

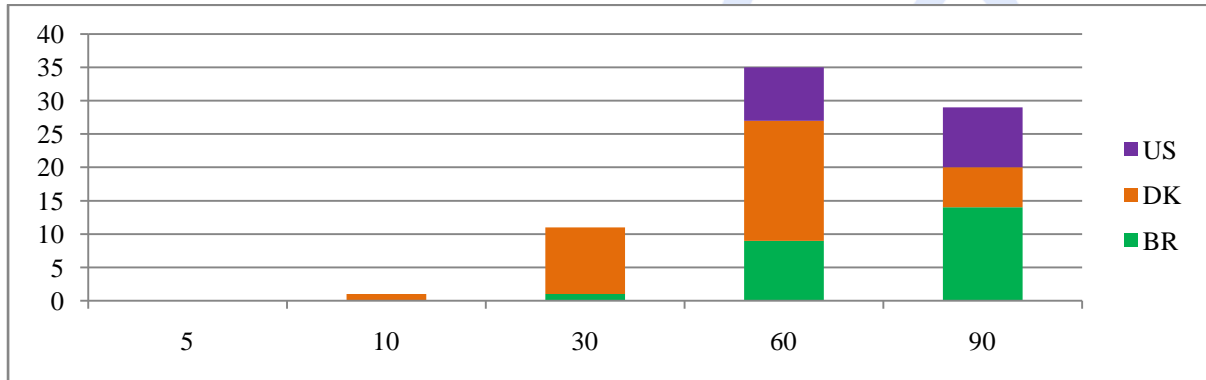
An Investigation into the Accuracy of Classical Behavioural Ecology Concepts, such as Ideal Free Distribution, using the Model Organism *Folsomia candida*

Since the days of early ethologists Karl von Frisch and Konrad Lorenz, behavioural ecologists have attempted to devise simple sets of rules to explain and predict the, often complex, behaviour of animals. One of the most prevalent of these sets of rules is the theory of Ideal Free Distribution (Fretwell & Lucas 1970); the theory predicts that individual organisms will arrange themselves proportional to the amount of resources in each separate 'patch'. In order to make this prediction, the theory relies upon the assumptions that: resources are distributed equally among patches; that all competitors are equal, negligible travelling costs, there is no depletion of resources and that predators of the subject are omniscient¹. These are unrealistic assumptions to make of a system in the wild, but how does the theory fare at predicting behaviour in a controlled system? This is the question the first section of this manuscript intends to answer. The second section will address the functional responses to prey density.

Results

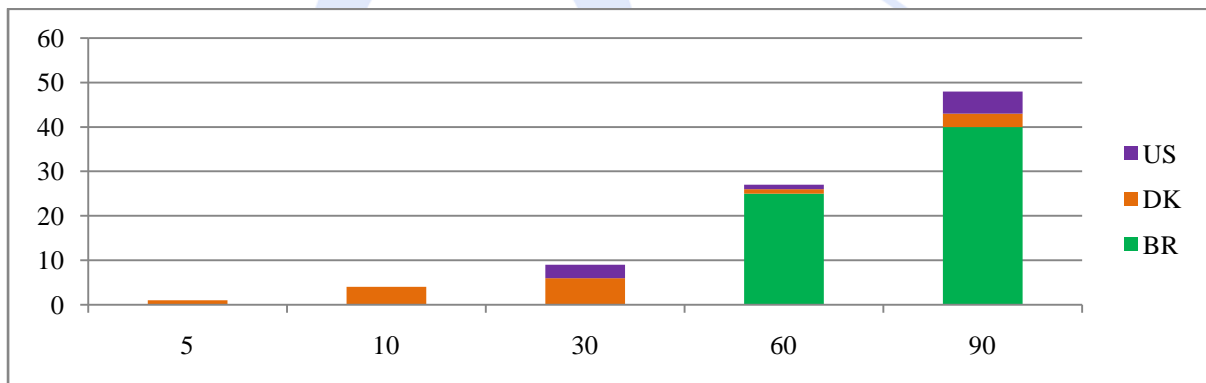
The following graphs show: x = time (min), y = numbers at the food patch

Low Density (1 microspatula)



