) scl(l) scl(P) BlckII BlcIII BlckIV Srvys2 SexMa1
s():(P
scale(grss) 0.076
scale(lgms) 0.039 0.241
scl(ttPrds) 0.026 -0.016 0.066
BlockII    -0.445 -0.045 -0.039 -0.074
BlockIII   -0.497 -0.100 0.044 -0.085 0.348

```

```

BlockIV      -0.581 -0.247  0.158  0.049  0.379  0.459
Surveys2     -0.343  0.071 -0.003  0.206 -0.009 -0.020  0.004
SexMale      -0.383 -0.009  0.004  0.000  0.006  0.013  0.003  0.013
scl(lg):(P)  0.065  0.068  0.173  0.226 -0.012  0.000 -0.044  0.010  0.004
scl(gr):s2   0.050 -0.566  0.007 -0.102  0.014  0.030 -0.006 -0.121  0.005
-0.034

```

```

> summary(glmer3Ee)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]
Family: poisson ( log )
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block + Survey + (1 | obs) + scale(grass):scale(totPreds) + Sex + Survey:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
Subset: Species == "Ee"

```

```

      AIC      BIC    logLik deviance df.resid
1549.0  1601.2   -762.5  1525.0     560

```

```

Scaled residuals:
  Min       1Q   Median       3Q      Max
-1.3513 -0.7054 -0.2668  0.5179  3.9077

```

```

Random effects:
 Groups Name      Variance Std.Dev.
 obs      (Intercept) 0.2221  0.4713
Number of obs: 572, groups: obs, 572

```

```

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept)    0.6715379  0.1039370   6.461 1.04e-10 ***
scale(grass)    0.0423578  0.0626670   0.676  0.49909
scale(legumes) -0.1919250  0.0601134  -3.193  0.00141 **
scale(totPreds) -0.1568968  0.0559740  -2.803  0.00506 **
BlockII        -0.8822885  0.1483888  -5.946 2.75e-09 ***
BlockIII       -0.6219576  0.1352448  -4.599 4.25e-06 ***
BlockIV         0.0997038  0.1221283   0.816  0.41428
Surveys2       -0.6484604  0.0972378  -6.669 2.58e-11 ***
SexMale        -0.3426167  0.0921127  -3.720  0.00020 ***
scale(grass):scale(totPreds) -0.0008307  0.0511258  -0.016  0.98704
scale(grass):Surveys2 -0.0721924  0.0942543  -0.766  0.44372
---

```

```

Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

```

Correlation of Fixed Effects:
          (Intr) scl(g) scl(l) scl(P) BlckII BlckIII BlckIV srvs2 SexMal
s():(P
scale(grss)  0.067
scale(lgms)  0.023  0.243
scl(ttPrds)  0.009 -0.039 -0.064
BlockII     -0.442 -0.042 -0.037 -0.084
BlockIII    -0.499 -0.093  0.044 -0.066  0.347
BlockIV     -0.579 -0.242  0.165  0.050  0.378  0.458
Surveys2    -0.340  0.067 -0.015  0.236 -0.021 -0.009  0.003
SexMale     -0.384 -0.009  0.005 -0.001  0.006  0.012  0.003  0.012
scl(gr):(P) -0.006  0.023  0.076 -0.269  0.028 -0.044  0.005 -0.132  0.004
scl(grs):s2  0.056 -0.557  0.017 -0.119  0.012  0.016 -0.011 -0.132  0.005
0.125

```

```

> summary(glmer4Ee)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]

```

```

Family: poisson ( log )
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +
Survey + (1 | obs) + Sex + Survey:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
Subset: Species == "Ee"

```

AIC	BIC	logLik	deviance	df.resid
1547.0	1594.9	-762.5	1525.0	561

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.3515	-0.7053	-0.2666	0.5182	3.9044

Random effects:

