
General Conclusions

In the previous chapters I have presented the findings from three studies on the evolutionary and behavioural ecology of *Dorylus* species. In the following I coalesce the main conclusions and point out further ideas on how future studies can build upon them.

What drives the evolution of worker morphology in *Dorylus* army ants? I managed to show a clear-cut trend of increasing relative length of several morphological features from hypogaeic to intermediate to epigaeic species. Thus the respective features very probably represent adaptations to the respective ecological niches. The correlation between relative leg length and ecological niche also holds on a finer scale when comparing two species usually categorized as having an epigaeic life-style. Therefore it is possible that the categorization of *Dorylus* species as hypogaeic, intermediate or epigaeic will finally have to make way for a more subtle system to describe their life-style when more detailed field observations are also carried out elsewhere. Although (fine scale) ecological niche and leg length allometries are uniformly continuously correlated and I proposed several possible complementary selective advantages of longer legs, providing evidence that any of these has been important in the evolutionary history of *Dorylus* is a difficult undertaking. Besides the general problem of linking performance to fitness in interpretations concerning the functional value of morphological features (Wainwright 1994) it will also be complicated to measure the performance of workers from species with hypogaeic and intermediate foraging habits in basically any task under realistic conditions. They are very hard to study in their natural environment, because even on the rare occasions when they can be observed on the surface they immediately withdraw into the leaf litter or underground when disturbed. Therefore I only worked with two epigaeic species when analysing the relationship between leg length allometries and load ratio during food transport. Obviously the selection pressures that have favoured the extremely long legs of *D. wilverthi* may have been different from the ones that favoured longer legs of intermediate species. Interestingly, the longer legs of *D. wilverthi* workers do not confer an advantage with respect to the size of the transported food items. The maximum size of a food item is therefore unlikely to be limited by front leg length in these species. Future studies should instead focus on the possibility that the extremely long legs of epigaeic army ants are necessary for swift climbing. Importantly, I examined within population variation of the leg length allometries in the comparison between *D. wilverthi* and *D. molestus* while in past studies allometries have often been viewed as fixed species specific traits. In future studies my approach should be extended to include colonies from different populations to elucidate the extent of geographic variation in these traits. In particular it

would be very interesting to compare the leg length allometries of the *D. molestus* population at Mt Kenya with those of other populations at sites where the species co-exists with other intermediate *Anomma* species. If competition with other species influences foraging stratum use as I suggested in Chapter II, it can be predicted that *D. molestus* colonies at these other sites are excluded from using the top-soil layers and leaf-litter, that they have a food spectrum more similar to the one of *D. wilverthi* at Kibale, and finally and most significantly that they should have longer legs in these populations.

There are still a large number of outstanding questions in ant polymorphism in general. The allometries as I measured them in a sense represent an epiphenomenon, because they reflect the outcome of a complex interplay of factors. The “growth” trajectories of female individuals as well as their predisposition to develop into an adult of a particular size are on the one hand influenced by genetic factors (Emlen & Nijhout 2000, Fraser et al. 2000, Hughes et al. 2003), but on the other hand appear to be plastic in response to food quality and / or temperature. The allometries as I measured them do not show individual “growth” trajectories but the emergent colony-level outcome of many different individual ontogenetic processes. Future research will have to elucidate the relative importance of all involved factors. In a similar way the size-frequency distribution of the standing worker population also represents the result of a complex interplay of different variables. The workers engaged in brood rearing can to some extent influence the size-frequency distribution of new callow workers through preferential feeding or oophagy. But the size-frequency distribution of workers is also affected by the longevity of workers of different sizes, which may differ physiologically and through task-dependent mortality. These issues will probably not be solved through studies on army ants because they do not lend themselves well to experimental manipulation in laboratory work.

The migration patterns of *D. molestus* turned out to be a very intriguing study system. The colony density at the Mt Kenya study site is the second highest ever reported for swarm raiding *Dorylus* species. Only Gotwald and Cunningham-van Someren (1990) gave an account of a short incidence of higher colony density for the same species. One explanation for the high density of *D. molestus* colonies is probably linked to the fact that it does in contrast to *D. wilverthi* not coexist with other *Anomma* species in that habitat. As colonies can therefore exploit a wider foraging stratum, their overall biomass density is expected to be higher. In a constellation with very high colony density and foraging distances that are potentially much higher than the usual nearest neighbour distance, fierce competition between colonies automatically ensues. But unlike e.g. harvester ants or weaver ants *D. molestus* army ants cannot be territorial and do not fight foreign colonies. They seem to follow a rather

different strategy to outcompete their neighbours in that they exploit profitable foraging grounds even close to neighbouring colonies and then move away from them to new areas rich in prey. As first steps to build upon and go beyond the findings presented here one should determine how much *D. molestus* swarm raids reduce the prey densities and how long these take to recover. Even more importantly it should then be tested through experimental manipulation whether colonies actually respond to gradients in prey density when foraging and migrating. In the long run it would be desirable to gather data on colony sizes, growth, reproduction rate and mortality to understand both population regulation as well as the evolutionary stable strategy in colony reproduction.