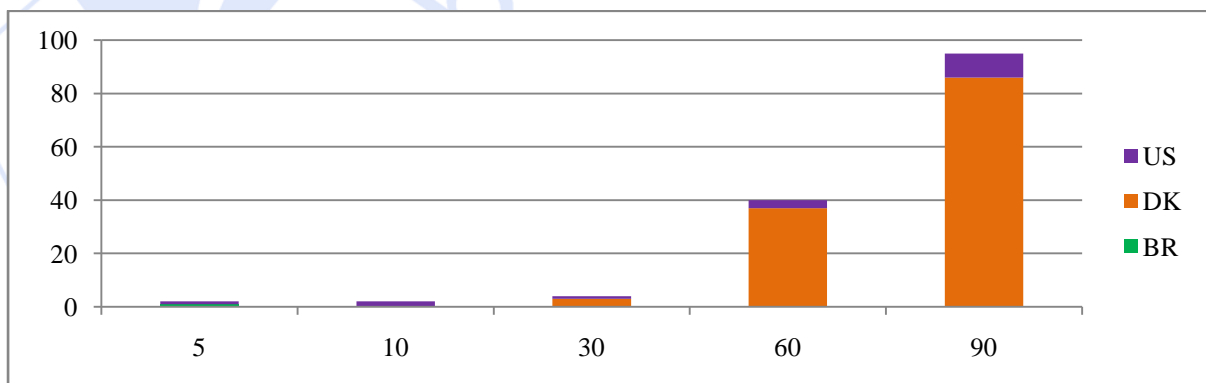
Total Number: 76

Medium Density (3 microspatulas)



Total Number: 89

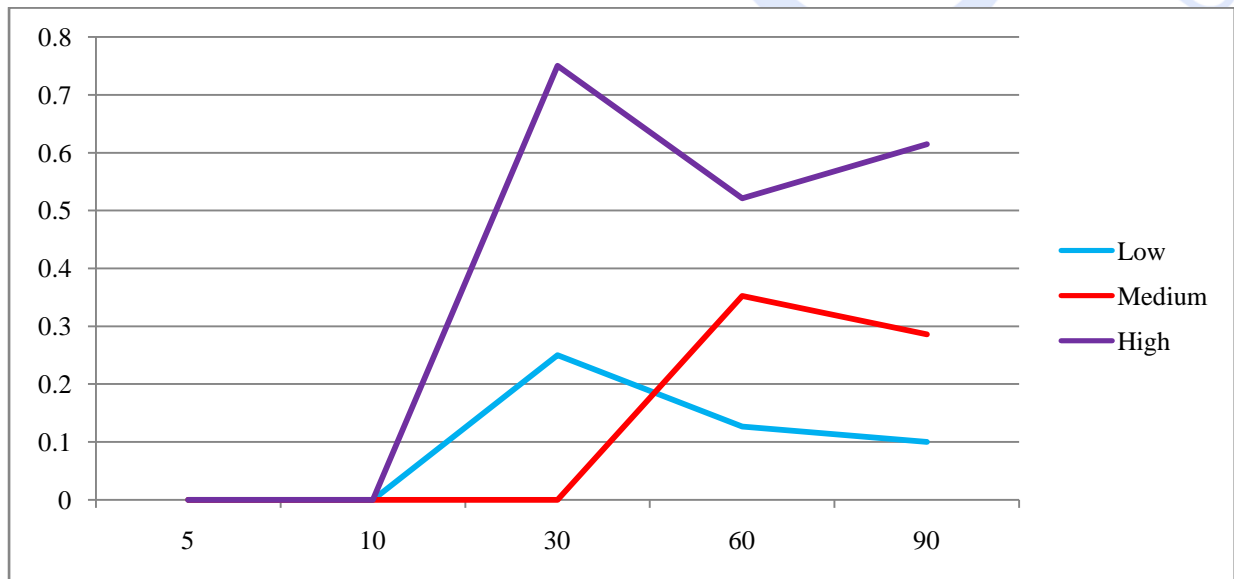
High Density (9 microspatulas)