Groups Name	Variance	Std.Dev.
obs (Intercept)	0.2222	0.4714

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	0.67153	0.10394	6.461	1.04e-10	***
scale(grass)	0.04238	0.06265	0.676	0.49877	
scale(legumes)	-0.19185	0.05994	-3.201	0.00137	**
scale(totPreds)	-0.15714	0.05392	-2.914	0.00356	**
BlockII	-0.88222	0.14834	-5.947	2.72e-09	***
BlockIII	-0.62206	0.13512	-4.604	4.15e-06	***
BlockIV	0.09971	0.12213	0.816	0.41425	
Surveys2	-0.64867	0.09640	-6.729	1.71e-11	***
SexMale	-0.34261	0.09212	-3.719	0.00020	***
scale(grass):Surveys2	-0.07200	0.09351	-0.770	0.44131	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	scl(g)	scl(l)	scl(P)	BlckII	BlckIII	BlckIV	srvys2	SexMa1
scale(grss)	0.067								
scale(lgms)	0.024	0.242							
scl(ttPrds)	0.007	-0.034	-0.045						
BlockII	-0.442	-0.043	-0.039	-0.079					
BlockIII	-0.500	-0.093	0.047	-0.081	0.348				
BlockIV	-0.579	-0.242	0.165	0.054	0.378	0.458			
Surveys2	-0.344	0.071	-0.005	0.211	-0.018	-0.015	0.003		
SexMale	-0.384	-0.010	0.005	0.000	0.006	0.013	0.003	0.013	
scl(grs):s2	0.058	-0.565	0.007	-0.089	0.009	0.022	-0.011	-0.118	0.005

```
> summary(glmer5Ee)
```

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [

glmerMod]

```

Family: poisson ( log )
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +
Survey + (1 | obs) + Sex + Survey:scale(grass) + Sex:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
Subset: Species == "Ee"

```

AIC	BIC	logLik	deviance	df.resid
1548.6	1600.8	-762.3	1524.6	560

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.3616	-0.7055	-0.2609	0.5091	3.7908

Random effects:

Groups Name	Variance	Std.Dev.
obs (Intercept)	0.2202	0.4693

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	0.67534	0.10394	6.498	8.16e-11	***
scale(grass)	0.01517	0.07479	0.203	0.839265	
scale(legumes)	-0.19200	0.05991	-3.205	0.001351	**
scale(totPreds)	-0.15688	0.05385	-2.913	0.003580	**
BlockII	-0.88237	0.14824	-5.952	2.64e-09	***
BlockIII	-0.62294	0.13502	-4.614	3.96e-06	***
BlockIV	0.09946	0.12199	0.815	0.414854	
Surveys2	-0.64865	0.09631	-6.735	1.64e-11	***
SexMale	-0.34980	0.09272	-3.773	0.000162	***
scale(grass):Surveys2	-0.07050	0.09340	-0.755	0.450334	
scale(grass):SexMale	0.06041	0.09107	0.663	0.507093	

 signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	sc1(g)	sc1(l)	sc1(P)	BlckII	BlckIII	BlckIV	srvys2	SexMal
s():s2									
scale(grss)	0.035								
scale(lgms)	0.023	0.206							
sc1(ttPrds)	0.008	-0.031	-0.046						
BlockII	-0.442	-0.034	-0.039	-0.079					
BlockIII	-0.499	-0.071	0.047	-0.081	0.348				
BlockIV	-0.579	-0.200	0.165	0.054	0.378	0.458			
Surveys2	-0.343	0.061	-0.005	0.210	-0.018	-0.015	0.004		
SexMale	-0.386	0.049	0.007	-0.001	0.007	0.014	0.005	0.013	
sc1(grs):s2	0.059	-0.484	0.007	-0.089	0.008	0.021	-0.011	-0.119	-0.001
sc1(grs):SM	0.047	-0.548	-0.006	0.006	-0.004	-0.012	-0.005	-0.001	-0.121

```
> summary(glmer1Cd)
```

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [

glmerMod]

Family: poisson (log)

Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +

Survey + (1 | obs) + scale(legumes):scale(totPreds) + Sex +

Survey:scale(legumes) + Survey:scale(grass)

Data: GHVegSurveyAllPreds

Control: glmerControl(optimizer = c("bobyqa"))

Subset: Species == "Cd"

AIC	BIC	logLik	deviance	df.resid
688.8	745.3	-331.4	662.8	559

Scaled residuals:

Min	1Q	Median	3Q	Max
-0.5972	-0.3752	-0.3188	-0.2549	3.1708

Random effects:

Groups Name	Variance	Std.Dev.
obs (Intercept)	0.9905	0.9952

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.97888	0.29703	-6.662	2.7e-11	***
scale(grass)	0.15664	0.14874	1.053	0.29231	
scale(legumes)	0.07325	0.15759	0.465	0.64208	
scale(totPreds)	-0.09726	0.11371	-0.855	0.39238	
BlockII	-0.06938	0.31101	-0.223	0.82347	
BlockIII	0.60831	0.27986	2.174	0.02973	*
BlockIV	0.14774	0.31598	0.468	0.64009	
Surveys2	-0.58902	0.21256	-2.771	0.00559	**
SexMale	0.17070	0.20137	0.848	0.39661	
scale(legumes):scale(totPreds)	0.17561	0.08706	2.017	0.04369	*

```

scale(legumes):Surveys2      -0.02800    0.22826   -0.123   0.90239
scale(grass):Surveys2       -0.37773    0.23687  -1.595   0.11079

```

```

---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Correlation of Fixed Effects:

```

(Intr) scl(g) scl(l) scl(P) BlckII BlckIII BlckIV Srvys2 SexMal
s():(P
scale(grss) 0.032
scale(lgms) -0.041 0.427
scl(ttPrds) 0.006 -0.079 -0.073
BlockII     -0.483 -0.032 -0.046 -0.081
BlockIII    -0.564 -0.070 0.033 -0.086 0.527
BlockIV     -0.532 -0.183 0.116 0.076 0.451 0.557
Surveys2    -0.282 0.041 0.024 0.198 -0.037 0.003 0.028
SexMale     -0.341 0.011 0.007 -0.006 -0.014 -0.016 -0.009 -0.009
scl(lg):(P) -0.066 -0.003 -0.296 -0.336 -0.036 0.062 -0.060 -0.048 -0.008
scl(lgm):S2 -0.003 -0.305 -0.651 -0.068 0.008 0.034 0.003 -0.034 0.003
0.224
scl(grs):S2 0.023 -0.605 -0.271 -0.047 0.010 0.035 0.030 0.059 -0.016
0.032

```

scl(l):S2

```

scale(grss)
scale(lgms)
scl(ttPrds)
BlockII
BlockIII
BlockIV
Surveys2
SexMale
scl(lg):(P)
scl(lgm):S2
scl(grs):S2 0.447

```

```
> summary(glmer2Cd)
```

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [

glmerMod]

Family: poisson (log)

Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block + Survey + (1 | obs) + scale(legumes):scale(totPreds) + Sex + Survey:scale(grass)

Data: GHVegSurveyAllPreds

Control: glmerControl(optimizer = c("bobyqa"))

Subset: Species == "Cd"

AIC	BIC	logLik	deviance	df.resid
686.8	739.0	-331.4	662.8	560

Scaled residuals:

Min	1Q	Median	3Q	Max
-0.5967	-0.3762	-0.3187	-0.2562	3.1896

Random effects:

Groups Name	Variance	Std.Dev.
obs (Intercept)	0.9904	0.9952

Number of obs: 572, groups: obs, 572

Fixed effects:

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.97917	0.29706	-6.663	2.69e-11	***
scale(grass)	0.15108	0.14156	1.067	0.28586	
scale(legumes)	0.06062	0.11957	0.507	0.61216	
scale(totPreds)	-0.09822	0.11350	-0.865	0.38687	
BlockII	-0.06907	0.31104	-0.222	0.82426	
BlockIII	0.60950	0.27969	2.179	0.02932	*
BlockIV	0.14784	0.31603	0.468	0.63991	
Surveys2	-0.58995	0.21240	-2.777	0.00548	**


```
SexMale 0.17078 0.20137 0.848 0.39639
scale(legumes):scale(totPreds) 0.17800 0.08482 2.099 0.03586 *
scale(grass):Surveys2 -0.36473 0.21185 -1.722 0.08514 .
```

```
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
Correlation of Fixed Effects:
```

```
(Intr) scl(g) scl(l) scl(P) BlckII BlcIII BlckIV Srvys2 SexMal
s():(P
scale(grss) 0.034
scale(lgms) -0.053 0.314
scl(ttPrds) 0.006 -0.105 -0.156
BlockII -0.483 -0.031 -0.054 -0.081
BlockIII -0.565 -0.062 0.072 -0.083 0.527
BlockIV -0.532 -0.191 0.156 0.076 0.451 0.557
Surveys2 -0.282 0.029 -0.004 0.197 -0.038 0.004 0.028
SexMale -0.341 0.012 0.011 -0.006 -0.014 -0.017 -0.009 -0.009
scl(lg):(P -0.067 0.070 -0.204 -0.332 -0.039 0.056 -0.062 -0.041 -0.008
scl(grs):s2 0.027 -0.550 0.034 -0.018 0.006 0.022 0.032 0.083 -0.020
-0.079
```

```
> summary(glmer3Cd)
```

```
Generalized linear mixed model fit by maximum likelihood (Laplace Approxim
ation) [
```

```
glmerMod]
```

```
Family: poisson ( log )
```

```
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block +
Survey + (1 | obs) + scale(grass):scale(totPreds) + Sex +
Survey:scale(grass)
```