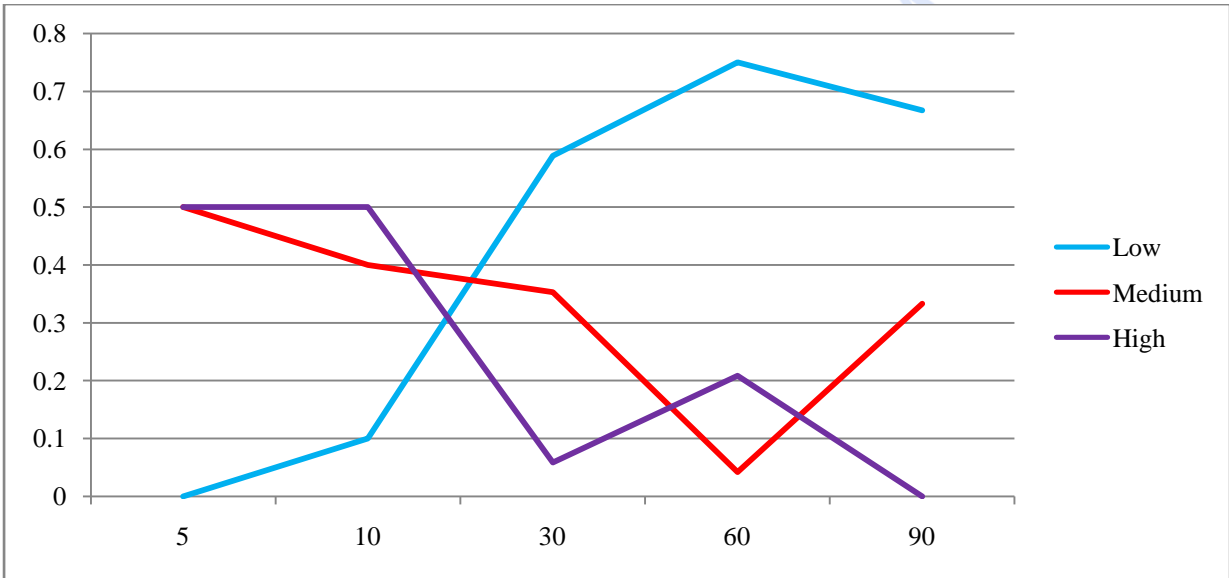
Total Number: 154

The following graphs show: x = time (min), y = proportion of population feeding

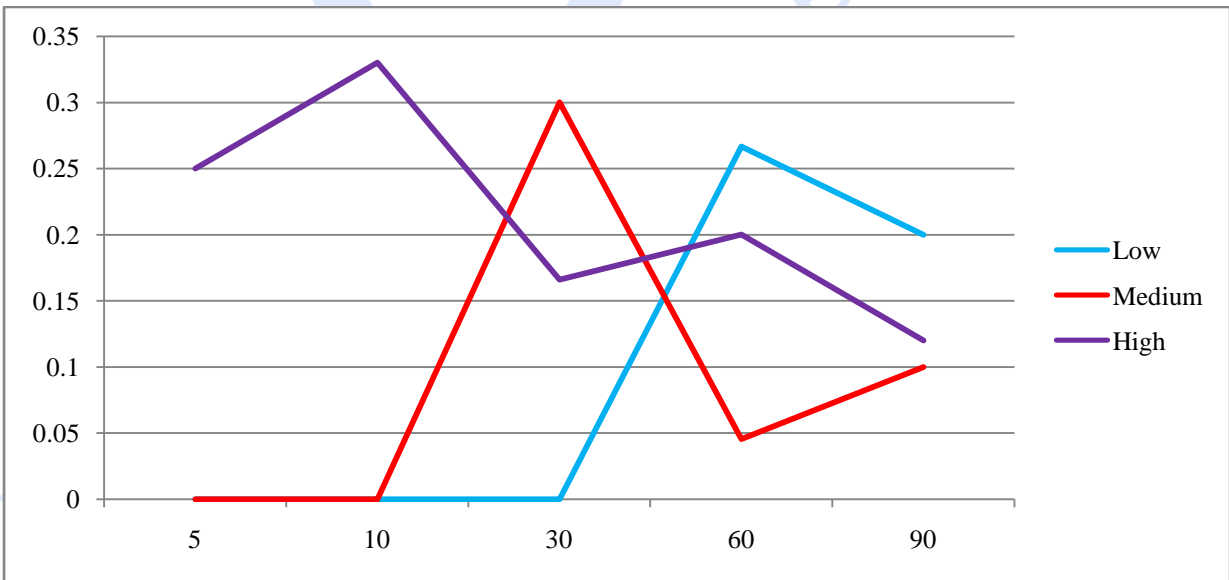
Clone: BR (Britain)



Clone: DK (Denmark)



Clone: US (United States of America)



Discussion

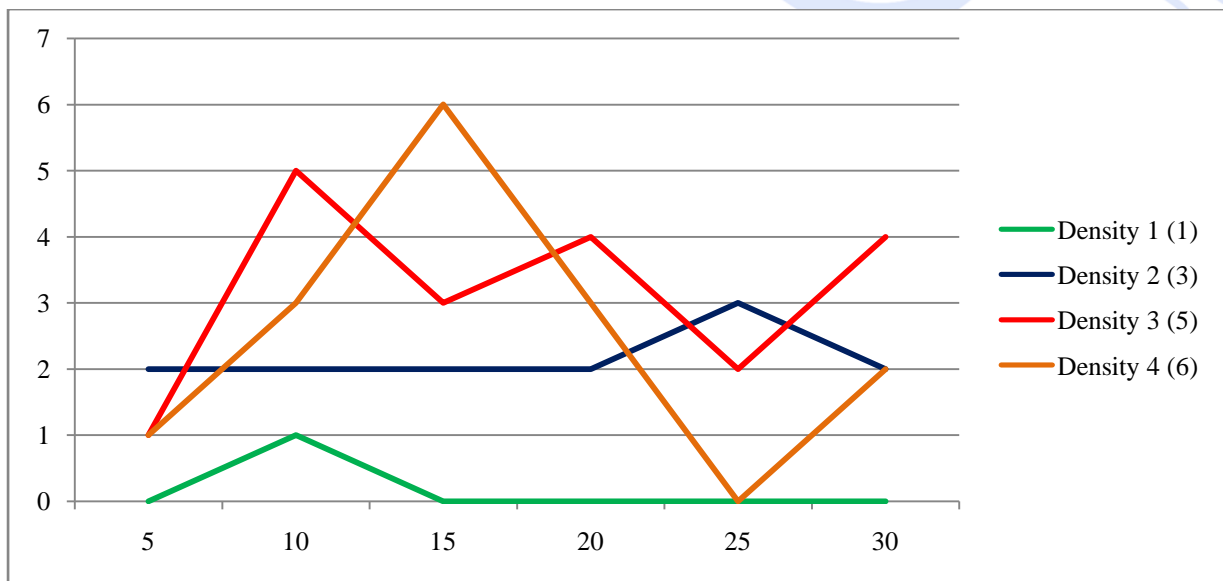
The Ideal Free Distribution

Under the predictions of the Ideal Free Distribution, we would expect a ratio of 1:3:9 from the low to the high food density. The observed ratio was 76:89:154. This incongruity is wholly unsurprising when we consider the assumptions the theory relies upon (see first paragraph). Competition is in effect between the different sized individuals of each species – this is a contributing factor to the ratio. The travelling cost between different food densities is also not negligible; it is approximately comparable to a human travelling 70m across unfamiliar ground for food when there is enough at hand. The last assumption is that negligible patch depletion occurs – this is fundamentally unrealistic in our experiment; but what consequences of patch depletion do we observe? If depletion were evident we would expect a fall in the number of individuals at each patch over time (according to Ideal Free Distribution), we do see a statistically significant reduction in numbers in the low food density after 90 minutes but we can only draw spurious conclusions from this result – the experiment must be prolonged in the future to investigate the effects of patch depletion. If the experiment were allowed to continue then we would expect a decrease in numbers around the low density food patch relative to the high density, despite the increased competition, as the smaller amount of food is depleted more quickly. In considering the foraging strategy of the different clones we must look at the relative proportions of individuals feeding at each density. Due to the fact that we did not replicate the experiment, any attempt to extrapolate possible meaning from the graphs would be contrived. Because biological systems are susceptible to multiple sources of variation, one experiment is not enough to conclude that the changes we are seeing are due to the differences between clones. We see that the whole population of DK and BR clones feed while only a small proportion of the US clones choose to feed but we do not know to what this is attributable. Many sources of differential stimuli are likely to have contributed to the variation in the data, such as: different levels of moisture (collembolans are known to cluster at the edges of an area in dryer conditions²), different light levels in different parts of the room and possibly many more factors of which we are unaware but that are evident to the experimental subjects (such as weak olfactory stimuli). We must also consider that the different clones were investigated by different groups with, invariably, slightly different experimental techniques. The effect of these differences could be profound, for example we recorded ‘one encounter’ when two subjects touched, but another