```
Data: GHVegSurveyAllPreds
```

```
Control: glmerControl(optimizer = c("bobyqa"))
```

```
Subset: Species == "Cd"
```

```
AIC BIC logLik deviance df.resid
690.8 743.0 -333.4 666.8 560
```

```
Scaled residuals:
```

```
Min IQ Median 3Q Max
-0.5627 -0.3713 -0.3219 -0.2571 2.6453
```

```
Random effects:
```

```
Groups Name Variance Std.Dev.
obs (Intercept) 1.059 1.029
Number of obs: 572, groups: obs, 572
```

```
Fixed effects:
```

```
Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.98823 0.29912 -6.647 2.99e-11 ***
scale(grass) 0.13280 0.14276 0.930 0.35224
scale(legumes) 0.09583 0.11713 0.818 0.41328
scale(totPreds) -0.02877 0.10738 -0.268 0.78875
BlockII -0.04837 0.31157 -0.155 0.87662
BlockIII 0.58711 0.28187 2.083 0.03726 *
BlockIV 0.18509 0.31772 0.583 0.56019
Surveys2 -0.57104 0.21378 -2.671 0.00756 **
SexMale 0.17372 0.20282 0.857 0.39170
scale(grass):scale(totPreds) -0.05801 0.10537 -0.551 0.58196
scale(grass):Surveys2 -0.34799 0.21497 -1.619 0.10549
```

```
---
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
Correlation of Fixed Effects:
```

```
(Intr) scl(g) scl(l) scl(P) BlckII BlcIII BlckIV Srvys2 SexMal
s():(P
scale(grss) 0.042
```

```

scale(lgms) -0.062 0.321
scl(ttPrds) -0.014 -0.060 -0.153
BlockII -0.494 -0.031 -0.057 -0.095
BlockIII -0.566 -0.072 0.082 -0.082 0.531
BlockIV -0.541 -0.190 0.156 0.059 0.453 0.559
Surveys2 -0.283 0.033 -0.023 0.195 -0.023 0.002 0.024
SexMale -0.344 0.012 0.011 -0.009 -0.015 -0.017 -0.009 -0.010
scl(gr):(P) 0.027 -0.057 0.138 -0.035 0.024 -0.023 0.031 -0.066 0.010
scl(grs):s2 0.021 -0.546 0.055 -0.068 0.016 0.035 0.035 0.063 -0.019
0.164

```

```

> summary(glmer4Cd)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [glmerMod]
Family: poisson ( log )
Formula: N ~ scale(grass) + scale(legumes) + scale(totPreds) + Block + Survey + (1 | obs) + Sex + Survey:scale(grass)
Data: GHVegSurveyAllPreds
Control: glmerControl(optimizer = c("bobyqa"))
Subset: Species == "Cd"

```

AIC	BIC	logLik	deviance	df.resid
689.1	737.0	-333.6	667.1	561

```

Scaled residuals:
  Min       1Q   Median       3Q      Max
-0.5344 -0.3726 -0.3233 -0.2548  2.5780

```

```

Random effects:
 Groups Name      Variance Std.Dev.
 obs      (Intercept) 1.057    1.028
Number of obs: 572, groups: obs, 572

```

```

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.98710    0.29913  -6.643 3.08e-11 ***
scale(grass)  0.12798    0.14285   0.896 0.37031
scale(legumes) 0.10454    0.11579   0.903 0.36659
scale(totPreds) -0.03195    0.10698  -0.299 0.76521
BlockII       -0.04421    0.31130  -0.142 0.88707
BlockIII      0.58304    0.28179   2.069 0.03854 *
BlockIV      0.18969    0.31745   0.598 0.55016
Surveys2     -0.57953    0.21300  -2.721 0.00651 **
SexMale      0.17484    0.20270   0.863 0.38838
scale(grass):Surveys2 -0.32881    0.21120  -1.557 0.11950
---

```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

Correlation of Fixed Effects:
      (Intr) scl(g) scl(l) scl(P) BlckII BlcIII BlckIV Srvys2 SexMa
scale(grss) 0.044
scale(lgms) -0.067 0.333
scl(ttPrds) -0.013 -0.080 -0.146
BlockII     -0.497 -0.030 -0.061 -0.093
BlockIII    -0.566 -0.075 0.087 -0.083 0.531
BlockIV     -0.542 -0.190 0.155 0.060 0.453 0.561
Surveys2    -0.282 0.026 -0.014 0.189 -0.019 0.001 0.026
SexMale     -0.344 0.013 0.010 -0.008 -0.015 -0.017 -0.009 -0.009
scl(grs):s2 0.016 -0.547 0.032 -0.068 0.017 0.040 0.032 0.071 -0.021

```

```

> summary(glmer5Cd)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) [