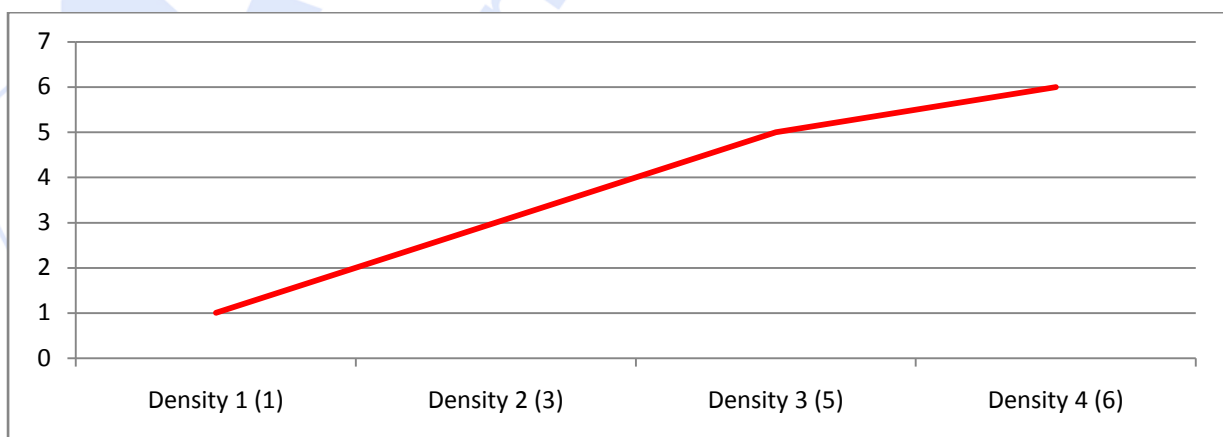
group may well have recorded one encounter at a certain distance apart e.g. approximately 1mm etc.

Functional Responses to Prey Density

This graph shows x = time (min), y = combined number of captures for both clones. The numbers in brackets show the peak number of captures



If the predictions of Holling's disc equation were fulfilled, we would expect an increase in captures until an asymptote is reached when handling time limits the rate of prey capture independent of further increasing density. If we plot peak captures (x) over increasing density (y); we see a linear increase between the first three densities followed by a shallower increase to the highest density:



If we had included greater prey densities than density 4 then we may well see the classic asymptotic trajectory. Other than handling time, the shape of the curves may be influenced, primarily, by decreasing prey density (as the collembolans are eaten) – this produces a similar result to that predicted by Holling as the mites (*Hypoaspis*) have to travel further between the remaining *F. candida* thus increasing handling time. Also the level of prey provided could have been sufficient to satisfy the hunger of the mites (we may be able to alleviate this e.g. by supplying only the smallest *F. Candida*). Similar to the Ideal Free Distribution, the predictions regarding Functional Responses to Prey Density rely upon unrealistic assumptions i.e. that prey are distributed randomly and that searching and handling are mutually exclusive activities. These are generally unreasonable assumptions in our experimental system; we know that the prey preferred the periphery of the area thus increasing the density around the edge and possibly making them more vulnerable to predation (because they have fewer escape options). However, it is somewhat pertinent to assume that searching and handling are exclusive in our system because the mites were incapable of searching for more prey when engaged upon consumption³.

References

¹ Kacelnick, A. & Krebs, J. R. (1992), The Ideal Free Distribution and Predator-Prey Populations. *Trends in Ecology & Evolution* 7, 50-55

² Bengtsson, G. *et al* (1994), Food and Density-Dependent Dispersal: Evidence from a Soil Collembolan. *The Journal of Animal Ecology* **63**, 513-520

³ Ferguson, S. H. & Joly, D. O. (2002), Dynamics of springtail and mite populations: the role of density dependence, predation, and weather. *Ecological Entomology* **5**, 565-573