```


INTERACTION BETWEEN RESIGHTING FREQUENCY ,TEMPERAMENT , SEX AND SPECIES

```
persData <- read.csv("Personality&ResightingData_20140916.csv")  
> glm1 <- glm(Nresights ~ Sex*Temperament*Species, data = persData, family = poisson)  
> glm1
```

Call: glm(formula = Nresights ~ Sex * Temperament * Species, family = poisson,
data = persData)

Coefficients:

(Intercept)	SexM
1.916923	-0.155935
Temperament	SpeciesE. elegantulus
0.153550	-0.114800
SpeciesP.giornae	SexM:Temperament
-0.733153	-0.282285
SexM:SpeciesE. elegantulus	SexM:SpeciesP.giornae
-0.497565	0.001784
Temperament:SpeciesE. elegantulus	Temperament:SpeciesP.giornae
-0.365466	-0.228658
SexM:Temperament:SpeciesE. elegantulus	SexM:Temperament:SpeciesP.giornae
0.649635	0.116231

Degrees of Freedom: 232 Total (i.e. Null); 221 Residual

(17 observations deleted due to missingness)

Null Deviance: 487

Residual Deviance: 349.8 AIC: 1115

```
> glm2 <- update(glm1, ~. - Sex:Temperament:Species)
```

```
> glm2
```

```
Call: glm(formula = Nresights ~ Sex + Temperament + Species + Sex:Temperament +  
Sex:Species + Temperament:Species, family = poisson, data = persData)
```

Coefficients:

(Intercept)	SexM
2.061857	-0.387359
Temperament	SpeciesE. elegantulus
-0.015560	-0.328926
SpeciesP.giornae	SexM:Temperament
-0.854253	-0.006945
SexM:SpeciesE. elegantulus	SexM:SpeciesP.giornae
-0.050114	0.121177
Temperament:SpeciesE. elegantulus	Temperament:SpeciesP.giornae
-0.066109	-0.095270

Degrees of Freedom: 232 Total (i.e. Null); 223 Residual

(17 observations deleted due to missingness)

Null Deviance: 487

Residual Deviance: 353.8 AIC: 1115

```
> glm3 <- update(glm2, ~. - Sex:Temperament)
```

```
> glm3
```

```
Call: glm(formula = Nresights ~ Sex + Temperament + Species + Sex:Species +  
Temperament:Species, family = poisson, data = persData)
```


-0.04772

0.11991

Degrees of Freedom: 232 Total (i.e. Null); 226 Residual

(17 observations deleted due to missingness)

Null Deviance: 487

Residual Deviance: 354.1 AIC: 1110

```
> glm5 <- update(glm4, .~. - Species:Sex)
```

```
> glm5
```

Call: glm(formula = Nresights ~ Sex + Temperament + Species, family = poisson,
data = persData)

Coefficients:

(Intercept)	SexM	Temperament	SpeciesE. elegantulus	SpeciesP.giornae
2.10002	-0.39133	-0.06273	-0.39587	-0.89775

Degrees of Freedom: 232 Total (i.e. Null); 228 Residual

(17 observations deleted due to missingness)

Null Deviance: 487

Residual Deviance: 354.8 AIC: 1106

```
> AIC(glm1,glm2,glm3,glm4,glm5) # model with lowest AIC value is best
```

```
df AIC
```

```
glm1 12 1115.339
```

```
glm2 10 1115.391
```

```
glm3 9 1113.394
```

```
glm4 7 1109.685
```

```
glm5 5 1106.349
```

```
> summary(glm5)
```

```
Call:
```

```
glm(formula = Nresights ~ Sex + Temperament + Species, family = poisson,  
     data = persData)
```

```
Deviance Residuals:
```

```
   Min      1Q  Median      3Q      Max  
-3.04387 -0.97703 -0.08218  0.76670  3.02833
```

```
Coefficients:
```

```
              Estimate Std. Error z value Pr(>|z|)  
(Intercept)      2.10002   0.07962  26.374 < 2e-16 ***  
SexM              -0.39133   0.06324  -6.188 6.10e-10 ***  
Temperament       -0.06273   0.07026  -0.893  0.372  
SpeciesE. elegantulus -0.39587  0.07362  -5.378 7.55e-08 ***  
SpeciesP.giornae  -0.89775   0.08589 -10.452 < 2e-16 ***
```

```
---
```

```
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
(Dispersion parameter for poisson family taken to be 1)
```

```
Null deviance: 486.95 on 232 degrees of freedom
```

```
Residual deviance: 354.78 on 228 degrees of freedom
```

```
(17 observations deleted due to missingness)
```

```
AIC: 1106.3
```